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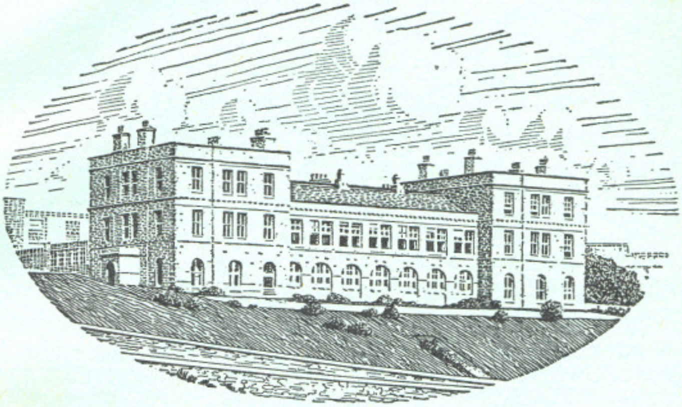

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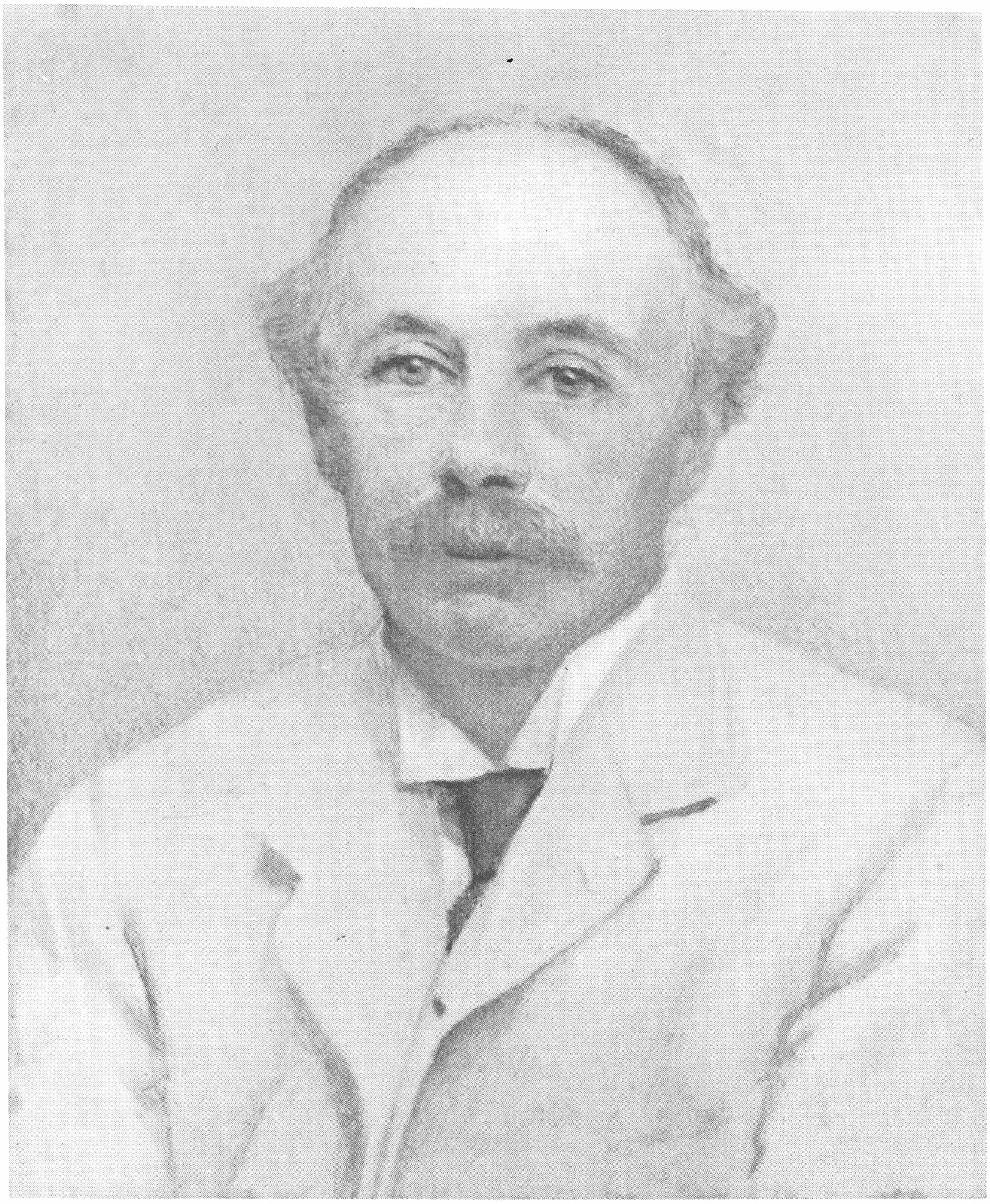

Edward G. Browne

EDWARD THOMAS BROWNE

1866–1937

Members of the Association, especially those who have served on the Council and many biologists who have worked at the Plymouth Laboratory during the last forty years, will have learned with sorrow and regret of the death of Edward Thomas Browne of "Anglefield", Berkhamsted, on December 10, 1937, in his 72nd year, following a short illness. As a student at Queen's College, Oxford, Browne did not read biology, but after graduation spent some years in London, where he developed an interest in microscopy and the study of freshwater pond life. He became a Fellow of the Royal Microscopical Society in 1884 and a member of the Quekett Club in 1887, and was an active worker with both these societies, serving for a time on the council of each and maintaining his interest in them throughout his life.

During the session 1891–92 Browne attended a full course of lectures and practical work in Zoology under Prof. W. F. R. Weldon at University College, London. In the autumn of 1892 he began investigations on coelenterates in the old research laboratory which had been arranged by Ray Lankester on the north side of the gallery surrounding the Zoological Lecture Theatre. In this narrow space tables were provided for six research workers, and it was here that I first met Browne. The rest of the party consisted of H. F. Thompson (now Sir Herbert Thompson), the late Miss Florence Buchanan, then working at marine Polychaetes but who subsequently did Physiological research with Burdon-Sanderson in Oxford, Miss Kircaldy of Oxford and Miss Margaret Robinson, a former Newnham student, who seventeen years later became Browne's wife. In addition to Prof. Weldon, who was full of enthusiasm for the Plymouth Laboratory and its work, Dr G. Herbert Fowler, Assistant Professor in the Department, and at the time Secretary of the Marine Biological Association, did much to encourage and help us all and to direct our attention to problems of marine animal life.

In the spring of 1893 Browne spent a month at the Marine Station at Port Erin, in the Isle of Man, and in September paid his first visit to the Plymouth Laboratory. A similar programme was followed in 1894, the intermediate months being spent at University College. In the spring of 1895 he went with W. I. Beaumont and F. W. Gamble to Valencia, on the south-west coast of Ireland, and also spent a month at Plymouth in the summer. In the following year a larger party was organized by him to carry out investigations at Valencia, the additional members being Prof. F. E. Weiss, A. O. Walker and M. D. Hill. The party received much help from the Misses Delap, who had previously taken great interest in the fauna of Valencia Harbour, and from them in later years Browne received constant supplies of new material with notes on observations made on the living organisms.

By this time Browne had settled down to specialize on the Medusae and Hydroids, and after the publication of his two papers in the *Proceedings of the Zoological Society of London* in 1896 and 1897 he was quickly recognized as a leading authority on these coelenterates. For many years he continued to work at University College during the winter half of the year, attending with great regularity from day to day. Already in 1896 and 1897 he was planning a monograph on the British Medusae, using every endeavour to follow their full life-histories and to connect them with their proper hydroids. As the illustrations to his published papers show he was a skilful artist. Many plates were prepared for use in the proposed monograph, and detailed notes were written. When, two or three years ago, he felt that he would not himself be able to complete the work, he arranged with Mr F. S. Russell to carry on the scheme, paying for a trained biological assistant to help him in the task. He has made provision also for the publication of the monograph when ready under their joint names, so that there is every hope that this part of his life work will not be lost.

In connexion with this work Browne continued to visit different marine laboratories, and made expeditions to places specially suitable for collecting the material he required. His visits to the Plymouth Laboratory as a worker continued from time to time during the next 15 or 20 years, and special mention should be made of the two papers "On keeping medusae alive in an aquarium" (1898) and "A new method for growing hydroids in small aquaria by means of a continuous current tube" (1907). In the first of these he emphasized the advantages of keeping small pelagic marine animals in constant movement by mechanical means in order to keep them healthy in an aquarium. For this purpose he designed an apparatus known as the "plunger-jar", which is still much used at Plymouth, as well as in other biological laboratories. Both this and the "continuous current tube" illustrate one side of his ability, the successful designing and handling of instruments and apparatus for the purposes of his research. His whole technique was excellent and he paid the greatest attention to detail and scientific accuracy. His early experience as a microscopist no doubt served him in good stead in his later work.

Special mention should be made of Browne's work with Rupert Vallentin, which belongs to this period. A series of papers on the Fauna of Falmouth Harbour was published in the *Report of the Royal Cornwall Polytechnic Society* and in the *Journal of the Royal Institution of Cornwall* between 1891 and 1897 (see 1899, p. 691 in list of works below), by Vallentin, which are liable to be lost sight of. Browne visited him and collected with him in Falmouth and they also spent some time together in the Scilly Islands (1904). Vallentin, who had studied Zoology in Munich under Richard Hertwig, visited the Falkland Islands in 1898–99, bringing back a fine collection of Medusae which he handed over to Browne. A preliminary report on these was published in 1902, and a manuscript with drawings for the full report was prepared but not published. This will probably be revised and arranged for publication by Dr P. L. Kramp of Copenhagen.

On his marriage in December 1909 to Miss M. Robinson, his colleague for many years in the research laboratory at University College, London, he made his home at "Anglefield", Berkhamsted, a house with a good garden on the outskirts of the town. Here he built a special laboratory for his work, and for the housing of his numerous collections and the fine special library on coelenterates which he had got together. Remarkably characteristic was the careful way in which the collections were preserved and arranged, and both these and the scientific pamphlets card-indexed, so that anything could be found at a moment's notice. He had also accumulated a great mass of typewritten notes, all arranged with equal care.

Owing to the reputation he had made as a specialist on the medusae, and the care and accuracy of his work, he at this time received numerous requests to report on collections of medusae from all parts of the world. Although the examination of these collections and the preparation of the reports on them interfered with the progress of the monograph on British medusae, he felt the work well worth undertaking, giving him as it certainly did a broader grasp of the group as a whole, and he hoped that the British monograph would gain greatly in the end by the delay. When therefore he was settled in his own laboratory at "Anglefield", he worked chiefly on foreign collections, and the reports he published, all of which are illustrated by his own beautiful and accurate figures, show that he put much time and effort into making them as perfect as the specimens allowed.

He was fortunate when he first went to Berkhamsted in having as a near neighbour the Rev. Canon A. M. Norman, in whom he found a marine naturalist after his own heart. The two became very close friends, for in addition to this bond, Browne and Norman were both keen gardeners and both found the care of their gardens a relief from the close work of systematic zoology. Norman's death was a great grief to Browne.

He became a Fellow of the Zoological Society in 1894, and when he was at University College he paid frequent visits to the Zoological Gardens. Among his other activities he was a good photographer and spent much time and effort in getting fine pictures of many of the animals in the Gardens in characteristic attitudes, and especially the birds.

After his marriage and settlement at "Anglefield", Browne, who was a good business man, took a special interest in the administration of several of the scientific societies of which he was a member. He was elected a Fellow of the Linnean Society in 1913 and served on the Council from 1915 to 1923, being a Vice-President from 1920 to 1923. He took great interest in the work of the Council, and was especially active as a member of the Library Committee.

He was also a member of the Challenger Society for the Promotion of Oceanography and a regular attendant at its meetings.

But I think we can claim that he gave his most active support to the Marine Biological Association and its Plymouth Laboratory. He became a member of the Association in 1893, the year in which he first visited the Laboratory, and from 1895 onwards he was always active and helpful in advising on business and administrative matters. He served as an ordinary member of Council from 1913 until 1919, in which year he supported his friend Dr G. P. Bidder, who was collecting a fund for the enlargement of the Laboratory buildings, by giving a donation of £500 which made the proposed scheme possible. By this donation he became a Life-Governor with a permanent seat on the Council of the Association. He gave substantial financial help to all subsequent efforts for the enlargement of the Laboratory and the extension of its work, spending also much time and thought on the various plans proposed. In all such matters his advice and business experience contributed greatly to the progress of the Association's work. His special donations made during his lifetime amounted to £2655, and in addition he provided funds to enable young naturalists to carry out particular lines of work in the Laboratory. Substantial sums have also been left to the Association in his will to enable these activities to continue.

Browne was a real "naturalist", in the old sense in which that word was understood, who, as a result of an academic training, early took a useful part in the transition that led to the "ecologists" of to-day. His interest was primarily in living animals and plants in their natural surroundings and for him work in the laboratory was undertaken as an aid to elucidating the relationships of the organism to the physical and biological conditions in which it lived. His interests were not confined to his hydroids and medusae, but extended to all the animals of the sea and equally to the birds and plants of the countryside and the garden.

As a man he was generous and good-hearted, the staunch friend of a large and varied group of biologists, whom he was always anxious to help in any way he could in their scientific work. His knowledge and experience were freely given to them all and especially he found great pleasure in helping those just entering on biological research. But it was not until one had the happiness to know him in his own charming home, with a wife who sympathized so fully with all his pursuits, that the full measure of his kindness was made plain.

E. J. ALLEN.

List of Papers by E. T. Browne

1895. Report on the medusae of the L.M.B.C. District. *Trans. Lpool Biol. Soc.*, Vol. IX, pp. 243–86.

—— On the variation of the tentaculocysts of *Aurelia aurita*. *Quart. Journ. Micr. Sci.*, Vol. XXXVII, pp. 245–51.

—— On the variation of *Haliclystus octoradiatus*. *Quart. Journ. Micr. Sci.*, Vol. XXXVIII, pp. 1–8.

1896. On British hydroids and medusae. *Proc. Zool. Soc. London*, pp. 459–500.

—— On the changes in the pelagic fauna of Plymouth during September, 1893 and 1895. *Journ. Mar. Biol. Assoc.*, Vol. IV, pp. 168–73.

—— The medusae of Valencia Harbour, County Kerry. *Irish Naturalist*, July, pp. 179–81.

1897. On *Tubularia crocea* in Plymouth Sound. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 54–5.

—— The hydroids of Valencia Harbour, Ireland. *Irish Naturalist*, pp. 241–6.

—— On British medusae. *Proc. Zool. Soc. London*, pp. 816–35.

—— Revised list of hydromedusae of L.M.B.C. District. *Trans. Lpool Biol. Soc.*, Vol. XI, pp. 147–50.

1898. On keeping medusae alive in an aquarium. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 176–80.

—— On the pelagic fauna of Plymouth for September, 1897. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 186–92.

1899. (With Beaumont, W. I. and Gamble, F. W.) The fauna and flora of Valencia Harbour on the west coast of Ireland. I. The pelagic fauna (1895–98). II. The medusae (1895–98). *Proc. R. Irish Acad.*, Ser. 3, Vol. V, pp. 667–93, 694–736.

1901. Variation in *Aurelia aurita*. *Journ. Biometrika*, Vol. I, pp. 90–108.

1902. A preliminary report on hydromedusae from the Falkland Islands. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. IX, pp. 272–84.

1903. Report on some medusae from Norway and Spitzbergen. *Bergens Mus. Aårbog*, No. 4, pp. 1–36.

1904. (With Vallentin, R.) On the marine fauna of the Isles of Scilly. *Journ. Roy. Inst. Cornwall*, Vol. L, pp. 120–32.

—— Hydromedusae, with a revision of the Williadae and Petasidae. *Faun. Geogr. Maldive Laccadive Archip.*, Vol. II, pp. 722–49.

—— Scyphomedusae. *Faun. Geogr. Maldive Laccadive Archip.*, Vol. II, Supp. pp. 958–72.

1905. A report on the medusae found in the Firth of Clyde (1901–2). *Proc. Roy. Soc. Edin.*, Vol. XXV, pp. 738–78.

—— Notes on the pelagic fauna of the Firth of Clyde (1901–2). *Proc. Roy. Soc. Edin.*, Vol. XXV, pp. 779–91.

1905 Report on the medusae (Hydromedusae, Scyphomedusae, Ctenophora) collected by Professor Herdman at Ceylon, in 1902. *Report on the Pearl Oyster Fisheries of the Gulf of Manaar Royal Soc. Suppl. Rep.*, Vol. XXVII, pp. 131–66.

1906. On the fresh-water medusa *Limnocnida tanganicae* and its occurrence in the River Niger. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XVII, pp. 305–6.

—— On the fresh-water medusa liberated by *Microhydra ryderi*, Potts, and a comparison with *Limnocodium*. *Quart. Journ. Micr. Sci.*, Vol. L, pp. 635–45.

—— Biscayan plankton collected during a cruise of H.M.S. *Research* 1900. Pt IX. The medusae. *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. X, pp. 163–187.

1907. A new method for growing hydroids in small aquaria by means of a continuous current tube. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 37–43.

—— The hydroids collected by the *Huxley* from the north side of the Bay of Biscay in August, 1906. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 15–36.

—— A revision of the medusae belonging to the family Laodiceidae. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XX, pp. 457–80.

1908. The medusae of the Scottish National Antarctic Expedition. *Trans. Roy. Soc. Edin.*, Vol. XLVI, pp. 233–51.

—— On the fresh-water medusa, *Limnocnida tanganicae*, discovered in the River Niger by the late J. S. Budgett. *Budgett Memorial Volume*, pp. 471–80.

1910. Coelenterata. V. Medusae. *Nat. Antarct. Exped., Nat. Hist.*, Vol. V, pp. 1–62.

1912. "The floating animals" and "Preservation of marine organisms." (With G. H. Fowler and E. J. Allen.) *Science of the Sea*. Prepared by the Challenger Society and edited by G. Herbert Fowler. London, Murray. 1912. Chapters V and XI, pp. 162–99 and 344–82. Second edition (revised). Oxford: Clarendon Press. 1928. pp. 206–40 and 386–425.

1916. Medusae from the Indian Ocean. (Collected by Prof. Stanley Gardiner in H.M.S. *Sealark*, in 1905.) *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. XVII, pp. 169–210.

—— Notes on some jelly-fishes from Okhamandal in Kattiawar collected by Mr James Hornell in 1904–5. *Rep. Govt. Baroda on Mar. Zool. Okhamandal in Kattiawar*, Pt. II, pp. 151–5.

1919–20. Ernst Heinrich Philipp August Haeckel. *Proc. Linn. Soc.*, Sess. 132, pp. 39–43.

1926. Siphonophorae from the Indian Ocean collected by Prof. Stanley Gardiner in H.M.S. *Sealark*. *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. XIX, pp. 55–86.

—— Report on the medusae, Cambridge Expedition to the Suez Canal. *Trans. Zool. Soc.*, London, Vol. XXII, pp. 105–15.

THE PLYMOUTH OFFSHORE MEDUSA FAUNA

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–5)

CONTENTS

INTRODUCTION

A system of regular weekly collecting with the 2 m. stramin ringtrawl was started in 1930 with the object of comparing fluctuations in the composition of the plankton over a number of years, in the hope that certain animals might thus be found which could be used as "an index of conditions that may lead to other fluctuations such as those of the fisheries" (Russell, 1933). A direct outcome of this work has been the recognition of a number of animals that can be used as indicators of water masses and the correlation of variations in their occurrence with the numbers of young fish in the plankton. In the preliminary paper quoted above it was noted that such changes as occurred in the composition of the plankton from year to year were especially noticeable in the medusa population. Medusae have been regarded by some workers (e.g. Kramp, 1927) as very valuable indicators, liberated at certain times from their hydroids in fixed localities and drifting in the water masses for periods that can be estimated with a correct knowledge of their life histories. Since the inception of this work in 1930 close attention has been paid to certain medusae which appeared to be spasmodic in their occurrence. But it was soon noticed that the differences between some years were so marked that it was advisable to distinguish all medusae occurring in the catches. The collections have also been supplemented since 1933 by almost daily examination of living plankton catches over long periods.

These observations have now been made for 8 years, with the result that it is now possible to obtain a fair view of the medusa fauna in offshore waters off Plymouth and its changes from season to season and year to year.

THE PLYMOUTH MEDUSA FAUNA

The "Plymouth Marine Fauna" (1931) records forty-one species of planktonic Hydromedusae, twenty-three Anthomedusae, fifteen Leptomedusae, two Trachymedusae and one Narcomedusa; four species of Siphonophora; and five species of planktonic Scyphomedusae. During the 8 years' observations since 1930 nine more species have been added to the fauna, viz.:

Anthomedusae: *Turritopsis nutricula* McCrady, *Pochella polynema* Hartlaub.

Leptomedusae: *Eucheilota clausa* (Hincks), *Helgicirrha schulzei* Hartlaub, *Aequorea vitrina* Gosse.

Trachymedusa: *Gossea corynetes* (Gosse).

Siphonophora: *Muggiaea kochi* (Will).

Scyphomedusae: *Pelagia noctiluca* Péron & Lesueur, *Discomedusa lobata* Claus.

Since 1930 I have myself taken all the species recorded at Plymouth except *Eucodonium brownei*, *Mitrocomella fulva*, *Solmaris corona*, and *Cyanea capillata*. (The specific names used in this report are those of the Plymouth Marine Fauna, except for *Zanclea* and *Eirene*.) The Siphonophora and Scyphomedusae are not referred to here except in the lists on pp. 416 and 417.

During the course of these 8 years' observations many data have accumulated on the occurrence of medusae in the different months of the year. By combining these results with the records given in the Plymouth Marine Fauna it has been possible to produce in Table I a reliable guide showing in which months of the year any species of medusa may be expected to occur and in which month any species has been recorded as being abundant. In this table the species have been arranged approximately in the order of their geographical distribution from north to south, and it can be seen at a glance that the more northerly species are usually present in the plankton earlier in the year than the more southerly. Table I thus gives a picture of the seasonal progression of the composition of the medusa fauna off Plymouth. The seasonal sequence according to geographical distribution is to be expected on account of the seasonal range of the temperature of the sea off Plymouth, and in this respect it is in agreement with the results already published for the young fish (Russell, 1930–7, Vol. xx, p. 147). But the information given in

Table I does not necessarily mean that all the species mentioned are certain to be found in any year. It must be supplemented by a close examination of the distribution of the species both geographically and with respect to the movements of the water masses in the English Channel. But as our knowledge of the plankton content of the different types of water grows we are becoming better able to say which are the species that are most likely to occur off Plymouth during any month in which specimens are required.

TABLE I. SEASONAL DISTRIBUTION OF PLYMOUTH MEDUSAE

× recorded as present; **x** months of greatest abundance; N.B., northern boreal; B., boreal; S.B., southern boreal; S., southerly; C., cosmopolitan.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
ANTHOMEDUSAE													
Rathkea octopunctata	×	×	×	**x**	**x**	..	..	..	..	..	×	×	N.B.
Hybocodon prolifer	..	×	×	×	**x**	×	..	..	..	..	..	..	N.B.
Euphysa aurata	..	..	×	×	×	×	..	..	×	..	..	..	N.B.
Steenstrupia nutans	..	..	..	×	**x**	**x**	×	×	×	..	..	..	N.B.
Podocoryne areolata	×	..	..	..	..	×	..	×	×	..	..	..	?N.B.
Podocoryne carnea	..	×	×	..	..	..	×	×	..	..	..	..	C.
Bougainvillia principis	..	..	..	×	×	..	..	..	..	..	..	..	N.B.
Sarsia tubulosa	..	..	×	×	×	×	×	..	×	×	×	..	N.B.
Sarsia eximia	..	..	..	×	×	×	×	..	×	..	..	..	?N.B.
Bougainvillia britannica	..	..	..	×	**x**	**x**	×	..	..	..	..	..	B.
Ectopleura dumortieri	..	..	..	×	×	..	..	..	×	×	×	..	?S.B.
Willia stellata	×	×*	×†	×	×	×	**x**	×	**x**	×	×	×	?S.B.
Lizzia blondina	..	..	×	**x**	**x**	**x**	**x**	×	**x**	..	×	..	S.B.
Leuckartiara octona	..	×	×	×	**x**	**x**	**x**	**x**	**x**	×	×	×	S.B.
Bougainvillia ramosa	..	..	..	×	×	..	..	×	×	×	×	..	S.B.
Purena gemmifera	..	..	..	..	×	**x**	**x**	..	×	..	×	..	S.B.
Amphinema rugosum	..	..	..	×	**x**	**x**	**x**	×	×	×	..	..	?S.B.
Zanclea costata	..	..	..	..	×	..	×	×	×	..	..	..	?S.B.
Sarsia prolifera‡	..	..	..	×	×	×	**x**	×	×	×	**x**	..	S.
Dipurena halterata	..	..	..	×	×	×	×	×	×	..	..	..	S.
Purena strangulata	..	..	..	..	..	×	×	..	..	..	..	..	S.
Amphinema dinema	×	..	..	..	..	..	×	..	**x**	**x**	×	..	S.
Turritopsis nutricula	×	..	..	..	..	..	..	×	×	**x**	×	×	S.
Eucodonium brownei	..	..	..	..	..	..	..	..	×	..	..	..	?
Pochella polynema	..	..	..	..	×	×	..	..	..	..	..	..	?
LEPTOMEDUSAE:													
Tiaropsis multicirrata	..	..	×	×	..	..	..	..	..	..	..	..	N.B.
Phialidium hemisphericum	×	×	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	×	×	B.
Obelia spp.	×	×	×	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	×	C.
Phialella cymbaloides	..	..	×	×	**x**	×	×	..	×	×	..	..	?B.
Cosmetira pilosella	..	..	×	**x**	**x**	**x**	**x**	**x**	×	×	..	..	S.B.
Mitrocomella brownei	..	..	..	×	×	..	..	×	×	..	..	..	?S.B.
Mitrocomella fulva	..	..	..	..	×	..	..	..	..	..	..	..	?
Saphenia gracilis	×	×	×	×	**x**	**x**	**x**	×	×	×	×	×	S.
Eutima insignis	..	..	..	..	..	×	..	×	×	×	..	..	S.
Aequorea forskalea	..	..	×	×	×	×	×	×	×	×	×	×	S.
Aequorea vitrina	..	..	..	..	..	×	..	..	..	..	..	..	S.
Laodicea undulata	..	×§	×	×	×	×	×	**x**	**x**	×	×	..	S.
Eucheilota clausa	×	..	..	×	..	×	×	..	×	**x**	×	×	?S.
Helgicirrha schulzei	..	..	..	..	..	×	×	×	×	×	..	×	S.
Eirene viridula	..	..	..	..	..	..	×	×	**x**	**x**	×	×	S.
Octorchis gegenbauri	×	..	..	..	..	..	×	**x**	×	×	..	..	S.
Agastra mira	..	..	..	..	..	..	×	×	..	..	×	..	?
TRACHYMEDUSAE:													
Aglantha rosea	×	×	×	×	×	**x**	**x**	**x**	**x**	×	×	×	S.B.
Liriope exigua	×	×	..	..	×	×	×	**x**	**x**	**x**	**x**	**x**	S.
Gossea corynetes	..	..	..	..	..	..	×	×	×	×	×	×	S.
NARCOMEDUSA:													
Solmaris corona	..	..	..	..	..	..	..	..	×	..	..	..	S.

* Hydroid with medusa ready for liberation. (E. T. Browne, MS. notes, February 22 1899.)
† Liberated from hydroid, March 30 1936.
‡ Plymouth Marine Fauna gives Jan.–Oct.; this is possibly a misprint for Jun.–Oct.
§ February 21 1938 one specimen.

The late Mr E. T. Browne laid a very sound foundation for a comparison of the different areas of distribution on the south and western shores of the British

Isles by his careful and prolonged studies, especially at Plymouth, Valencia, Port Erin and Millport. In a comparison of the faunas of Plymouth and Valencia, Browne (1900) gave the following species as occurring at Valencia but not at Plymouth: *Bougainvillia pyramidata*, *Dipleurosoma typicum**, *Melicertum octocostatum*, *Laodicea undulata*, ?*Aequorea forskalea*, *Aglantha rosea* and *Gossea corynetes*. Of these only *Bougainvillia pyramidata*, *Dipleurosoma typicum* and *Melicertum octocostatum* now remain not recorded from Plymouth, but to the list of those found only at Valencia must be added *Leuckartiara nobilis* and *L. breviconis* (see Hartlaub, 1911). The only species recorded from Plymouth and not from Valencia are *Turritopsis nutricula*, *Pochella polynema*, *Eucheilota clausa* and *Helgicirrha schulzei*; of these the last three have been described as new species since Browne's observations were made and *Eucheilota clausa* has now been found at Valencia (see p. 432). Browne's observations at Valencia were further supplemented by the Misses Delap (1905, 1906).

Browne (1906) also made a comparison between the medusae recorded from the English Channel and those taken in the Bay of Biscay on the cruise of H.M.S. *Research*. Of those species living within 100 fathoms of the surface in the Bay *Aglaura hemistoma* and *Rhopalonema coeruleum* had not been recorded in the Channel and they still remain unrecorded from Plymouth.

But such faunistic comparison is not sufficient in itself; to it must be added a knowledge of the comparative abundance of the species in the different localities. Unfortunately, I cannot give numerical data for many of the smaller species, but data for all those species occurring in the stramin ringtrawl catches will be found in Tables II and III. From the examination of townet catches and of the previously published records a good idea can, however, be obtained as to which species are common and which scarce. But while one species may be common in one year it may be very scarce the next. A comparison of the Plymouth medusa fauna with that of other regions, coupled with a knowledge of the occurrence of the hydroids of some species and a critical analysis of the data in Table III, enables us now to explain to some degree these changes in the composition of the fauna from year to year. There are some species which can undoubtedly be regarded as visitors to the area, but owing to Plymouth's geographical position it is difficult to decide for all species which are visitors and which may be called truly indigenous. This circumstance is brought about by the complicated hydrographic conditions existing in the Channel area, and in order to understand the composition of the medusa fauna off Plymouth we must have some idea of these conditions.

Through oceanic circulation and wind effects there is a resultant flow of water through the straits of Dover into the southern North Sea. The supply from which this water is ultimately drawn enters the western mouth of the

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* This species was recorded off Brighton in 1879 by Haeckel in his *System der Medusen*, p. 636.

Channel either from the west or the south-west. It is generally conceded that more water enters the Channel than can pass through the Dover straits, and this surplus probably drifts north-west or north past the Scillies—Land's End region, though the actual state of affairs here is still not clear (Carruthers, 1934). To the west of the mouth of the Channel is an anticyclonic swirl lying over the shallow continental plateau south of Ireland. This swirl varies in its extent and position; at times it appears to block the mouth of the Channel and at others it apparently retreats farther north, thus laying the Channel mouth open to more oceanic water from the south and south-west. When there is a strong flow through the Dover straits, water may move up Channel past Plymouth either from the swirl or from the ocean according to the conditions existing off the Channel mouth. In the Channel itself there must be a body of water constantly being added to from the west and dissipated to the east, or hemmed into the coast to allow for passage of more oceanic water. The circulation of water in the Channel itself is clearly very variable from time to time.

It has been shown (Russell, 1936 *a*) that the various water types carry their own faunistic associations of plankton or indicators and, of these, three types have so far been elucidated:

(1) "Channel" water, characterized by *Sagitta setosa* and a poverty of plankton.

(2) "Elegans" (swirl) water, characterized by *S. elegans* and a number of associated species and a rich plankton.

(3) "Oceanic" water, characterized by salps and doliolids and their associated fauna.

There have also been during the past 3 years indications of the possible existence of a fourth type in which there are always large numbers of pilchard eggs and few *Sagitta* of either species; but its relationship in the general scheme is not yet clear.

These different types have also different species of medusae associated with them, and it is this fact that makes the true character of the Plymouth medusa fauna difficult to decide. The "*elegans*" water for instance contains in the summer great numbers of *Cosmetira* and *Laodicea*. In years in which this water is drifted past Plymouth it is natural to suppose that a stock of their hydroids should be produced on the sea bottom off Plymouth. Thus if a period of several years of absence of "*elegans*" water off Plymouth follows there is at first a good stock of hydroids to liberate medusae, but the numbers of adult medusae thereafter decrease. Presumably there is either an insufficient food supply or the type of water is for some reason harmful and not many medusae grow to maturity. The stock of hydroids will thus gradually diminish, but it is unlikely that for common species sufficient time ever elapses off Plymouth to allow the stock to die out before there is an importation of large numbers of fresh medusae from the west.

Similarly *Turritopsis* appears to be a species characteristic of "Channel" water, associated with *Sagitta setosa.* In periods when Channel water predominates off Plymouth it is thus possible that a local population of *Turritopsis* hydroids may arise. But *Turritopsis* is never very abundant, so that it is probable that its hydroid may die out at Plymouth after a prolonged continuation of "*elegans*" conditions.

This colonization of the grounds by hydroids from drifting medusae must be constantly borne in mind, and it can be understood that it is difficult to decide which species can be regarded as permanently indigenous to the waters off Plymouth. Even such medusae as *Phialidium* and *Obelia*, which are always present, become much more abundant during periods of predominance of "*elegans*" water presumably on account of the increased supply of food.

With these difficulties in mind I have attempted to draw up the following preliminary list of Plymouth medusae divided into indigenous and visiting species and indicating whether they are common or scarce. It is likely that in time, as our knowledge of their distribution increases, more of those species here listed as indigenous will be shown to be visitors.

Indigenous

Common

*Sarsia prolifera**
Purena gemmifera†
*Steenstrupia nutans**
Hybocodon prolifer
*Rathkea octopunctata**
Lizzia blondina†
*Bougainvillia britannica**
*Amphinema dinema**
*Leuckartiara octona**
Phialidium hemisphericum†
*Phialella cymbaloides**
Obelia spp.†
*Eucheilota clausa**
*Saphenia gracilis**
*Eirene viridula**
Aurelia aurita
Cyanea lamarcki
Chrysaora isosceles

Scarce

Sarsia tubulosa
Sarsia eximia
Zanclea costata
Ectopleura dumortieri
Bougainvillia ramosa
Podocoryne carnea
Willia stellata
Mitrocomella brownei
Octorchis gegenbauri
Helgicirrha schulzei
Gossea corynetes

Very rare (position uncertain)

Eucodonium brownei
Pochella polynema
Mitrocomella fulva
Agastra mira

* Abundant at times. † Very abundant at times.

Visitors

Abundant at times

Amphinema rugosum
Laodicea undulata
Cosmetira pilosella
Aglantha rosea
Liriope exigua
Muggiaea atlantica
Muggiaea kochi

Common at times

Turritopsis nutricula

Scarce

Dipurena halterata
Purena strangulata
Euphysa aurata
Bougainvillia principis
Podocoryne areolata
Tiaropsis multicirrata
Aequorea forskalea
Aequorea vitrina
Solmaris corona
Pelagia noctiluca
Discomedusa lobata

The above visitors can probably be divided among the three types of water as follows:

"Channel"	"*Elegans*"	"Oceanic"
Turritopsis nutricula	*Dipurena halterata*	*Aglantha rosea*
	Purena strangulata	*Liriope exigua*
	Euphysa aurata	*Solmaris corona*
	Bougainvillia principis	*Muggiaea atlantica*
	Podocoryne areolata	*Muggiaea kochi*
	Amphinema rugosum	*Pelagia noctiluca*
	Laodicea undulata	*Discomedusa lobata*
	Cosmetira pilosella	
	Tiaropsis multicirrata	
	Aequorea spp.	
	Aglantha rosea	

The above lists require one or two words of comment. The reservation must be made that at any time occasional specimens of visiting species may be found, but their presence in larger numbers is a sure indication of water movement.

As regards the indigenous medusae this list needs the qualification that in some years, owing to certain hydrographical conditions (see p. 419), all species may appear to be scarce. As regards the *relative* abundance of the different species it should however still hold good.

The scarcity of *Sarsia tubulosa* and *S. eximia* in offshore waters is probably due to the very littoral or estuarine distribution of their hydroids. These are quite common inshore. It is also rather remarkable that while the hydroids of *Zanclea costata*, *Bougainvillia ramosa*, and *Podocoryne carnea* are common off Plymouth the medusae themselves seem to be rather scarce. It may possibly be accounted for by the fact that the medusae, especially those of *P. carnea*, may often mature at a very undeveloped stage, thus only being present in the plankton for a very short time.

It is also to be noted that in the above list *Aglantha rosea* has been included as an indicator both of "*elegans*" and of "oceanic" waters. *Aglantha* is essentially an oceanic medusa, nevertheless a large stock appears to flourish in the water south of Ireland. It may thus possibly be drawn from two sources, though results seem to show that it is more usually associated with "*elegans*" conditions.

Euphysa aurata and *Bougainvillia principis* have never been recorded commonly off Plymouth, yet they are common south of Ireland. The reason for their continuous scarcity at Plymouth is not clear.

The occurrence of the oceanic indicators is not yet fully elucidated. For instance, *Liriope* has so far only appeared abundantly off Plymouth during periods of essential "*elegans*" predominance (see p. 423).

Before passing on to the details of the ringtrawl catches mention should be made of an interesting feature of the Plymouth medusa fauna as a whole. This is that of the northern species by far the majority are Anthomedusae. This fact led me to make a casual survey of the medusae of cold waters (see e.g. Thiel, 1932; Browne, 1902, 1910). It is evident that of the medusae liberated from hydroids the majority in cold waters are Anthomedusae or so-called "primitive" Leptomedusae such as laodiceids and mitrocomids. This difference between the medusa faunas of cold and warm waters seems worthy of a closer investigation. In this respect it is interesting to note that all the laodiceids and mitrocomids whose hydroids are so far known have "*Cuspidella*" hydroids. It may well be that this is the primitive type from which many of the campanulate hydroids have evolved and that the evolution of the Leptomedusae has taken place mainly in warm waters. Being of more recent evolution than the Anthomedusae they have not yet given rise to many cold-water species.

THE RINGTRAWL CATCHES, 1930–7

The average catches for each month in the years 1930–7 are given in Table III, p. 436. These are based on half-hour oblique hauls taken usually each week at a position 2 miles east of the Eddystone (for the actual dates of hauls see Russell, 1930–8). The sums of the average monthly catches of each year are given in Table II.

Before discussing the results of these collections a few remarks must be made on the identification of species. As already mentioned, owing to the size of the mesh employed only the larger species are represented in these catches. Such species as *Purena gemmifera*, *Rathkea octopunctata* and *Lizzia blondina*, the majority of which are not retained by the net, have not been counted, although when they are very abundant in the plankton a few may be found in the catches. Owing at times to the large masses of other plankton animals in the catches the medusae are often in a very bad state of preservation, and when numerous themselves could not be subjected to so close a critical examination as is to be desired. Long experience of dealing with such catches in bulk has, however, enabled me to be fairly certain that the identifications are correct, and the re-examination at a later date of previously sorted material, and frequent observations of living samples taken at the same times as the catches which were preserved, have convinced me that a reliable picture has been produced of the medusa fauna taken by the ringtrawl. There are, however, one or two species that can only be separated for certain by a critical examination under the microscope. These are *Mitrocomella brownei*, *Eucheilota clausa* and *Phialella cymbaloides*, which in bulk catches sorted with the naked eye may easily be mistaken for *Phialidium hemisphericum*. No regular attempt was made to discriminate between these species and all have been counted under *Phialidium*. As *Phialidium* is by far the most abundant the inclusion of the other species has probably not produced a very false impression. Of the other species *Phialella cymbaloides* and *Eucheilota clausa* are quite common at times, but *Mitrocomella brownei* is scarce. *Saphenia gracilis* and *Eutima insignis* have also been counted together as *Saphenia*. They are often in too bad a state to be sure of the number of tentacles as the manubria become twisted together, and it is indeed uncertain whether they are distinct species.

When we examine the results as a whole (see Table II) the most striking feature is the great decrease in the numbers of total medusae in the years 1935, 1936 and 1937 as compared with the previous years. The high numbers in the years 1930, 1931 and 1932 are in part made up by the abundance of *Laodicea*, *Cosmetira*, *Aglantha* and *Liriope*, which were visitors to the area associated with the predominance of "*elegans*" and "oceanic" water. But when we regard the commonest truly indigenous species, such as *Leuckartiara*, *Phialidium* and *Obelia*, we notice that in the later years there has on the whole been a great decrease in numbers. The decrease in the numbers of young fish in the plankton during this period has already been noted (Russell, 1936 *a*), and there can be little doubt that the decrease in numbers of medusae is an associated phenomenon. At the foot of Table II are included the corresponding numbers for all young fish (less clupeids) taken in the same series of collections. The low numbers of young fish in the years 1935, 1936 and 1937 closely parallel those for the medusae. The abundance of young fish has been shown to follow closely the winter maximum of phosphorus content of the water (Russell, 1936 *a*), and it seems quite evident that this lack of nutrient matter has resulted in a decreased supply of planktonic food for such predatory organisms as fish and medusae and affected their survival rate.

TABLE II. SUMS OF AVERAGE MONTHLY CATCHES OF MEDUSAE IN THE RINGTRAWL FOR EACH YEAR AT PLYMOUTH

	1930	1931	1932	1933	1934	1935	1936	1937
Steenstrupia nutans	46	123	64	18	1,232	6	15	59
Bougainvillia britannica	296	112	402	4	1,285	33	2	2
Turritopsis nutricula	..	..	..	17	1	3	25	34
Amphinema dinema	..	..	6	8	7	107	55	70
Amphinema rugosum	473	1	21	13	2	..	7	2
Leuckartiara octona	658	513	403	218	108	102	68	16
Laodicea undulata	5,141	2,527	22	70	282	208	4	18
Cosmetira pilosella	891	2,111	2,599	326	342	41	6	7
Obelia spp.	15,418	1,311	18,656	2,730	13,649	1,935	797	2,151
Phialidium hemisphericum	8,950	12,554	5,862	9,512	5,179	600	948	2,605
Saphenia gracilis	157	22	28	67	34	39	136	108
Octorchis gegenbauri	..	28	+	8	10	36	14	25
Eirene viridula	..	1,314	83	56	1	7	2	39
Helgicirrha schulzei						3	2	1
Aequorea forskalea	+	13	4	..	+	1	2	+
Gossea corynetes	..	12	1	4	11	6	1	13
Aglantha rosea	38,439	143	..	1	32	22	425	60
Liriope exigua	15,522	327	..	3	+	+	..	..
Total medusae	85,991	21,111	28,151	13,055	22,175	3,149	2,509	5,210
Total young fish (less clupeids)	1,517	1,625	1,556	1,337	1,144	430	487	557

If we examine the list in Table II in greater detail other points of interest are to be found. In the year 1934 *Steenstrupia nutans* and *Bougainvillia britannica* were both unusually abundant; in that year there were more *Sagitta elegans* present in May than in recent years. The sudden appearance of *Turritopsis* in 1933 and its persistence thereafter is to be associated with the prevalence of Channel water. There has been a sudden increase in abundance of *Amphinema dinema* in 1935, 1936 and 1937, while *A. rugosum* was very abundant in 1930 during the year of greatest "*elegans*" predominance. The year 1931 was outstanding for the numbers of *Eirene viridula*; it is to be noted that this abundance coincided with the presence of *Salpa mucronata* and *Doliolum gegenbauri* which occurred only in that year. No attempt can be made to explain all these differences from year to year, but they are here noted for comparison with future years.

Observations on Certain Medusae

In the following pages are given further details on the biology of some of the Plymouth medusae together with a few observations of note on structural details.

Purena gemmifera (Forbes).

I have noticed that the tentacles of living medusae of *Purena gemmifera* show a characteristic vibrational movement. This movement is produced by cilia on the tentacles. These cilia which appear to be confined to the nematocysts clusters and terminal knob can already be seen on the tentacles while the young medusae are still attached to the stomach of the parent. A careful examination of living specimens of other medusae has so far shown no similar ciliation in other Sarsiid species.

Zanclea costata Gegenbaur.

In a previous publication (Russell & Rees, 1936) *Zanclea gemmosa* McCrady with two tentacles was provisionally kept distinct from *Zanclea costata* Gegenbaur until it could be shown either that the latter was liberated from the hydroid with four tentacles, or that a medusa with four tentacles could develop from one with two. In 1937 I obtained a complete series of *Zanclea* medusae from the plankton showing the development of a two-tentacled medusa into one with four tentacles. Among these specimens a medusa 1·5 mm. in height had two opposite perradial tentacles, another 2 mm. in height had two fully grown opposite perradial tentacles, and on the other two perradial bulbs there were very short tentacles just developing. Another 3·1 mm. in height had four tentacles of nearly equal size. There seems therefore to be little doubt that the medusae with two and those with four tentacles are the same species and referable to *Zanclea costata* Gegenbaur.

It is hoped to deal with the questions raised by Weill (1936) and Ranson (1937) about the nematocyst armature on the umbrella in a future publication.

Bougainvillia britannica Forbes.

The year 1934 was outstanding for the abundance of this species and the presence of such large numbers furnished an opportunity to study the growth and development of the medusa in the plankton. Measurements of height and width were made on a large number of preserved specimens from the plankton on April 20 and May 3, 16 and 24. The actual period when the medusae were present in the plankton and their numbers in the weekly catches were as follows:

April 6	10	May 2	1567
,, 12	4	,, 9	41
,, 16	4	,, 16	2731
,, 26	233	,, 24	1528
		,, 29	244

When alive the medusa is usually somewhat higher than it is wide; when preserved, however, contraction causes them often to be as wide as they are high. In order to range the medusae after measurement the height of each specimen was multiplied by its width and the square root of the product taken. Thus the measurements of the medusa diameter given in the table on p. 422 and Fig. 1 are for spherical medusae and would probably have been very slightly greater if the measurements of height had been made on living material. The data have been supplemented by some material collected on April 20 when the ringtrawl was not used.

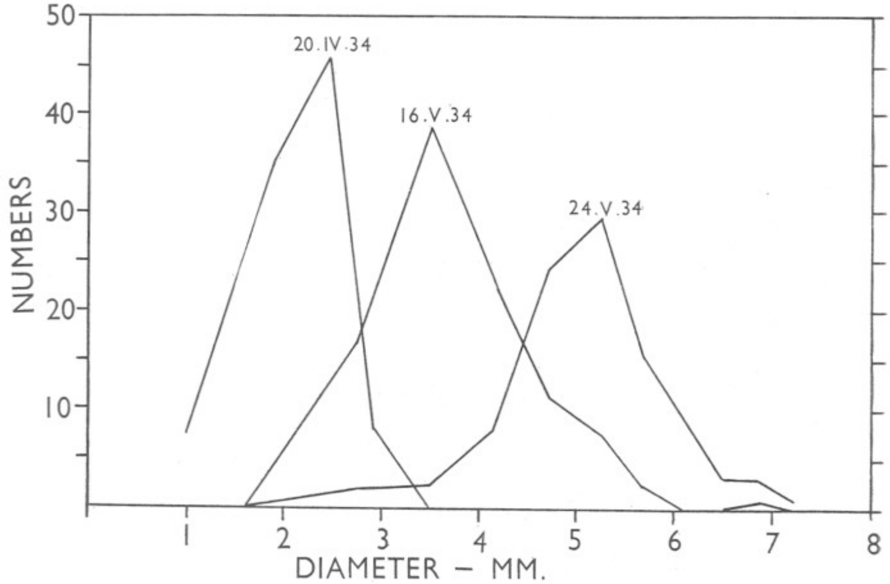

Fig. 1. Growth of *Bougainvillia britannica* from samples collected in the plankton off Plymouth, 1934. The curves show the numbers of specimens of different diameters on April 20, May 16 and 24.

Growth. The results of measurements made on April 20, May 16 and 24 are shown in Fig. 1. The growth of the medusae is well illustrated, the mode increasing successively from 2·5 to 3·5 and 5·25 mm. on each successive date. The maximum size attained is about 7 mm. The medusa had disappeared from the plankton completely by June 6. Thus the period from the date of first appearance (April 6) was 2 months. By May 16 some of the gonads were mature and planulae were reared. The dates of appearance of the medusa in the plankton coupled with the gradual increase in size shown in Fig. 1 afford fair evidence that the length of life of the medusa *Bougainvillia britannica* in Plymouth waters is not more than 2 months. Kramp (1927) has said that in Danish waters "it lives presumably for about 2 months, but we know nothing certain as to this".

Development. The medusa when first liberated from its hydroid has four single marginal tentacles and four unbranched oral tentacles. As growth proceeds the number of marginal tentacles increases on each of the four tentacular bulbs and the oral tentacles branch dichotomously. Observations were made on a large number (140) of medusae of different sizes and the sequence of their development found. The examination gave the following results:

Diameter (mm.)	Number of tentacles on each marginal bulb	Number of times oral tentacles are branched
1·5	3	1–1(+)
1·75	3– 4	1–2
2·0	4– 5	1–2(+)
2·25	4– 5	(1)–2
2·5	4– 6	(1)–2–2(+)
2·75	5– 6	2
3·0	5– 7	2
3·25	5	2
3·5	8– 9	3
4·0	9–11	3–3(+)
4·5	10–11	3(+)–4
5·0	10–12	3(+)–4
6·0	11–13	4–4(+)
7·0	14–15	4
7·5	16–17	5(+)

Note. (+) implies that some of the branches are just starting to subdivide. Numbers in brackets are exceptional occurrences.

It is evident from this table that full-grown medusae will have about eleven to seventeen tentacles on each marginal bulb, and the oral tentacles will be dichotomously branched four or five times. This agrees with observations by Hartlaub (1911) on a swarm in the North Sea. His specimens had well-developed gonads and averaged 5–7 mm. in height, and the number of tentacles on each marginal bulb averaged twelve to sixteen. Hartlaub gives 12 mm. in height as the largest size, the tentacles on each marginal bulb up to 30 in number, and oral tentacles branching at most seven times. Such individuals must be exceptional.

Bougainvillia principis (Steenstrup).

This species appears to be very rare at Plymouth. One specimen was taken in May 1935, one* in May 1936 and one in April 1937. The only previous record is the end of April 1893 (Garstang, 1894). In its distribution it is much more northerly than *B. britannica*, although it occurs more commonly at Valencia than at Plymouth.

Turritopsis nutricula McCrady.

This species has not been recorded in the Plymouth fauna prior to this series of observations. It was first seen in 1933, and has occurred each year since. The species is indigenous in the southern North Sea and eastern end of the English Channel, where it has been used by Kramp (1930), Wulff, Bückmann, and Künne (1934) and Künne (1937) as an indicator of water movements. Its first appearance here and its continuation is coincident with the decrease in "*elegans*" water which has been so noticeable after the year 1932. Browne (1898) did not find the species at Plymouth in the years 1893, 1895 and 1897 although working in September, a month in which *Turritopsis* occurs in the plankton. Browne's records show that those years were characterized by the presence of *Liriope*; this would explain the absence of *Turritopsis* at that time, since *Liriope* has only appeared in numbers during the last eight years in 1930–1 when "*elegans*" conditions were most predominant. Künne (1934) states that *Turritopsis* penetrated farther into the southern North Sea in 1932 than in 1933, in which year it appeared off Plymouth.

There has in the past been some discussion as to the identity of the European species of *Turritopsis*, which was described under the specific name *polycirrha*. Although Mayer (1910) could detect no specific differences between *polycirrha* and the American *nutricula*, Hartlaub (1911) kept them distinct. He maintained that in *polycirrha* the endodermal mass was not in four sections, and that the radial canals did not penetrate the endodermal mass or widen into chambers as figured by Brooks. Later (1917) he recorded a specimen from Heligoland that agreed with Brooks' figure as regards the widening of the radial canal, though he maintained that the identity of the two species still remained unproved. Their identity has, however, been accepted by Mayer (1910), Bigelow (1913) and Kramp (1930); it is accepted here on the grounds that all specimens seen at Plymouth showed the endodermal mass divided into four sections which were traversed by the radial canals. Cavities were also frequently seen in the endodermal mass, which when radially disposed could give rise to the appearance figured by Brooks.

Amphinema rugosum Mayer.

In earlier literature there has been considerable confusion between this species and *A. dinema* (see Rees and Russell, 1937). Since I was myself at

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* I am indebted to Dr P. L. Kramp for confirmation of the identification of this specimen.

first confused by Hartlaub's (1911) description of one species under the name of the other I have found it necessary to re-examine all the previous samples on which any data have been published; as I expected to find, all species under the specific name *dinema* should have been *rugosum* (a revision of my data will be found in the footnote*).

From the occurrence of *A. rugosum* in such numbers in 1930 it appears probable that the species is associated with "*elegans*" conditions. The true distribution of the species is not yet known, but in 1933 while cruising in Col. E. T. Peel's yacht *St George* I took a plankton sample on July 9 at a position north of the Fair Isle Channel (59° 42′ N.; 2° 10′ W.). This was a typical *elegans* association and there were a number of *A. rugosum* present. The species is therefore not likely to be normally indigenous to Plymouth, and it is perhaps significant in this respect that the only two records of its hydroid off Plymouth are on floating objects that may have drifted into the area (see Rees and Russell, 1937).

A detailed examination was made of a number of specimens taken off Plymouth in June and July 1930. The numbers of marginal tentaculae were counted on sixty-three specimens with the following results:

Total number of marginal tentaculae	Number of individuals	Distribution of tentaculae on either side of large tentacles	Number of individuals
11	1	5+6	1
12	2	5+7	1
13	6	5+8	1
14	14	6+6	1
15	10	6+7	5†
16	7	6+8	1
17	8	7+7	13
18	4	7+8	10
19	4	7+9	2†
20	1	8+8	5
21	3	8+9	8
22	3	8+11	1
		9+9	4
		9+10	3
		9+12	1
		10+10	1
		10+11	2
		11+11	3

† One abnormal.

From these figures it is evident that there is considerable variation in the number of tentaculae, which have been recorded up to twenty-four in number, the most frequent numbers here being fourteen to seventeen. The

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* I have examined the medusae in my collections and find that in all my previously published papers the medusae recorded under the names *Stomotoca dinema* or *Amphinema dinema* were in fact *A. rugosum*. These records are in this *Journal*, Vol. XIII, p. 781, July 15–16 1924; Vol. XIV, p. 569, June 17, 19; July 1, 16, 29 1925; Vol. XV, Table I, June 17, 18, 19 1925; Vol. XIX, Table I, June 10, 19, July 14, 23, 29, August 14 1930.

number must naturally vary with the age and size of the medusa, but the preserved specimens were too contracted to measure.

An analysis of the distribution of the marginal tentaculae gives the following results:

Equal numbers on either side of two main tentacles	27
A difference of one on either side of two main tentacles ...	28
A difference of two on either side of two main tentacles ...	3
A difference of three on either side of two main tentacles ...	3

Thus it appears that the normal increase of the number of tentaculae is by the addition of one tentacula at a time on either side of the medusa.

A. rugosum appears to be rather prone to abnormality. Of the two abnormal specimens mentioned in the above table, one had the following arrangement: one large tentacle with single radial canal, eight marginal tentaculae with no radial canal, one large tentacle with radial canal which bifurcated near its origin from the stomach with the two branches rejoining at the tentacle bulb, one marginal tentacula, one half-size large tentacle with a radial canal, eight tentaculae with the normal radial canal among them. In the other, one of the tentacular radial canals had bifurcated giving rise to a fully developed large tentacle at the end of each branch; its arrangement was one large tentacle, two tentaculae, one large tentacle, five tentaculae, one large tentacle, seven tentaculae. Other abnormal specimens were seen, one in which there was only one large tentacle, the place of the missing tentacle being taken by a tentacula; and two in which there were three large tentacles, in one of which the additional large tentacle was adradially situated and not opposite a radial canal.

Pochella polynema Hartlaub.

In May 1934 a specimen of *P. polynema** was taken off Plymouth. The medusa (Fig. 2*a*) was 2·7 mm. in diameter; it had thirty tentacles, fifteen large and fifteen small, each springing from a brown marginal bulb. The four radial canals were not observed to be branched, and the preserved specimen is too contracted to show branches if they were present.

This species was described by Hartlaub (1917) from seventeen specimens collected from the northern North Sea in June 1905. It has never been recorded since from European waters.

In 1936 while I was in Edinburgh Mr P. Gray showed me a number of slides of medusae that he had collected from the Firth of Clyde. Among these were two labelled *Pochella? polynema*. Mr Gray very kindly gave me one of these slides, a drawing of which is reproduced in Fig. 2*b*. This specimen, a female collected in Loch Fyne in April 1934, has twenty-seven tentacles, sixteen of which are large and eleven smaller. It is 2·4 mm. in height (mounted on slide). The ovaries are interadially situated on the stomach. The solid core of endoderm cells in the tentacles is to be clearly seen.

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* Is this *Oceania pusilla* of Gosse, "Devonshire Coast", 1853, p. 384, Pl. 13, figs. 11–14?

There can be little doubt that these specimens are the same species as Hartlaub's medusae.

Hartlaub states that occasionally the radial canals were branched, the branches starting about at the middle of the canal and running outwards towards the umbrella edge; some were short and blind, and some longer. In the mounted specimen that I have there is definitely no branching of the radial canals. When, however, I showed these medusae to Mr E. T. Browne he turned up from his collection two specimens taken 40 years ago at Plymouth and labelled by him as a new species of *Proboscidactyla*. These specimens differ in no respect from mine except that very delicate branches can be seen on some of the radial canals, much as described by Hartlaub. The specimens are too contracted to allow detailed observation of the branching system.

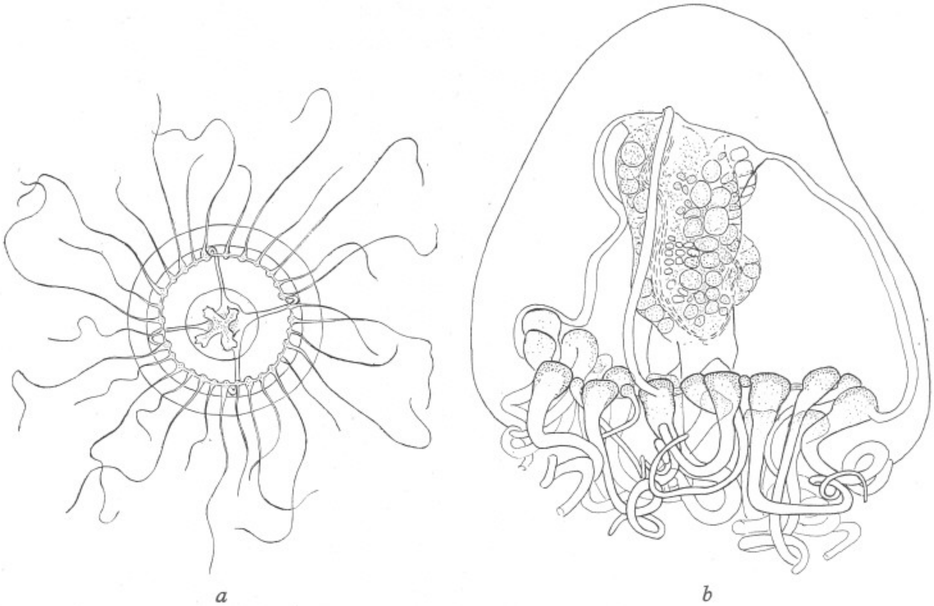

Fig. 2. *Pochella polynema*. *a*, living medusa 2·7 mm. in diameter caught off Plymouth May 25 1934. *b*, mounted specimen collected by Mr P. Gray from Loch Fyne, April 1934.

One of the specimens, taken by Mr Browne on June 30 1898, is 2·0 mm. in height (preserved in formalin) and has thirty-two tentacles, larger and smaller ones approximately alternating. It is a mature male. The four gonads are situated on the interradii of the stomach (Fig. 3 *a*). Two opposite gonads have the form of large cushions with their thickest parts at the upper ends. The other two gonads are thickest at their lower ends so that when viewed laterally they may be seen projecting as lobes on either side of the lower halves of the other two gonads (Fig. 3 *b*). The other specimen, taken on May 26 1898, is 1·4 mm. in height (preserved in alcohol) and has thirty-three tentacles.

In none of the above specimens was there any indication of exumbrella nematocyst canals, neither did Hartlaub find any. Until more specimens are obtained we cannot state whether the ring canals are solid. The systematic position of this species still remains problematical until more of its life history is known. There is, of course, the possibility that the medusae with unbranched radial canals may be different species from those in which the radial canals are branched. The fact that Hartlaub caught his seventeen specimens all together, some of which were with branched canals and others without, rather suggests, however, that they were all one species.

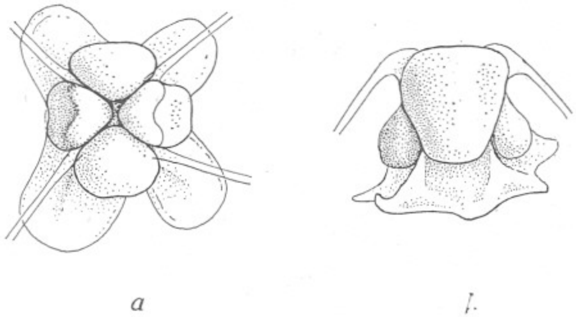

Fig. 3. *Pochella polynema*, Plymouth, June 30 1898 (E. T. Browne's collection). *a*, aboral view of gonads; *b*, lateral view.

The species has been recorded from Departure Bay, on the Pacific coast of North America, by Foerster (1923, p. 30), who called it *Proboscidactyla polynema*. In his specimens there were fine thread-like branches from the radial canal "invisible except under the high power of the microscope". The medusae were 2–4 mm. in diameter and there were 12 tentacles in each quadrant.

Foerster placed the species in the genus *Proboscidactyla*, but the gonads are not radial outgrowths from the stomach, neither are there exumbrella nemetocyst channels. On account of these differences it seems better to keep the genus *Pochella* distinct. In its affinities it is perhaps nearest to the Williidae, and if future research should show that it belongs to that family the characters of the family will have to be emended to take it.

Laodicea undulata (Forbes & Goodsir).

The probability that *L. undulata* cannot be regarded as a truly indigenous species off Plymouth has already been mentioned (p. 415). Kramp (1930) concluded that the species was indigenous in the southern North Sea because it was abundant in 1906, a year in which the influx of water from the Channel into the North Sea was only slight. It is, however, noteworthy that 1906 was the year following two successive years, 1904 and 1905, in which the influx was above the normal. It is thus possible that this may have been an instance of hydroids having developed on the sea bottom from mature medusae carried into the area in previous years. Kramp states that the medusae produced in the southern North Sea were considerably dwarfed, the majority being less than 8 mm. in diameter. In 1937 none of the *Laodicea* seen off Plymouth exceeded 7 mm. in diameter, and it appears that this is a parallel phenomenon with that observed by Kramp. It is probably an indication that the conditions of Channel water are not suitable for the successful growth of the medusa. In years when *Laodicea* occurs off Plymouth in large numbers the medusae are up to 15–20 mm. in diameter.

Cosmetira pilosella Forbes.

Two species of *Cosmetira* are recorded from the north Atlantic, *C. pilosella* Forbes and *C. megalotis* (Maas). The usual distinctions given between these two species in recent literature are (see e.g. Hartlaub, 1909, and Kramp, 1933):

	C. pilosella	*C. megalotis*
Umbrella diameter	*ca.* 20 mm.	30–40 mm.
Number of tentacles	*ca.* 64	*ca.* 100
Gonads/radial canal	$\frac{3}{4}$	$\frac{1}{3}-\frac{1}{2}$

This appears to overlook Forbes' (1848) original description of *C. pilosella* in which he gives the number of tentacles as $(24 \times 4 + 4)$, i.e. 100, and whose figure of the medusa shows at least eighty-two tentacles.

Diameter mm.	Tentacles and Developing Bulbs									Length of gonad mm.	Sex
	Numbers between every two marginal vesicles								Total		
15	8	8	9	7	8	8	12	8	68	6	♀
15	11	7	9	6	11	6	11	6	67	4	♀
16	11	6	10	6	10	9	11	8	71	4	♂
16	13	10	12	11	11	9	12	10	88	6·5	♂
16	13	11	12	9	13	9	11	11	89	..	..
17	12	9	13	11	25*	20*			90	5	
17	10	11	7	11 : 2† : 7		11	8	8 : 1†	76	5	♂
17	10	9	12	9	11	15*	8		74	5	♂
18	12	13	10	12	10	11	11	13	92	7	♂
18	11	12	13	14	8	15	7	12	92	7	♂
18	10	8	12	9	9	8	11	9	76	5·5	♂
18	10	8	9	7	13	11	11	8	77	6	♂
18	11	8	12	8	13	9	12	8	81	5·5	♂
18	11	11	12	21*	10	11	8			6·5	♀
19	10	10	12	11	16	10	14	10	93	Short	♂
19	11	7	7	9	12	8	11	7	72	5	♂
19	13	12	12	11	13	11	16	11	99	7	♂
19	13	9	10	9	10	9	12	9	81	6·5	♀
20	11	9	11	11	11	8	10	9	80	5·5	..
20	12	7	12	7	13	8	9		68	5·5	♂
21	12	9	13	9	12	8	11	8	82	6·5	♂
21	15	3	15	11	11	9	11	10	85	8·5	♀
22	13	7	10	4	10	8	10	6	68	4·5	
22	11	11	11	10	9	8	8	9	77	7	♂
22	13	11	12	9	12	8	12	8	85	6	♂
23	11	10	8	12	11	9	11	9	81	..	..
23	11	9	11	10	12	9	11	9	82	7	..
24	10	8	12	8	14	9	19*		80	7	♀
24	11	9	13	9	12	10	11	12	87	8	♂
26	10	9	14	9	20*	10	7		79	8	♂

* Marginal vesicle missing. † Extra marginal vesicle.

On August 17 1932 a number of *C. pilosella* caught off Plymouth were preserved for careful examination. The results are shown in the above table, in which are given the diameter of the medusa, the numbers of tentacles and developing bulbs between every two marginal vesicles beginning with a radial canal octant, the total number of tentacles and bulbs, and the lengths of the gonads.

This table shows that the diameters of the medusae varied between 15 and 26 mm., and that the numbers of tentacles and bulbs ranged from sixty-seven to ninety-nine. The length of the gonads varied from 0·2 to 0·4 of the diameter of the umbrella, or taking the radial canal length as approximately half that of the umbrella *ca.* 0·4–0·8 of the radial canal, or slightly less allowing for the width of the stomach. It is probable that in the preservation some medusae have contracted more than others.

Thus the number of tentacles and size of the gonads of *C. pilosella* at Plymouth overlap those given for *C. megalotis*, and the only remaining difference between the two species is in the size of the umbrella. Incidentally in this respect the Misses Delap (1905) record specimens from Valencia up to 48 mm. in diameter which were fully mature.

Künne (1937), using *Cosmetira* as an indicator of northern water in the southern North Sea, decided that his specimens were *C. megalotis*. While cruising in Col. Peel's yacht *St George* in 1933 I obtained some specimens of *Cosmetira* from north of the Fair Isle Channel (July 9 1933; 59° 42′ N., 2° 10′ W.). The diameters, numbers of tentacles and bulbs, and length of gonads (when not lost) were as follows:

mm.		mm.
15	63	..
15	68	..
15	71	4·5
17	80	5·5
18	81	..
19	84	7·5

These figures agree closely with those for the Plymouth medusae, and there can be no doubt that they were *C. pilosella*.

Tiaropsis multicirrata (M. Sars).

This species has only once been recorded at Plymouth: by Dr E. J. Allen in April 1895. On April 21 1934 a very small specimen was taken in the Sound. This was 1·39 mm. high and 1·25 mm. wide and had about twenty-four tentacles. The presence of so small a specimen must have been an indication that the hydroid was living in the locality. Its hydroid is unknown, but the extreme rarity of the medusa shows that it cannot normally be indigenous off Plymouth.

Phialidium hemisphericum (L.).

Phialidium is, with *Obelia* spp., by far the commonest species of medusa off Plymouth, and it may be taken in any month of the year. There is, however, a great decrease in numbers in the winter months, and it may sometimes be entirely absent in January and February. Observations by Orton (1920) showed that its hydroid, *Clytia johnstoni*, liberates medusae from March to October, and I have seen them liberated in November.

Two rather different forms are found in the plankton: a large form with elongated gonads, especially in the spring and early summer, and a small form with short oval gonads in the autumn. This has in the past given rise to the idea that there may be two species (see Browne, 1896, p. 489), but it is now generally agreed that there is only one. The difference is due to seasonal variation in size and the following observations confirm this.

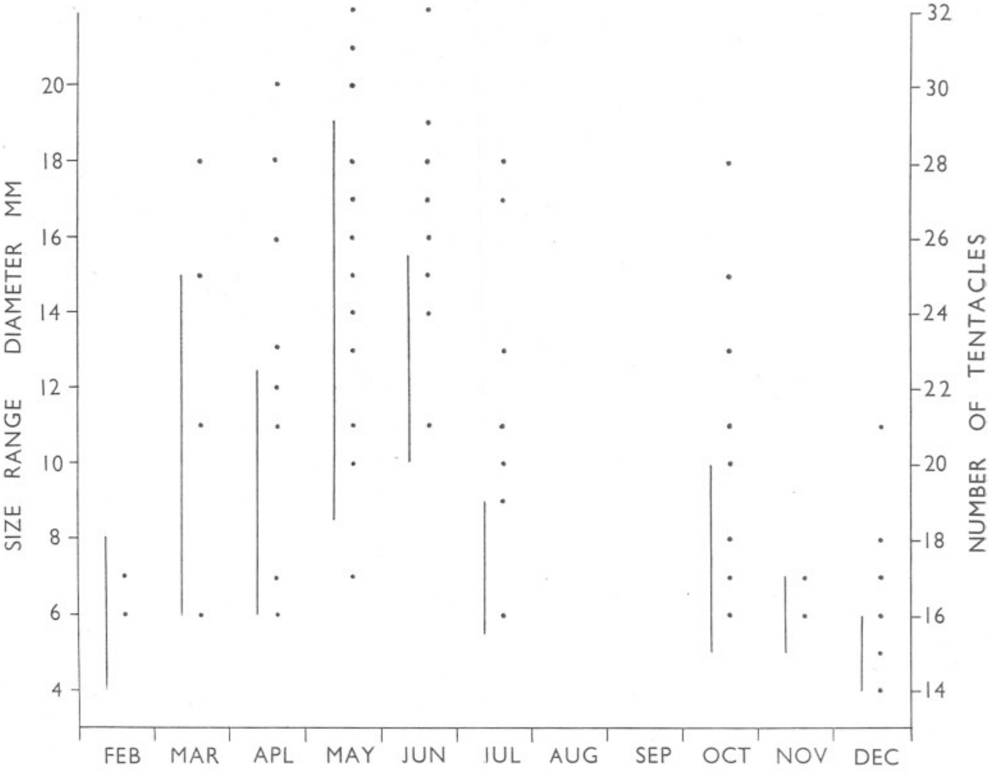

Fig. 4. Seasonal variation in diameter and number of tentacles of *Phialidium hemisphericum* in the plankton off Plymouth 1933 and 1934. The continuous lines show the size range and the dots the range of tentacle numbers.

During 1933 and 1934 a large number of living *Phialidium* were measured and their tentacles counted. The results are given in Fig. 4, which shows the size range for mature medusae in each month of the year (except August and September) and the numbers of tentacles (including developing bulbs) that they had. It shows clearly that in the spring and early summer the medusae grow to a larger size than at other times of the year. The maximum size reached was 19 mm. diameter in May. Also, as might be expected, the largest medusae have the greatest number of tentacles. These reached a maximum of thirty-two in May and June, while by October they were usually sixteen to eighteen fully formed tentacles, any larger numbers being made up with developing bulbs.

Browne (1900) found that at Valencia the largest specimen taken, in May, was 20 mm. in width and had thirty-eight tentacles, the average size of the adult being 10–15 mm. with about thirty-two tentacles. Similarly at Port Erin (1896, p. 490) he found the largest specimen to be 21 mm. and to have thirty-eight tentacles.

As observed by Browne I have occasionally seen specimens at Plymouth having one or two marginal vesicles containing two concretions. The largest number of marginal vesicles seen in any one specimen at Plymouth was eighty-nine (two of which each had two concretions); this was in a specimen 19 mm. in diameter taken on May 15 1934, which had thirty-two tentacles.

Measurements made on the gonads of medusae of different sizes gave the following results:

Umbrella diameter mm.	Gonad length (mm.)			Ratio diameter*: av. gonad length
	Average	Range	Observations	
4·1– 5	0·30	0·21–0·76	11	15·0
5·1– 6	0·59	0·4 –0·75	15	9·3
6·1– 7	0·67	0·3 –1·1	17	9·9
7·1– 8	0·98	0·75–1·5	6	7·7
8·1– 9	0·94	0·5 –1·5	8	9·0
9·1–10	1·26	0·5 –3·0	13	7·5
10·1–11	1·25	0·75–2·0	8	8·4
11·1–12	1·43	1·0 –2·0	14	8·0
12·1–13	1·64	1·0 –3·0	13	7·6
14·1–15	1·75	1·5 –2·0	2	8·3
15·1–16	2·1	1·5 –3·0	7	7·4
16·1–17	2·25	2·0 –2·5	2	7·3
18	3·0		1	5·8
19	3·5		1	5·4

* Diameters taken as 4·5, 5·5, 6·5, 7·5 mm., etc.

Except for the smallest and the largest individuals the ratio of the average gonad length to the umbrella diameter thus appears to be fairly constant with a slight tendency to decrease with size. The figures for the smallest specimens are probably vitiated by the inclusion of immature specimens, while those for the two largest sizes are each based on a single observation.

The above observations on size of medusa, number of tentacles and gonad length, are somewhat different from those given by Kramp (1927) for Danish waters. There, while the smaller specimens (6–7 mm. diameter) occurred in summer, the larger specimens (11–12 mm. diameter) were found in winter, though they reached 16 mm. in spring. While in July the number of tentacles rarely exceeded sixteen, in November they were as a rule twenty-four to twenty-eight. Kramp also says that the gonads are about one-quarter the length of the radial canals. This agrees approximately with the results for Plymouth, where the gonad length averages about one-eighth of the diameter of the umbrella of which a radial canal occupies approximately one half.

Kramp (1927) pointed out that the ratio of the width to the length of the gonads varied at different times of the year. Assuming that there is no very great difference in the size of the eggs at different times of the year it seems natural to expect the smaller gonads to be wider in relation to their length than the longer gonads.

The trend of the seasonal change in size at Plymouth is quite what is to be expected from observations on other plankton animals such as *Calanus*, *Sagitta* and *Aglantha*. It is shown by *Phialidium*, since this is one of the few medusae apart from *Obelia* which is consistently liberated from its hydroid into the plankton almost all the year through. It seems probable that *Obelia* should also show similar seasonal variation but this cannot be proved owing to the difficulty of identifying the species.

Eucheilota clausa (Hincks).

The existence of this species at Plymouth has only recently been brought to notice (Russell, 1936 *b*, *c*). Other records of its seasonal occurrence have since been obtained and these have been incorporated in Table I. As the distribution of the species is not known the following information is worthy of note. In September 1936 I received a letter from Mr J. S. Barlee saying that he had caught a specimen 1 mm. in diameter at Valencia. On September 10 he obtained two specimens, 1 and 4 mm. in diameter respectively, in Dalkey Sound, Co. Dublin, and on September 15 a dozen larger specimens off Sandycove, near Kingstown, Co. Dublin. Mr Barlee kindly sent me the specimens, which were *E. clausa*. Later he sent me another specimen from Kingstown which was more fully developed than any so far recorded. It had fifteen fully developed tentacular bulbs and seven smaller ones and its gonads were 1·2 mm. long and 0·65 mm. wide.

Helgicirrha schulzei Hartlaub.

In 1934 Künne drew attention to the distinction between *Eirene viridula** and Hartlaub's species *Helgicirrha schulzei*, which had been rather overlooked. Careful examination revealed the fact that *Helgicirrha* occurs off Plymouth. I had not realized the existence of this species until I saw Künne's paper, and my records for the species only date from 1935. A few specimens were found in each of the years 1935–7, and they occur in the plankton in the months of June to October inclusive. Its seasonal distribution thus overlaps that of *Eirene*, which reaches its maximum abundance in September and October, and the two species are likely to be found together. A re-examination of samples

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* No attempt has been made in this report to distinguish *E. viridula* and *E. pellucida* on the preserved material; they are possibly the same species.

for the years previous to 1935 showed that the great majority of the specimens identified as *E. viridula* were correct. An occasional specimen of *Helgicirrha* was, however, found, but it is quite certain that they were too few to affect the general picture of the seasonal distribution of *Eirene* given in Table III.

In living specimens of *Helgicirrha schulzei* there are fine specks of deep indigo pigment all round the extreme margin of the umbrella. This pigment was not present in living specimens of *Eirene pellucida*.

The genera *Eirene* and *Helgicirrha* have recently been revised by Kramp (1936). He pointed out that Hartlaub's spelling *schulzii* should be more correctly *schulzei*.

Aglantha rosea (Forbes).

In 1930 *Aglantha*, which always accompanies "*elegans*" water, was present off Plymouth throughout most of the year. The opportunity was taken to see whether size measurements would throw any light on the life history of this medusa. The umbrella height was accordingly measured on samples from each catch. In Fig. 5 a curve is given showing the actual numbers caught between February and October. The numbers were low until June when they began to increase very rapidly, reaching a maximum of many thousands in August. Curves are also given in Fig. 5 for the height measurements of the medusae on each date. From February to April the *Aglantha* were large, being 12–18 mm. in height. A new brood, presumably arising from these large individuals, appeared in April, and these medusae reached a size of 6–8 mm. in May. Thereafter reproduction was rapid and the production of successive generations probably overlaps. Nevertheless, the height measurements do appear to give some indication of successive generations. In Fig. 5 a large dot is placed on the base line opposite the highest peak for each curve. It can be seen that there are three definite series in June, July and August each one of which starts at a small size and shows a gradual increase to a maximum. Perhaps too much stress should not be laid on these until they can be repeated in another year, but the indications are that three successive generations arose in June, July and August, each taking about 1 month to grow up. In September there was a slight increase in the size of the medusae, and it is probable that these live through the winter to grow into the large individuals found in February.

The annual sequence thus seems to be as follows: The year starts with large individuals 12–18 mm. in height which were produced by the last spawning of the previous year. These large medusae spawn in late March and their offspring mature in May, after which there are three, or possibly four, successive generations produced in the summer. These summer medusae only grow to a height of about 5–7 mm. Five or six generations are thus produced in a year.

The large individuals found from February to April were strong and muscular, a characteristic of deep water medusae. Kramp (1927) records

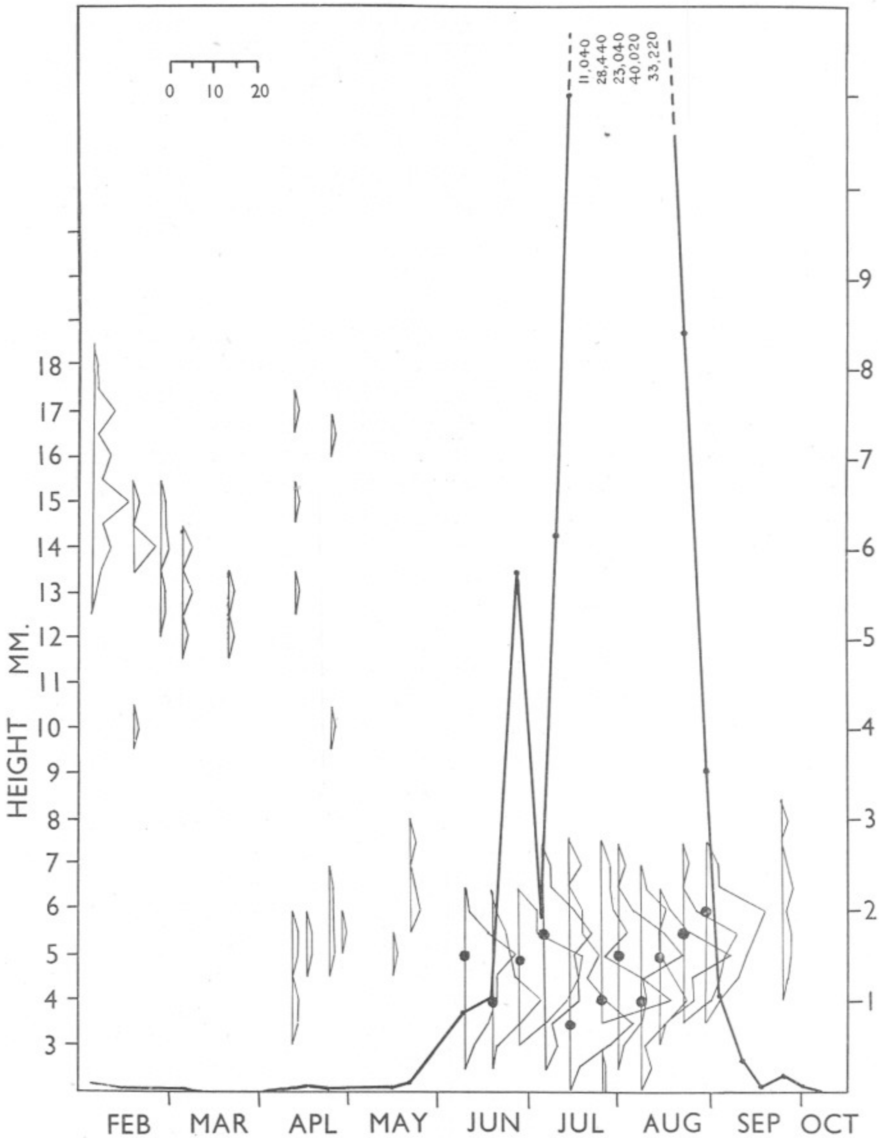

Fig. 5. Numbers and size of *Aglantha rosea* in half-hour oblique hauls with the 2 m. stramin ringtrawl off Plymouth in 1930. The thick curve gives the numbers caught in thousands; the small curves show the size distribution in each catch, the scale for numbers being in the top left-hand corner.

that two forms are to be found in Danish waters, one inhabiting the North Sea and upper water layers of the Skagerrak reaching a height of 16 mm. and a smaller form found in the Kattegat and Belt Sea hardly growing to more than 12 mm. in height. He makes the suggestion that it is the shallowness of the water that renders the Belt Sea unsuitable as a permanent habitat for *Aglantha*. It may well be that the large medusae found off Plymouth had come from deep water where they need to retire for the winter months, and that this necessity prevents them from becoming permanently established in the waters off Plymouth. Günther (1903) says concerning *A. rosea* off the west of Ireland: "It seems possible that fully developed *Aglantha* may live near the surface during the summer months, but may sink into deeper waters with the advancing season."

It is uncertain whether *A. rosea* should be regarded as a variety of *A. digitalis* or as a distinct species. The chief structural difference, apart from size, is that while in *A. digitalis* there are only four marginal sense organs, in *A. rosea* there are eight. In March 1936 I obtained some very young specimens of *A. rosea* off Plymouth and was able to examine them alive. Specimens up to just under 4 mm. in height, with twenty to thirty tentacles, had only four sense organs; a specimen 4·4 mm. in height with thirty-four tentacles had five sense organs, while specimens 5 and 6 mm. in height had eight. It is evident that the number of marginal sense organs increases from four to eight when the medusa is somewhere between 4 and 5 mm. high. Since *A. rosea* begins by developing four sense organs and not eight it is unnecessary to suppose that, if it is a variety, *A. digitalis* must have lost four sense organs during the course of its development. It must remain therefore a matter of opinion whether the two are to be regarded as varieties or distinct species on account of their different distribution and habits.

SUMMARY

The composition of the medusa fauna in offshore waters off Plymouth is reviewed. A table is given showing the months in which the different species have been recorded and those months in which they are most abundant.

A preliminary list has been drawn up attempting to discriminate between those species which are regularly indigenous off Plymouth and those which are brought from elsewhere by water movements.

The results of weekly hauls with the 2 m. stramin ringtrawl during the years 1930–7 inclusive are given. The years 1935, 1936 and 1937 have been noteworthy for the paucity of all species of medusae.

Observations on the structure and biology of certain species of medusae are recorded.

TABLE III. AVERAGE CATCHES FOR EACH MONTH IN THE YEARS 1930–7

Half-hour oblique hauls with 2 m. stramin ringtrawl

	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Steenstrupia nutans	1930		..	..	..	..	20	24	2	+	..	..	..	46
	1931	..	..	..	..	110	13	..	..	..	..	..	..	123
	1932	..	..	..	..	10	54	..	..	..	..	..	..	64
	1933	..	..	..	15	2	..	1	..	..	..	..	..	18
	1934	..	..	..	13	1219	+	..	..	..	..	..	..	1232
	1935	..	..	..	..	6	..	..	..	..	..	..	..	6
	1936	..	..	..	+	4	11	+	..	..	..		..	15
	1937	..	..	..	..	37	22	..	..	..	..	..	..	59
Bougainvillia britannica	1930		..	..	..	157	107	32	..	..	..	..	..	296
	1931	..	..	..	6	9	97	..	..	..	..	..	..	112
	1932	..	..	..	..	155	247	..	..	..	..	..	..	402
	1933	..	..	..	+	4	..	..	..	..	..	..	..	4
	1934	..	..	..	63	1222	..	..	..	..	..	..	..	1285
	1935	..	..	..	..	33	..	..	..	..	..	..	1	34
	1936	..	..	..	..	1	1	..	..	..	..		..	2
	1937	..	..	..	+	1	1	..	..	..	..	..	..	2
Turritopsis nutricula	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	..	..	..	..	..
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	..	..	..	..	+	8	5	3	1	17
	1934	1	..	..	..	..	..	..	..	..	+*	+*	..	1
	1935	..	..	..	..	..	..	..	..	2	1	..	..	3
	1936	..	..	..	..	..	..	..	+	4	21		..	25
	1937	..	..	..	..	..	..	..	1	14	15	3	1	34
Amphinema dinema	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	..	..	..	..	..
	1932	..	..	..	..	..	..	..	..	..	6	..	..	6
	1933	..	..	..	..	..	..	..	..	1	4	3	..	8
	1934	..	..	..	..	..	..	..	..	1	6	..	..	7
	1935	..	..	..	..	..	..	..	..	11	96	..	..	107
	1936	+	..	..	..	..	..	..	..	11	44		..	55
	1937	..	..	..	..	..	..	..	..	48	22	+	..	70
Amphinema rugosum	1930		..	..	..	..	7	466	+	..	..	..	..	473
	1931	..	..	..	..	1	..	..	..	..	..	..	..	1
	1932	..	..	..	..	..	21	..	..	..	..	..	..	21
	1933	..	..	..	13	..	..	..	..	..	..	..	..	13
	1934	..	..	..	..	2	..	..	..	..	..	..	..	2
	1935	..	..	..	..	..	..	..	..	..	..	..	..	..
	1936	..	..	..	..	..	..	..	..	..	7		..	7
	1937	..	..	..	..	..	..	..	..	+	2	..	..	2
Leuckartiara octona	1930		..	..	1	47	296	164	81	61	5	3	..	658
	1931	..	5	6	12	77	173	63	63	90	24	..	+	513
	1932	..	..	3	8	100	133	55	30	62	10	1	1	403
	1933	..	+	1	25	59	104	7	4	16	2	+	..	218
	1934	..	..	..	1	66	23	4	4	..	10	..	..	108
	1935	..	..	..	+	48	39	6	3	2	4	..	..	102
	1936	..	..	+	..	6	60	2	..	+	..		..	68
	1937	..	..	1	1	2	9	+	1	1	1	..	..	16
Laodicea undulata	1930		..	..	2	10	10	..	1040	4079	..	..	..	5141
	1931	..	..	15	20	..	..	3	363	1944	182	..	..	2527
	1932	..	..	..	..	..	7	..	1	14	..	..	..	22
	1933	..	..	..	1	8	..	..	60	1	..	..	..	70
	1934	..	..	5	+	1	..	6	265	5	+	..	..	282
	1935	..	..	+	..	+	..	+	1	206	1	..	..	208
	1936	..	..	1	..	1	..	..	..	+	2		..	4
	1937	..	..	+	2	+	..	5	4	6	1	+	..	18
Cosmetira pilosella	1930		..	..	66	52	83	672	15	3	..	..	..	891
	1931	..	..	..	528	900	520	25	100	38	..	..	..	2111
	1932	..	..	..	70	1055	300	765	401	8	..	..	..	2599
	1933	..	..	..	93	12	220	1	..	..	..	..	..	326
	1934	..	..	3	11	328†	..	..	..	..	..	..	..	342
	1935	..	..	..	..	41	..	..	+	..	..	..	..	41
	1936	..	..	..	..	2	4	..	..	..	+		..	6
	1937	..	..	1	3	2	1	..	..	+	..	..	..	7
Obelia spp.	1930		..	..	..	573	455	14206	123	53	8	..	..	15418
	1931	..	..	35	..	449	7	60	760	..	..	..	..	1311
	1932	..	..	..	745	14040	3587	45	40	66	123	5	5	18656
	1933	5	..	48	1096	153	40	40	34	263	718	330	3	2730
	1934	2	+	9	2092	10788	393	13	87	8	85	170	2	13649
	1935	..	+	5	226	1176	10	43	10	108	356	..	1	1935
	1936	..	..	10	26	543	180	33	5	..	..		..	797
	1937	..	..	1	47	718	115	255	165	213	388	163	3	2068

* Seen in townet catches.

† I had in my notes a record for May 29 "many". I have given this number as 1000.

TABLE III (*cont.*)

Half-hour oblique hauls with 2 m. stramin ringtrawl.

	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Phialidium hemisphericum	1930		..	..	68	415	510	3442	2855	1305	310	15	30	8950
	1931	20	30	3170	3006	1378	2807	1393	443	83	..	60	164	12554
	1932	10	..	5	133	1885	1247	510	80	1106	795	70	21	5862
	1933	69	54	67	1145	998	4000	2115	71	536	138	271	48	9512
	1934	18	2	131	508	4144	85	150	38	15	19	69	..	5179
	1935	3	6	7	53	89	18	148	28	135	92	1	20	600
	1936	32	29	6	2	253	148	52	5	29	392		+	948
	1937	..	..	116	13	267	124	88	48	591	1267	80	11	2605
Saphenia gracilis	1930		..	..	8	37	4	66	22	20	..	..	..	157
	1931	..	..	..	..	7	..	..	15	..	..	..	..	22
	1932	..	..	..	..	15	..	..	10	2	..	1	..	28
	1933	..	..	..	16	2	..	45	1	1	+	2	..	67
	1934	..	..	..	4	11	..	7	2	4	5	1	..	34
	1935	..	..	..	..	3	..	9	2	19	6	..	..	39
	1936	+	+	+	8	17	65	42	2	2	..		..	136
	1937	..	..	+	9	40	29	14	7	8	1	..	..	108
Octorchis gegenbauri	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	15	8	5	..	..	28
	1932	..	..	..	..	..	..	..	..	..	+	..	..	+
	1933	..	..	..	..	..	..	2	5	1	..	..	..	8
	1934	+	..	..	..	..	..	8	..	..	2	..	..	10
	1935	..	..	..	..	..	..	3	28	4	1	..	..	36
	1936	..	..	..	..	..	..	..	..	8	6		..	14
	1937	..	..	..	..	..	..	1	13	11	..	..	..	25
Eirene viridula	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	5	608	701	..	..	1314
	1932	..	..	..	..	..	..	..	1	70	6	3	3	83
	1933	..	..	..	..	..	..	..	+	34	11	10	1	56
	1934	..	..	..	..	..	..	1	..	..	+	..	..	1
	1935	..	..	..	..	..	..	..	1	4	2	..	..	7
	1936	..	..	..	..	..	..	..	..	..	2		..	2
	1937	..	..	..	..	..	..	..	1	14	23	1	..	39
Helgicirrha schulzei	1935	..	..	..	..	..	..	+	..	2	1	..	..	3
	1936	..	..	..	..	..	2	+	+	+	..		..	2
	1937	..	..	..	..	..	..	..	1	..	..	..	..	1
Aequorea forskalea	1930		..	..	..	..	..	+	+	..	..	..	..	+
	1931	..	..	..	1	..	..	..	1	7	3	1	..	13
	1932	..	..	..	..	..	..	..	+	1	1	1	1	4
	1933	..	..	..	..	..	..	..	..	..	..	..	..	..
	1934	..	..	..	..	..	..	..	..	..	+	..	..	+
	1935	..	..	1	..	..	..	..	..	..	+	..	..	1
	1936	..	..	..	..	+	2	..	..	..	..		..	2
	1937	..	..	..	..	..	..	..	+	+	+	..	..	+
Gossea corynetes	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	4	8	..	..	12
	1932	..	..	..	..	..	..	..	..	+	1	..	..	1
	1933	..	..	..	..	..	..	1	1	2	+	..	..	4
	1934	..	..	..	..	..	..	..	8	1	1	1	..	11
	1935	..	..	..	..	..	..	..	..	5	1	..	..	6
	1936	..	..	..	..	..	..	..	..	1	..		..	1
	1937	..	..	..	..	..	..	1	11	1	..	..	..	13
Aglantha rosea	1930		17	2	9	43	2529	14120	21285	413	18	3	..	38439
	1931	..	..	..	..	..	..	128	15	+	..	..	..	143
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	1	..	..	..	..	..	..	..	..	1
	1934	..	..	..	..	..	..	..	3	4	22	2	1	32
	1935	+	..	..	..	+	..	21	1	..	+	..	..	22
	1936	..	..	6	+	9	93	201	116	..	..		..	425
	1937	..	1	+	+	3	27	29	..	..	..	..	..	60
Liriope exigua	1930		..	..	..	1	+	+	6332	5610	1655	1183	741	15522
	1931	325	1	..	..	..	..	..	..	..	1	..	..	327
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	..	..	..	..	..	..	+	3	+	3
	1934	+	..	..	..	..	..	..	..	..	..	..	..	+
	1935	+	..	..	..	..	..	..	..	..	..	..	..	+
	1936	..	..	..	..	..	..	..	..	..	..		..	..
	1937	..	..	..	..	..	..	..	..	..	..	..	..	..

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ON THE DEVELOPMENT OF *MUGGIAEA ATLANTICA* CUNNINGHAM

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(Text-figs. 1–6)

In September 1937 *Muggiaea atlantica* Cunningham was very abundant off Plymouth. The presence of large numbers of eudoxids in the plankton afforded an opportunity to rear the early stages of this siphonophore. The development of *M. kochi* (Will) was worked out by Chun (1882, 1913), and he also described the eudoxid of that species. The eudoxid of *M. atlantica* has, however, never been described for certain. The allocation of eudoxids collected in the plankton to their respective species is necessarily fraught with uncertainty when more than one species is present. Throughout the whole of September 1937 *M. atlantica* was the only species of siphonophore to be found off Plymouth, and there can be no reasonable doubt that the eudoxids described below belonged to that species and that the development of the early stages from their eggs is that of *M. atlantica.*

For the terminology used in the description of the eudoxid I have followed Totton (1932), to whom I am grateful for helpful advice.

THE EUDOXID

The *bract* (Fig. 2 *a*) is cone-shaped with a broad flat suture running from its apex to the base. The edges of the suture are raised into a slight flange. The right edge is continued downwards into a sweeping curve while the left edge cuts away horizontally at its lower end; the bract is thus asymmetrical. There is a slight cavity on the lower surface in which the somatocyst is centrally placed. The general form of the bract can also be seen in the different views of the whole eudoxid given in Fig. 1. The largest bract seen had an overall height of 1·9 mm.

The *gonophore* bell (Fig. 1) is cylindrical and has four longitudinal ridges running from the apex to the velar opening with a spiral twist to the right. The two ventral ridges are prolonged below the velar opening and join to form a short curved mouth-plate. The right ventral ridge is more strongly developed than any of the others (Fig. 2 *b*). Specimens with left-handed twisting, or "mirror images", are common (Fig. 2 *c*) and are presumably the second gonophores to be budded. The edges of the ridges are quite smooth, although some may show very faint traces of irregularity. The manubrium in fully developed gonophores extends more than two-thirds the length of the subumbrella cavity and has a pink tip. The radial canals follow the spiral courses of the ridges.

The height of the whole eudoxid is usually about 2–2·5 mm.; isolated gonophore bells have been found up to 2·2 mm. in height. One eudoxid was seen with twenty-one nematocyst batteries on its tentacle.

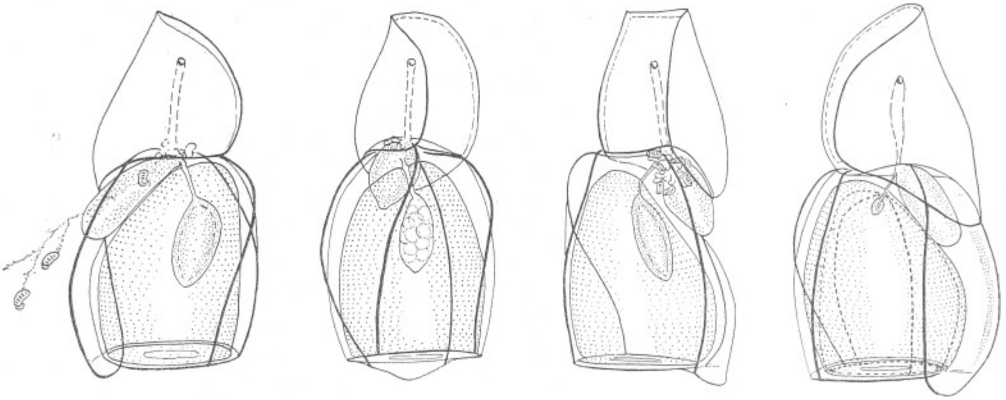

Fig. 1. Different views of eudoxids of *Muggiaea atlantica*, Plymouth, Sept. 1937. Height of original specimens from left to right 2·5, 2·5, 2·4 (bract somewhat twisted above gonophore) and 1·8 mm.

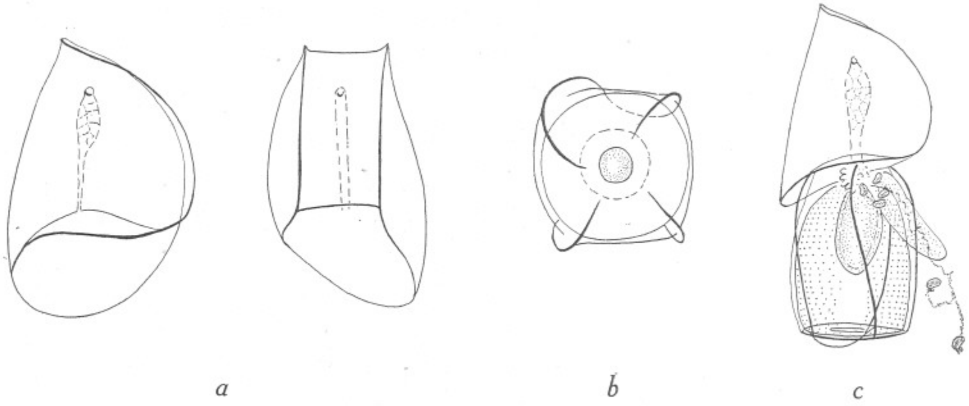

Fig. 2. Eudoxid of *Muggiaea atlantica*, Plymouth, Sept. 1937. *a*, lateral and ventral views of bract; overall height 1·7 mm.; *b*, apical view of gonophore; the ventral side is uppermost; *c*, eudoxid with "mirror image" gonophore; total height 2·2 mm.

The figures given here are drawings of living specimens; when preserved the gonophore bell appears much more angular and the ridges are more prominent owing to the contraction of the bell. In many dead or dying gonophores the apex showed the inflated condition figured by Totton (1932, fig. 33 *B*) for *Lensia subtiloides*.

No essential difference can be seen between my figures and the drawing given by Chun (1882) of the eudoxid of *Muggiaea kochi*. The only difference in Moser's (1925) account of the eudoxid of *M. kochi* is that the gonophore bell is laterally flattened; this, however, is probably an effect of preservation.

As already stated the circumstances under which my eudoxids were obtained practically remove all doubt that they belong to *M. atlantica*. Since for some years previous to 1936 *M. kochi* completely took the place of *M. atlantica* off Plymouth (Russell, 1934), I have been able to refer to previous collections. Some eudoxids were found with a sample of *M. kochi* taken on October 12 1933. When these were placed beside eudoxids of *M. atlantica* caught this year no differences could be detected, and we must conclude that the eudoxids of the two species are probably indistinguishable, at any rate in their grosser features.

THE EARLY DEVELOPMENT

A number of successful fertilizations from the eudoxids of *M. atlantica* were made in the Laboratory in September 1937, and the development was observed until the first appearance of the secondary nectophore.

The eggs are transparent, 0·25 mm. in diameter, and float near the surface of the water. Segmentation is regular, a spherical ciliated embryo being formed 0·27 mm. in diameter; this quickly becomes pear-shaped and within 24 hours develops into a typical elongated planula *ca.* 0·37 mm. in length. The rudiments of the primary nectophore soon appear as slight bulges on one side of the planula and proliferation of the posterior cells to form the siphon takes place. At this stage there is a pinkish tinge along that side on which development occurs. In less than 36 hr. the cavity of the primary nectophore is already formed and the somatocyst appearing (Fig. 3). Within 48 hr. the nectophore is fully formed (Fig. 3) and pulsating. The whole larva, umbrella included, is ciliated, so that when not moving by pulsation it rotates slowly by ciliary action. A cushion develops on the exumbrella on either side of the remains of the planula and a hydroecial groove is formed. By the next day all signs of the original tissue of the planula have disappeared and the primary nectophore is fully developed with somatocyst, siphon, tentacle with seven or eight nematocyst batteries and the rudiments of the secondary nectophore. Figs. 3, 4 show the course of development of specimens reared in the laboratory from the planula to the fully developed primary nectophore. The latest stage there shown is apparently abnormal, for specimens taken from the plankton at the same stage of development were larger and much higher (Fig. 5). In those from the plankton there was also an oil globule in the somatocyst showing that the animals had fed. The laboratory reared specimens were not fed and later development has probably taken place at the expense of the tissues, resulting in abnormal shape in the bell. After examination of a number of specimens from the plankton ranging between 0·9 and 1·3 mm. in height it

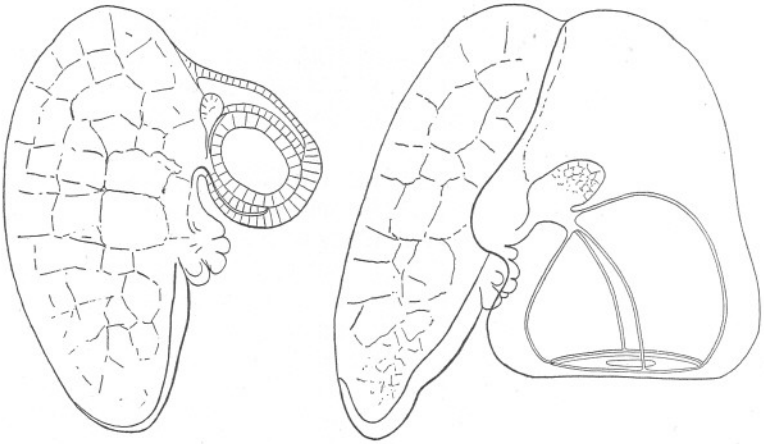

Fig. 3. Developing embryos of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Left, *ca.* 36 hr. old, length of planula 0·37 mm. Right, less than 48 hr. old, umbrella height 0·38 mm.

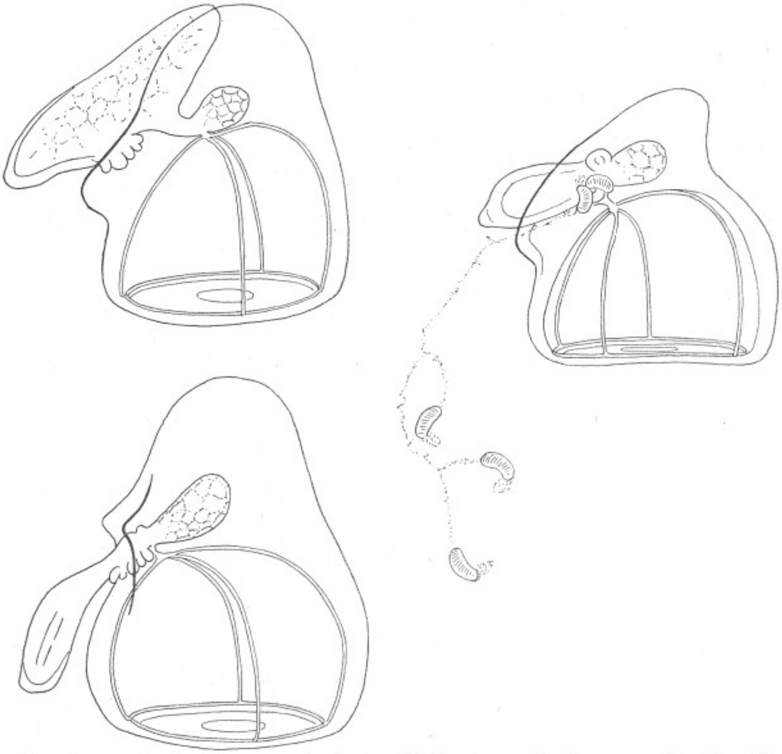

Fig. 4. Development of primary nectophore of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Lower left, 0·56 mm. high; right 0·5 mm. high, shape of umbrella abnormal; the developing secondary nectophore is just appearing.

appears that the normal shape is that shown in Fig. 5, though an occasional specimen more like that reared in the laboratory was found.

No specimens were seen in which the primary and fully developed secondary nectophores were both present together. But very small secondary nectophores were found with the remains of their attachment to the primary nectophore still present (Fig. 6), and many cast primary nectophores were also seen loose in the plankton. In the smallest secondary nectophore, which was 0·4 mm. in height, the somatocyst already extended to the top of the subumbrella cavity and the species could thus be identified as *M. atlantica.*

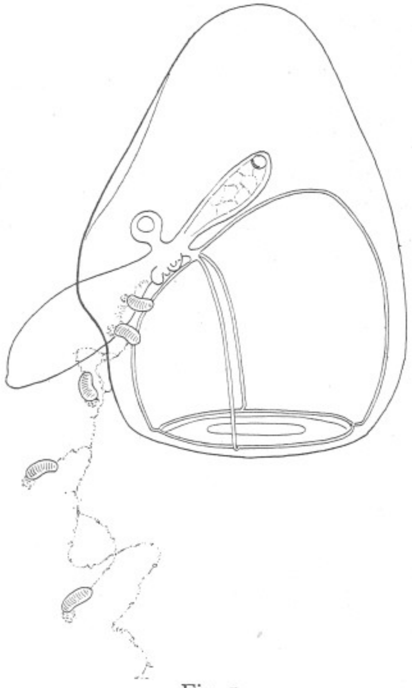

Fig. 5.

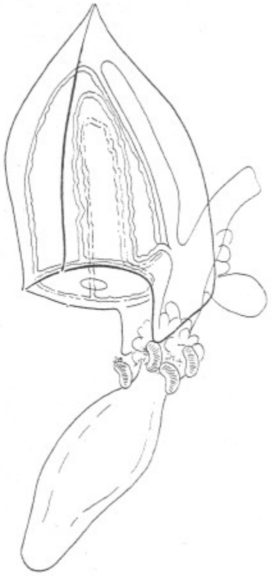

Fig. 6.

Fig. 5. Primary nectophore of *Muggiaea atlantica* 1·3 mm. high, normal shape, from plankton, Plymouth, Sept. 1937.

Fig. 6. Secondary nectophore of *Muggiaea atlantica* recently separated from primary nectophore; height from apex to velar opening 0·67 mm., from plankton, Plymouth, Sept. 1937.

The course of development here outlined agrees with that given by Chun (1882) for *M. kochi*. The normal shape of the primary bell of *M. atlantica* differs from Chun's drawing of that of *M. kochi* in that the apical process is more dome shaped. In view of the variability of this character it is not certain whether Chun's figure is that of a normal specimen and it is possible that the two species would be hardly distinguishable at this stage unless it be in the microscopic structure of the nematocyst batteries. Once the secondary nectophore is developed, however, the two species become at once recognizable by the difference in the lengths of the somatocyst, that in *M. kochi* being much the shorter.

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THE LIFE HISTORY OF *KELLIA SUBORBICULARIS*

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(Text-fig. 1)

Kellia suborbicularis (Montagu) has long been known to be viviparous. Lovén (1848) mentions this fact and Jeffreys (1863, p. 227) quotes Mr Clark who "found in the ovary of one individual ova in an advanced state with fully formed testaceous fry". It is probable, however, that these shelled larvae were in reality contained in the gill pouch where later workers have found them. Pelseneer (1935, p. 517) says that the eggs are incubated in the internal gill lamella, and this was also observed by myself.

It is striking that although the shelled larva is extremely small when liberated (shell 0·064–0·08 mm. in length), the late planktonic larva is very large (shell 0·30–0·37 mm. in length) and one of the most conspicuous bivalve veligers in the plankton. This indicates a prolonged free-swimming life quite unlike that of the oyster, *Ostraea edulis*, whose shelled larvae are liberated only to lose the velum in a few days. These late larvae of *Kellia* have been kept in bowls and plunger jars in the Plymouth Laboratory until they metamorphosed and for months afterwards, growing into beautifully clear and transparent individuals which undoubtedly belonged to this species.

Kellia suborbicularis is placed by Winckworth (1932) in the Erycinidae, but this family is closely related to the Leptonidae, Montacutidae and Galeommatidae, most or all of whose members are viviparous. Lovén (1848) described the young shelled stage of *Montacuta ferruginosa* and *M. bidentata*, the latter species now being referred by Winckworth to *Mysella*. Both keep their young in the gill pouch until the shelled stage and Lovén's beautiful figures show that the early shelled stage in each of them is very like that of *Kellia*. Both, however, are larger when ejected and more developed (*M. ferruginosa* 0·14 mm. long, *M. bidentata* 0·15 mm. long, *Kellia suborbicularis* 0·064–0·08 mm. long). After being fed on flagellates *Kellia* at 0·12 mm. had developed further, although smaller than either of the others. The shape of the newly ejected shell is similar in all three. *Kellia* grows rounder as it develops. The later stages of the other two are not known; but certain large veligers in the Plymouth plankton, now being investigated, seem to belong to *Mysella bidentata*, and if this is proved to be the truth we have another species, similar to *Kellia*, in which there is much growth in the free-swimming stage before metamorphosis.

When we realize that Lovén's work is now ninety years old it is somewhat astonishing that so little has been added to our knowledge of these most interesting larvae. *Lasaea rubra* incubates its eggs until a very late stage. *Galeomma turtoni* gave out embryos during the night of September 13 1937, which were in a much less advanced state than those of *Kellia*, having no shell although moving freely, the round embryo measuring 0·07 mm. across (these facts were kindly communicated by Miss Popham who is working at the group). A young *Turtonia minuta*, belonging to the same family as *Kellia*, grown in a plunger jar but in which the free-swimming stage was not noted, measured only 0·64 mm. in length and was just like the adult.

Kellia suborbicularis is fairly abundant at Plymouth on rocky shores in crevices and in dead shells and is also frequently dredged from deeper water in the Sound and outside, especially from the Stoke Point Grounds in crevices of red rock or in empty burrowing shells. Developing eggs were found in the gill pouches in May, July and August, but no eggs were seen in the winter months although several specimens contained active sperm in October. Shelled larvae were given off in September and October. Late larvae are present in the plankton in any month of the year both inside and outside the Sound, but especially in summer and early autumn. At this time they are some of the most conspicuous bivalve veligers, occurring with others of about the same size (*Lima*, *Saxicava* and, possibly, *Montacuta*). The breeding season appears to be spring, summer and early autumn with occasional larvae in winter.

Odhner (1914) found *Kellia suborbicularis* ripe in April at Rovigno, but does not mention the young in the gills. He notes the benthonic young in May with almost circular form, diameter (=length) 0·31 mm.; having a violet streak below the middle of the umbo and a greenish liver, and later stages with a red-brown pigment fleck under the adductors. It is at about this size that the larvae begin to lose the velum at Plymouth, but the violet streak and red spot were not noticed although there is frequently a red colour just inside the mantle edge.

The smallest developing egg seen from the gill pouch measured 0·025 mm. across and had divided into two segments; but in the same brood there were many celled spherical embryos 0·05 mm. across. On September 14 1937 Miss Popham found newly extruded larvae which had hatched out in a bowl during the night. Another brood was given out on October 11–12 during the night. Those from the September brood were very numerous and were swimming actively. The oval shell (Fig. 1 *a*, *b*) was perfectly transparent, smooth and colourless, the hinge line nearly straight, the length 0·064 mm. The organs were only feebly differentiated; but the velum, which was nearly half the length of the shell, was a fairly strong swimming organ surrounded by long and powerful cilia. A long and stronger cilium (the flagellum) was situated in the centre of the velum. The velar muscles were strongly developed.

The larvae given out in October were slightly larger and more developed

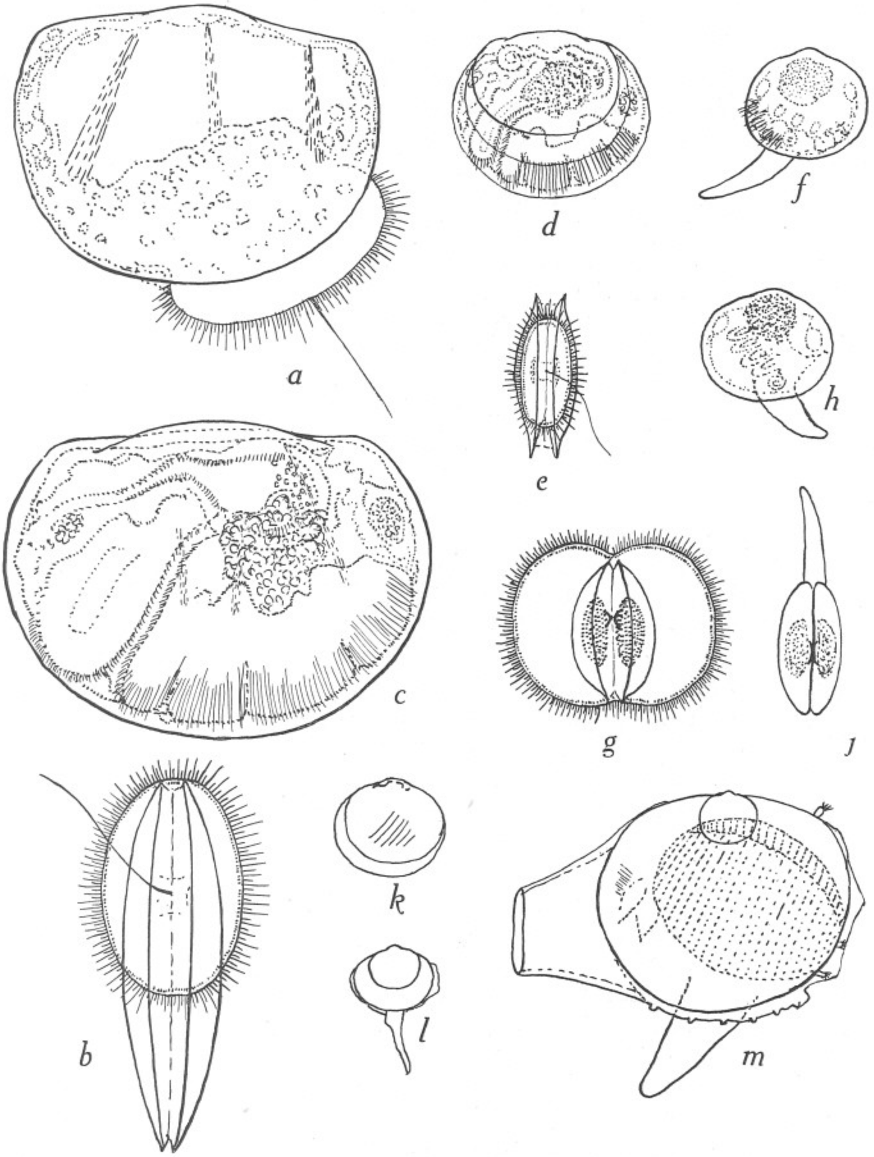

Fig. 1. *a*, veliger of *Kellia suborbicularis* newly extruded from parent's pouch, 0·064 mm. long, lateral view, September; *b*, the same, ventral view, swimming; *c*, veliger one day after extrusion, 0·08 mm. long, lateral view, October; *d*, veliger reared in plunger jar, extruded by parent in October, 14 days old, lateral view, 0·16 mm. long; *e*, the same, ventral view, swimming; *f*, late veliger from plankton, lateral view, 0·36 mm. long; *g*, the same, swimming, ventral view; *h*, newly metamorphosed larva, lateral view, 0·37 mm. long; *j*, the same, dorsal view; *k*, young shell, reared from planktonic veliger, 0·32 mm. long; *l*, slightly older shell, reared from planktonic veliger, 0·48 mm. long; *m*, older shell reared from planktonic veliger, 1·2 mm. long

than the September brood. These were placed in a plunger jar and given very small flagellates as food. On the morning of October 13, being one day old, they were swimming freely and feeding. The larva (Fig. 1 *c*) measured 0·08 mm. in shell length. The stomach, mouth and intestine were developed and were strongly ciliated, the stomach being full of flagellates. The liver was beginning to appear as a roundish mass at the side of and below the stomach. The anterior adductor muscle was fairly well developed, the posterior just beginning to appear below the end of the intestine. The velar muscles could still be seen, although hidden to a certain extent by the developing organs, and the velum was considerably larger. These larvae grew slowly but were active and fed well, the food being renewed every few days. When 14 days old they measured 0·11 mm. in shell length and 0·08 mm. in depth. The liver and stomach were turning a pale yellow, the stomach still being full of the flagellate food; the intestine was becoming twisted and the posterior adductor muscle was larger. The velum had increased in size and was held more centrally than in the very early larva, the flagellum being still conspicuous. At 3 weeks old the largest larva (Fig. 1 *d*, *e*) measured 0·16 mm. in shell length, but some were much smaller. At this point they ceased to grow, although still active and feeding, and they lived for a further 6 weeks. The larva at this size is very like the smallest recognized in the plankton; it has gradually grown from an oval to a round shape, the velum growing larger until it projects well beyond the shell.

It is probable that growth in the plunger jar is much slower than it is in nature, although the larva probably stays for a considerable time in the plankton in order to attain such a large size before metamorphosis. Veligers about 0·20 mm. in shell length may be recognized in the plankton and these are very similar to the largest reared in the plunger jar. They are, however, at this stage not very easy to differentiate from other species. The late larvae are easily recognizable. The largest veliger (Fig. 1 *f*, *g*) was 0·37 mm. in shell length, slightly less in breadth, and nearly spherical. From a shell length of 0·30–0·37 mm. the larva is ready to metamorphose. It has a faint yellowish tinge with touches of red irregularly present and is sometimes red all round the inside of the mantle margin. The general effect is colourless. The digestive gland is very conspicuous, forming two large greenish grey masses on each side just below the umbo. There are two to four gill slits, well-formed adductor muscles and a long contractile foot. The velum is very large and is slightly divided centrally at the anterior and posterior ends, the beginning of a bilobed structure usual in gastropods but very rare in bivalves. The velum is surrounded by powerful cilia and has lost the central flagellum; the whole organ projects far beyond the shell on each side. At this stage the animal can either crawl or swim and is now ready to metamorphose. The umbos of the shell are peculiarly prominent. The velum is now lost and the animal descends to the bottom.

These late veligers rapidly metamorphosed in plunger jars (Fig. 1 *h*, *j*) and the shell put on growth all round (Fig. 1*k*, *l*); the gills increased quickly and the mantle began to close up, showing the typical anterior and posterior siphons, the foot projecting from a central opening. At a length of 1·2 mm. the shell and animal are those of a typical *Kellia*, the embryonic shell still showing conspicuously at the apex (Fig. 1*m*). One specimen, kept for 6 months, measured 3·25 mm. in length and except for the absence of reproductive organs was in every way like the adult. Here again growth is probably slow, compared with that in natural surroundings, and it seems likely that the shell grows to its full size in a year. One female collected in August contained developing embryos and measured only 4 mm. in length, the largest being about 9 mm.

Newly metamorphosed *Kellia* were frequently found crawling on and in the red rock dredged from the Stoke Point Grounds. The smallest had a length of 0·32 mm. and intermediate stages between these and adults also occurred frequently; all were exactly similar to those reared in the plunger jars.

It seems certain that the young enter the holes and empty shells at a very early stage—a fact already noted by Montagu (1863, p. 39) who first described the species and stated that "it is to be found in holes in limestone the entrance being much smaller than the shell so that it must have entered in a young state".

It is thus established that *Kellia suborbicularis*, although it incubates its eggs until the larvae have formed a shell, must none the less remain in the plankton for a long time. It possesses a late veliger which is one of the largest planktonic bivalve larvae seen, and as the larvae are large and very numerous and occur practically throughout the year they must be important economically. The adult *Kellia* is known to form part of the food of the haddock (Jeffreys, 1863, p. 227).

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EVOLUTION OF CILIARY FEEDING IN THE PROSOBRANCHIA, WITH AN ACCOUNT OF FEEDING IN *CAPULUS UNGARICUS*

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(Text-figs. 1–6)

CONTENTS

INTRODUCTION

Ciliary feeding, of such widespread occurrence in the Lamellibranchia, is confined in the Gastropoda to a few scattered groups. In freshwater Pulmonata, such as *Limnaea*, cilia on the foot assist in feeding when the animal is creeping suspended from the surface film (Brockmeier, 1898). Thecosomatous Pteropoda feed exclusively by the aid of cilia on the unpaired middle lobe and the paired side lobes of the foot, and an evolutionary series—*Cavolinia-Cymbulia-Gleba*—can be traced in which there is a progressive elaboration in the perfection of this mechanism and an accompanying reduction in the buccal mass and associated structures handed down from carnivorous ancestors (Yonge, 1926). Only in the few prosobranchs which have acquired ciliary feeding mechanisms do these represent a modification of the ctenidia as in the Lamellibranchia. They also, as it is the aim of this paper to show, represent a modification of the rejection currents present in the mantle cavity of typical prosobranchs.

REJECTION CURRENTS IN THE MANTLE CAVITY OF THE PROSOBRANCHIA

In typical Prosobranchia a respiratory current, created by the beating of the lateral cilia on the gill filaments, is drawn into the mantle cavity by way of the inhalent opening (frequently prolonged into a siphon, e.g. in *Buccinum*) on the left side of the head and, after passing between the gill filaments where respiration takes place, passes out by the exhalent opening on the right side. Any sediment present in the water must inevitably be drawn in with this current and, if the gills and other important organs in the mantle cavity are not to be smothered by it, it is essential that mechanisms should exist for its rapid and efficient removal. In a recent paper on *Aporrhais* (Yonge, 1937) it was shown that disposal of suspended matter is brought about by the following three well-defined sets of ciliary currents:

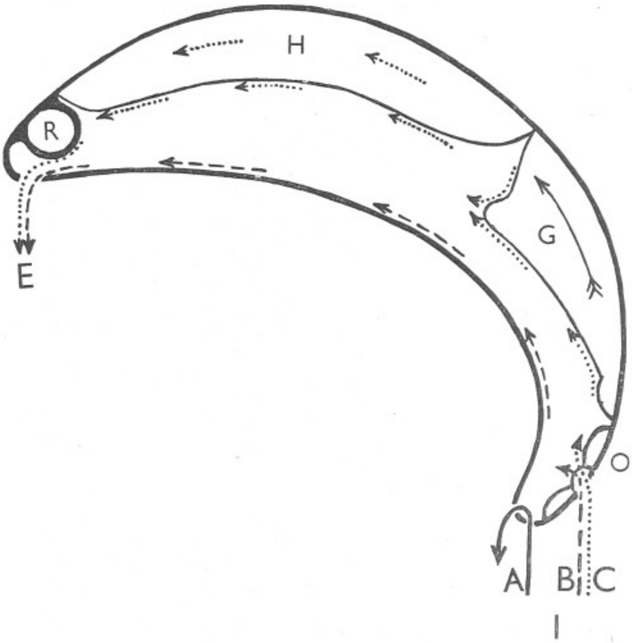

Fig. 1. Semi-diagrammatic representation of course of the ciliary currents within the mantle cavity of a typical pectinibranch prosobranch. A, B, C, three sets of rejection currents represented by unbroken, broken and dotted arrows respectively; E, exhalent current (downward arrows representing outward current at right angles to plane of figure); I, inhalent current (upward arrows representing inward current as before); G, gill filament (feathered arrow representing respiratory current created by lateral cilia); H, leaflet of hypobranchial gland; O, osphradium (with paired lateral plates as in *Buccinum*); R, rectum.

A. Cilia on the margin of the inhalent region carry the largest and heaviest particles, which tend to settle almost at once, directly to the exterior, i.e. by way of the inhalent opening.

B. Cilia on the floor of the mantle cavity carry medium-sized particles, which settle farther within the cavity, across to the right side where they are caught in forwardly directed currents and conveyed to the exhalent opening.

C. Frontal cilia on the gills and cilia on the folded surface of the hypobranchial gland carry the lightest particles, which still remain in suspension when the water passes between the gill filaments, across the roof of the mantle cavity. These minute particles become entangled in the mucus produced by the hypobranchial gland—hence the size and importance of this gland—and, so consolidated, are carried to the right side where they are conveyed forward and out together with the medium-sized particles and the faeces.

The relation of these three sets of currents to one another is shown diagrammatically in Fig. 1. It will be noted that the osphradium (o) represents the line of division between currents B and C.

The same general arrangement of rejection currents has been found in such typical pectinibranch Prosobranchia as *Littorina littorea*, *L. rudis*, *Nucella* (*Purpura*) *lapillus*, *Nassarius* (*Nassa*) *reticulatus* and *Buccinum undatum* by Mr G. C. E. B. Hulbert while working under the direction of the author. The only organ in the mantle cavity which shows marked variation in form is the osphradium. It is suggested, on biological grounds, that the function of the osphradium is to determine the amount of sediment which enters the mantle cavity (Hulbert & Yonge, 1937). This varies widely according to the habitat of the animal.

EVOLUTION OF CILIARY FEEDING

A consideration of the above facts has indicated the possible mode of origin of the ciliary feeding mechanisms which have been described in *Crepidula* and *Calyptraea* (Orton, 1912, 1914), *Vermetus novae-hollandiae* (Yonge, 1932), and briefly noted in *Capulus ungaricus* by Orton (1912). Further observations were made by the author on the last-named during a visit to the Bergens Museum Biological Station at Herdla in 1936, and also on specimens obtained from the marine laboratories at Plymouth and Millport. The author wishes to acknowledge his indebtedness to Prof. A. Brinkmann, Director of the Bergen Station, and also, for financial assistance, to the Colston Research Society, Bristol.

All of these animals are specialized herbivores. This fact is established by the universal presence in them of a crystalline style, characteristic (Yonge, 1932) of herbivorous Gastropoda "which feed by ciliary mechanisms, or by the slow but almost continuous action of a radula". Ciliary feeding representing a further specialization associated with a sedentary mode of life, it follows that we must consider the ancestors of animals feeding in this manner to have been primitive herbivorous prosobranchs, possessing styles, but probably feeding by means of a radula and jaws. The single pectinibranch gill of such a form would be concerned solely with its primitive function of respiration and ciliary currents in the mantle cavity only with rejection of sediment.

Such primitive herbivorous prosobranchs appear to have evolved in various directions. One line of evolution is represented by animals such as *Pterocera* and other Strombidae (Yonge, 1932): they possess a proboscis and use the jaws to crop fine algae which are broken down in the stomach by a cellulase. The radula shows little sign of wear "evidently acting as a conveyor belt" (Peile, 1937). Another line of evolution is represented by *Aporrhais* (Yonge, 1937), which burrows in mud and collects detritus of plant origin with the aid of an extensile proboscis possessing grasping jaws and radula. Other lines are represented by groups—not necessarily closely related to one another—which have lost the power of movement, either as a result of cementation to the substratum as in the Vermetidae, or effectively as in the Calyptraeidae and Capulidae. In these families, as in the Lamellibranchia, the gills and the ciliary currents in the mantle cavity have become modified to enable the animals to collect fine particles, chiefly phytoplankton, from the surrounding water.

Vermetus novae-hollandiae.

The simplest case would appear to be that of *Vermetus novae-hollandiae* (Yonge, 1932). This large species lives, cemented to dead coral rock, on the exposed outer faces of Indo-Pacific coral reefs. Unlike the smaller *V. gigas* which lives in still waters in the Mediterranean and, as recently conclusively demonstrated by Boettger (1930), collects plankton by means of long

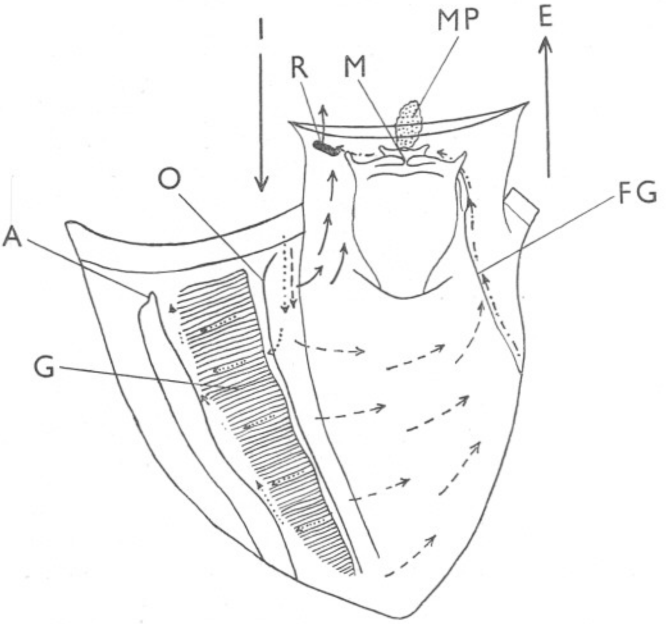

Fig. 2. *Vermetus novae-hollandiae*, mantle cavity opened along right side, seen from above. × 1½. A, anus; E, exhalent current; FG, food groove; G, gill; I, inhalent current; M, mouth; MP, mucus from pedal gland; O, osphradium; R, position where large particles collected prior to rejection by action of current A. Various currents represented by same type of arrows as in Fig. 1. (Figure modified after Yonge, 1932.)

mucous threads extruded from the pedal gland, *V. novae-hollandiae* is a ciliary feeder. As shown in Fig. 2, heavy material is accumulated on the left side of the head and then rejected; this represents current A. Medium-sized material is carried across the floor of the mantle cavity in current B, where it passes into a food groove which carries it to the mouth. Finely divided material—which will include phytoplankton on which the animal chiefly feeds—is carried by frontal cilia on the gill filaments to the free edge of the gill where other cilia carry it anteriorly. In life this free edge is in close apposition to the food grove (FG) on the right side of the mantle cavity. This current clearly represents a modification of current C. It should further be noted that there is *no* hypobranchial gland. The increased size of the gill—the result of its added function as a collector of food—leaves no space for this organ, which is in any case unnecessary because material is no longer passed completely across the roof of the mantle cavity but carried at right angles, anteriorly, along the free edge of the gill.

Food which enters the food groove from either current B or C is carried round the right-hand side of the head to the mouth (M). As food streams approach, the small introvert is extruded over the opening of the pedal gland, the mouth opens and the exposed radula seizes the food which has been mixed with mucus from the pedal gland (MP). Any excess of material passes farther to the left and joins the material rejected by current A. The secretion of the pedal gland, no longer required to provide lubrication for movement, is thus concerned with the consolidation of food particles but *not* with its direct capture as in *V. gigas*.

Crepidula fornicata and other Calyptraeidae.

In *Crepidula fornicata* (Orton, 1912, 1914) the elaboration of the ciliary feeding mechanisms has been carried several stages farther. The mantle cavity is of relatively enormous size, extending over the entire visceral mass and also over the elongated "neck" region. This provides for the accommodation of the gill, which is many times larger than that of typical prosobranchs of the same body size (it is also relatively larger than that of *V. novae-hollandiae*, though not to the same extent). This increase in the gill is due to the greater current needed for feeding and the increased surface for food collection. The modifications of the individual filaments will be discussed later. The osphradium (Fig. 3, O) is reduced to a small area at the anterior end of the gill, but an endostyle (EN) extends along the entire base of the gill.* This structure, described in detail by Orton (1912, 1914), is confined to the Calyptraeidae (*Crepidula* and *Calyptraea*) and represents a special adaptation for ciliary feeding in these animals, producing mucus which is carried on to the ventral, frontal surface of the gill filaments.

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* In *V. novae-hollandiae* an elongated osphradium (Fig. 2, O) runs along the base of the gill, *not* an endostyle as described in my paper (Yonge, 1932). I am glad to have an opportunity of correcting this error. There are always abundant mucous glands in this region.

Food reaches the mouth by one of two routes. Large particles are carried direct into a food pouch (FP) in the mantle edge, which is situated, in life, just anterior to the mouth. They are there worked up into a pellet with mucus and passed to the mouth. If food is not required or excess of material is present, it is carried out by a current which runs parallel to and slightly anterior to the food pouch. It is clear that this feeding current represents a modification of rejection current A. Medium and fine particles are carried over the floor of the mantle cavity in current B, but chiefly, entangled in mucus secreted by the endostyle, by way of the frontal cilia of the gill filaments (i.e. current C). By both routes particles pass into the food groove (FG) and are carried forward by the combined action of its cilia and those on the tips of the gill filaments. The food particles are here worked up into pellets with mucus and are passed from time to time to the mouth (M). There they are grasped and passed into the buccal cavity by the radula and retained there by the jaws prior to swallowing. Peile (1937) has remarked on the absence of wear in the teeth of the radula in both *Crepidula fornicata* and *Calyptraea chinensis*. There is no trace of a hypobranchial gland.

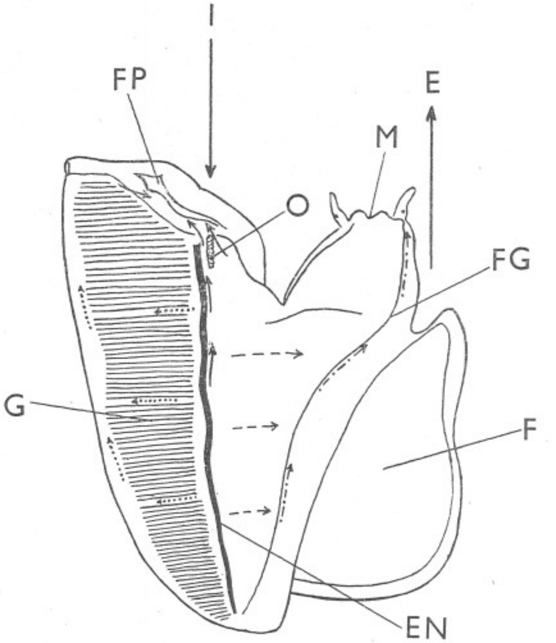


Fig. 3. *Crepidula fornicata*, mantle cavity opened along right side, seen from above. × 1½. EN, endostyle; F, foot; FP, food pouch. Other lettering as in Fig. 2. (Figure modified after Orton, 1914.)

Orton found essentially the same conditions in *Calyptraea* and they almost certainly prevail throughout the Calyptraeidae. Kleinsteuber (1913), in a comparison of the genera of this family, has pointed out that in *Calyptraea*, *Crepidula* and *Janacus* the length of the gill filaments is about one-half, in *Trochita* some three-quarters and in *Crucibulum* twelve-thirteenths the width of the body.

Capulus ungaricus.

The only existing account of feeding in this very interesting species being confined to a brief statement by Orton (1912), a more detailed account would appear to be well justified, apart from its importance in connexion with the general subject-matter of this paper. The animal has very limited powers of movement and is often found attached to the free edge of the valves of Lamellibranchia. The appearance of the animal from the dorsal aspect after the limpet-like shell has been removed is shown in Fig. 4, which also indicates the

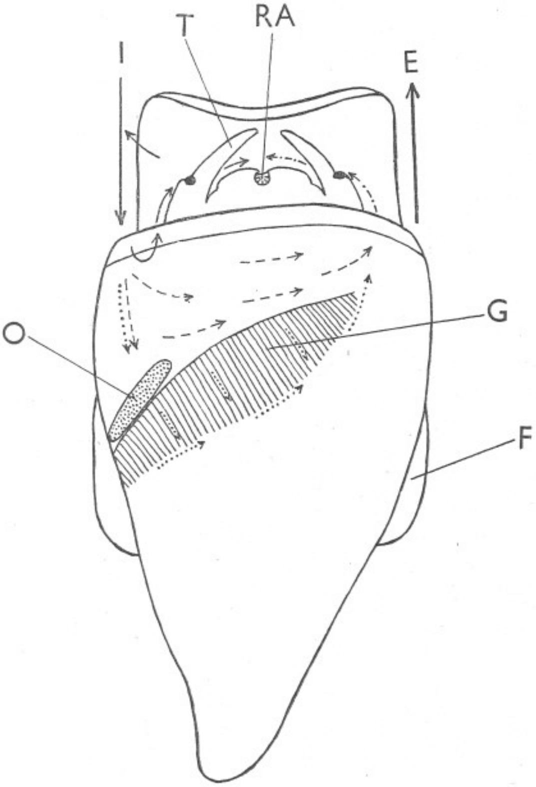


Fig. 4. *Capulus ungaricus*, animal seen from above after removal of shell; organs and currents in mantle cavity shown. ×3. RA, radula; T, tentacle. Other lettering as before.

position, within the mantle cavity, of the gills (G) and osphradium (O). The head with the stout tentacles (T) projects a little beyond the mantle edge. The position of the mouth and contained radula (RA) is shown but not that of the remarkable grooved proboscis. The proboscis appears in Fig. 5 (P), drawn after it and the foot had been extended anteriorly. It is formed of the prolonged lips and extends downwards, the tip lying on the flat, upper surface of the anterior prolongation of the foot. The gill is very large and extends obliquely across the roof of the mantle cavity, instead of along the left side as in a typical prosobranch or in the other ciliary feeding species. This would appear to be a direct consequence of its large size; it could not be accommodated in the restricted mantle cavity were it not so disposed. There is a conspicuous osphradium (Figs. 4 and 5, O) but no hypobranchial gland.

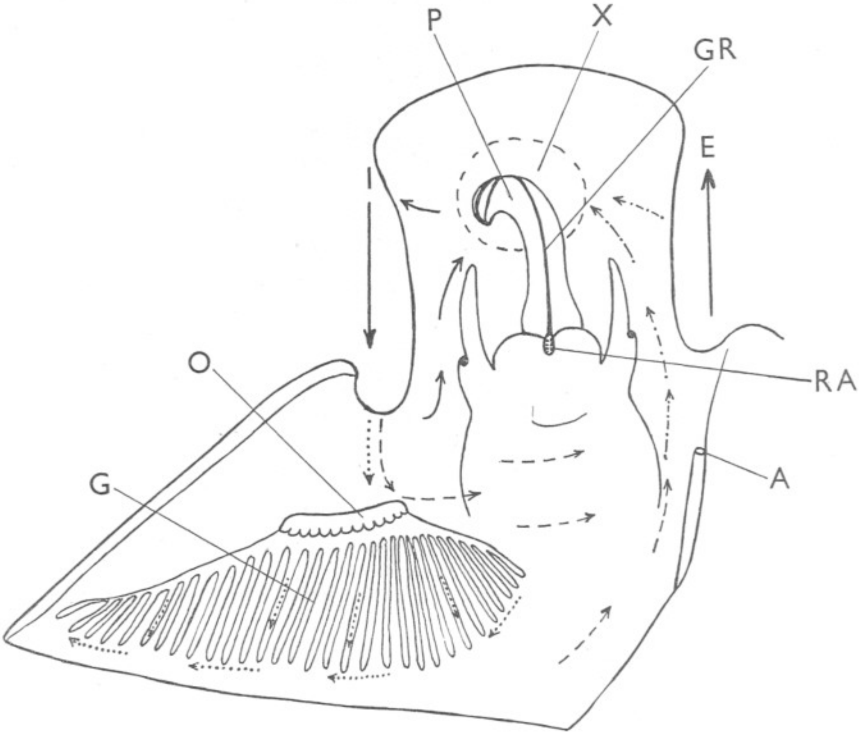


Fig. 5. *Capulus ungaricus*, mantle cavity opened along right side, seen from above. ×3. GR, groove along proboscis; P, proboscis; X, region of propodium, below proboscis, where food material collects. Other lettering as before.

The powerful inhalent current (I), created by the lateral cilia on the gill filaments, enters the mantle cavity on the left side and impinges almost at right angles on the obliquely situated osphradium. The heaviest suspended material does not reach this organ, but is caught in current A and carried round the upper surface of the anterior prolongation of the foot to the region of the tip of the proboscis. The osphradium represents the division between currents B and C, the former carrying medium-sized particles over the floor of the mantle cavity and the latter consisting of currents on the gills. These last currents are produced by frontal cilia which carry fine particles to the tips of the filaments; here particles come under the influence of currents caused by conspicuously large cilia and are conducted, embedded usually in mucous strings, along the tips of the filaments in an obliquely anterior direction towards the exhalent opening. There are also abfrontal cilia, smaller than those on the frontal surface, which carry particles to the tips of the filaments.

Material in currents B and C unites in a common stream near the exhalent opening and passes anteriorly round and beneath the head to join material from current A on the upper surface of the propodium (in the region marked X in Fig. 5). Material here collects in mucus-laden masses—sections reveal abundant mucous glands in and below the epidermis in this region—and on these the animal feeds by means of the proboscis. Food passes up the groove in the proboscis (GP) by means of ciliary, possibly aided by muscular, action; the radula appears to have an essentially conveying function. Peile (1937) states that in "*Capulus ungaricus* the teeth are slightly blunted in a few of the front rows".

Orton (1912) states that the proboscis "appears to be held along the right side of the animal to collect the food-particles from the tips of the gills when the animal is feeding". Nothing corresponding to this was observed in any of the three specimens examined. Orton, however, admits that he had no opportunity of investigating *Capulus* fully.

Unlike the Calyptraeidae further evolution within the Capulidae has been towards parasitism. Certain species of *Capulus* have been described as parasites, but this may be due to a misinterpretation of the true function of the proboscis; there is, however, no question as to the ecto-parasitic habits of all species of the allied genus *Thyca*. Here the animal is attached throughout adult life to the body of echinoderms. The foot is correspondingly reduced; the radula is lost, but the proboscis is elongated and penetrates deep into the body of the host, apparently sucking in the coelomic fluid (see Schepman & Nierstrasz, 1909; Koehler & Vaney, 1912). The species of the allied but completely sedentary family Hipponycidae probably feed in a similar manner to *Capulus*.

Modification of gill filaments.

The elaboration of ciliary feeding mechanisms in these Prosobranchia has involved, above all else, modifications of the gill filaments. The nature of these modifications can best be discussed by reference to Fig. 6, in which appear lateral views of complete filaments and also transverse sections near the base, from the gills of the three species already discussed. Similar figures of *Buccinum undatum*, as an example of a pectinibranch prosobranch in which the gills are exclusively concerned with their primitive function of respiration, are also given. The filaments of *Littorina littorea* and of *Aporrhais pespelecani*, which were also examined, do not differ essentially from those of *Buccinum*. Except for *Vermetus*, the drawings of the complete filaments were all made from living tissue.

The first point of interest is the progressive increase in the length of the filaments in comparison to width at the base. In *Buccinum* (Fig. 6 A), and similar Prosobranchia, the filaments are roughly triangular with the base and height about equal; the other extreme is represented by *Crepidula* (Fig. 6 D), where the filament is narrow throughout and greatly elongated. The ratio of height to maximum width is in *Buccinum* (A) 1:1, in *Vermetus* (B) 2·75:1, in *Capulus* (C) 3:1 and in *Crepidula* (D) 26:1. In *Vermetus* the figures given are based on measurements of preserved filaments which, as indicated by the transverse section, contract considerably in width; they are thus not strictly comparable with the others and the ratio should certainly be lower and so nearer to conditions in *Buccinum*.

In the general distribution of the main tracts of cilia, frontals (*f*), laterals (*l*) and abfrontals (*a*)—the last being always somewhat shorter and more sparse than the frontals—and in the presence of the internal chitinous supporting rods (*c*), the various filaments do not differ fundamentally. In all the frontals and abfrontals beat towards the tips of the filaments and the laterals transversely. In *Buccinum* the particles carried to the tip are then carried over farther to the right (when the gill is *in situ*) and so on to the hypobranchial gland as shown in Fig. 1. But in the other three genera particles are carried forward along the tips from filament to filament at the region marked *x* (indicated approximately only in *Vermetus*).

Passing to a more detailed examination of the individual filaments, in *Buccinum* (A) there are well-developed frontal, lateral and abfrontal cilia. Between the regions occupied by the last two is a wide area which is sparsely ciliated (as noted in living material but never revealed in sections). This region is chiefly notable for the presence of many large mucous glands (*m*) and the irregular nature of the epithelium, in sharp contrast to its regular arrangement in the other ciliated regions. Dakin (1912), who studied sections cut parallel to the longitudinal axis of the filaments, speaks of the epithelium of the gill leaflet (the frontal region), the area of ciliated cells (the lateral region) and the area of glandular cells. His sections did not pass through the abfrontal region. Within the cavity of the filament are many blood corpuscles and much coagulated blood plasma, notably in the "glandular" region, which is presumably concerned with respiration and also with the entangling, in mucus, of any particles which are carried between the filaments in the current created by the lateral cilia. There are no mucous glands in the frontal or abfrontal regions, although they are abundant at the sides of the abfrontal epithelium. Muscular activity was observed in living tissue and there

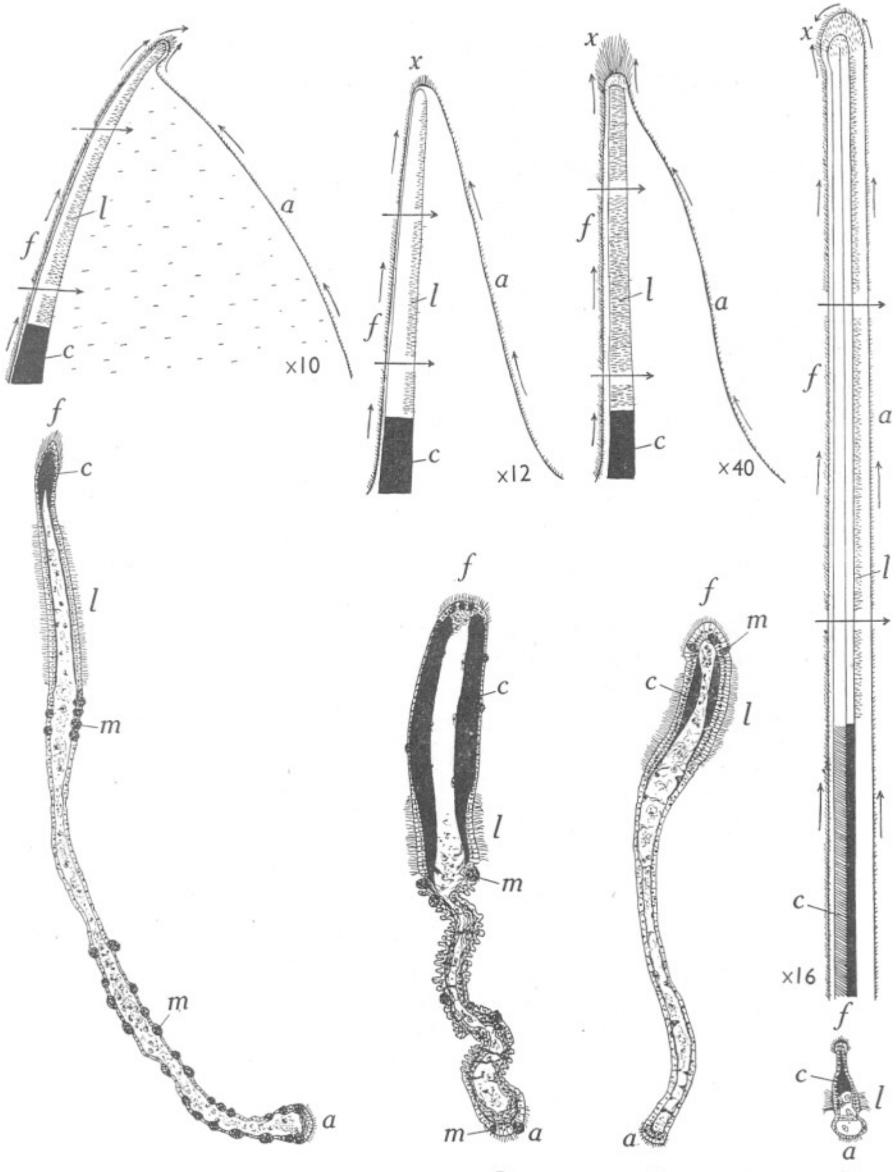


Fig. 6. Lateral view (above) and transverse section near base (below) of gill filaments of A, *Buccinum undatum*; B, *Vermetus novae-hollandiae*; C, *Capulus ungaricus*; D, *Crepidula fornicata*. Sections all ×55; magnifications of whole filaments shown in figure. *a*, abfrontal cilia; *c*, chitinous supporting rods; *f*, frontal cilia; *l*, lateral cilia; *m*, mucous gland cells; *x*, region of anteriorly directed current at tips of filaments.

are indications of muscle in the section, notably at the base of the abfrontal epithelium.

In *Vermetus* (B) the chitinous rods are exceptionally thick and broad and the area occupied by the lateral cilia is reduced and confined to the abfrontal third of the region supported by these rods. Mucous glands occur in all regions except in the epithelium which bears the lateral cilia. Their presence in both frontal and abfrontal epithelia indicates that their secretion assists in the entanglement of food particles in these regions. As already noted the filament has great powers of contraction, made possible by the presence, in the "glandular" and abfrontal regions, of longitudinal and transverse fibres and also others running across the central cavity. The wrinkled condition of the section indicates the effect of the contraction of the second and third of these sets of muscles.

In *Capulus* (C) conditions, in transverse section, approximate more to those in *Buccinum*, but mucous glands are here confined to the frontal region. It may be assumed, therefore, that collection of food particles by the frontal region is so efficient that few pass between the filaments, as they presumably do in the other two species. Muscle occurs, but not to the same extent as in the other two, although muscular movements were observed when living filaments were examined. An important feature is the great length of the terminal cilia, which exceed 100μ.

Finally in *Crepidula* (D), where the filament is no longer triangular, mucous glands are rare, a condition clearly correlated with the presence of the endostyle (Fig. 3, EN), a mucus-producing organ which has been described in detail by Orton (1912, 1914). The lateral cilia here lie nearer to the abfrontal region and beyond the region of the chitinous rods. There is little indication of muscle either in the behaviour of the living filaments or in sections. The tips of the filaments are flattened somewhat laterally, as shown in Fig. 6, but much more so dorso-ventrally, as described and figured by Orton (1912, Fig. 3). The filaments of *Crepidula* have clearly been modified to a much greater extent than those of *Vermetus* or *Capulus*.

The change in shape of the gill filaments from triangular to linear has had the important effect of increasing the extent of the region carrying lateral cilia—and so increasing the water current created in the mantle cavity—and also the extent of frontal and abfrontal regions, thereby augmenting the collecting surface. The accompanying reduction in the middle, or "glandular", region represents a reduction in the respiring surface. This is to some extent made good by the increased length of the gill (though not so in *Crepidula*) but, owing to the sedentary habits of these ciliary feeding Prosobranchia, the need for respiration will be distinctly less than that in actively moving genera, such as *Buccinum*. There is a tendency also for a relative increase in thickness of the chitinous supporting rods, necessary owing to the increased length of the filaments. The change in the distribution of the mucous glands may also be correlated in all three genera with feeding on fine particles, culminating in

Crepidula with the acquisition of an endostyle and the loss of mucous glands on the filaments. The change in the beat of the terminal cilia has already been noted.

It has thus been possible for the purely respiring gill filament of *Buccinum* and similar Prosobranchia to be converted into an organ of food collection by essentially minor modifications, representing the conversion of ciliated rejection tracts into food-collecting tracts. The process, incidentally, indicates the manner in which the gill of the Filibranchia and Eulamellibranchia probably evolved (starting from a paired aspidobranch gill and not from the unpaired pectinibranch gill here considered). The most important differences in these groups are the folding back of the filaments, their increased cohesion by means of interlamellar and interfilamentary junctions of various kinds, and the appearance of latero-frontal cilia. The latter, which appear to be universally present in these two groups, although very small in more primitive Filibranchia such as *Glycymeris* and *Arca* (Atkins, 1936), probably developed owing to the need for a straining mechanism, in the absence of which the narrow spaces leading to the suprabranchial cavity in these complex gills would become blocked. There is clearly no such need in the unfolded and unattached gill filaments of these Prosobranchia.

Discussion

The mode of feeding in the three families here discussed, the Vermetidae, Calyptraeidae and Capulidae, is in essentials the same, and undoubtedly represents a modification of ciliary mechanisms originally concerned with the rejection of sediment from the mantle cavity. There appears to be no reason for postulating a common origin for these families; the Vermetidae are admittedly widely removed from the other two, and they, though often grouped together (e.g. by Thiele (1925) in the Calyptraeacea), have many significant differences, their more superficial resemblances being very possibly the result of convergence due to similar modes of life and not of common origin. Lebour (1937) has recently shown that the larvae of *Capulus* possess an echinospira shell indicating relationship to the Lamellarioidea.

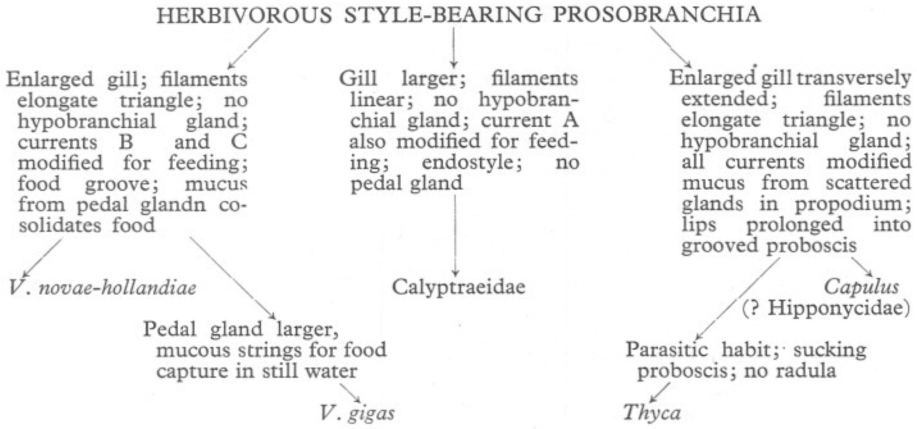
Modification of the ciliary mechanisms and associated changes are always correlated with complete or effective loss of the power of movement and with life in comparatively clear water. Loss of movement has involved the necessity of drawing food to the animal by means of ciliary currents (and by the unique method of mucous strings in *Vermetus gigas*), and this is possible only if the animal lives in water reasonably free from sediment which would clog the feeding tracts. Thus the Vermetidae live cemented to rocks and the Calyptraeidae and *Capulus* are frequently attached to the shells of Lamellibranchia, such as *Ostrea* or *Pecten*, or to stones, and so raised above the bottom deposits. Those living on Lamellibranchs will profit by the currents they create.

The necessity for providing powerful feeding currents and extensive collecting surfaces has been met by the elongation of the original broadly triangular gill filaments and by the greater extent of the entire gill. But there has been no change in the direction of the ciliary currents except for the anteriorly directed current along the tips of the filaments, a current which corresponds in function to those present in the food grooves along the free edges of the demibranchs in the Lamellibranchia. In the Calyptraeidae food collection has been further assisted by the appearance of an endostyle. In all genera current B, essentially unmodified, assists current C in the collection of food—a ciliated tract on the floor of the mantle cavity carrying food finally towards the mouth—while in all but the Vermetidae current A, by modification of its direction, also assists in this process.

The invariable absence of a hypobranchial gland, so very well developed in typical Prosobranchia, is correlated with the increased size of the gill, the filaments of which extend to the right side of the mantle cavity. Moreover, being an essential part of the original cleansing and rejection mechanism, as postulated in the case of *Aporrhais* (Yonge, 1937), it is no longer necessary.

The radula and jaws have been retained but are modified in function. Peile (1937) has described the conspicuous absence of wear in the teeth of the radula of all of these animals and concludes, "we may sum up the function of the radula as grasping, not rasping". Thus, although the gills have become modified in the direction of those of the Lamellibranchia and give some indication of the manner in which they have evolved, the actual taking in of food at the mouth consists of the grasping, by radula and jaws, of mucus-laden masses which are passed back into the oesophagus by the conveying action of the radula. Nothing in the nature of a selective mechanism, represented in the Lamellibranchia by the labial palps, the complex ciliated tracts on which rigorously control the passage of material to the mouth, has been evolved in these Gastropoda.

The evolution of ciliary feeding has taken significantly different directions in the three families. In the Vermetidae it is associated with a retention, and remarkable enlargement, of the pedal gland, which provides mucus for the consolidation of food particles in species such as *Vermetus novae-hollandiae*, while in *V. gigas* a still greater enlargement of this gland permits direct feeding by its secretion. In the Calyptraeidae the elaboration of ciliary feeding mechanisms has been taken to the highest degree of perfection recorded in the Prosobranchia: by the enlargement of the mantle cavity and of the gill, modification of the filaments, possession of an endostyle and conversion of all three rejection tracts into food streams. Finally in the Capulidae an increase in the size of the gill has been made possible by its oblique position in the mantle cavity; but the most characteristic feature is the remarkable grooved proboscis, the further evolution of which has resulted in the parasitic habit found in *Thyca*. The trends of evolutionary change in all three families may suitably be indicated diagrammatically as follows:



SUMMARY

1. Ciliary currents concerned with rejection of sediment from the mantle cavity of pectinibranch Prosobranchia consist of A, currents carrying heavier particles to the inhalent opening; B, currents carrying medium particles across the floor of the mantle cavity; C, currents carrying fine particles over and between the gill filaments for later consolidation by the mucus from the hypobranchial gland. Material in currents B and C is rejected from the exhalent opening.

2. The feeding currents in ciliary feeding Prosobranchia represent modifications of these rejection currents.

3. In *Vermetus novae-hollandiae* currents B and C only are modified, material being passed to the mouth region, where it is mixed with mucus from the large pedal gland, by way of a food groove.

4. In *Crepidula fornicata* and other Calyptraeidae all currents are modified for feeding and there is an endostyle for mucus secretion.

5. In *Capulus ungaricus* all currents are modified, food collecting on the upper surface of the propodium, where mucus is secreted and mucus-laden masses are passed to the mouth by way of the grooved proboscis.

6. In ciliary feeding species the gill is enlarged and the filaments tend to become longer and linear. This results in the production of an increased feeding current and collecting surface and the loss of the hypobranchial gland. Cilia at the tips of the filaments beat anteriorly. The distribution of mucous glands on the filaments can be correlated with the change in their function.

7. The possible mode of evolution of the lamellibranch gill is discussed in the light of these findings.

8. In the ciliary feeding Prosobranchia radula and jaws are retained for the grasping of the mucus-laden food masses; nothing equivalent to the labial palps of Lamellibranchia is present.

9. Evolution of ciliary feeding has probably been independently achieved in the three families considered. In the Vermetidae further development of the pedal gland enables direct mucus feeding, as in *Vermetus gigas*; in the Capulidae evolution culminates in a parasitic habit as in *Thyca*; only in the Calyptraeidae, where ciliary feeding mechanisms are most highly organized, do all genera and species appear exclusively to be ciliary feeders.

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Note. Since this paper went to press I have had the pleasure of seeing the manuscript of a forthcoming paper by Mr A. Graham on ciliary feeding in *Turritella communis*. Essentially the same mechanisms are involved as in the species here considered, but there are most interesting modifications due to the fact that this animal is adapted for ciliary feeding in a *muddy* environment.

THE FATE OF THE LARVAL ORGANS IN THE METAMORPHOSIS OF *OSTREA EDULIS*

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(Text-figs. 1–8)

INTRODUCTION AND REVIEW OF PREVIOUS WORK

It has long been realized that the free-swimming larva of the European oyster (*Ostrea edulis*) must undergo considerable anatomical reorganization when it attaches itself as spat and takes on the fixed life of the adult oyster. The details of these changes have remained obscure. The fully developed "ansatzreifen" oyster larva has been admirably described and illustrated by Erdmann (1934). The smallest settled spat of which there is an adequate description is that figured by Yonge (1926). This specimen had a shell 1·2 mm. in length and must have been fixed for not less than 5 or 6 days, and possibly considerably longer; it had in most respects the structure of the adult oyster. It is clear that there is a considerable gap in our knowledge. A preliminary note by the writer (1937) gave information on a few points, particularly the rate of development of the gills and the changes in the adductor muscles. A further note (Cole, 1938) described a pair of sense organs of a new type found in the early fixed stages. In this, the first part of this study, the fate of the characteristic larval organs—the velum, foot, eyespots and adductor muscles—is described. The changes in gills, mantle, digestive system, etc., which take place during the first few days after attachment will be described in another publication.

Our knowledge of the metamorphosis of the larva of the American Atlantic oyster (*O. virginica*) is considerable, due chiefly to the efforts of Ryder (1882–84), Jackson (1888–90), and particularly Stafford (1913). In his monograph on *The Canadian Oyster* (*O. virginica*), Stafford gives a full account of the anatomy of both the fully developed larva and the earliest settled spat, and discusses the transition in detail. During recent years Prytherch (1934) has devoted further attention to this species. Although concerned mainly with the physiological requirements during attachment and metamorphosis, Prytherch gives a description and figure of the fully developed larva and discusses the fate of some of the larval organs, in particular the so-called pigment spots.

Roughley (1933) in his account of the life history of the Australian oyster (*O. commercialis*) gives a good description of the larva, but deals only briefly with the anatomical reorganization at fixation. The course of events in this species was in general so similar to that described by Stafford for *O. virginica* that he did not consider it necessary to give a detailed description. Hori (1926) gives some figures of the larva and spat of the common Japanese oyster (*O. gigas*) but does not consider the anatomical changes. In a later paper (1933) he describes also the development of the larva up to the setting stage in *O. lurida*, his figures being reproduced by Hopkins (1937). Although there are numerous other well-known species of oysters in no instance has the metamorphosis received any attention.

It has been customary (see Yonge, 1926) to assume that the metamorphosis of *O. edulis* follows very closely that of *O. virginica*, but it will be seen from the subsequent pages that this is not so, although it is possible that a re-investigation of certain points in the development of *O. virginica* may bring these two closely related species into line.

MATERIAL AND METHODS

The source of all material, both larvae and early spat, has been the oyster-breeding tanks of the Ministry of Agriculture and Fisheries at Conway. Since 1918 experiments in breeding *O. edulis* have been carried out in large concrete tanks, a description of which was published by the writer in 1936. Fully developed larvae were obtained by townet from the tanks and were fixed in Bouin's solution. No special precautions were taken to fix larvae in the expanded condition, since the collection of suitable material had to be carried out in odd moments during the summer when the breeding experiments were in progress. Larvae were simply dropped into tubes of Bouin's solution, and in practice the fixation was excellent and no trouble was experienced in determining the relations of the different organs in the contracted condition. For the study of the early spat stages, oyster shells which had been in the tanks a few days while settlement was in progress, and which were liberally sprinkled with spat, were immersed in Bouin's solution and later transferred to alcohol. In consequence of the decalcification of the surface layers of the shells, brought about by the acid in the fixative, it was later possible to brush off the spat without damage. Such shells yielded spat of all ages down to those which were in the act of settling, and, in fact, gave also some larvae which were merely wandering over the surface of the shell in search of a suitable place for attachment. More than a hundred such early spat were later embedded in paraffin and sectioned at a thickness of 8–10 μ. A large number of eyed larvae were also sectioned for comparison. No attempt was made to orientate the larvae or spat, as it was expected that a sufficient number would be cut in all planes to present an adequate picture of their anatomy. This in practice proved to be the case. Sections were stained with Ehrlich's acid haematoxylin and eosin. A large number of larvae and early spat were also prepared as whole mounts, Ehrlich's acid haematoxylin or alum-carmine being used for staining. A certain number of spat were caught on glass slides immersed in the tanks, and these slides were removed at known intervals and placed in fixative. These spat of known age were subsequently prepared as whole mounts and gave useful information on the speed of metamorphosis. Spat of known age for sectioning were obtained by immersing shells for fixed periods and later detaching the spat set thereon. Some aspects of the metamorphosis could be studied in living material, e.g. the disappearance of the eyespots, the growth of the shell and gills, etc.

The illustrations have in all cases been prepared from *camera lucida* drawings.

BRIEF DESCRIPTION OF THE LARVA OF *OSTREA EDULIS*

Although the fully developed oyster larva has been so well described by Erdmann, it will be necessary to give here a brief description of its outstanding features. The larva is characterized first of all by the possession of a large and muscular ciliated velum, which when protruded from the shell serves for both locomotion and food collection. When the shell is closed the velum occupies the fore-part of its cavity. The mouth is situated at the base of the velum on its *posterior* surface, between the velum and the foot—a long strap-shaped organ which develops only during the last day or so before attachment. The interior of the foot is occupied by the byssus gland which provides the secretion with which attachment is effected. On each side of the body of the larva a large eyespot develops a few days before attachment and is easily seen on account of the transparency of the shell and mantle at this stage. There are two adductor muscles, anterior and posterior, symmetrically placed in relation to the hinge. The anus is posterior, slightly dorsal to the posterior adductor. The nervous system in the larva consists of cerebral and pleural ganglia in the velum, pedal ganglia in the base of the foot, and visceral ganglia near the posterior adductor. There is a pair of statocysts in the base of the foot, near the pedal ganglia. Gills are not well developed in the larva, but Erdmann figures a row of six extremely short knob-like processes along the left side. During the process of attachment the larva comes to lie on the left or more convex valve of the shell.

The Velum

The fate of the velum of the lamellibranch larva, and in particular of its contained apical sensory area, has been the subject of considerable speculation. The suggestion that in *Ostrea* the velum was cast off was first put forward by Davaine (1852). A few years previously Lovén (1848) had suggested that in the forms studied by him the labial palps of the adult were derived from the apical area of the velum. This view was, however, rejected by later workers, among them Ryder (1882), who studied the metamorphosis of *O. virginica*, and it was not until the publication in 1901 of Meisenheimer's great work on the life history of *Dreissensia polymorpha* that the subject received the attention that it deserved. Meisenheimer described and illustrated the disintegration and absorption of the velum of *Dreissensia*, and showed clearly that the apical area was not lost but came to lie astride the oesophagus, and later fused with the upper lip of the mouth and did in fact form the basis of the labial palps.

Meisenheimer's work was apparently unknown in America for several years, as Sigerfoos (1908) and Stafford (1913), in discussing the metamorphosis of *Ostrea virginica*, make no reference to it. Sigerfoos, in his work on the development of shipworms (Teredinidae), refers incidentally to observations which he had made on *O. virginica*. He considered that the velum disappeared in its entirety very soon after attachment. He did not consider it possible that any part of the velum should give rise to the palps. Stafford (1913) gives a full account of the changes taking place at fixation in *O. virginica*. He states that after attachment the velum quickly atrophies, and in spat which had still in most respects the structure of the larva the velum was already shrunken and collapsed, the outline being rather vague. Immediately the spat began to grow, probably only a few hours after fixation, the velum was "so far gone as to be unrecognizable", and by the time the spat had increased its size by one-eighth "there remained only vestiges, chiefly of its muscles". Stafford discusses at length the possible loss of a part of the whole of the velum by "dehiscence", but came to the conclusion that no such "dehiscence" occurred. His material, however, was limited, consisting of sections of six spat only of the requisite size. Stafford, although unfamiliar with Meisenheimer's work, was acquainted with the views of Lovén regarding the origin of the palps. He was, however, of the opinion that the apical area of the velum played no part in the development of the palps. He found their origin in a thick-walled invagination dorsal to the oesophagus which later spread around and enveloped the mouth, giving rise to upper and lower palps by the growth of the outer and inner edges of the cavity. Concerning the interpretation of Stafford's sections further remarks will be made later in this paper.

Field (1922) in his study of *Mytilus edulis* came to the conclusion, from the examination of whole mounts only, that the labial palps of the adult were derived in the manner described by Meisenheimer. As far as I am aware no further attention has been paid to the subject during recent years.

A close study of my sections of very early spat makes it clear that in *Ostrea edulis* at least, the upper palps develop in a manner similar to that described by Meisenheimer for *Dreissensia*. Immediately after attachment the apical area of the velum becomes detached from the surrounding tissue and sinks into the interior of the velum, coming to lie dorsal to the oesophagus some distance from the surface of the body (Figs. 1 and 2). Here it is still associated with the cerebro-pleural ganglia of the larva. At the same time the velum collapses and is carried forward and upward by the rotation of the body. The mouth comes to lie just below the anterior adductor with the velar

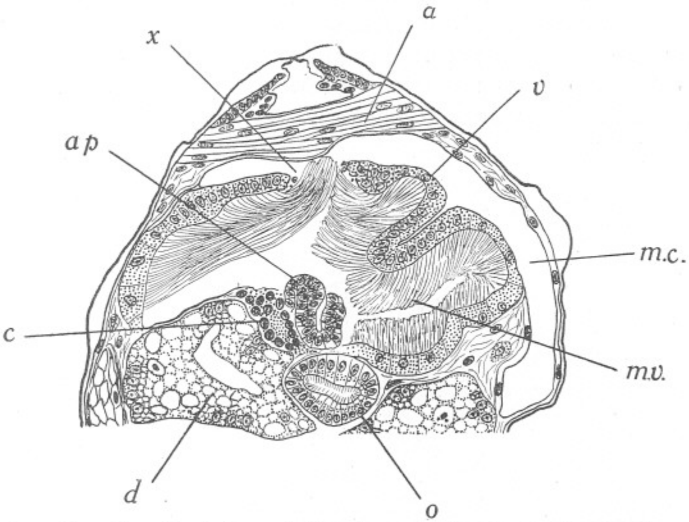

Fig. 1. Horizontal section of anterior end of oyster spat a few hours after attachment, showing the apical area of the velum detached from the surrounding tissues and lying astride the oesophagus. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pedal ganglion; *d*, digestive diverticulum; *m.c.*, mantle cavity; *m.v.*, muscle fibres of velum; *v*, velum; *x*, former position of apical area of velum.

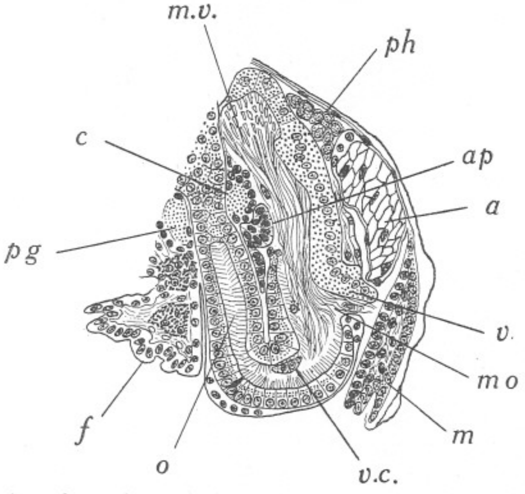

Fig. 2. Sagittal section of anterior end of oyster spat a few hours after attachment, showing the oesophagus bent round on itself, with the mouth directed inwards and blocked by velar muscles and detached cells. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pleural ganglion; *f*, foot; *m*, mantle; *mo*, mouth; *m.v.*, muscle fibres of velum; *o*, oesophagus; *ph*, phagocytes; *v*, velum; *v.c.*, detached velar cells.

remnants occupying a position between them. As the velar remnants sink more deeply into the body, the mouth, which is closely bound up with the stalk of the velum, is dragged in also and the oesophagus is for a while bent round so that the mouth faces inwards instead of outwards (Fig. 2). Due to the sinking of the apical area of the velum and the general collapse and disintegration of the latter organ, the muscle fibres which filled its cavity project from the body wall as a shaggy mass. While the mouth is bent inwards in the manner described above, it is practically blocked by these fibres and by detached velar cells, and, with the rapid dissolution of the velar tissues which is going on, it seems fairly certain that some of the remnants are swallowed. Such an occurrence would be by no means unusual in the metamorphosis of marine larvae. This bent position of the oesophagus does not persist for long, certainly not more than 24 hr., for the tension is relieved by the dis-

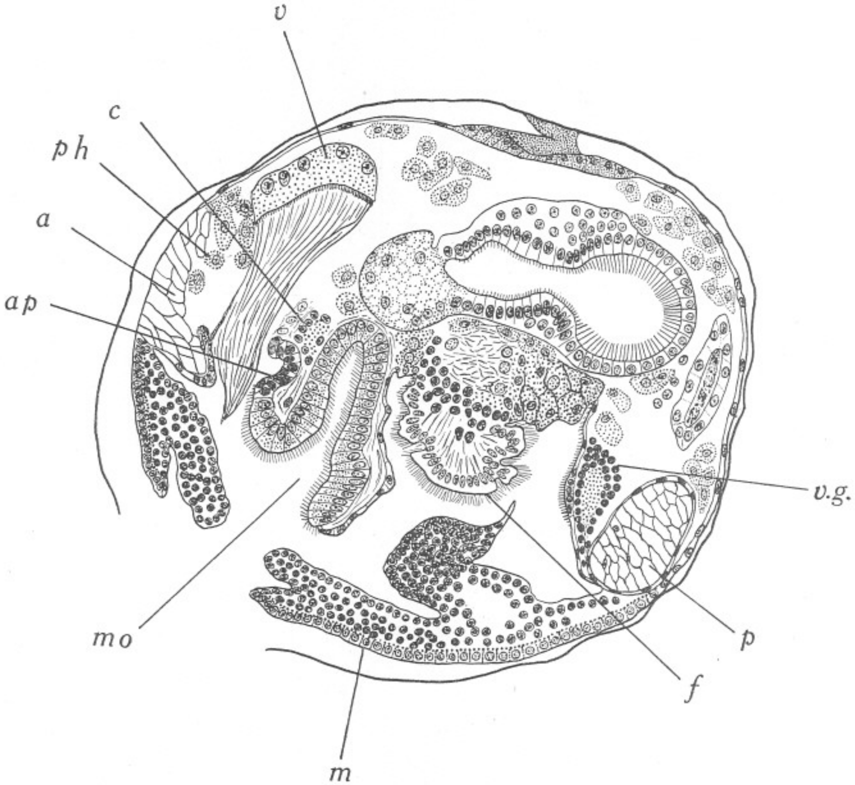

Fig. 3. Sagittal section of oyster spat about 24 hr. after attachment, showing the degenerating foot, the velar remnants practically enclosed within the body, and the apical area of the velum fusing with the upper lip of the mouth. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pleural ganglion; *f*, foot; *m*, mantle; *mo*, mouth; *p*, posterior adductor muscle; *ph*, phagocytes; *v*, velum; *v.g.*, visceral ganglion.

integration of the velar tissues. The apical plate moves along the oesophagus until it occupies a position directly above the mouth. Underlying it at this stage traces of the cerebro-pleural ganglia may still be seen. The apical plate now fuses with the epidermis of the upper lip (Fig. 3). At this stage, which is reached about 24 hr. after fixation, the velar remnants consist of a little of the typical epithelium of the thickened edge and some of the muscle fibres of the interior. These latter still project from the body wall between the mouth and the degenerating anterior adductor. Subsequently the much thickened upper lip spreads out laterally, and gives rise to short rounded lobes which project, one on each side, at the upper corners of the mouth (Fig. 5). These are the rudiments of the upper, or outer, palps of the adult oyster. This stage is reached 48 hr. after attachment. During this period the velum also disappears completely, and a thin epithelium grows across between the palps and the remnant of the anterior adductor (Fig. 4). There can be no doubt that a great deal of the velar tissue breaks up and is lost or eaten. From a close study of Stafford's figures, and the text which accompanies them, I am of the opinion that it is not improbable that a re-examination of the development of the palps in *Ostrea virginica* will show that it follows a course very similar to that described above.

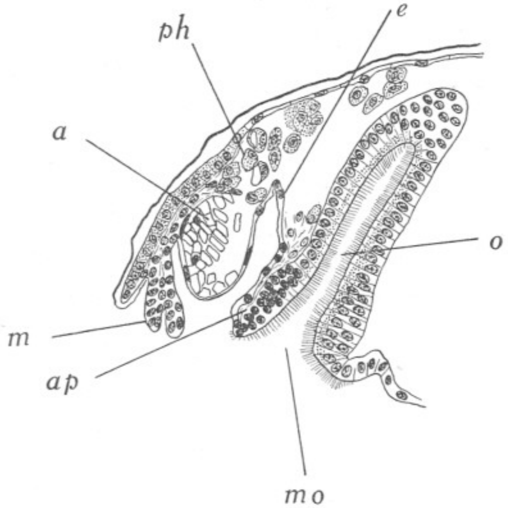

Fig. 4. Sagittal section of anterior end of oyster spat 48 hr. after attachment, showing the apical area of the velum completely incorporated with the upper lip of the mouth, and the epithelium of the body wall closed over the area formerly occupied by the velum. *a*, anterior adductor muscle; *ap*, apical area of velum; *e*, epithelium covering area formerly occupied by the velum; *m*, mantle; *mo*, mouth; *o*, oesophagus; *ph*, phagocytes.

Later spat show the upper palps slightly more elongated and pointed (Fig. 6), the upper lip being drawn forward to form a hood over the mouth. Spat 3 or 4 days old show, however, no trace of the inner palps, unless the thickened

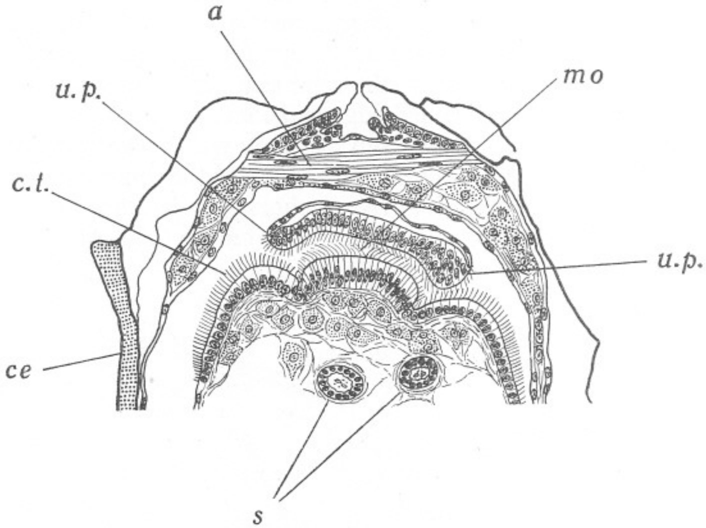

Fig. 5. Horizontal section of anterior end of oyster spat about 48 hr. after attachment passing just below the mouth, showing the lateral spreading of the upper palp rudiments, and the position of the statocysts. *a*, anterior adductor muscle; *ce*, cementing material; *c.t.*, ciliated tract at base of gills; *mo*, mouth; *s*, statocysts; *u.p.*, upper palps.

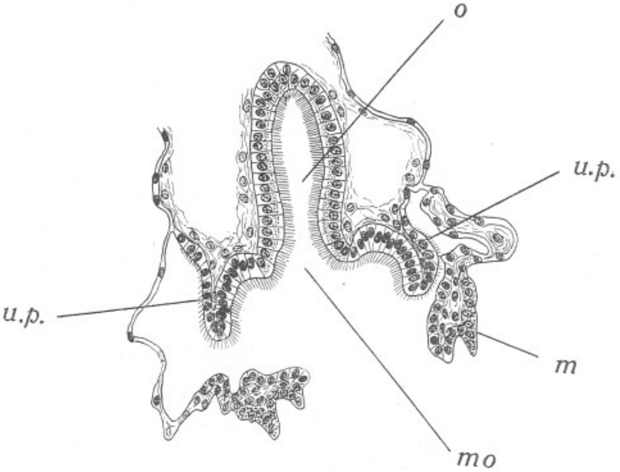

Fig. 6. Frontal section of oyster spat 3–4 days after attachment, showing the mouth and upper palps. *m*, mantle; *mo*, mouth; *o*, oesophagus; *u.p.*, upper palps.

nature of the rim round the mouth and in particular of the lower lip is an indication of their derivation from this source. In *Dreissensia* Meisenheimer states that the lower palps develop some time after metamorphosis as outgrowths from the upper palps. My material unfortunately does not extend beyond spat of 3–4 days old, none of which have the lower palps developed. These spat had shells about 0·6 mm. in length, while the smallest spat described by Yonge had a shell 1·2 mm. across. This individual had, however, relatively enormous palps, both upper and lower palps being well developed. It is probable that it had been settled not less than 5 or 6 days, but even so it is clear that the growth of the palps must be very rapid after the changes associated with metamorphosis have been completed.

The Foot

The foot develops very rapidly in the larva during the last 24 hr. or so before settlement. In the fully developed larva the foot is a long strap-shaped organ which projects from the body in the region between the mouth and the posterior adductor muscle. It is capable of being protruded between the valves for a distance at least equal to the diameter of the shell. Besides serving for locomotion on the substratum immediately prior to attachment, the foot is a highly sensory and glandular organ. The greater part of the base of the foot is occupied by the byssus gland which opens along the sole by a ciliated groove. Although the actual process of attachment in *Ostrea edulis* has not been described, there is no longer any doubt (see Erdmann, 1934) that this gland produces the cement with which the left shell of the larva is attached permanently to the substratum. Spat fixed to shells and subsequently detached by decalcification show a definite thick pad of homogeneous cement underlying the left valve (see Fig. 5). After fixation a little cement remains in the byssus gland and on staining takes up eosin with great avidity. The fate of this residual cement is easy to follow as in slightly more advanced spat phagocytes may be seen crammed with an eosinophilous substance which has every indication of being residual byssus material. The foot gradually shrinks in size following fixation and is carried forward by the rotation of the mouth until it occupies an almost mid-ventral position, projecting from the body wall behind the mouth as an irregular crumpled mass clothed with rather shaggy cilia (Fig. 3). The regular columnar epithelium which clothes the foot remains distinct for some time. Internally the pedal ganglia may be distinguished for about 24 hr. after fixation, although their outlines are rather vague. At this stage the glandular cells of the byssus cavity are also still quite distinct. In spat which have been attached 48 hr. the foot projects only slightly from the body and its free border is rather vague, suggesting the loss of some of the tissues making up the distal part. Internally, the tissues of the byssus cavity may still be seen, but the pedal ganglia are no longer distinguishable. The whole region is much invaded by phagocytes, some of which contain recognizable elements of the byssus gland. The last traces of the foot are absorbed and the epithelium assumes a smooth outline before the spat is 72 hr. old. The absorption of the foot in *O. virginica* is apparently not complete until much later, as Stafford states that traces may be seen in spat up to a size of 1 mm. Otherwise the details of the process appear to be very similar.

Of the sensory structures of the larval foot only the statocysts persist in the adult. In the larva they are closely applied to the sides of the pedal ganglia, although innervated from the visceral ganglia (Erdmann, 1934), and open on the base of the foot by a small pore. Following fixation and absorption of the foot they sink more deeply into the body until they come to lie below the root of the first gill filaments, ventral and slightly posterior to the mouth (Fig. 5). Their connexion with the exterior is lost. Such statocysts have already been described by Carazzi (1902) in the adult *O. edulis*, and were found also in *O. chilensis* by Dahmen (1923). I have received also a private communication from Prytherch which indicates their persistence in *O. virginica*. It seems probable that they are of frequent occurrence in oysters, although it is difficult to see what their function can be. They are stated not to occur in the adult *O. cucullata* (Awati & Rai, 1931). It is possible that they may serve as organs for the detection of movement in the surrounding medium, but the special pallial sense organs described by the writer (1938) would seem to be better equipped for this purpose, inasmuch as they are situated on the mantle and are separated from the external medium by a thin epidermis only, while the statocysts on the other hand are rather deeply set and must be correspondingly insensitive to small disturbances.

The Adductor Muscles

Huxley (1883) was the first to suggest that the single adductor of the early oyster larva did not correspond to the single adductor of the adult. The posterior adductor of the late larva was discovered by Jackson (1888) working with *O. virginica*. Since that time it has been recognized that the single adductor muscle of the early larva corresponds to the anterior adductor of dimyarian molluscs, while the adductor of the adult oyster corresponds to the posterior adductor of these forms. It has further been recognized that the late larva of all species of oysters possesses two adductors more or less symmetrically placed with regard to the hinge. In the eyed larva of *O. edulis* at the time of settlement the two adductor muscles are approximately equal in size. Following fixation the anterior adductor begins to degenerate and at the same time is crowded to the edge of the shell (Fig. 3). The posterior adductor enlarges and moves ventrally and anteriorly towards the centre of the shell. In spat which are between 24 and 48 hr. old the sizes of the posterior and anterior adductors are in the ratio of 3 : 2. Forty-eight hours after settlement a fringe (dissoconch) has usually been added to the larval shell or prodissoconch. Thereafter the degeneration of the anterior adductor proceeds rapidly. Spat which have been fixed 3 days usually show a few fibres only at the extreme edge of the shell, while at 4 days all traces of the anterior shell muscle have disappeared. The posterior adductor has increased in size and moved ventrally until it lies just outside the prodissoconch attached to the dissoconch or definite shell of the adult. Such 4 days' old spat may be 6 mm. in diameter. At this stage sections of the adductor muscle show no differentiation into "quick" and "catch" components.

The Eyes, with Remarks on their Function during Attachment

The eyes develop in the larva only during the last few days before settlement. They are a pair of spherical densely pigmented organs, situated in the body wall just dorsal to the attachment of the gill rudiments. In the living larva, when the velum is retracted, each eyespot can be seen underlying the valve of the shell at about its centre. The structure, function, and fate subsequent to metamorphosis of these organs have been the subject of considerable difference of opinion (see Prytherch, 1934). In *O. edulis* the eyes are described in detail and figured by Erdmann (1934), each eyespot consisting of an almost spherical cup of pigmented epithelium filled with a gelatinous matrix and having its aperture closed by a lens-like body. It gives the writer great pleasure to confirm Erdmann's description, as considerable doubt has been thrown upon his interpretation of their structure. The degree of pigmentation and the situation of the pigment in the epithelium of the cup appear to vary somewhat in different individual larvae. In some instances the nuclei of the epithelium are so densely pigmented as to show little structure, while the cytoplasm above the nuclei may be practically free from pigment. In others the pigment is dense in the cytoplasm while the nuclei are more lightly pigmented.


Fig. 7. Section through the eyespot of oyster spat just settled.

In a recent paper (1934) the structure of the eyespots in the larva of *O. virginica* is discussed in detail by Prytherch. He describes in this species pigment spots which are "found on each side of the body as very conspicuous larval organs". According to this author they have not the structure of eyes and have been incorrectly described as such. In support of his contention he states that in the course of experiments over a period of 8 years he has found no evidence that oyster larvae are sensitive to light intensity or colour. It must be admitted in this connexion that no such phototropic responses have been demonstrated in the larva of *O. edulis*, but this may largely be explained by the fact that the possibility of such responses existing has not yet been explored. There can, however, be no doubt whatever about the eye-like structure of the "pigment spots" in this species (see Fig. 7). Hopkins (1937) has studied experimentally the setting of larva of *O. lurida* under natural conditions, and concludes that "light is not an orienting factor in the setting behaviour of larvae of this species". Although he made no detailed study of the pigment spots he concludes that they are not light sensitive organs, and is inclined to support Prytherch's view that they have an entirely different function. Nelson (1925), on the other hand, is of the opinion that the eyed larva of *O. virginica* exhibits a negative phototaxis, which is not apparent in younger larvae without eyespots. Regarding the eyespot and its function Nelson states: "This spot, although unable to form an image like a true eye, is sensitive to light....In the presence of light these 'eyed' larvae of the oyster are stimulated and continue moving until they get into a shaded place, where they become quiescent." In this way he accounts for the preference exhibited by larvae for shady situations for attachment. It is clear, however, that the freedom of shady overhung situations from silt and encrusting growths is also an important factor in determining the density of settlement. Larvae of all species of oysters attach themselves only to clean surfaces, whether they are shaded or not. Roughley (1933) working with *O. commercialis* noted a tendency for the larvae to set in small depressions on the shells offered, as for example in the indentations between the teeth along the inner margins of the shells. A similar phenomenon has also been noted by Hopkins (1935). Roughley correlates this tendency with the increased protection against abrasion afforded by such situations. Hopkins (1935) has shown that the angle of inclination of the surface to the horizontal has an important effect on the intensity of setting in *O. lurida*. The more nearly the surface approaches the horizontal so does the intensity of setting on it increase. The present writer's experience with *O. edulis* in tanks has been similar, e.g. if two similar slates are put into the water, one at an angle of 45° and the other horizontal, then the intensity of setting on the under side of the horizontal slate will be considerably greater than on the same side of that set at an angle. Further, on the under side of the half-round limed tiles in use at Conway the intensity of setting is always greater along the ridge of the tile where the surface is horizontal, than along the sides where the surface is at an angle. The nature of the surface presented, i.e. whether it is rough or smooth, seems also to be of importance, and the writer has noticed that among some test slates placed horizontally in the Conway tanks, one which had been ground smooth caught far less spat than others the surfaces of which had not been touched. Hopkins (1935) further produces experimental evidence in support of his contention that the greater intensity of setting of *O. lurida* on the underside of horizontal surfaces is not due to negative phototaxis. He compared the setting on horizontal glass plates placed in the sea for 24 hr., some of which were coated on the upper surface with black paint, while others were plain. The results showed a slightly *greater* number of larvae setting on the underside of the plain glass in the unshaded situation. He considers that the greater intensity of setting on the underside of horizontal surfaces which is generally experienced to be due to the fact that larvae swim with the velum and foot uppermost and thus the foot most frequently comes into contact with horizontal surfaces. In a recent paper (1937) the same author gives further details of his experiments but the conclusions are the same. There is, however, a great deal of evidence for the view that larval oysters exercise some selection in the choice of the site to which they eventually become attached. They do not attach themselves to the first surface with which they come into contact as Hopkins implies. Before attachment larvae of *O. edulis*, and indeed apparently of most species of oysters, pass through an exploratory phase, during which they crawl over the surface of the substratum, with the foot protruded in front and apparently acting as an important tactile organ. Further, the writer is of the opinion that, in *O. edulis* at least, attachment may be postponed for a while if a suitable surface is not presented. Such an ability to delay metamorphosis until a suitable surface is available is possessed by the larvae of several species of polychaete worms, and in the opinion of Wilson (1937) has an important influence on the survival rate after metamorphosis. It is clear that the whole question of the factors influencing oyster larvae at the time of attachment needs to be examined more closely.

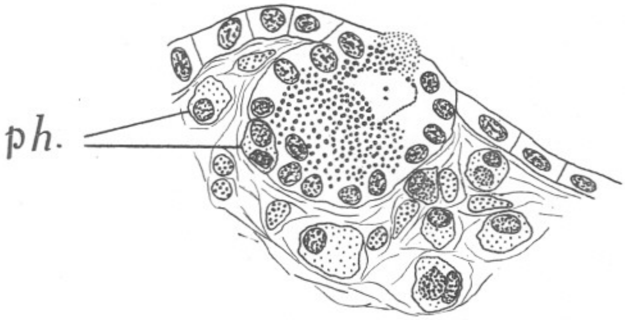

Fig. 8. Section through degenerating eyespot of oyster spat, a few hours after attachment. *ph*, phagocytes.

Prytherch describes in detail the dispersal of the pigmented cells in *O. virginica*, and their migration to the blood stream. In this species the break-up of the pigment spots is very rapid as the following statement shows: "When setting is in progress, the pigmented cells in each spot gradually enlarge, separate and one or two break away and are carried forward by the blood stream into the mantle. After attachment the pigment spot breaks apart more rapidly, and all the cells become distributed in a short time into the circulatory system, as the process of transformation of the larva is in full swing. Each pigment spot consists of approximately 300 cells, which after separation resemble in many respects the leucocytes of the spat and adult oyster." It is unfortunate that Prytherch should not have figured sections of larvae and early spat which would support his findings, but in a recent private communication to the writer he re-affirms his view that "these structures are not light sensitive organs, but function chiefly as leucocyte-generating tissue from which cells migrate to the blood stream during metamorphosis".

Concerning the fate of the eyespots Stafford offers no information, nor in fact does any writer other than Prytherch. In *O. edulis* the eyespots disappear as such after the first 24 hr. of attached life. Soon after attachment the eyes become less conspicuous due apparently to some loss of the black pigment. They tend also to sink below the epithelium of the body which later closes over them. There seems to be no reason to doubt that they are broken down *in situ* and the pigmented cells ingested by phagocytes. The details of this breakdown process naturally vary in different spat. The pigment usually disappears quickly from the nuclei. The outline of the epithelial cup becomes irregular and invading phagocytes may be seen (Fig. 8). With the breakdown of the cells, the pigment is liberated into the centre of the cup and lies in irregular clumps, the granules of which are considerably larger than those in the functional eye. Phagocytes are very numerous in the connective tissue underlying the eye. The final stages of the disintegration is represented by a group of phagocytes many of which contain cells and nuclei with much black pigment, which have every appearance of having formed part of the larval eyespot. That such phagocytes while still containing the remains of the pigmented epithelium of the eye may wander to other parts of the body is not unlikely, and this may create the illusion that the pigmented eye-cells are actually functioning as leucocytes. No separation and dispersal of the pigmented cells, such as Prytherch describes, has however been observed, the disintegration and absorption of the eyespots going on *in situ*.

SUMMARY

This is the first part of a study of the metamorphosis of the larva of the European flat oyster (*Ostrea edulis*) and deals with the fate of the larval velum, foot, adductor muscles and eyespots.

The apical area of the larval velum forms the basis of the upper labial palps of the spat.

The bulk of the velar tissue is broken up and cast off or eaten; the total dissolution of the velum being complete within 48 hr. of attachment.

The larval foot after effecting attachment rapidly shrinks in size and disappears within 72 hr. of attachment. Partial loss of its tissues probably occurs.

The statocysts persist in the spat.

Following fixation the anterior adductor muscle rapidly degenerates.

The so-called pigment spots of the larval oyster have the structure of eyes. During metamorphosis they degenerate rapidly *in situ*.

A discussion of the function of the eyespots during attachment reveals the need for further critical experiments.

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ON TWO SPECIES OF THE TREMATODE GENUS *DIDYMOZOON* FROM THE MACKEREL

By H. A. Baylis, M.A., D.Sc.

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(Text-figs. 1–6)

Taschenberg (1879) briefly described, under the name of *Didymozoon scombri*, a trematode which he recorded as occurring in pairs in cysts on the inside of the gill-covers of *Scomber colias* at Naples. Odhner (1907) found what he believed to be the same species not uncommonly in small specimens of *S. scombrus* off the west coast of Sweden, but was unable to find it in the larger fish taken in the early summer. He gives a minute description and excellent figures of the worm. Johnstone (1914) has also given a good, though diagrammatic, figure of its anatomy. Odhner describes the worm as occurring most commonly in paired cysts on the upper pharyngeal bones, but also in exceptional cases in cysts on the inside of the gill-covers and on the outside of the head, close behind the eye. About half the cysts examined by him contained two worms, the rest from three to seven. Johnstone describes the cysts as being most commonly situated "on the roof of the mouth beneath the pharyngo-branchials", but also sometimes on the basi-branchials, on the external surfaces of other parts of the gill-bars, or on the internal surface of the operculum. One cyst contained as many as sixteen worms. According to Dollfus (1926), he and Monod found cysts containing one, two, three or more worms in the mucosa of the mouth, palate and gills of *S. scombrus*, and also single unencysted worms under the transparent skin behind the eye.

Thus at least two authors record the same worm as occurring both inside the mouth and on the outside of the head, behind the eye. The writer has observed specimens in both situations in mackerel (*S. scombrus*) from the English Channel, but considers that they represent two different species. By far the commonest occurrence is to find a pair of cysts in the roof of the pharynx, at the anterior end of the pad which carries the upper pharyngeal teeth. The symmetrical position of these cysts suggests that they occupy a pair of organs normally present in the mackerel—in all probability a pair of lymphatic glands. A variable number of worms may be found in each cyst, and these vary considerably in size. They agree in all essential features with the descriptions given by Odhner and by Johnstone, and are considered to belong to the species *scombri* Taschenberg, 1879, *sensu* Odhner.

In a small percentage of the mackerel examined one or more elliptical yellowish bodies, about 3–7 mm. long and 1–1·5 mm. wide, were observed beneath the transparent outer skin of the head, behind the eye. These, on being dissected out, were found to be cysts containing from one to four worms closely resembling *Didymozoon scombri*, but differing from it in a number of respects. The worms are very tightly packed in the cyst. Moreover, the cyst-wall is relatively tough and the worms extremely fragile, so that in preserved material it is almost impossible to extract the worms without damaging them. Further, the same cyst often contains two or more worms so enormously different in size that it is very difficult to detect the small individuals and to separate them from the large, to which, when preserved, they may be firmly adherent. These difficulties, however, can be overcome by opening the cysts in the fresh condition, when the worms are usually quite readily separated.

The following is a description of the species occurring in these "facial" cysts, which it is proposed to name

Didymozoon faciale, sp.n.

The length of the worms (after mounting in Canada balsam) varies between about 0·71 and 16·3 mm. The largest individuals measure (when slightly flattened under cover-glass pressure) up to about 1·4 mm. in maximum width, the smallest only 0·08 mm. Specimens under 3 mm. in length are generally without eggs, and in most of them the female portions of the genital apparatus are undifferentiated. The testes, however, are generally well developed and functional. This was so even in a specimen only 1·1 mm. long (Fig. 2). While in one specimen 4·6 mm. long even the testes could not be made out, another measuring only 3 mm. in length already had fully-developed female organs and was producing eggs. In the smallest specimen seen, which was 0·71 mm. long, the testes appeared to be quite undifferentiated. Fig. 1 gives an idea of the variation in size which may occur among the worms in a single cyst. In some the disparity is even greater, a minute "male" worm little more than a millimetre long being found together with a fully-developed hermaphrodite individual measuring up to about 16 mm.

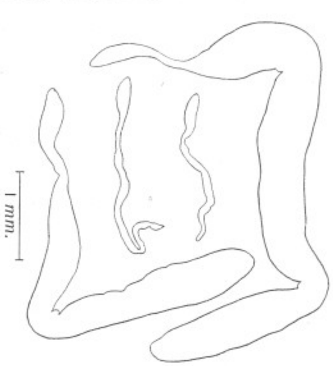

Fig. 1. *Didymozoon faciale*. Outlines of the four individuals from a single cyst, drawn to the same scale, to show relative sizes.

The anterior portion, or "forebody", is somewhat flattened dorso-ventrally and lanceolate in outline. It is joined by a narrower "neck" to the "hindbody", which is generally cylindrical. With increasing age the "hindbody" undergoes much more rapid growth than the "forebody", so that in a large worm there is a much greater difference in their relative proportions than in small specimens. The larger individuals, owing to their close confinement within the cyst, are generally bent sharply upon themselves in two places, so that the anterior and posterior ends tend to overlap.

At the anterior extremity there is a small oral sucker (Figs. 2, 3, 4, 5, *su*). This is oval or pear-shaped, instead of being subglobular, as in *D. scombri*. It is also very much smaller than in that species. It measures 0·04–0·08 mm. in length and 0·03–0·052 mm. in maximum width, its dimensions being roughly proportional to the size of the specimen.* The sucker is immediately followed by a small hemispherical pharynx (Fig. 5, *ph*), measuring about 0·018–0·024 mm. in diameter.† A narrow oesophagus connects the pharynx with the intestine, which at its anterior ends forms a wide tube running transversely (Figs. 2, 4). From this two caeca (*c*) run posteriorly as delicate, thin-walled tubes which are thrown into numerous short dorso-ventral loops, giving them a sacculated or moniliform appearance. The caeca are conspicuous only in the forebody, and, except in the youngest and smallest specimens, are difficult to detect in the hindbody, almost the whole of which is occupied by the genital apparatus. The excretory system has not been made out.

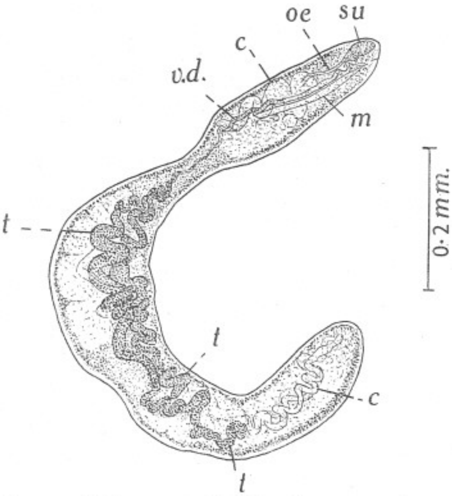

Fig. 2. *Didymozoon faciale*. Young specimen in which only the male organs are fully developed. *c*, intestinal caecum; *m*, metraterm; *oe*, oesophagus; *su*, sucker; *t*, testes; *v.d.*, vas deferens.

The arrangement of the genital organs is the same as in *D. scombri*. Ventrally to the oral sucker there is, in the medium-sized and larger specimens, a rounded muscular papilla (Figs. 3 and 4, *p*) on which the genital pore is situated. Running almost straight back from this papilla down the middle line of the forebody is the metraterm (Figs. 2, 3, 4, *m*), or terminal portion of the uterus. This is apparently the first part of the female genital apparatus to be differentiated, and is visible even in such a young specimen as that shown in Fig. 2. It has, for the greater part of its length, a rather stout coat of

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* In *D. scombri* Odhner (1907) found the diameter of the sucker to be 0·3–0·4 mm. From the scale of magnification it appears to have been about 0·47 mm. long and 0·53 mm. wide in the specimen figured by Johnstone (1914). In specimens examined by the writer it measures 0·21–0·6 mm. in length and 0·25–0·55 mm. in width. Johnstone gives the dimensions of the worms as 15–20 × 0·5–over 1 mm., Odhner as 25–35 × 1·2–1·75 mm. The writer has seen much larger specimens, one of which measured 55 mm. in length and 2 mm. in breadth when mounted in balsam.

† In the writer's specimens of *D. scombri* the pharynx has a diameter of 0·08–0·1 mm. It is difficult to detect in the larger specimens when mounted whole, as it appears to become hidden by a dense coat of cells, and also to become more intimately fused with the sucker. According to Odhner its diameter is 0·06 mm.; according to Johnstone's figure apparently about 0·14 mm.

circular muscles, but the muscles become sparser near the anterior end. Dorsally to the metraterm, and running roughly parallel to it, but with a more convoluted course, is the vas deferens (Figs. 2, 3, 4, *v.d.*). This also has a somewhat muscular wall, but is a much narrower and more transparent tube than the metraterm. Passing through the narrow "neck" of the worm, it divides just behind it into two vasa efferentia, each of which is continuous with one of the two long, coiled, tubular testes (Figs. 2, 3, *t*). In young specimens (Fig. 2) these occupy the greater part of the body. In older individuals (Fig. 3), however, owing to the great growth of the hindbody, they extend only about as far as the anterior third of the total length.

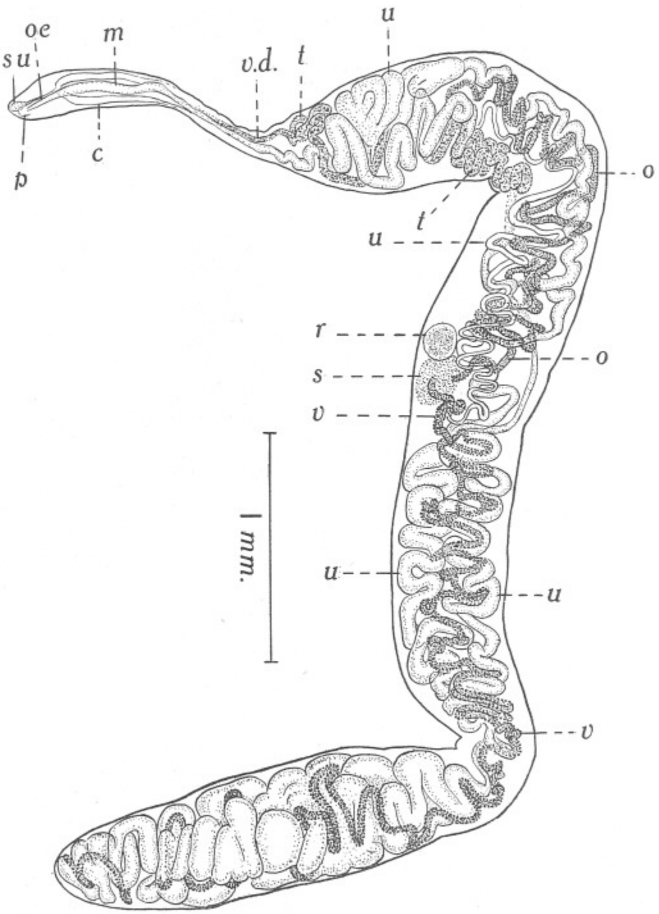

Fig. 3 *Didymozoon faciale*. Mature hermaphrodite individual. *c*, intestinal caecum; *m*, metraterm; *o*, ovary; *oe*, oesophagus; *p*, genital papilla; *r*, receptaculum seminis; *s*, shell-gland; *su*, sucker; *t*, testis; *u*, uterus; *v*, vitelline gland; *v.d.*, vas deferens.

The ovary (Fig. 3, *o*) and the vitelline gland (*v*) are both long, convoluted, tubular organs, the former beginning some distance in front of the posterior ends of the testes, the latter close to the hinder extremity of the body. They converge towards a point a little in front of the middle of the body, where they are connected with the oviduct, with which are also connected the "shell"-gland (*s*) and a well-developed and more or less globular receptaculum seminis (*r*). The uterus runs forward from the shell-gland complex as a much convoluted tube almost to the anterior end of the hindbody. Here it doubles back and runs to the extreme posterior end, whence it doubles forward and pursues a much convoluted course to about the level of the shell-gland complex. From this point it appears to straighten out somewhat, and its terminal portion forms the metraterm, as already described.

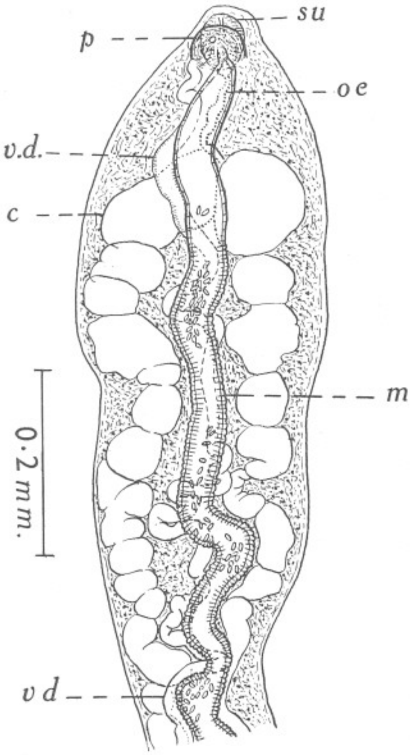

Fig. 4.

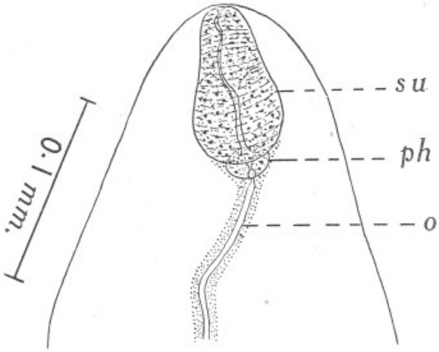

Fig. 5.

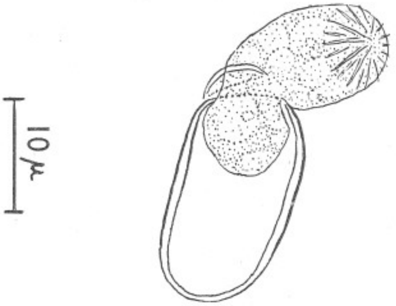

Fig. 6.

Fig. 4. *Didymozoon faciale*. Forebody of mature specimen; ventral view. *c*, intestinal caecum; *m*, metraterm *oe*, oesophagus (dotted outline); *p*, genital papilla; *su*, sucker; *v.d.*, vas deferens.

Fig. 5. *Didymozoon faciale*. Anterior extremity, showing *su*, sucker; *ph*, pharynx, and *oe*, oesophagus.

Fig. 6. *Didymozoon faciale*. Egg, with embryo escaping under pressure of cover-glass.

The eggs are exceedingly numerous and very small. Their shells are relatively thick and of a yellow colour, and are almost elliptical in shape. They measure about 0·018–0·02 × 0·011 mm.,[*] and have an operculum at one pole. In embryos liberated from the shells by cover-glass pressure (Fig. 6), it appeared possible to confirm an observation made by Wagener (in Lieberkühn, 1854) regarding a related species found in the flying-fish, *Exocoetus exsiliens*. Wagener describes and figures a crown of fine spines or hooks, "wie ein Tänienhakenkranz", round the "head" of the embryo. Under high magnifications the appearance of such a crown of spines was seen in the embryos both of *Didymozoon faciale* and of *D. scombri*. Owing to their minute size it was not possible to determine the precise form of these spines, or their number, but they appeared to be of two sizes, the longer and shorter spines alternating.

Taxonomy and Nomenclature

After a study of the literature the generic name *Didymozoon* Taschenberg, 1879, has been provisionally adopted for the species described above. Odhner (1907) designated the species *scombri* as type of *Didymozoon*, and the genus has been accepted in this sense by Dollfus (1926) and other authors. Ishii (1935), on the other hand, refers *scombri* to *Nematobothrium* v. Beneden, 1858,[†] at the same time retaining *Didymozoon* Taschenberg (which he unnecessarily emends to *Didymozoum*) as an independent genus, with *D. sphyraenae* Taschenberg as its genotype.[‡]

According to Stiles & Hassall (1908), Taschenberg, in erecting the genus *Didymozoon*, was merely renaming the genus *Wedlia* Cobbold, 1860, and the type of both these genera is *Wedlia bipartita* (Wedl, 1855). This species is the first mentioned under the genus *Didymozoon* by Taschenberg, who renames it *D. thynni*. Moreover, he quotes Cobbold's reference and mentions that that author had referred this species to *Wedlia*. Poche (1926), however, rejects the suggestion of Stiles & Hassall, and points out that Taschenberg neither expressly states that he is renaming *Wedlia* nor admits that *Wedlia* and *Didymozoon* are synonymous. It is true that Taschenberg does not definitely designate a genotype of *Didymozoon*, and unfortunately Cobbold (1860) also fails to make a definite designation in the case of *Wedlia*, though from his text it is quite evident that he regarded *bipartita* as the typical species.

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[*] The eggs of *D. scombri* are slightly smaller, measuring 0·016–0·0175 × 0·01–0·0105 mm., or, according to Odhner, 0·015 × 0·01 mm.

[†] Within the genus *Nematobothrium* Ishii proposes two new subgenera, *Benedenozoum* and *Maclarenozoum*, placing *scombri* in the former. Article 9 of the International Rules of Zoological Nomenclature lays down that "if a genus is divided into subgenera, the name of the typical subgenus must be the same as the name of the genus". Hence the subgenus *Benedenozoum*, which contains the genotype of *Nematobothrium*, is incorrectly named, and should be called *Nematobothrium*.

[‡] Yamaguti (1934) also defines *Nematobothrium* and *Didymozoon* as distinct genera, and gives *D. auxis* Taschenberg as "type by elimination" of the latter.

Didymozoon cannot, therefore, be disposed of without question as a synonym of *Wedlia*.*

The question whether *Didymozoon* (*sensu* Odhner) and *Nematobothrium* are congeneric cannot, as it seems to the writer, be determined without a fuller knowledge of the morphology of *N. filarina* v. Beneden, the type of *Nematobothrium*. v. Beneden's (1858, 1861) description of this form is admittedly very incomplete, and the species does not appear to have been redescribed. v. Beneden was unable to find even an oral sucker or an intestine, whereas some of the species attributed to *Nematobothrium* by later authors possess not only these organs but also a ventral sucker.

Although Ishii (1935) places *Nematobothrium* and "*Didymozoum*" in distinct subfamilies, his diagnoses of these two genera are almost identical, and the distinctions between them and between the subfamilies appear to be based on extremely unsatisfactory characters. The diagnosis of *Nematobothrium*, however, is necessarily based mainly on species other than the genotype, while "*Didymozoum*", as we have seen, is quite different from the *Didymozoon* of Odhner.

Yamaguti's (1934) definition of *Didymozoon* appears to be based mainly on the characters of a new species (*D. minor*) described by him, and in any case his designation of *D. auxis* Taschenberg as genotype is inadmissible in view of Odhner's earlier designation of *D. scombri* (*vide* International Rules of Zoological Nomenclature, Art. 30, II, *g*). The same remark applies to Ishii's designation of *D. sphyraenae*.

In view of these considerations it seems best to retain *Didymozoon*, *sensu* Odhner, as distinct from *Nematobothrium* v. Beneden, until more conclusive evidence is brought forward to show that these genera are identical. The new species here described is unquestionably congeneric with the *Didymozoon scombri* of Odhner, and is therefore referred to *Didymozoon*.

For the material on which this paper is based the writer is greatly indebted to Mr P. G. Corbin, of the Laboratory of the Marine Biological Association, Plymouth, and to Miss Miriam Rothschild. For some excellent preparations of *Didymozoon scombri* thanks are due to Mr L. A. Harvey, of University College, Exeter; and for a remarkably good preparation of *D. faciale* the writer wishes to thank Mr W. J. Rees, of the Plymouth Laboratory. The specimens of both species collected by Mr Corbin and by Miss Rothschild came from mackerel landed at Plymouth and at Newlyn in November 1936 and in February, March, May, October and November 1937.

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* *Wedlia* is reduced by Ishii (1935) to a subgenus of *Köllikeria* Cobbold, 1860, the only other subgenus being named *Köllikerizoum*. This action again contravenes Article 9 of the International Rules, since there is no subgenus *Köllikeria*. The genotype of *Köllikeria* (*K. filicollis*) is placed in *Köllikerizoum*, which name consequently must be replaced by *Köllikeria*. On similar grounds Ishii's subgenus *Atalosparganum* should be replaced by *Atalostrophion* MacCallum, 1915.

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ON THE SEASONAL ABUNDANCE OF YOUNG FISH. V. THE YEAR 1937

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–4)

The present report continues the observations on the seasonal abundance of the pelagic young of teleostean fish in the plankton off Plymouth (Russell, 1937) and gives the results for the year 1937. These results are published in the same form as in previous reports. The dates on which collections were made with the 2-metre stramin ringtrawl are given in Table I and the monthly average catches of the young fish per half-hour haul in Table II. In Fig. 1 is given the curve for the average catches for each fortnight of all young fish, excluding clupeids, and superimposed upon this the corresponding curve for the average catches over the period 1930–1934 inclusive.

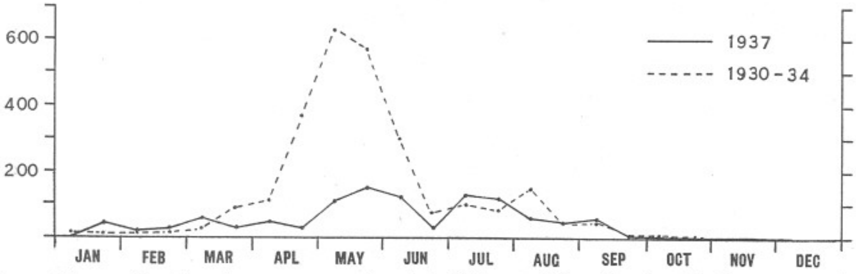

Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2-metre ring-trawl for each fortnight for all young fish, excluding clupeids, in 1937 (——) and the same averaged over the period 1930–1934 inclusive (-----).

The results for 1937 are almost a repetition of those for 1936. Once more there was an almost complete absence of the usual peak of the young of spring spawners and there were again slightly higher numbers of the young of summer spawners. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive, excluding clupeids, was 174 in 1937 as against 115 in 1936. These numbers were mainly made up by *Arnoglossus* sp., *C. trachurus*, *C. rupestris*, *S. scombrus*, and *B. gattorugine*. There thus appears to be a gradual swing over to better conditions for summer spawners in contrast to spring spawners the significance of which is not yet apparent.

The sums of the average monthly catches of the more important species for the year 1937 divided by the corresponding average sums for the period

1930–1934 inclusive are given below. In the second column are the figures for the best year divided by the worst year from 1930 to 1937 inclusive.

	1937 / Av. 1930–34	Best / Worst
G. merlangus	0·19	23·6 ('32/'36)
G. minutus	0·15	40·3 ('31/'35 & '36)
Onos spp.	0·40	13·0 ('30/'35)
Arnoglossus spp.	1·09	11·5 ('31/'35)
S. norvegicus	0·14	10·7 ('32/'37)
P. limanda	0·35	14·0 ('31/'35)
P. microcephalus	0·04	41·0 ('32/'37)
S. variegata	0·24	6·5 ('32/'37)
Callionymus spp.	0·28	3·8 ('30/'37)
S. scombrus	1·68	11·2 ('30/'35)
Gobiid spp.	0·02	119·0 ('30/'37)

The year 1937 has been the worst during the period 1930–1937 for *S. norvegicus*, *P. microcephalus*, *S. variegata*, *Callionymus* spp., and Gobiid spp. Except for *Callionymus*, however, the numbers of these species are becoming so low, even in some species reaching unity, that undue significance should no longer be placed on high values for the calculated figures for best divided by worst years.

The numbers of *Callionymus* have fallen from an average of 548 for the period 1930–1934 to only 155 in 1937. This decrease is very noticeable in the catches because young *Callionymus* usually bulk so largely that they are a characteristic feature of Plymouth plankton. But in spite of their decrease in actual numbers their proportionate representation is still 0·28 of the catches of all young fish, excluding clupeids, as compared with 0·38 for the period 1930–1934. The fact that this, the most abundant species, still forms approximately the same proportion of the young fish population indicates that the decrease in the numbers of young fish during the last few years has been due to some factor adverse to all species of fish indiscriminately. Indeed, if this decrease had been due to an overfishing of the reproducing stock it might have been expected that there would have been a corresponding increase in the proportionate numbers of the young of those species of fish which are not taken by the trawl. The gobies for instance might have benefited, whereas actually their numbers have dwindled to insignificance. This adds further support to the argument that it is the decrease in the amount of available phosphorus in the water which is the root cause of the poor survival of young fish.

In 1937 both *Arnoglossus* and *Scomber* were slightly above the average for 1930–1934, but the latter came nowhere near the high figure of 344 recorded for 1926. A noteworthy feature in 1937 was the unusual abundance of the young of *Serranus cabrilla* of which a catch of 24 was made on September 1.

The results for all species of young fish for the last eight years are summarized in Fig. 2. This figure shows the yearly averages for total young fish (excluding clupeids), for the young of summer spawners, and for total young fish less the young of summer spawners. It shows clearly how the drop in numbers after 1930 occurred first among the young of summer spawners, and that the decrease in the numbers of other species, mainly spring spawners, started later, reaching a very low level in 1935 at which it has remained while the summer spawned fish have slightly improved.

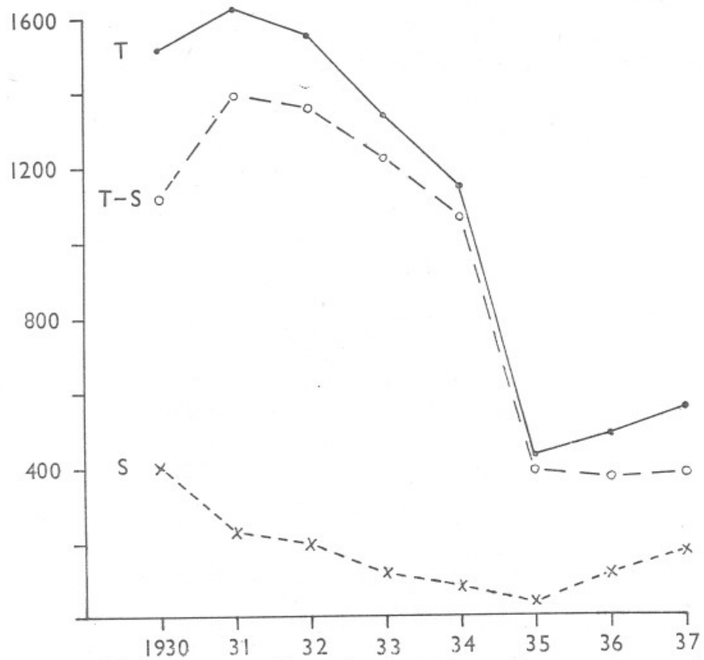

Fig. 2. The sums of the average monthly catches for each year from 1930 to 1937 in half-hour oblique hauls with the 2-metre ringtrawl for: *T*, total young fish (excluding clupeids); *S*, the young of summer spawners; and *T–S*, total young fish less the young of summer spawners.

In previous reports it was suggested that we must await a fresh inflow of water from the south of Ireland into the Channel to replenish the supply of phosphorus before there will be a return to conditions for good survival of young fish. It seemed most likely that this replenishment will come from the "elegans" water. So far there are no indications of a return to the conditions of 1930 when "elegans" water predominated off Plymouth. Figs. 3 and 4 give data on the occurrence of plankton indicators in the catches off Plymouth in 1937 in continuation of those given in the last report (1937, Figs. 2 and 3). The year 1937 was very similar to 1936. The numbers of both species of *Sagitta* were extremely low until August, when *S. setosa* became abundant, and

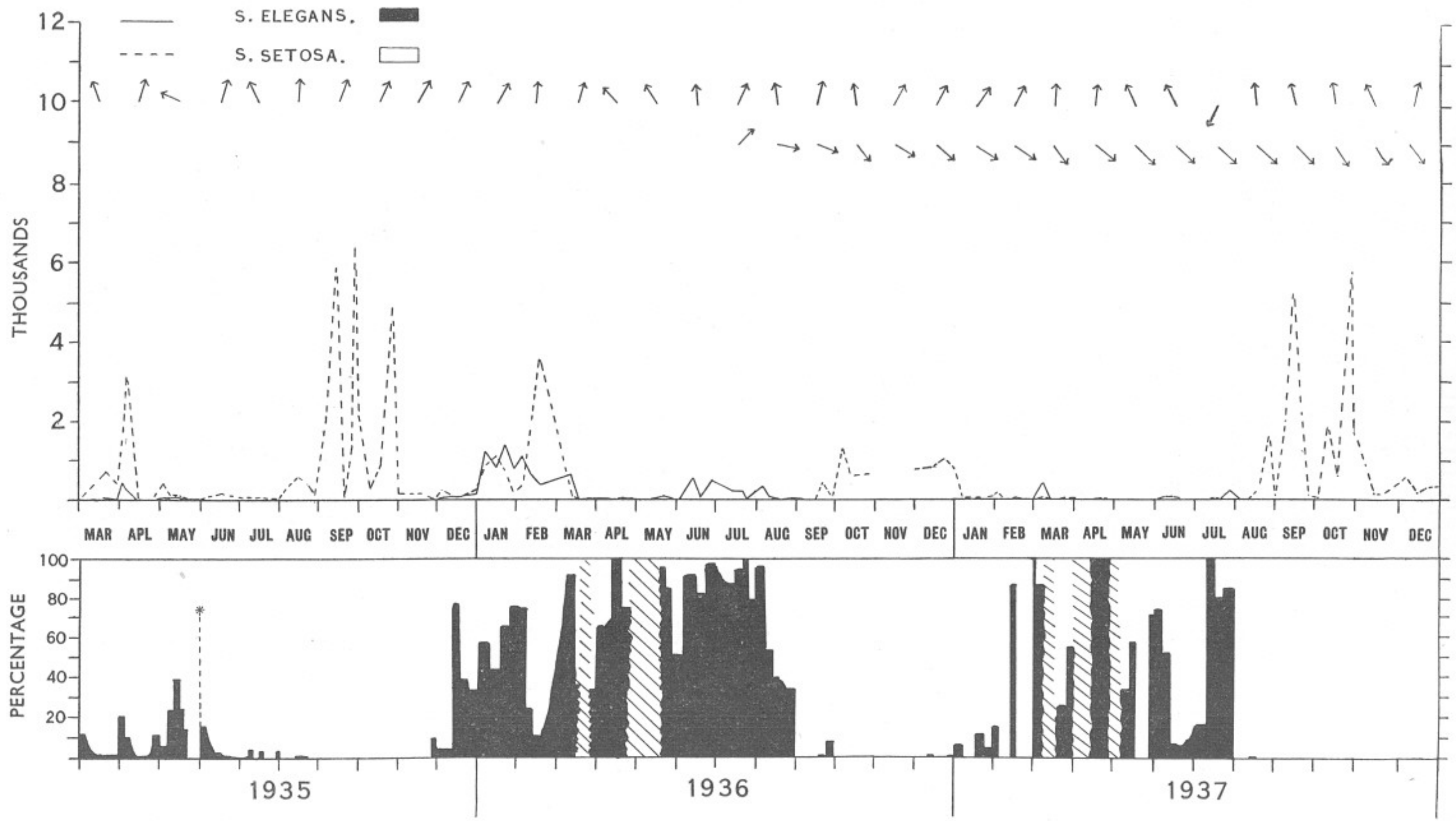

Fig. 3. Above, curves showing the actual abundance of *S. elegans* (——) and *S. setosa* (------) in half-hour oblique hauls with the 2-metre ringtrawl during the period March 1935 to December 1937.

Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched.

At the top of the diagram the arrows indicate the mean directions (true) of the flow of water past the Varne Lightship (above) and the Royal Sovereign Lightship (below) from data kindly supplied by Dr J. N. Carruthers. (Continued from Russell, 1937, p. 681, Fig. 2.)

what *S. elegans* there were were much fewer than in 1936. The siphonophore *Muggiaea atlantica* was again abundant in the later summer and autumn. As in 1936 the low numbers of *S. elegans* in the first half of the year were accompanied by the appearance of unusual species. On February 24 another specimen of the scyphomedusa *Discomedusa lobata* was caught and several *Pelagia* were present in April. These two species were recorded in 1936 for the first time off Plymouth. In addition, in 1937 one specimen of the copepod *Rhincalanus nasutus* was taken on February 9; this is the first time the species has been recorded off Plymouth. It is perhaps also of interest that on February 23 the *Salpa* landed a catch with many small hake.

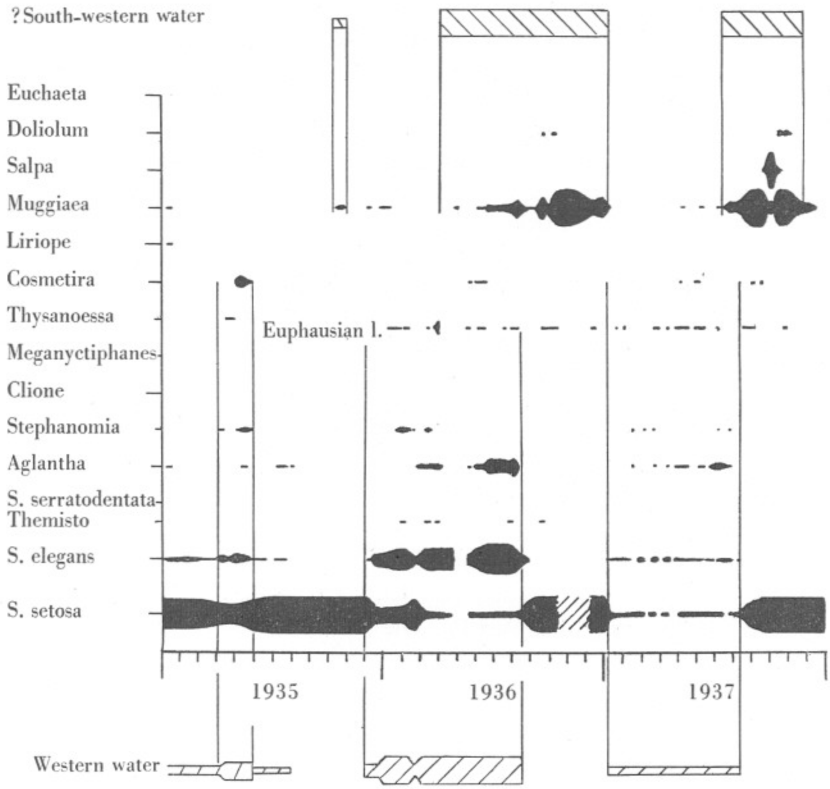

Fig. 4. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the years 1935, 1936 and 1937. (Continued from Russell, 1937, p. 682, Fig. 3.)

The *Muggiaea* species were *M. kochi* up to January 1937, and thereafter *M. atlantica*, the salps were *S. fusiformis*, and the doliolids *D. nationalis*.

On September 20 *Salpa fusiformis* appeared in the catches and had disappeared by October 19. Although the salps were not found off Plymouth on

September 13 they were present on the next day off Looe. This is the first appearance of salps off Plymouth since 1932.

As in 1936 also, pilchard eggs were a distinct feature in the plankton in 1937. They were present continuously from April to December, the approximate numbers on the different dates being as follows: April 14 (280), 26 (2320); May 3 (2360), 10 (37, 300), 19 (1000), 24 (2800), 31 (4200); June 6 (480), 14 (30,000), 18 (19,220); July 5 (14,960), 13 (7920), 19 (few), 26 (few); August 4 (1220), 11 (880); September 1 (1000), 7 (few), 13 (few), 20 (few), 27 (90); October 4 (100), 11 (320), 26 (few); November 1 (2420), 8 (300), 15 (670), 19 (20); December 6 (4), 13 (1), 31 (11).

The continuous appearance of such large numbers of pilchard eggs under conditions when the numbers of both *S. elegans* and *S. setosa* are conspicuously low deserves special mention, as it appears possible that we have here a body of water distinct from either of those characterized by the presence of *S. elegans* or *S. setosa*. If this be so, or whatever be the origin of this water, it is proposed that it should for the time being be called "pilchard" water, since it is evident that it is well worth watching in the future for the conditions that favour this great production of pilchard eggs off Plymouth.

In spite of the large number of eggs there are no indications in the ring-trawl catches that the young were abnormally abundant. The possibility that the low numbers of *S. setosa* may also be owing to their poor survival must not be lost sight of, but we do not know how abundant they were in the eastern half of the Channel.

REFERENCE

RUSSELL, F. S., 1937. The seasonal abundance of the pelagic young of teleostean fishes in the Plymouth area. Part IV. The year 1936, with notes on the conditions as shown by the occurrence of plankton indicators. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 679–86.

Table I. Dates on which Collections were made, 1937

All 2 miles east of Eddystone unless otherwise stated

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
6*	2	1	6	3	6	5	4	1	4	1	6
12*	9	8	14	10	14	13	11	7	11	8	13
20	16	19‡	19§	18	18	19	18	13‖	19	15	20
27†	24	23	26	24		26	25	20	26	19¶	31
		30		31				27			

* L4–L5.
† Bolt E × S: Stoke Pt. N.
‡ L3–L4.
§ Off Revelstoke, 25 fathoms.
‖ 4–5 miles south of Breakwater.
¶ 3 miles west of Rame.

TABLE II. AVERAGE MONTHLY CATCHES OF POST-LARVAE PER HALF-HOUR

Oblique hauls with 2-metre Ringtrawl, 1937

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total Young Fish	37	116	430	56	182	150	207	60	40	40	9	1	1328
Ditto, less Clupeids	21	22	39	36	132	89	124	53	36	2	2	1	557
All Clupeid spp.	17	94	391	20	50	58	83	7	5	39	6	1	771
Clupea harengus	3	1	1	..	..	..	..	..	..	..	..	..	5
Gadus pollachius	..	..	+	1	+	+	..	..	..	..	..	..	1
Gadus merlangus	..	..	2	5	21	7	2	..	..	..	..	..	37
Gadus minutus	..	..	10	2	1	1	+	..	..	..	..	..	14
Gadus luscus	..	+	+	..	1	+	+	+	..	+	1	1	3
Gadus callarius	..	+	..	..	..	..	..	..	..	..	..	..	+
Onos spp.	..	..	1	1	13	3	2	1	..	..	..	..	21
Molva molva	..	..	..	..	+	..	..	..	..	..	..	..	+
Merluccius merluccius	..	..	..	..	..	..	..	+	..	+	..	..	+
Raniceps raninus	..	..	..	..	..	..	+	..	..	..	..	..	+
Capros aper	..	..	..	..	..	..	..	1	+	..	..	..	1
Zeus faber	..	..	..	..	..	..	..	..	..	+	..	..	+
Arnoglossus spp.	..	..	..	..	..	+	17	9	10	+	..	..	36
Rhombus spp.	..	..	..	..	..	+	2	3	2	..	..	..	7
Scophthalmus norvegicus	..	..	..	..	3	4	1	..	..	..	..	..	8
Zeugopterus punctatus	..	..	..	+	1	..	..	..	..	..	..	..	1
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes limanda	..	..	+	6	9	4	..	..	..	..	..	..	19
Pleuronectes flesus	..	..	+	1	..	..	..	..	..	..	..	..	1
Pleuronectes microcephalus	..	..	..	..	+	1	..	..	..	..	..	..	1
Solea vulgaris	..	..	1	2	..	..	..	..	..	..	..	..	3
Solea variegata	..	..	..	3	7	8	1	1	..	..	..	..	20
Solea lascaris	..	..	..	..	..	..	..	..	+	..	..	..	+
Solea lutea	..	..	..	..	+	..	+	..	..	..	..	..	+
Serranus cabrilla	..	..	..	..	..	..	..	+	5	..	..	..	5
Caranx trachurus	..	..	..	..	..	..	3	8	6	+	..	..	17
Mullus surmuletus	..	..	..	..	..	..	..	+	..	..	..	..	+
Morone labrax	..	..	..	..	..	..	..	..	..	..	..	..	..
Ammodytes sp.	21	21	23	4	..	..	3	3	1	..	1	..	77
Ammodytes lanceolatus	..	..	..	1	4	3	1	1	..	..	..	..	10
Cepola rubescens	..	..	..	..	..	..	1	..	1	..	..	..	2
Callionymus spp.	..	..	..	10	69	46	12	15	2	+	1	..	155
Labrus bergylta	..	..	..	..	..	+	..	..	..	..	..	..	+
Labrus mixtus	..	..	..	..	..	+	..	..	..	..	..	..	+
Ctenolabrus rupestris	..	..	..	..	..	3	17	1	..	..	..	..	21
Crenilabrus melops	..	..	..	..	..	..	2	..	..	..	..	..	2
Centrolabrus exoletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachinus vipera	..	..	..	..	..	..	2	2	2	..	..	..	6
Scomber scombrus	..	..	..	..	5	24	5	3	..	..	..	..	37
Gobius spp.	..	..	..	..	+	+	1	..	+	..	..	..	1
Lebetus scorpioides	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius ocellaris	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	1	2	..	..	..	..	..	3
Blennius gattorugine	..	..	..	..	..	3	33	+	+	..	+	..	36
Chirolophis galerita	..	1	..	..	..	..	..	..	..	..	..	..	1
Agonus cataphractus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	..	+	+	..	..	..	..	..	+
Cottus sp.	+	+	2	1	..	+	..	..	..	..	..	..	3
Liparis montagui	..	..	..	..	..	..	..	..	..	..	..	..	..
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	+	..	+	..	..	..	..	..	..	+

THE ECOLOGY OF THE TAMAR ESTUARY

I. INTRODUCTION

By P. H. T. Hartley, B.Sc. and G. M. Spooner, M.A.

From the Plymouth Laboratory

(Plate XVIII)

During 1936 and 1937 extensive physical and faunistic studies of the Tamar Estuary were made by several workers at the Plymouth laboratory. These investigations, though conducted independently and with different immediate aims, proved to have considerable bearing on one another, and each worker benefited by occasions for co-operation. As the work proceeded it became clear that one of the most important aspects of each investigation was the bearing it had on the balance of life in the estuary as a whole. It was decided to publish the results of these studies in a series of papers in which each contributor should lay due emphasis on data having possible bearings on the problems studied by the others, so as to present as complete a picture as possible.

Studies have been made of salinity, temperature, penetration of daylight, macro- and micro-fauna of the intertidal zone, the sessile flora and fauna of the buoys, the fishes and their food, and the birds which frequent the flats and channels. Other studies are contemplated. In the work on light penetration and on quantitative estimates of the fauna of the mud-flats, no comparable data have hitherto been procured in this country.

The Tamar is the largest of the rivers which flow into the west end of Plymouth Sound. It is tidal for nearly 19 miles (30 km.) of its course. Rather over 3 miles (5·5 km.) from the sea it is joined by the River Lynher to form the Hamoaze, an estuary common to the two rivers. About 6 miles (9·5 km.) from the sea it is joined by its main tributary, the River Tavy. The Tamar flows over geological formations of Devonian and Carboniferous slates, shales, and grits. The Tavy flows over the same formations but rises among the peat bogs overlying the Dartmoor granite. The Lynher and its tributary, the St Germans River, also rise on granite, but they run for most of their length over Carboniferous rocks.

Estuarine Deposits

Among the more conspicuous features of the whole estuarine area are the mud-flats, often of considerable extent, which border the river channel. Mud has been so extensively deposited as to constitute the predominating element of the bottom in the intertidal zone. Even in the lower reaches of the estuary the deposits extend well up into the high-water zone, impregnating the "shillet" or stony ground which is characteristic of long stretches of shore-line. There is a marked contrast with the conditions in the Kingsbridge Estuary, where a zone of clean stones and gravel, bearing rich growths of algae, extends down to below high-water neaps. In the Tamar and its branches rocky outcrops clear of silt at the higher levels are relatively infrequent, but occur as far up the river as Neal Point. As the river mouth is approached the mud deposits do not give place to sand, as in neighbouring estuaries such as the Erme and Avon.

As may be seen on the accompanying plan (Plate XVIII), the intertidal areas occupy a large fraction of the estuary bed, and by far the greater part of these consist of the deposits referred to. They fill all the inlets and irregularities in the contours of the shore-line, tending to confine the main flow of the river and tidal streams to a central channel. Owing to their large area and to the abundance of the fauna for which they provide a habitat, these mud-banks acquire considerable importance in the ecology of the estuary; and while it would be out of place here to enter into details of their physiography, certain general features may be pointed out.

It may be noticed that the contours of the mud-banks are rarely such that a cross-section of the estuary bed shows an even decrease of level from the shore towards mid-channel; the banks tend to flatten out and acquire a steeper slope on their outer face. The levelling process has often gone so far that in any place a large proportion of the surface of the mud-bank will lie between certain narrow limits of vertical height. Since change in vertical height implies change in the amount of exposure to the air on the ebb tide, or of exposure to varying salinities on the flood, this factor is important in faunistic studies. For brevity we may refer to those regions of the mud-banks where the gradient is at a minimum as "flats". As a general rule not only do the flats include a considerable fraction of the total area of a bank, but also, as they are apparently usually subjected to least disturbance from currents, they provide the most favourable habitat for the mud fauna. Consequently it is important to note, in any area, the levels at which the flats occur.

In the first place it emerges that though, where the estuary is broad, the flats may extend well below the permanent water channel (as off West Muds, and at the junction of the Tavy), they are more usually mainly or entirely intertidal. Secondly, as the estuary is ascended, and as the rock bed of the estuary rises, so rises the average level of the mud-flats. One effect of this is that an increasing proportion of the intertidal zone is uncovered at half-tide. In many places the approximate level of the half-tide line has been ascertained and is shown on the plan (Plate XVIII). Both the estuaries of the Tamar and Tavy above their junction show this phenomenon fairly diagrammatically, while smaller branches such as St John's Lake and Millbrook Lake provide excellent examples in miniature. Above a certain point the area between half-tide and the channel comprises a nearly uniform narrow zone with a relatively steep gradient; while the greater part of the mud-bank lies above, with a lesser gradient which varies with the breadth of the tidal zone. A great proportion of the fauna of these mud-banks is thus saved from the low salinities which prevail on the ebb tide. Also, as the river is ascended, birds have increasing opportunities over fish as predators of the mud fauna.

Another aspect of the up-river rise of the level of the mud-banks is that, unless currents interfere, mud is more freely deposited near high-water springs. As a result the substratum in the zone between high-water springs and neaps becomes increasingly favourable, where the gradient permits, for the development of saltings. The salting flora, of which *Salicornia* is the pioneer, is able to establish itself on flat stretches below the level of ordinary tides, where it is uncovered for no more than two or three consecutive days. Up river all the flatter (and so broader) ground between ordinary high water and springs is occupied by saltings. It is common knowledge that once saltings have become established they accelerate the deposition of silt, and so rise more rapidly than the adjoining areas of clear mud. At the same time erosion of the edges produces an increasingly abrupt transition line between the clear mud and the salting, the boundary of which comes to be marked by a "salting cliff". Various stages in this process may be seen passing from Salt Mill to Egypt Salt Marsh to Clifton. In the latter vicinity the salting cliff attains the height of 1 m. In the upper reaches of the estuary the top of the salting cliff approximately coincides with the level of ordinary tides (+1·7 m. O.D.). The greater part of the saltings on the Tamar above Cargreen, and on the Lynher above Sheviock Wood, are uncovered for the whole week of neap tides.

Saltings tend to fill up all the irregularities in the contours of the spring-tide shore-line. This natural, but slow, process of land reclamation has in some places been completed artificially by the construction of embankments and drainage ditches (at Landulph, on the north side of Kingsmill Lake; and opposite Pentillie). A large inlet cut off by Ernesettle railway embankment has also been reclaimed during the past century.

In the upper reaches the river is in many places bounded by steep slopes. The mud-banks here are narrower, but still show an increasing gradient on their outer face. For considerable stretches steep hanging woods extend to the river's edge. In winter great quantities of sodden leaves accumulate in the river, and are deposited in the mud on the inner sides of curves near low-water mark, as well as along the channel in deeper water.

When a winter flood is beginning to decrease a layer of fine, sticky, grey mud, locally called "slurry", is deposited on the flats, and lies there until scoured away by the next spring tides. This may be responsible for temporary fluctuations in the level of certain flats.

In general the mud-banks appear to have considerable stability, and their growth, below the level of saltings at least, appears to be extremely slow. It is difficult to detect any appreciable changes during recent years. Signs of growth might be expected in a situation such as the east shore above Saltash, where a railway embankment raised from a level lying below half-tide has provided a new shore-line. The survey of a traverse in 1937 can be compared with the Admiralty Chart surveyed in 1894. Though a significant difference is found, it cannot be considered great. The bank appears to have risen nearly a metre in the centre, but scarcely at all on the face of the embankment. The result is that the bank rises somewhat more steeply from the river, is more level on its main expanse, but still remains well below the half-tide level.

The consistency of the mud deposits may be described as "soft", as contrasted with that of stiffer muds which contain a large admixture of fine sand. Progress over the banks is often difficult, a man usually sinking above the ankles at each step, and often to the knees. Surface samples from different situations vary most in the materials which are mixed with the silt. Valves of mollusc shells are almost always present, sometimes comprising the main bulk of the deposit. Vegetable residues ranging from very finely divided shreds to whole leaves and pieces of twig are always present, though in extremely variable quantities. But there is a marked absence of admixture of sand particles, and gravel is only obtained from sievings of samples taken near high water in the lower reaches. Thus the more solid components of the mud deposits consist almost entirely of valves of mollusc shells and their fragments. *Cardium edule*, *Scrobicularia plana*, *Peringia ulvae*, and *Littorina littorea* are the main species concerned. Their abundance is sometimes such that they form a conspicuous feature of the landscape, as they lie thickly strewn on the surface of the flats, or accumulated in a mass along the course of drainage channels.

Depth of the Channel and Tidal Range

In the harbour area (Hamoaze) the river channel attains a considerable depth, attaining 37·8 m. (124 ft.) near Devil's Point. The depth steadily decreases northward. Beyond 5 km. from the mouth only two small depressions exceed 15 m. (49 ft.). The Lynher shallows to a maximum of 5 m. at the point where it widens, and to the order of 1 m. at Sheviock Wood. The main river shallows rapidly above Saltash Bridge, and above the junction of the Tavy only just exceeds 5 m. in two places. At Cargreen there is a slight indication of a decrease in average tidal fall (see Table II), but this does not become pronounced until the bend in the river above Clifton. However, at Pentillie Quay, 16·5 km. from the mouth, it is only 0·62 m. less than at Devonport. The subsequent rise of the river bed relative to sea-level is very gradual in the winding Tamar, and the influence of the tide does not die out until 30 km. from the mouth. The bed of the Tavy, however, rises much more quickly. Even at Bere Ferrers it has apparently risen above Chart datum. Tidal influence soon disappears after the narrowing of the river at Lopwell, at some 17 km. from the mouth.

The depth of the channel in the harbour area ensures a strong tidal scour of the lower reaches of the estuary, and checks the encroachments of the mud-banks. Dredging operations help in the same direction, and there has apparently been little change in the bed of the Hamoaze in recent years. However, from the junction of the Lynher to Saltash an appreciable shallowing has taken place. In the upper reaches, too, the local watermen say the channel is becoming shallower. They attribute this to the fact that small paddle steamers no longer run between the villages along the shores. The churning of the paddle wheels may well have artificially affected the depth of the channel at some points, but noticeable changes subsequent to the removal of this influence are more likely to involve a return to a normal equilibrium than a renewal of a progressive silting.

The data relating to the tide levels are given in Table I. It will be observed that the mean range of tide is 4·73 m. (15·52 ft.) for spring tides, and 2·34 m. (7·65 ft.) for neaps, extremes in 1937 being 5·55 and 1·44 m. respectively. Table II gives the relative tidal range at seven positions in the tidal area, following the Channel Pilot.

TABLE I. TIDAL LEVELS AT DEVONPORT IN RELATION TO ORDNANCE SURVEY DATUM

	Metres	Feet
Highest predicted tide 1937	+2·53	+8·3
Mean high-water springs	2·22	7·28
Mean high-water ordinary tides*	1·70	5·58
Mean high-water neaps	1·17	3·83
Lowest predicted high tide 1937	0·70	2·3
Mean sea-level	0·22	0·73
Land Survey (Ordnance) Datum	0·0	0·0
Mean tide, Devonport	−0·08	−0·27
Highest predicted low tide 1937	−0·77	−2·52
Mean low-water neaps	−1·165	−3·82
Mean low-water ordinary tides*	−1·82	−6·00
Mean low-water springs	−2·51	−8·24
Admiralty Datum	−2·566	−8·42
Lowest predicted tide 1937	−3·02	−9·9

* The high- and low-water contours are inserted on the plan (Plate XVIII), following the practice of Ordnance maps.

TABLE II. RELATIVE TIDAL RANGES AT SPRINGS

Position	Distance from mouth in km.	Tidal range	
		Metres	Feet
Devonport Dockyard	3	4·7	15·5
Saltash, River Tamar	6·8	4·6	15·0
Cargreen, River Tamar	11	4·5	14·75
Pentillie, River Tamar	16·5	4·1	13·5
Calstock, River Tamar	22	3·8	12·5
Warleigh Quay, River Tavy	10·5	4·4	14·5
Maristow, River Tavy	14	2·6	8·5

There is considerable eddying of the tidal stream within the river. Close inshore there is a current running in the opposite direction to the set of the tide—the so-called "eddy tide". When much fresh water is coming down, the flood tide will move up on one side of the river before its influence reverses the direction of the surface flow upon the other. The two bodies of water may be distinguished by the line of floating leaves and debris where they meet and by the muddiness of the fresh water. The upward flow of the rising tide is first felt along the bottom of the river.

A southerly gale will choke back the tide in the estuary so that the water level at the slack of the ebb may be several feet above that predicted. When the next rising tide drives in before the storm, considerable flooding may take place. A northerly gale will cause a stronger ebb than usual and a depression of high-tide level.

The greatest speed of the tidal stream within the harbour is 2¾ knots (Channel Pilot).

RAINFALL

Along the valleys of the Tamar and its tributaries the mean annual rainfall is from 950 to 1150 mm. per annum: but the drainage area lies between two of the wettest places in the west of England—Dartmoor and the Cornish moors. At Princetown, on Dartmoor, the normal rainfall is 2079 mm. per annum, and at Altarnun on the Cornish side, 1503 mm. In Table III is shown the rainfall at Plymouth near the mouth of the river (normal annual rainfall: 933 mm.) and at Princetown.

TABLE III

	Plymouth			Princetown		
Months	Normal	1936	1937	Normal	1936	1937
Jan.–Mar.	233	388	431	568	612	941
Apr.–June	166	87	189	339	218	332
July–Sept.	213	254	126	439	622	324
Oct.–Dec.	321	199	304	733	604	411

During the first three months of both years the rainfall was greatly in excess of the normal. In July 1936, the rainfall was greater than normal and floods of thick, brown water came down from the moors. The rest of the summer of 1936 and the summer of 1937 were drier than usual.

HUMAN ACTIVITIES

A small and diminishing population of fishermen work in the estuaries of the Tamar and Lynher. Large seines for salmon and sprats are used, and a modified shore-seine, the "Saltash Tuck Seine", is used for the capture of flatfishes. In the autumn, herrings are caught in drift-nets. Motor boats from Plymouth trawl for prawns in the harbour area, and some shrimps and prawns are taken in hand-nets during the summer. On the flats of West Muds winkles and cockles are gathered; cockle beds outside Skinham Creek are also picked over occasionally. Mussels from the river are not saleable, and the oyster beds (near Saltash) are worked out. After December 1937, the sale of all shellfish from the estuaries was prohibited by the local medical authorities. Only one professional punt-gunner now works in these waters, and there is very little shore-shooting. Above Hole's Hole rotten leaves are collected from the flats for use as manure.

The eastern side of the Hamoaze from Devil's Point to Bull Point is covered by the quays and buildings of Devonport Dockyard. There is no pollution of the rivers by commercial effluents. A number of sewers release crude sewage into the channels: much of this matter is at once eaten by the mobs of gulls which haunt the outfalls. Unlike certain other rivers which flow off Dartmoor and the Cornish moors, those in this watershed never carry the milky white suspension derived from China-clay washings. Pollution by crude oil residues, as far as it can be determined by the presence of oiled sea-birds or stranded clots, is not found in the estuary. Small quantities of lighter oils are constantly being discharged in the harbour area from motor-driven vessels, but it is extremely questionable whether these have any harmful effects, and even if proof of such is ever obtained, the extent to which it occurs is very probably negligible.

PREVIOUS BIOLOGICAL WORK

Duncker (1899) made a statistical examination of flounders caught in the Tamar. Ford (1928) fished for young herring with a small-meshed seine-net in the Tamar, Tavy, and Lynher, and published his results in the fourth paper of "Herring investigations at Plymouth". In 1929 Percival published the results of an investigation of the fauna of the Tamar and Lynher, carried out between June and November, 1928. The paper contains a description of the area, an annotated faunistic list, and some observations on salinity variations. Percival points out that 1928 was an unusually dry summer. Certain analyses of his data are made in the Survey of the River Tees, Part II (pp. 79–81). After Serventy (1935) had recorded the occurrence of *Gammarus zaddachi* in the Tamar, Crawford (1937) made a more detailed study of the distribution of certain Crustacea (Tanaidacea, Isopoda, and Amphipoda) in the estuarine zone of the three main rivers. Moore's studies on the biology of *Balanus* (1936) and *Littorina littorea* (1937) deal with populations of these animals from Henn Point and Treval respectively.

Note

In the spelling of place-names we follow the Ordnance Survey, but it should be pointed out that for some names alternative spellings are still in use. Thus Neal Point is variously "Neil" (Admiralty Chart) or "Neille" (Percival, 1929; Crawford, 1937). Another locality appears to be "Treval" or "Trevol", according as it is approached from the land or the water! There are names such as Warren Point which recur in this and other estuaries with inconvenient frequency, and care should be employed in their use. In Crawford's map (1937, p. 649) the names Bull Point and Weston Mill Lake are misplaced.

Various information, such as depths, has been derived from the following

Admiralty Charts: Plymouth Sound and Hamoaze, surveyed 1898–9, with large corrections to 1931, and small corrections to 1937; Tamar River (Saltash to Cargreen), surveyed 1894, with additions to 1905; entrance to St Germans or Lynher River, surveyed 1923, with small corrections to 1937.

The information given here on intertidal levels, e.g. the half-tide line, is based on the survey of certain traverses made in 1936–7, supplemented by observations on the state of the tide in a general view of stretches of estuary, at the appropriate time and in suitable weather conditions. No great exactness is claimed.

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PLAN OF THE TAMAR ESTUARY BASIN

The *Intertidal zone* between *Ordinary High and Low Water* marked in fine stipple.

Saltings indicated by coarse irregular stippling.

Only the main streams through the intertidal zone are inserted. Ramifying channels through saltings are omitted. Fresh-water streams flowing into the estuary are not traced to their source.

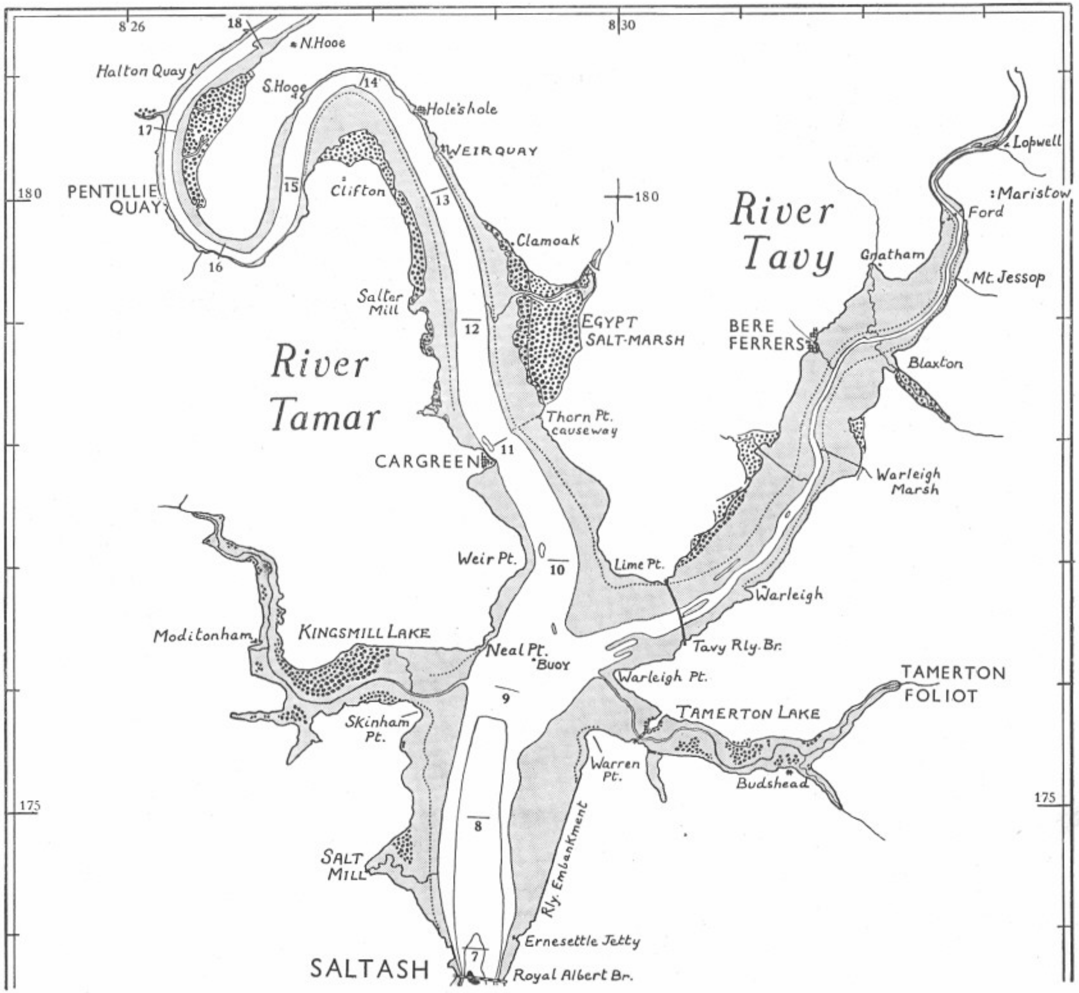
The dotted line dividing the intertidal zone represents *the approximate position of half-tide* where this has been ascertained.

Contours in the permanent channel are given at intervals of 5 m. depth below Admiralty datum. The deeper part of the channel exceeding 15 m. (approximately 8 fathoms or 50 ft.) is blackened.

The course of the main river, the Tamar, is marked in *kilometre intervals* from the mouth (zero position at the level of Devil's Point).

Certain *mooring buoys* from Plymouth Sound to Saltash are marked as follows. *D* 1 *to* 4: Drake's Island Buoys. *Cr. By.*: Cremyll Buoy. *H* 1 *to* 15: Hamoaze Buoys, Nos. 1 to 15.

The plan is orientated (2° W. of N.) with respect to the Ordnance Survey National Grid, of which 1000 yard intervals are marked along the border. The lower section covers 820·5–833·66 (thousand yards) E. and 166·86–174·06 N. The upper section covers 825·1–833·66 E. and 173·57–181·5 N.



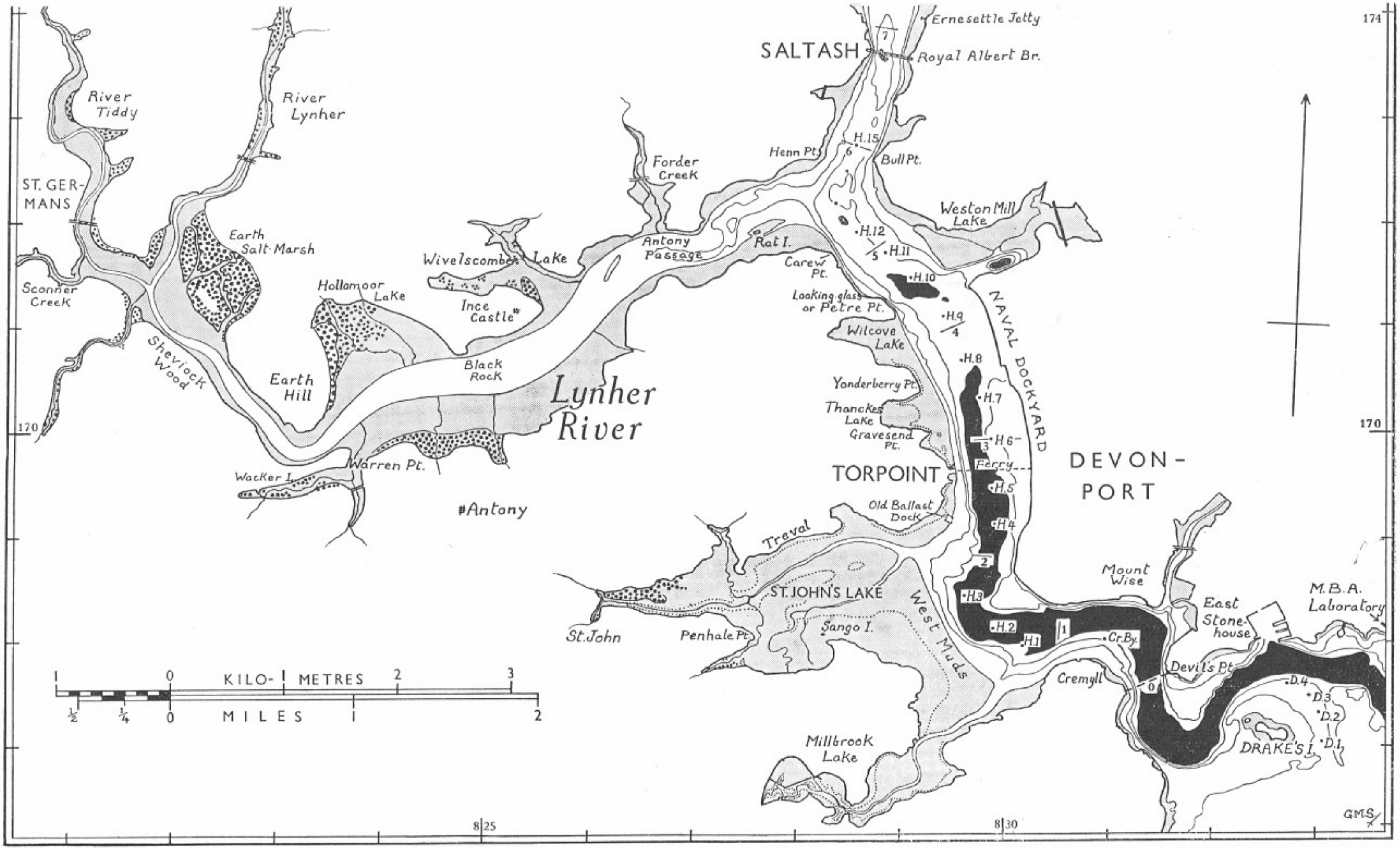

SALTASH
Ernesettle Jetty
Royal Albert Br.
7
174
River Tiddy
River Lynher
ST. GERMANS
Earth Salt Marsh
Forder Creek
Henn Pt.
H.15
6
Bull Pt.
Weston Mill Lake
Antony Passage
Rat I.
H.12
5
H.11
Wivelscombe Lake
Carew Pt.
H.10
Sconner Creek
Hollamoor Lake
Ince Castle
Looking glass or Petre Pt.
H.9
4
NAVAL DOCKYARD
Sheviock Wood
Wilcove Lake
H.8
Black Rock
Earth Hill
Lynher River
Yonderberry Pt.
H.7
Thanckes Lake
Gravesend Pt.
H.6
3
170
DEVON-PORT
Warren Pt.
TORPOINT
Ferry
Wacker I.
H.5
Old Ballast Dock
#Antony
H.4
Treval
2
Mount Wise
M.B.A. Laboratory
ST. JOHN'S LAKE
West Muds
H.3
East Stonehouse
St. John
Penhale Pt.
Sango I.
H.2
H.1
1
Cr.By.
KILO- METRES
1
0
1
2
3
Cremyll
Devil's Pt.
0
D.4
D.3
D.2
D.1
MILES
½
¼
0
1
2
Millbrook Lake
DRAKE'S I.
8|25
8|30
G.M.S.

PLATE XVIII

THE ECOLOGY OF THE TAMAR ESTUARY
II. UNDER-WATER ILLUMINATION

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From the Plymouth Laboratory

(Text-figs. 1–6)

Studies on illumination in the waters of the open sea made from this and other laboratories (cf. Atkins & Poole, 1933) have stressed the profound effects of varying transparency of sea water upon plant growth. Therefore during ecological investigations in the Tamar Estuary or Hamoaze, some measure of the light available for plants growing on the banks and in midstream on mooring buoys was sought. For work in shallow turbid water, the photoelectric method has certain disadvantages due to shading by the boat and the necessity of measuring the depth of the cell on a scale of centimetres rather than of metres. Steemann Nielsen (1935) has used the Zeiss Pulfrich photometer for measuring the extinction coefficients of blue and green light in Icelandic waters. For measuring the turbidity of North Sea water Kalle (1937) also has used this photometer in combination with the red S 72 light filter. In the present investigation the photometer has been used for measuring the transmission of light throughout the visible spectrum. The results can be linked up with photo-electric measurements.

Method of Measurement

The photometer measures directly the absorption or extinction coefficient of a coloured or turbid solution compared with distilled water; 0·25 m. twin absorption tubes have been employed. As commonly used the distilled water tube serves to give a balanced optical system and to eliminate from the measurement the undesired absorption by water itself, but for our purpose this absorption must be considered. When the instrument is correctly set up, the intensities of light of given wave-length entering the twin tubes, each of length d metres, will be identical, I_0, but after passing through d metres of distilled water or of sea water, the intensities will be reduced to I_1 and I_2 respectively. The following relations then hold:

$$d\mu_{DW} = \log_e \frac{I_0}{I_1}, \qquad \ldots\ldots(1)$$

$$d\mu_{SW} = \log_e \frac{I_0}{I_2}, \qquad \ldots\ldots(2)$$

where μ_{DW} and μ_{SW} are the extinction coefficients of distilled water and sea water respectively for light of a given wave-length. The measurements compare the intensities of light which emerge from the tubes, that is

$$d\mu_M = \log_e \frac{I_1}{I_2}, \qquad \ldots\ldots(3)$$

where μ_M is the extinction coefficient as measured. A simple rearrangement shows that

$$\mu_{SW} = \mu_M + \mu_{DW}. \qquad \ldots\ldots(4)$$

The transmission curves for the eight spectral filters used are shown in Fig. 1, reproduced by permission of Messrs Carl Zeiss (Jena). In most cases the cut off is very sharp. For this investigation the S 66·6 filter was not available.

Sawyer (1931) has summarized measurements of the extinction coefficients of distilled water. His own measurements extend up to 650 mμ. and appear amongst the most suitable for our purpose. Later Dawson & Hulburt (1934) redetermined μ_{DW} in the visible spectrum between 540 and 690 mμ. (Table I). Lange & Schusterius (1932) published results for an extinction coefficient, ϵ_{DW}, defined by the equation: $x\epsilon_{DW} = \log_{10} \frac{I_0}{I_1}$, where x is measured in centimetres (see their correction redefining their coefficient). Using the relation $\mu_{DW} = 2{\cdot}3 \times 100\, \epsilon_{DW}$, their graph gives μ_{DW} as approximately 0·27, 0·18, 0·50 and 2·8 at 500, 560, 670 and 750 mμ. respectively. On many occasions throughout the visible spectrum, as far indeed as 800 mμ., considerably lower values of vertical extinction coefficients in the open sea have been found by Poole & Atkins, Utterback, and Clarke. Since the extinction coefficients of distilled water are unlikely to exceed these values, Lange & Schusterius' figures have had to be rejected. The accepted figures in Table I for the filters S 43–61 were based solely on Sawyer's data, since we had not

TABLE I. EXTINCTION COEFFICIENTS OF DISTILLED WATER, μ

Spectral filter	Wave-length at centre of gravity of filter mμ	μ		
		Sawyer (1931)	Dawson & Hulburt (1934)	Accepted value
...	400	0·072	0·08	...
S 43	440	0·023	...	0·02
S 47	460	0·015	...	0·02
S 50	490	0·015	...	0·02
S 53	530	0·021	...	0·02
...	540	0·024	0·04	...
S 57	570	0·038	...	0·04
...	589	0·082	0·14	...
S 61	620	0·178	...	0·18
...	650	0·21	...	...
...	670	...	0·34	...
...	690	...	0·39	...
S 72	*ca.* 720	...	...	0·47
S 75	*ca.* 750	...	...	0·54

then discovered Dawson & Hulburt's paper. For our purposes the differences between the two sets of measurements are too small to warrant recalculation

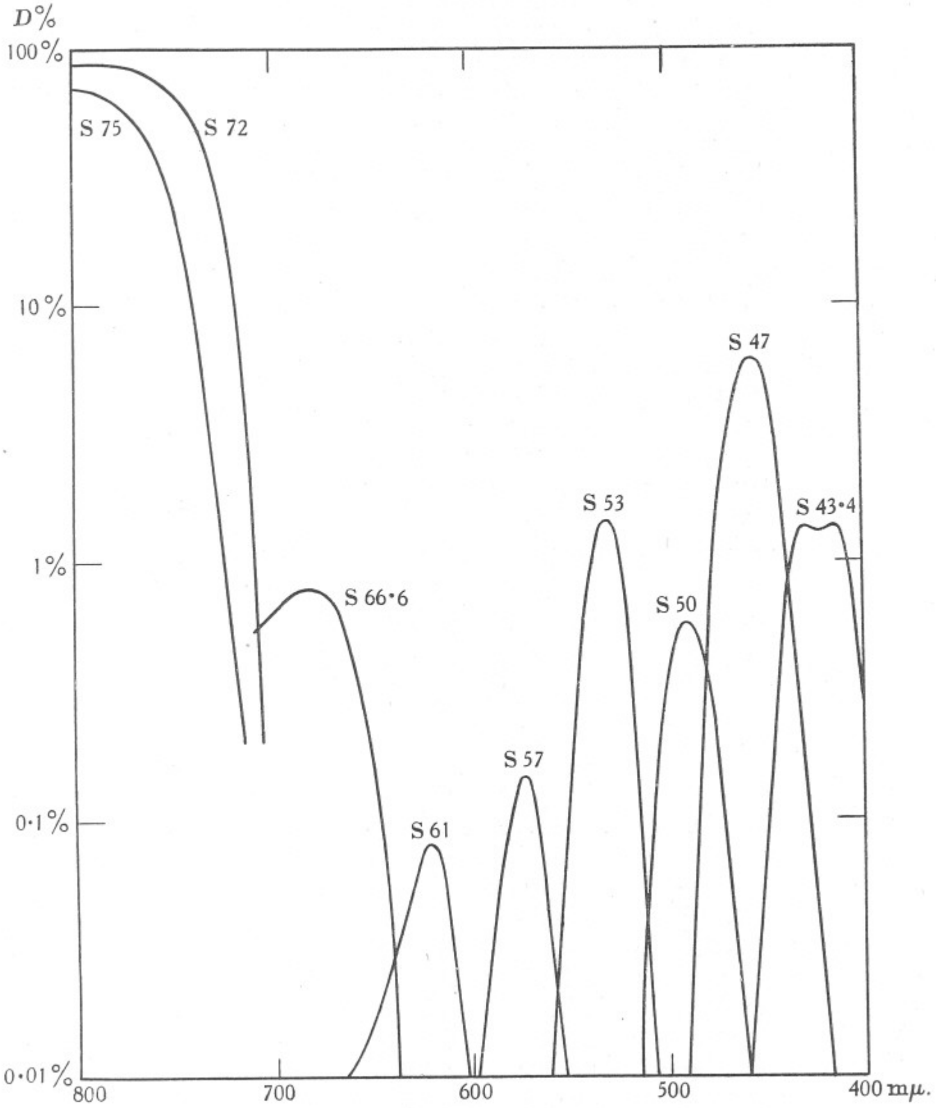

Fig. 1. Transmission curves for the spectral filters used with the Pulfrich photometer (supplied by Messrs Carl Zeiss).

of our results. The new results at 670 and 690 mμ. are of much value in arriving at the correction factors for the S 72 and S 75 filters. If, as would appear, the coefficient in this region is increasing linearly with wave-length,

μ_{DW} would be about 0·47 at 720 mμ. and about 0·54 at 750 mμ. These values have been used for the correction factors which must at present remain somewhat uncertain. Aschkinass (1895) found very high values for the extinction coefficient of pure water above 720 mμ. ($\mu_{DW} > 1$). Dr Atkins has very kindly examined for us the transmission curves of the Schott and Gen RG 7 and RG 8 filters used in his work on the transmission of red light in the sea. From his records it would seem that sea water shows nothing like such a high extinction coefficient. Thus Atkins & Poole (1933, p. 152) found vertical extinction coefficients 0·435, 0·480 and 0·567 at 660, 700 and 760 mμ. respectively. Pure water is unlikely to be more opaque than this.

Different samples of distilled water no doubt vary considerably in transparency. Our laboratory still gives water of excellent quality, so that for this investigation where the correction makes only a small change in the final value, Table I is appropriate. Should the method be used for more transparent waters, the distilled water correction would require further study.

Usually the two sides of the photometer will not be in exact optical balance. In consequence four readings with each of the eight spectral filters were made consecutively with the tube containing distilled water on the right hand. The tubes were then interchanged and a further similar series of observations made. To prevent settling of sediment, they were rotated through about 45° after every four readings. For each filter μ_M is therefore the mean of eight readings.

Comparison with the Photo-electric Method

Both methods give results in terms of an extinction coefficient μ defined by the equation

$$\mu = \log_e \frac{I_0}{I} \Big/ d.$$

Poole & Atkins use a quantity, μ_v, which they earlier (1926) described as the "vertical absorption coefficient" and now (1937) prefer, in agreement with Pettersson, to call the "vertical extinction coefficient"; μ_v is defined by the above equation in which d represents the difference in depth and not the unknown length of path travelled by the light. They concluded (1933) that for off-shore measurements below 10 m. with photometers limited to a restricted spectral range, μ_v as a measure of opacity is unlikely to be in error by more than a few per cent. It had been found by experiment to be practically independent of the angle of incidence at the surface.

Light passing through water may be transmitted, absorbed by the water, or absorbed or scattered by suspended solids. If a beam follows an oblique but straight path for n metres, the true extinction coefficient due to absorption only, $\mu_{n\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ n$, will be less than the vertical extinction coefficient due to absorption only, $\mu_{v\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ d$.

That part of the light scattered will become omni-directional but will not be lost unless it is reflected back out of the water. Nevertheless, in turbid water scattering will greatly increase the length of path of a ray passing downwards, so providing the opportunity for proportionately great absorption. The milky appearance of turbid water both in the estuary and in the photometer tubes shows this scattering to be considerable. If we consider a cylindrical sample of turbid water surrounded, as in the estuary, by similar water, as much light will be gained from the surrounding water by scattering as will be lost to it. For such a sample in a glass absorption tube in a dimly lit room, light incident on the water/glass surface at less than a certain angle will be completely lost from the water. If the water/glass and glass/air surfaces were plane and parallel, the limiting angle of incidence on the water/glass surface would be the critical angle for water/air, 48·5°. However, due to the curvature of the walls, the limiting angle of incidence for light not originating on, or from the direction of, the axis of the tube may be somewhat greater than this. As against this, the aperture of the measuring diaphragm receives only light which has traversed the central portion of the tube where conditions are more like those in nature, so that, although the measured extinction coefficient may be somewhat too great, due to loss of scattered light, the error is unlikely to be serious. Both methods are subject to inherent errors, but these are considered to be sufficiently small not to invalidate comparison between extinction coefficients determined by them.

Position of Observations

The exact positions examined will be found in Part I (Plate XVIII). The lowest is near the western end of Plymouth Breakwater and 2·0 km. to the N.N.E., still within Plymouth Sound, is Drake's Island No. 1 Buoy. Relative to the estuary this buoy is situated − 2·5 km. from the adopted zero line at the mouth, following the continuation of the main channel. Hamoaze No. 1 Buoy lies off Cremyll, No. 7 off Thanckes Lake, No. 15 below Saltash, and Neal Point Buoy in midstream at the junction of the Tavy, at distances of + 1·2, 3·4, 6·0, and 9·25 km. respectively from the estuary mouth.

Influence of Stratification

Observations in Plymouth Sound, even in the winter rainy season, have shown that the salinity varies little in the first metre or so below the surface. Salinity stratification increases in the up-river direction, and above Saltash bridge may become considerable during a winter spate (see Part III). In the Tamar Estuary, the maximum stratification may be expected at the upper limit examined, Neal Point Buoy. It will be shown in Part III that even in time of rainfall, equivalent to normal winter fall, the variations in salinity down to 1·8 m. are small and, for the top metre, negligible. Solid matter in suspension in an estuary arises from the inflowing river water and by tidal scouring of the muddy banks and bottom. The mixing processes are complex, but the amount of solid matter in any sample of water taken from the estuary is more or less directly dependent upon the degree of mixing of sea water with river water which, in times of spate, may be heavily laden with silt, and upon the time the various waters have spent in the estuary. Of this mixing the salinity is a measure, so that it is reasonable to suggest that waters of similar salinity carry, in general, much the same amount and kind of suspended solids. The considerable turbulence always present in isohaline water in a strongly tidal estuary would tend to keep conditions in the uppermost metre uniform. We therefore feel justified in considering our 0·3 m. samples representative of conditions down to rather more than 1 m. Whether there are more or less suspended solids at greater depths requires further investigation. In Gullmar Fjord Pettersson's observations showed that the underlying water may be much clearer but tidal forces are there much weaker than in the Hamoaze.

The relation between extinction coefficients and salinity is shown in Fig. 2 for green light measured with the S 50 filter. Below about $30^{\circ}/_{\circ\circ}$ salinity a fair degree of inverse proportionality exists. With more saline water, in which sediment from the river has had a greater and more variable time in which to settle, no simple relation holds. The extinction coefficients for January 25, although of less accuracy than those determined later, are of much interest (Fig. 2). On this occasion silt determinations were also made by filtering 2–3 l. of estuarine water through a small tared No. 42 Whatman filter paper, washing with distilled water and drying at 100° C. to constant weight.

At the Breakwater (0·3 m.) salinity was very low, indicating a thin layer of river water spreading over the salter water beneath. This upper layer of water was associated with 5·3 mg./l. of silt and high extinction coefficients for light of all wave-lengths ($\mu_{500}=5\cdot0$; $\mu_{720}=3\cdot8$). Near Drake's Island the surface water was more saline and more transparent, yet carried more silt. Thence up-river to Hamoaze No. 7 Buoy, salinity, silt content and extinction coefficients varied in the way one would have forecast. Still further up-river at No. 15 Buoy, the water was still fresher but, to our surprise, contained less silt and was less opaque (Table II).

TABLE II. HAMOAZE POSITIONS, JANUARY 25 1937

	No. 1 Buoy	No. 7 Buoy	No. 15 Buoy
State of tide, hours flood	4	4·5	5
$S\ ^{\circ}/_{\circ\circ}$	20·4	14·1	11·6
Silt, mg./l.	10·5	18·5	10·4
μ_{500}	5·1	9·0	8·4
μ_{720}	4·4	6·7	5·8

EXTINCTION COEFFICIENT

Throughout the visible spectrum the extinction coefficients in the Hamoaze (Fig. 3) are always higher, often much higher, than in the English Channel. The coefficients increase in the up-river direction and with falling tide because, first, the river is the chief contributor of suspended matter and secondly, the proportion of sea water, originally relatively clean, decreases.

In the winter of 1936–7 excessive rainfall (see Part III) saturated the watershed; most of this must have run straight off the ground into the river bringing with it a heavy load of silt. In February the surface waters of the estuary became so turbid that at low water at Neal Point with a salinity of 7·8 ‰ the intensity of red and blue light entering the water was cut down to one-thousandth within 0·6 and 0·4 m. respectively ($\mu = 12·2$ and $16·5$). Even

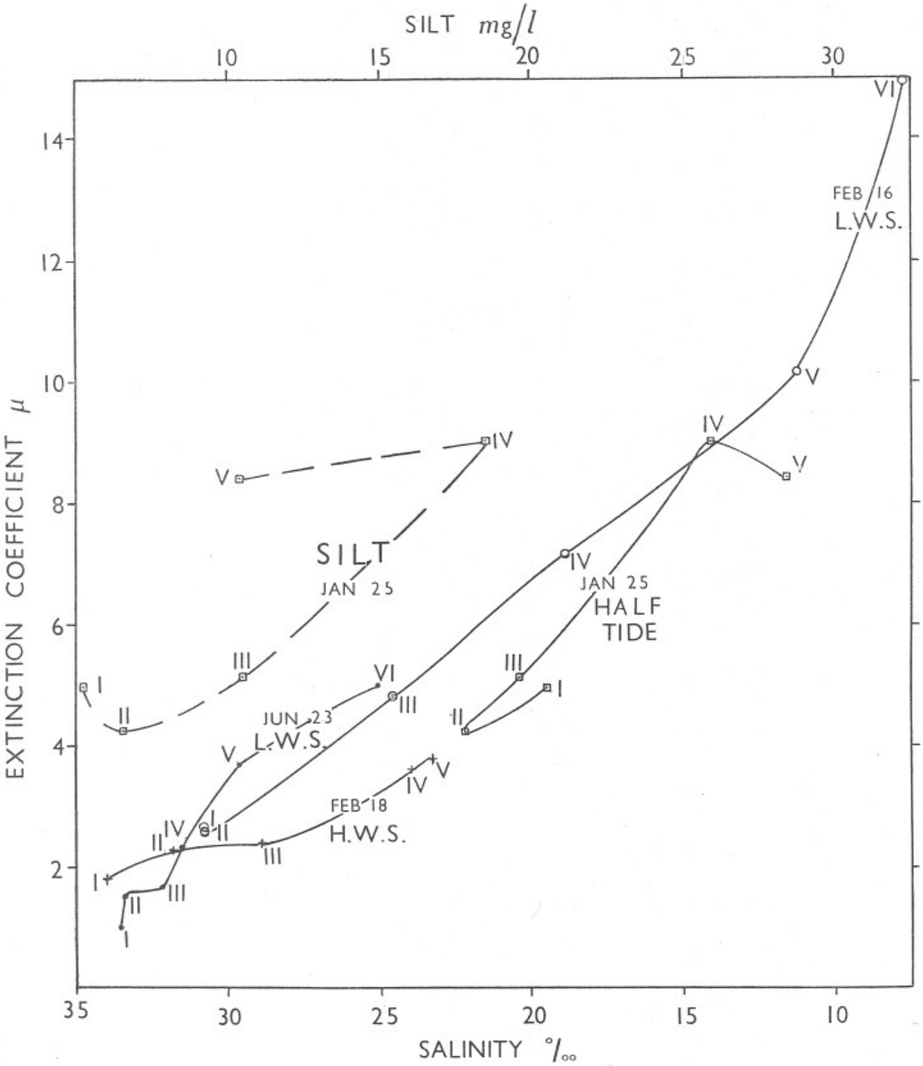

Fig. 2. Relation between extinction coefficient for green light (500 mμ.) and salinity, and also silt content on January 25 (pecked line). For key to positions of observations, see Fig. 3.

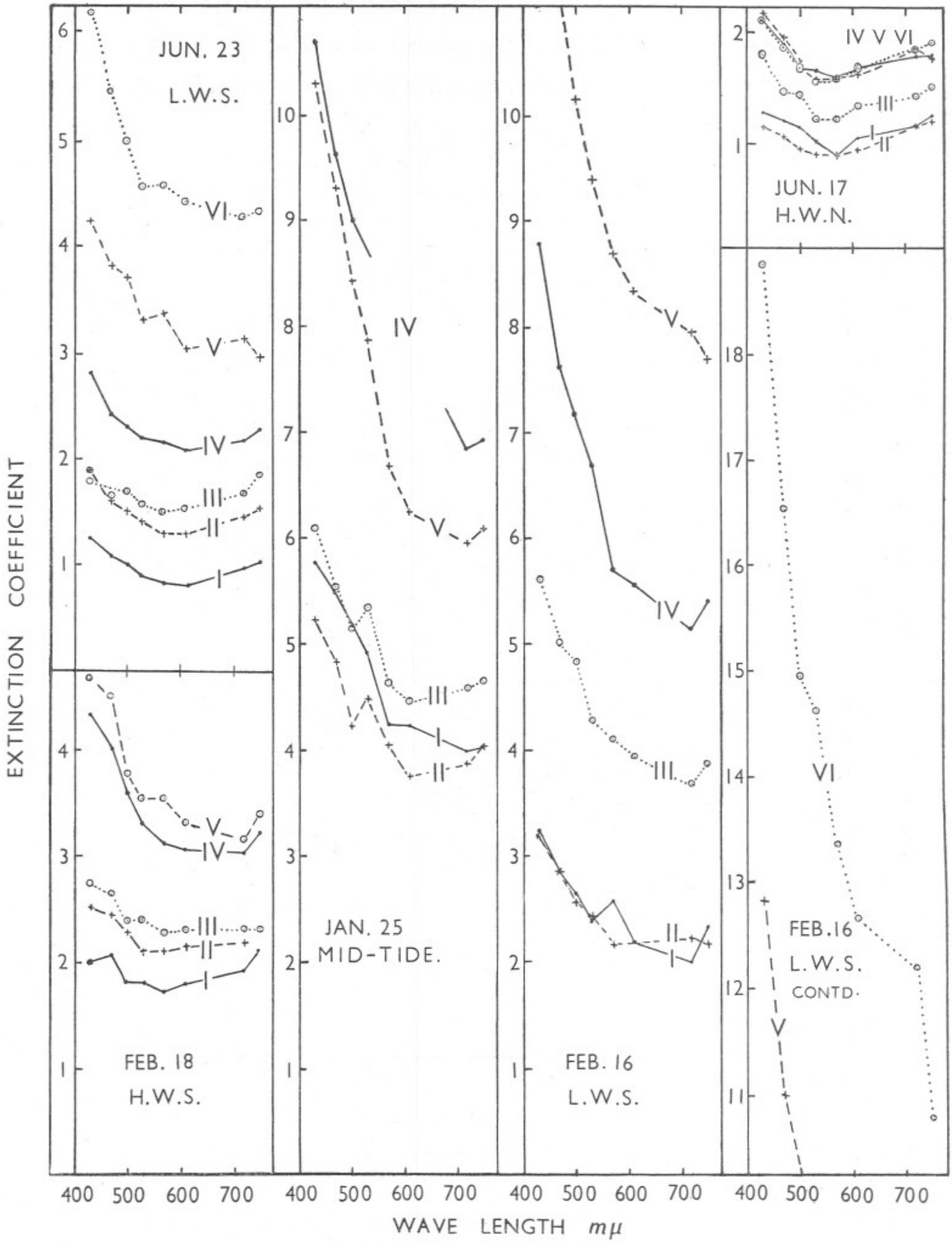

Fig. 3. Extinction coefficients in Plymouth Sound and Hamoaze.

I ——•—— Breakwater No. 1 Buoy.
II ----+---- Drake's Island No. 1 Buoy.
III ····○···· Hamoaze No. 1 Buoy.
IV ——•—— Hamoaze No. 7 Buoy.
V ----+---- Hamoaze No. 15 Buoy.
VI ····○···· Neal Point Buoy.

H.W.S. = High-water springs. L.W.S. = Low-water springs. H.W.N. = High-water neaps.

The curves for February 16 in the third panel are continued in the fourth.

at the two surface stations in Plymouth Sound, the coefficient for blue light was 2·85. This compares with the value for daylight, 2·52, found at the surface in Gullmar Fjord under somewhat similar weather conditions by Pettersson (1935).

The June measurements were made during a very dry spell (see Part III). The little rain that fell must have been absorbed by the soil, so that the fresh water draining to the river would be the minimum flow and composed of clear spring water and seepage from the moors. In consequence in June even at low water at Neal Point Buoy the surface salinity was no less than 25·1 °/₀₀, and the extinction coefficients were similar to those at high water in February. The February and June results probably represent the extremes of conditions likely to be encountered in the estuary.

RELATIVE EXTINCTION OF DIFFERENT WAVE-LENGTHS

Visible light of shortest wave-length is transmitted by the violet S 43 filter, but within this wave-band the sensitivity of the eye and the composition of light in air are changing rapidly. Measurements made with that filter are therefore liable to considerable error. We have accordingly preferred to arrange our February and June results in order of increasing absorption of blue light (filter S 47). These have been divided into three groups having $\mu_{470} = 1\text{–}2{\cdot}1$, 2·4–2·9 and 3·8–16·5. The ratio of the extinction coefficient for each spectral filter relative to that for S 47 has been calculated for every sample. In each group the mean value for the ratio μ_λ/μ_{470} and the standard error when this is of interest have been computed (Table III). It will be seen that for light having μ_{470} greater than unity, light in the spectral region 400–570 mμ. (violet to orange) is always extinguished in the same proportions, viz. 1·11, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively. This is so no matter what the absolute magnitude of the coefficient may be, provided that it exceeds unity. For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to that for blue (or for that matter green). The greater the wave-length within the visible spectrum the greater this difference becomes. For the group having $\mu_{470} = 1\text{–}2{\cdot}1$, the figures

TABLE III

	Mean ratios of μ_λ/μ_{470} for values of μ_{470} between			
Filter	1·0 and 2·1	2·4 and 2·9	3·8 and 16·5	Entire series
S 43	1·110	1·097	1·112	1·107
S 47	1·000	1·000	1·000	1·000
S 50	0·928	0·924	0·917	0·923
S 53	0·861	0·874	0·847	0·856
S 57	0·821 ± 0·015	0·854 ± 0·025	0·805 ± 0·015	0·823
S 61	0·860 ± 0·018	0·829 ± 0·024	0·766 ± 0·010	0·812
S 72	0·962 ± 0·019	0·830 ± 0·037	0·739 ± 0·016	0·855
S 75	1·010 ± 0·020	0·881 ± 0·043	0·742 ± 0·018	0·889

for the S 72 and S 75 filters may be in some error due to the uncertain distilled water correction. This source of error will be negligible in the other two groups and it does not apply to filter S 61.

Suspended particles affect the extinction of visible light in air and in water in the same way, favouring the transmission of red and yellow rather than blue and green. In marked contrast to pure clear air, pure water itself absorbs light in the extreme visible red and in the infra-red, so that such light is practically completely absorbed within 1 or 2 m., no matter what the turbidity may be (Poole & Atkins, 1937). In water, therefore, the region of optimum transmission will result from two opposing factors—absorption by suspended matter cutting out the blue and green and absorption by the molecules of water and dissolved salts cutting out the infra-red and often much of the visible red. Unlike foggy air, turbid water is unlikely ever to show an optimum transmission in the infra-red.

DEPTH AT WHICH SURFACE LIGHT IS REDUCED TO 1 %

The depths in metres (d_1) at which the intensity of light of given wave-length was cut down to one-hundredth of that incident on the surface are set out in Table IV in which the following assumptions are implicit:

(1) That the loss of light at the surface is 15 % of that incident there. Powell & Clarke (1936) have discussed in detail the various surface losses.

(2) That the water down to the depth given was uniform with that sampled at 0·3 m. (see p. 514).

(3) That the vertical depth is a sufficient measure of the effective path of the downward penetrating light. The arguments advanced by Atkins & Poole (1933, p. 140) for open sea water below 10 m. are considered to apply at a much lesser depth when scattering, as here, is so much greater.

The equation, $\mu = 4{\cdot}44/d_1$, may be used to recalculate from Table IV the extinction coefficients which have been plotted in Fig. 3. Also the depth, d_x metres, at which the intensity of light of given wave-length is reduced to x % of that incident on the surface may be found from the relation.

$$d_x = d_1\,(1 - 0{\cdot}518 \log_{10} x).$$

PERCENTAGE ENERGY COMPOSITION OF TRANSMITTED LIGHT

Abbot (see *Seventh Internat. Congress of Photography*, 1929) has measured the relative spectral energy composition of mean noon sunlight. If we take the relative energy figures appropriate to each of our filters, we can calculate the spectral energy composition of the light transmitted to any depth. Owing to the much greater transmission of light at about 720 than at 500 mμ. in very turbid water, it is not practical to express our results as did Poole & Atkins (1937, fig. 2). In Fig. 4 we show the spectral energy composition of mean noon sunlight reaching 1 m. at the more transparent stations relative to the energy at 500 mμ. in air as 100 %. For the more turbid stations, logarithmic

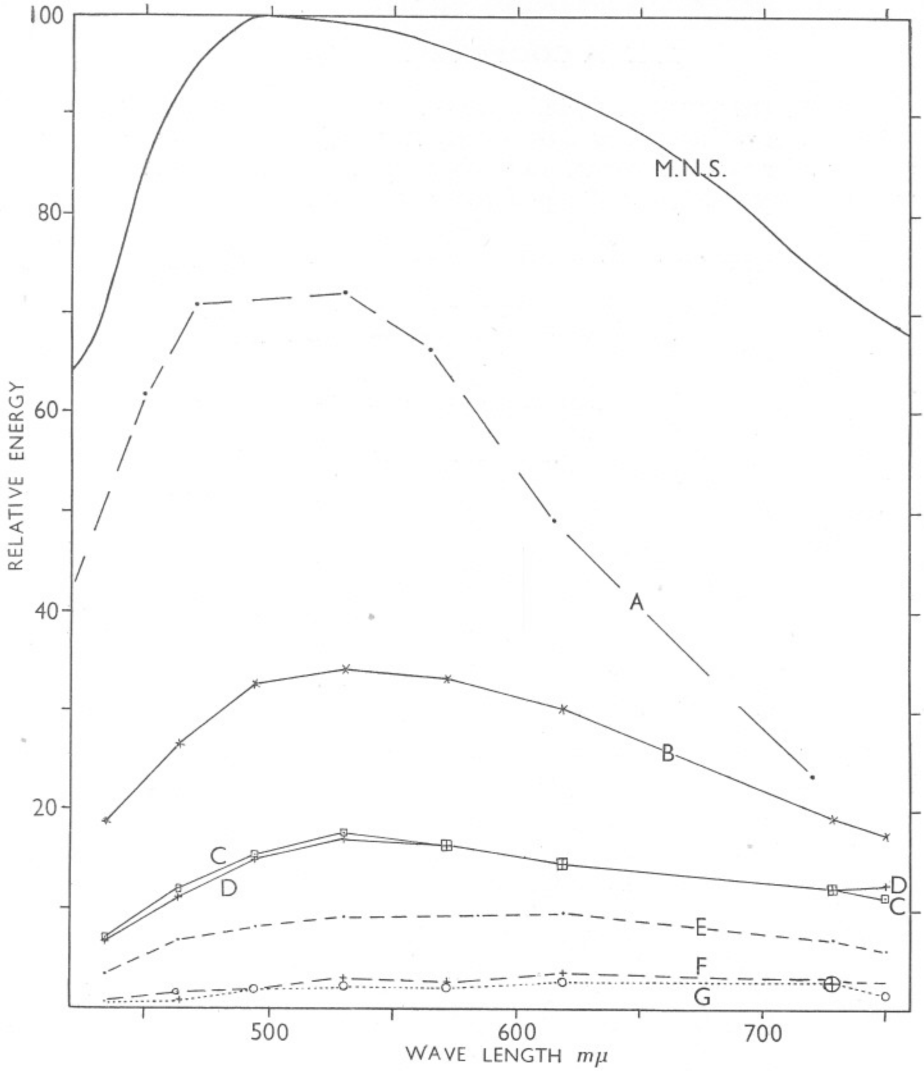

Fig. 4. Relative energy of mean noon sunlight at various wave-lengths transmitted to one metre. Allowance has been made for 15 % surface loss.

Key to Figs. 4 and 5.

June positions, high water: ———— February positions, high water: · · · · · · · · · · · ·
June positions, low water: — — — — — February positions, low water: —· · ·—· · ·—

Curve *M.N.S.*	Mean noon sunlight in air (Abbot).
A	Photo-electric measurements by Poole & Atkins (1937), half mile east of Eddystone September 21 1936.
B	Drake's Island, No. 1 Buoy, high water June 17 1937.
C	Hamoaze, No. 15 Buoy, high water June 17.
D	Neal Point Buoy, high water June 17.
E	Hamoaze, No. 7 Buoy, low water June 23.
F	Hamoaze, No. 15 Buoy, low water June 23.
G	Hamoaze, No. 15 Buoy, high water February 18.
H	Neal Point Buoy, low water June 23.
K	Hamoaze, No. 7 Buoy, low water February 16.
L	Hamoaze, No. 15 Buoy, low water February 16.
M	Neal Point Buoy, low water February 16.

plotting is necessary (Fig. 5), and some curves are included in both figures to facilitate comparison. They show clearly how little of the incident spectral energy under estuarine conditions reaches even to 1 m. and also the extent to which red light (> 600 mμ.) is preferentially transmitted.

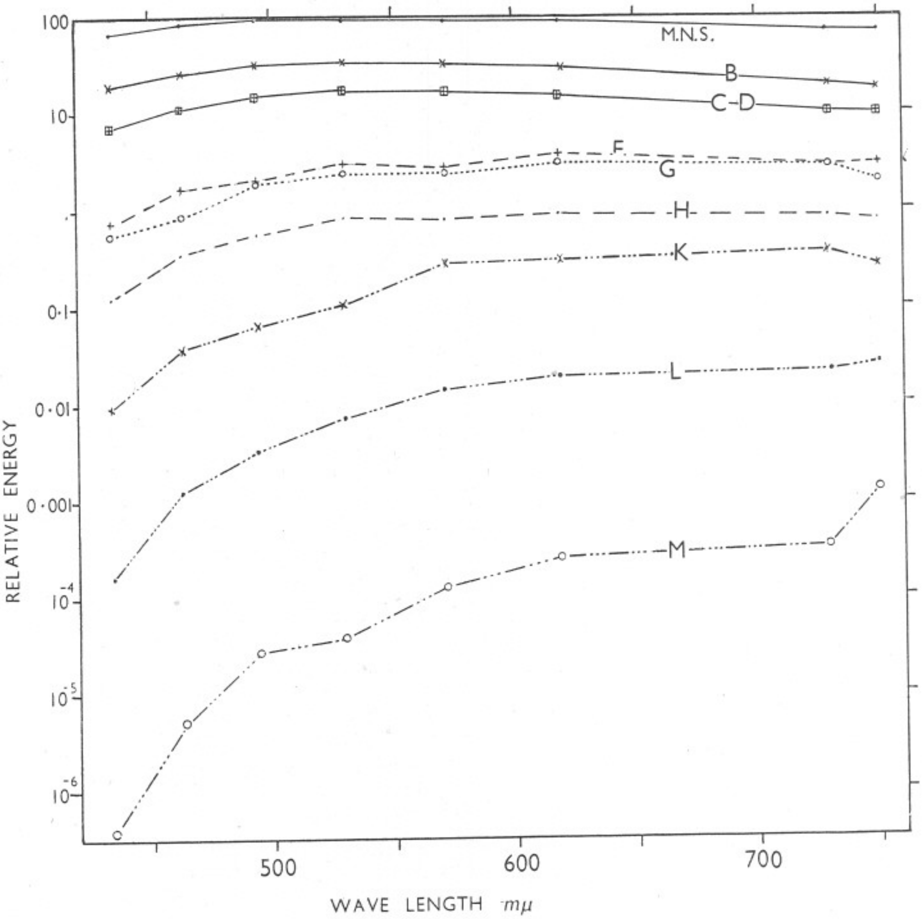

Fig. 5. Legend as for Fig. 4 except that relative energy is plotted on a logarithmic scale in order to include waters having high extinction coefficients.

If the extinction coefficients determined at Hamoaze No. 15 Mooring Buoy in February and in June are respectively plotted against salinity (as in Fig. 2), two curves are obtained which may be used to derive, from salinity records made on other occasions, extinction coefficients and the light intensities at 1 m. plotted in Fig. 6. It must be stressed very emphatically that this graph is intended to convey only a general picture of conditions in the

Hamoaze in the spring of 1937, when extensive ecological investigations were in progress, and not to represent exact results.

Preliminary experiments by H. Pettersson, Höglund & Landberg (1934) suggest that the compensation intensity at which photosynthesis just balances respiration by diatoms lies in the neighbourhood of 400 lux. The depths at which light energy incident on the surface is reduced to this value is therefore a rough measure of the compensation depth. The accurate calculation of this depth is very tedious, but a fair approximation may be made by taking the extinction coefficient for orange-red light (S 61 filter) as representing that of all the light transmitted by the turbid water found in our estuary. The figures for this filter in Table IV will then be a very rough measure of the compensation depth when the illumination in air is 40 kilolux. Such an illumination approximates to that of a bright sunny day at the end of February or of an overcast day in summer (Atkins & Poole, 1936). On a cloudless summer day an intensity of 120 kilolux in air may be exceeded, and the compensation depth would lie about 25 % deeper.

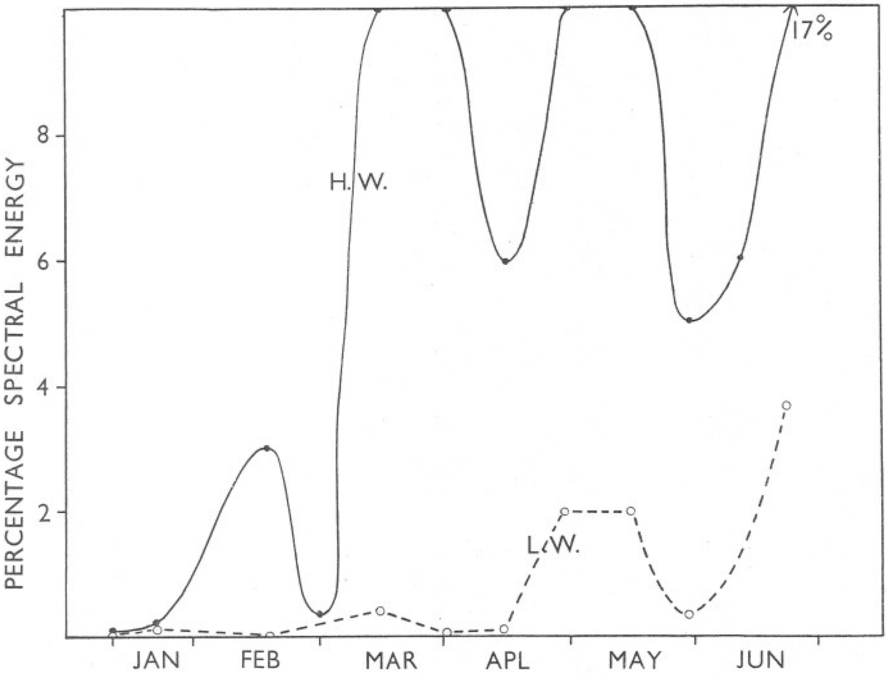

Fig. 6. Percentage spectral energy between 410 and 760 mμ. transmitted to one metre at high and at low water near Mooring Buoy No. 15 in Hamoaze, January to June 1937. Based on salinity records (see text).

TABLE IV. DEPTH IN METRES AT WHICH INTENSITY OF LIGHT IS REDUCED TO 1 % OF THAT INCIDENT ON THE SURFACE

Assuming 15 % Surface Loss; $\mu d_1 = 4·444$

Centre of gravity of filter mμ.	Breakwater	Drake's Island	Hamoaze			Neal Point Buoy
	No. 1 Buoy	No. 1 Buoy	No. 1 Buoy	No. 7 Buoy	No. 15 Buoy	
	February 18 1937. Spring tide. High water					
434	2·20	1·76	1·62	1·02	0·95	...
463	2·06	1·81	1·67	1·09	0·98	...
494	2·45	1·95	1·85	1·23	1·17	...
530	2·45	2·12	1·85	1·34	1·25	...
572	2·58	2·12	1·95	1·42	1·25	...
619	2·48	2·06	1·93	1·45	1·34	...
729	2·31	2·02	1·92	1·46	1·41	...
750	2·11	1·79	1·91	1·38	1·31	...
	February 16 1937. Spring tide. Low water					
434	1·37	1·39	0·79	0·51	0·35	0·24
463	1·56	1·55	0·89	0·58	0·40	0·27
494	1·68	1·73	0·92	0·62	0·43	0·30
530	1·86	1·82	1·04	0·67	0·47	0·30
572	1·72	2·05	1·08	0·78	0·51	0·33
619	2·02	2·03	1·12	0·80	0·53	0·35
729	2·22	1·99	1·20	0·86	0·56	0·36
750	1·90	2·03	1·14	0·82	0·58	0·41
	June 17 1937. Neap tide. High water					
434	3·44	3·83	2·48	2·09	2·02	2·10
463	3·64	4·15	3·00	2·34	2·27	2·38
494	3·86	4·68	3·04	2·60	2·58	2·60
530	4·40	4·93	3·61	2·64	2·76	2·81
572	5·00	4·93	3·58	2·76	2·77	2·77
619	4·23	4·73	3·28	2·61	2·69	2·62
729	3·76	3·77	3·08	2·48	2·41	2·40
750	3·52	3·63	2·90	2·48	2·50	2·33
	June 23 1937. Spring tide. Low water					
434	3·52	2·36	2·50	1·57	1·05	0·72
463	4·11	2·78	2·68	1·83	1·16	0·81
494	4·40	2·94	2·63	1·92	1·20	0·89
530	5·05	3·17	2·84	2·02	1·34	0·96
572	5·42	3·47	2·97	2·06	1·32	0·96
619	5·62	3·47	2·92	2·14	1·46	1·00
729	4·67	3·08	2·66	2·04	1·42	1·03
750	4·35	2·90	2·40	1·95	1·50	1·02

ZONATION OF ALGAE ON BUOYS

The flora on the mooring buoys in Plymouth Sound and the Hamoaze may be divided into three zones with clearly marked boundaries.* The depths of these zones vary and may be correlated with differences in illumination.

The daylight factors (percentages of vertical white light having the spectral composition of mean noon sunlight) have been worked out for each of the zonal boundaries (Table V); the zones and their daylight factors vary little within Plymouth Sound, mean figures for which are given. The similarity of

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* Paper in preparation by A. M.

the daylight factors in the Sound and at No. 7 Buoy in the Hamoaze on three occasions—at high and low water in June and at high water in February—shows that variations in illumination are adequate to account for the zonation found. The plants in Zone I require a surprisingly high proportion of the incident light. Even at the top of Zone III, a daylight factor as high as 67 % can occur.

TABLE V. DAYLIGHT FACTORS AT BOUNDARIES OF ALGAL ZONES ON BUOYS

No correction for surface loss

	Zone I		Zone II	
	Plymouth Sound	Hamoaze No. 7 Buoy	Plymouth Sound	Hamoaze No. 7 Buoy
Depth of bottom of zone, m. ...	0·18	0·097	0·356	0·223
Daylight factor, %:				
June 17 (high water)	83·6	84·6	68·5	67·4
June 23 (low water)	80·8	80·6	65·5	60·4
February 18 (high water)	69·0	72·2	47·2	47·3
February 16 (low water)	64·6	54·6	42·3	25·3

The algae composing Zone III were found in a flourishing condition right to the bottom of all the buoys examined. The daylight factors at the bottom of the two deepest buoys are set out in Table VI. Account has been taken neither of surface losses nor of shading by the buoys themselves. Some of the adult algae no doubt float upwards into water receiving more light than shown, but in their young stages they must be able to grow in water having a daylight factor always less than 1·5 % and often less than 0·5 %.

TABLE VI. DAYLIGHT FACTORS AT BOTTOM OF TWO BUOYS (WITHIN ZONE III)

	Mallard Buoy (Plymouth Sound)			Hamoaze No. 7 Buoy		
Date and state of tide	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.
June 17 (high water)	2·19	10·16	570	2·47	1·35	580
June 23 (low water)	2·19	7·59	580	2·47	0·42	630
February 18 (high water)	2·19	1·16	580	2·47	0·035	650
February 16 (low water)	2·19	0·59	650	2·47	0·000093	720

SUBMARINE DAYLIGHT IN THE NORTH SEA

The numerous determinations of turbidity made in the southern North Sea by Kalle (1937) in January 1935 and February 1936, using the Pulfrich photometer with the red S 72 filter, may be used to derive the extinction coefficient for red light for comparison with results elsewhere. He reported his results as "*K*-values" which are a measure of the extinction as measured in a 0·25 m. tube. When the extinction coefficient as measured is defined by equation (3), it may be shown that $\mu_M = \frac{9{\cdot}2\,K}{1000}$. From equation (4) the true extinction coefficient for the sea water

$$\mu_{SW} = \frac{9{\cdot}2\,K}{1000} + \mu_{DW},$$

and the depth in metres at which the light is reduced to 1 % of that incident on the surface (as in Table IV)

$$d = \frac{4440}{9{\cdot}2\,K + 1000\,\mu_{DW}},$$

where K is Kalle's measure of turbidity. These expressions may not be accurate for values of K less than 100, since any error in the correction factor, μ_{DW}, becomes large and a surface sample only will be inadequate to characterize all the water concerned in the absorption of light. Moreover, for such waters a 0·25 m. absorption tube may be too short.

Assuming, as in our work, that $\mu_{DW} = 0{\cdot}47$, the true extinction coefficients have been calculated for some of Kalle's more turbid stations (Table VII). These appear to be of two types, one being practically isohaline and showing greater turbidity and light extinction coefficient at the bottom than at the surface, the second having much lower salinity and higher extinction coefficient at the surface and resembling our own conditions in Hamoaze. Water of the

TABLE VII. A COMPARISON BETWEEN EXTINCTION COEFFICIENTS FOR RED LIGHT (S 72 SPECTRAL FILTER) IN THE NORTH SEA (DERIVED FROM KALLE 1937) AND IN THE HAMOAZE

Station	Date	Position	Depth m.	Salinity ‰	Extinction coefficient μ_{SW}
		Group 1			
12d	i. 35	52° 53′ N 2° 27′ E	0	34·71	3·5
			34	34·71	5·0
13	i. 35	52° 41·5′ N 2° 17·5′ E	0	34·66	3·6
			48	34·60	12·9
16	i. 35	52° 16·7′ N 1° 50′ E	0	34·45	7·8
			28	34·49	12·9
17	i. 35	52° 10·1′ N 2° 12′ E	0	35·16	2·4
			43	35·01	6·3
27	i. 35	51° 30·8′ N 1° 26·1′ E	0	35·05	3·2
			14	35·01	6·2
		Group 2			
60	i. 35	Off Rhine-Meuse Delta	0	25·63	4·3
			22	33·86	1·5
70	ii. 36	Channel N. of Sylt off	0	30·01	7·9
71	ii. 36	Schleswig	0	28·35	10·0
84	ii. 36	Off Mouth of Elbe	0	23·55	7·8
85	ii. 36	,,	0	15·50	12·0
86	ii. 36	,,	0	16·04	12·0
		Hamoaze, No. 15 Buoy:			
—	ii. 37	High water	0·3	23·3	3·1
—	ii. 37	Low water	0·3	11·2	8·0
—	ii. 37	Neal Point, low water	0·3	7·7	12·2

first type occurred off the East Anglian coast, and most of the suspended matter must have been stirred up from the bottom by tidal or storm action. Extinction coefficients calculated only from surface data will be too low. Part of this region of high absorption is associated with the north-west Southern Bight Eddy which Kalle discovered as a result of these cruises.

Water of the second type was found at the mouths of the Elbe and of the Rhine-Meuse delta. As in the Hamoaze, also in February, the suspended matter had no doubt been brought down by flood water from the rivers. Since these are much larger than those feeding the Hamoaze, the region of low salinity and high absorption extended farther to sea. In the North Sea off East Anglia and in the sea off these continental river mouths the light absorption may be as high as in the Hamoaze under extreme conditions (Table VII). The special distribution of plants in estuaries is usually attributed primarily to reduced salinity. Whilst this is often true, there may be cases where the distribution is the result not of reduced salinity but of increased light absorption resulting from the associated silt. A study of the flora of buoys situated off the East Anglian coast along the lines followed by one of us (A. M.) in the Hamoaze might go far towards a solution of the problem.

SOME BIOLOGICAL INDICATIONS

From Table IV it will be seen that even under optimum conditions light is always reduced to 1 % or less within 5 m. at Drake's Island No. 1 Buoy and within 3 or 4 m. further up the Hamoaze. In Table VIII a comparison is made with conditions in other waters determined photo-electrically by various workers. Whereas the same intensity of blue light (450 or 470 mμ.) was found

TABLE VIII. DEPTH IN METRES AT WHICH LIGHT OF VARIOUS WAVE-LENGTHS IS REDUCED TO 1 % (AS IN TABLE IV)

Station	Date	Wave-length mμ.							
		400	450	470	530	570	600 +	675 +	700 +
Coasts of Iceland*	May 1934	...	...	2·0–12·0	2·4–19·3	...	...	...	...
Plymouth Breakwater†	Oct. 1932	...	6·3	...	10·7	...	4·6	3·0	...
Puget Sound, Pillar Point‡	June 1934	...	8·7	9·7	12·2	13·3	8·8	...	...
Puget Sound, Pillar Point	Jan. 1934	...	21·5	26	30	26	13·0	...	...
Puget Sound, Hood Canal‡	Apl. 1934	...	6·6	9·4	17·7	14·5	8·2	...	...
Puget Sound, Hood Canal	Mar. 1934	...	18·9	21	29	23	12·7	...	...
English Channel, Eddystone†	Sept. 1936	14·8	34	38	41	31	10·5	...	3·6
Pacific Ocean, 47° 26′ N., 126° 26′ W.§	...	...	63	62	59	43	14·7	9·1	...
Sargasso Sea‖	...	100	148	...	85	...	17	...	...

* Measurements with Pulfrich photometer by Steemann Nielsen (1935). Results at 490 mμ. entered as 470 mμ.

† Photo-electric measurements by Poole & Atkins (1937).

‡ Photo-electric measurements by Williams & Utterback (1935). Records at 460, 480 and 565 mμ. entered as 450, 470 and 570 mμ. respectively.

§ Photo-electric measurements by Utterback & Jorgensen (1934).

‖ Photo-electric measurements by Clarke (1936). Read from a graph of μ_v.

at 0·27 m. at Neal Point Buoy under the worst conditions and at 148 m. in the Sargasso Sea (ratio 1 : 550), the corresponding figures for red light were 0·36 and 17 m. (ratio 1 : 48).

Not only will the reduced light intensity compress the zonation of plants in estuarine waters but the season of active growth should be shorter than in the open sea. Moreover, both these effects should become more marked in an up-river direction, and species dwelling near the level of low water should be more affected than those nearer high-water mark.

We are much indebted to Dr W. R. G. Atkins and Dr H. H. Poole for their helpful advice.

SUMMARY

The Zeiss Pulfrich photometer, with its eight spectral filters covering narrow spectral bands within the visible spectrum, has been used to investigate the penetration of light into an estuary under winter and summer conditions.

Throughout the visible spectrum, extinction coefficients in Hamoaze are always higher, in winter often very much higher, than in the English Channel. In marked contrast to the open sea, red light penetrates as well or better than green, and blue is cut down most rapidly. Highest and lowest values of μ found at two estuarine stations were:

		Hamoaze No. 1 Buoy		Neal Point Buoy	
Colour		Lowest	Highest	Lowest	Highest
Blue	440–480 mμ.	1·48	5·01	1·87	16·5
Green	515–550 mμ.	1·23	4·28	1·58	14·6
Red	610–640 mμ.	1·35	3·94	1·69	12·7
Dark red	710–760 mμ.	1·44	3·69	1·85	12·1

The intensity of incident daylight in the Hamoaze appears always to be reduced to 1 % within 4 m., often in less than 2 m. and at low water when the rivers are in spate in less than 0·5 m.

For water having an extinction coefficient for blue light (470 mμ.) greater than unity, the light within the spectral range 400–570 mμ. is always extinguished in the same proportions (μ_λ/μ_{470} = 1·11, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively).

For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to blue (or for that matter green). The greater the wave-length within the visible spectrum the greater the difference becomes.

Zonation of algae on buoys may be correlated with variations in illumination.

Measurements of turbidity in the North Sea by Kalle have been recalculated to give the extinction coefficient for red light. Off the East Anglian coast and off the mouths of the Elbe and the Rhine-Meuse delta, very turbid waters showing values of μ_{720} as high as 12·9 were encountered.

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THE ECOLOGY OF THE TAMAR ESTUARY

III. SALINITY AND TEMPERATURE CONDITIONS IN THE LOWER ESTUARY

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(Text-figs. 1–5)

CONTENTS

In the Tees Survey (Alexander, Southgate & Bassindale, 1935) the general salinity conditions of the Tees Estuary have been clearly described, and it was suggested that conditions in the Tamar might be somewhat similar. Observations during 1936–37 confirm this similarity. Here, therefore, it is only necessary to discuss those data which will give some idea of the actual salinity fluctuations (rate of change as well as magnitude) affecting the fauna and flora of the section of the Tamar Estuary now considered in these papers.

The Tees Survey gives maximum, minimum, and average salinities, but such data are not the only aspects to be considered from the point of view of salinity effects on organisms, for it is well known that some aquatic animals can be acclimatized to almost any salinity from above that of sea water down to fresh water, provided that the change is brought about gradually. The actual range of salinity may not be so important as rate of change.

Salinity Conditions in a Cross-section of the Estuary

In the Tees Estuary (1935, p. 76) "The salinity variation to which an organism is subjected depends, therefore, on the position in the intertidal area at which the species normally lives. A mean value has been taken as the difference between salinity at the surface at low water under normal winter conditions and at a depth of one fathom at high water under normal summer conditions. Organisms living near high-water mark suffer a smaller, and those living near low-water mark a greater variation than this mean value." To give a more complete picture of events in the Tamar Estuary, two investigations of salinity conditions at various depths in a cross-section of the river at a representative estuarine position were made on a rising tide and on a falling tide. The rainfall was slightly above normal in the former and normal in the latter (see rainfall in Fig. 3). The first of these sets of observations was carried out on May 24 1937, when the predicted height of the tide was 4·35 m., and the second on June 3, when it was 3·76 m. Normally tidal heights range from about 3 to 5 m. above chart datum.

For the positions mentioned in this paper the map reproduced in Part I of this series (Hartley & Spooner, 1938) should be consulted.

That the area under consideration in this ecological study is a natural compartment or division of the estuary is emphasized by the following extract from Percival (1929): "It would appear that the main body of incoming sea water does not pass Cargreen. A considerable portion goes into the Lynher and Tavy and covers the mud-flats on each side between Saltash and Neille* Point. A further large quantity is held over the flats between Neille Point and Hole's Hole." Our observations were made about midway between Saltash Bridge and Neal Point (7·7 km. from mouth of estuary), a position chosen because it lies near the middle of the area under consideration and in a fairly straight stretch of the river. Collections were taken (at hourly intervals) at nine points, marked by buoys, in the cross-section—one in mid-river and four in each of the intertidal areas from high-water mark to low-water mark. Sampling was done by means of a reversing bottle at ½ or 1 m. intervals from the bottom to the surface. Salinities were determined with immersion hydrometers and temperature corrections made. Depth was plotted against time for each of the nine stations and, upon these, isohaline curves were superimposed by means of salinity-depth curves; finally isohalines on a cross-section of the river at intervals of 1 hr. were drawn as in Fig. 1.

It is seen that on a rising tide the Cornish margin is a little less saline than the Devon, and on a falling tide the reverse is true. This lag may be explained by the contour of the river and does not alter the general fact that when the tide is rising there is an "up-bulging" of the more saline layers from the bottom in the middle; and when it is falling there is a "down-bulging" of the less saline or fresh layers of the river. This bulging is produced by friction at the edges, where the water is shallow, tending to retard water movement in that region as compared with the middle or deeper part. It must be remembered that the bulging is exaggerated in Fig. 1 owing to the differences between the horizontal and vertical scales.

Owing to this bulging the surface water tends to be a little more saline in mid-river than at the edges at high water, and *vice versa* at low water. Fig. 1 shows that, in this region of the estuary, salinity stratification in mid-river at low water is much more pronounced than at high water, the range being greater though the salinity is less. The action of the river interferes slightly with the usual tidal oscillation.

It would be interesting to know the magnitude, range and duration of

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* In these reports, following recent Ordnance maps, the spelling "Neal" is adopted.

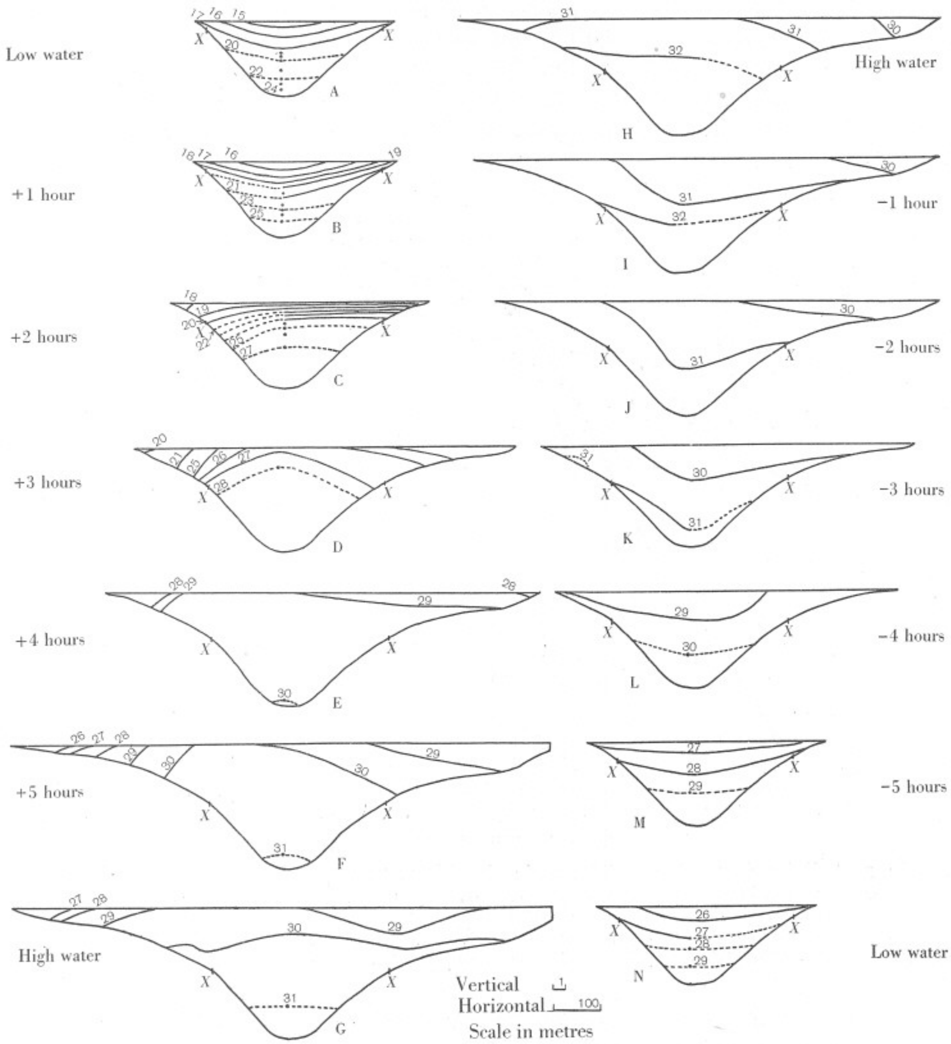

Fig. 1. Isohalines on a cross-section of the Tamar Estuary (midway between Saltash and Neal Point). *A–G* on May 24, *H–N* on June 3 1937. *X* is low-water mark of equinoctial spring tides. Cornwall to the left, Devon to the right of each section. Dotted lines indicate insufficient data—sometimes only one record at the level in question. Single dots between isohaline curves indicate intermediate salinities, e.g. in Section A two dots between isohalines 17 and 20 show the levels in mid-river at which salinities of 18 and 19°/₀₀ were obtained. The sections represent conditions at hourly intervals between high and low water.

incidence of salinities experienced by organisms at various points on the estuary bed over a period of several years. The work attached to such an investigation is not practicable, but some insight into the problem may be got by a study of data compiled from Fig. 1 (see Fig. 2 and Table I). The positions chosen were (*a*) bottom mid-river, (*b*) mean high water of spring tides, (*c*) mid-tide mark, and (*d*) mean low water of spring tides. The fluctuation in the water layers above bottom mid-river need not be studied because this region is inhabited principally by plankton which moves with the currents and therefore stays in water of more or less suitable salinity. The only animals of importance in this region are fishes which can avoid low salinities by going deeper, and also the organisms living on the mid-river buoys (the latter are dealt with in Part IV of this series). Fig. 2 is drawn from data obtained on the Devon shore on May 24; the conditions on the Cornish bank were similar.

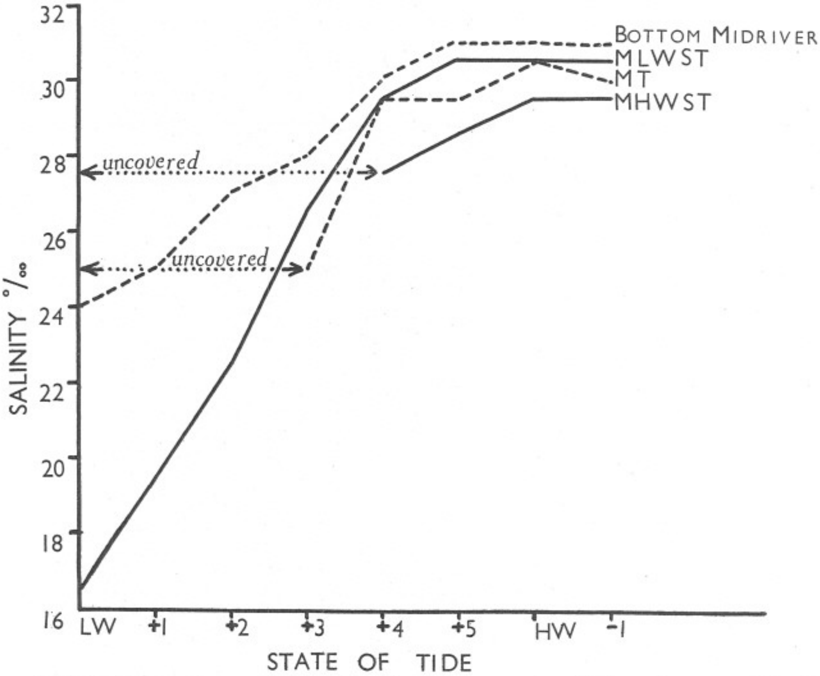

Fig. 2. Salinity fluctuation at different levels. May 24 1937. Midway between Saltash and Neal Point, Devon bank. The periods during which H.W.M. and M.T. mark are uncovered by the tide are indicated. M.L.W.S.T. is mean low-water (mark) of spring tides. M.H.W.S.T. is mean high-water (mark) of spring tides. M.T. is mid-tide mark. L.W. is low water; H.W. is high water. Numbers 1–5 represent hours.

In this section of the estuary, near high-water mark, organisms suffer least fluctuation, and those near low-water mark suffer most; while those at mid-tide mark experience a fluctuation intermediate between these two. That is, there is a fluctuation gradient decreasing from low-water mark to high-water mark. An organism at low-water mark experiences the greatest and least salinities possible in the intertidal area and indeed in the entire estuary bed; at high-water mark, while the fluctuation is very much less, it is important to note that it is also in the higher end of the salinity range. On proceeding from low-water mark to high-water mark the upper limit of the salinity range falls only very slightly, while the lower rises considerably. Thus the higher the level in the intertidal area at which an organism lives the more favourable the salinity conditions it will meet.

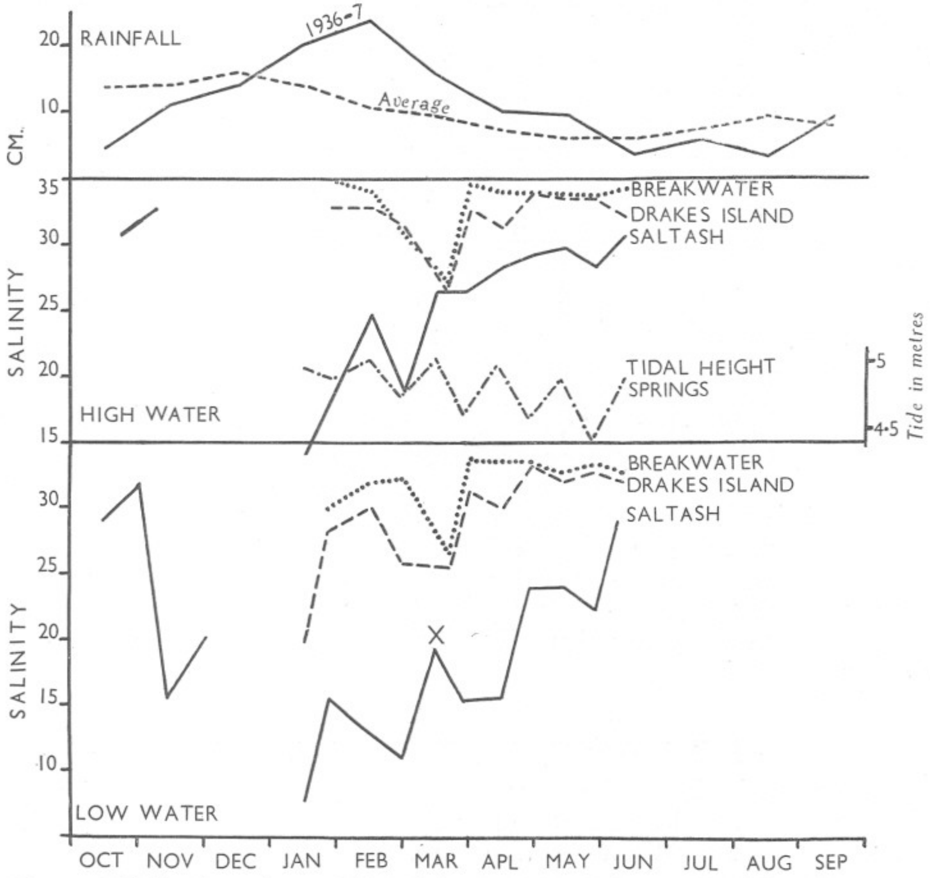

Fig. 3. Salinities for springs at high and low water—a continuous record from January to June 1937. Tidal height in metres. Total monthly rainfall for Tamar Valley Area (average of eight stations) 1936–7; and normal average monthly rainfall for Egloskerry (one of these stations). Point *X* is referred to in the text.

Another aspect of possible biological importance is the duration of the period of fluctuation. Near high-water mark, not only is the fluctuation smaller than at points lower in the intertidal area and higher in the salinity range, but organisms are subjected to fluctuation for a shorter time. Owing to stratification, the farther down one goes in the intertidal area the longer is the duration of incidence of the high salinity (cf. Figs. 1 and 2); this will be more evident in winter than in summer for stratification is more pronounced in rainy periods.

Fig. 2 shows that organisms at bottom mid-river and at mid-tide mark (in this section of the estuary) experience a salinity fluctuation similar in range. The salinity change at mid-tide mark, however, takes place at approximately twice the rate of the change at the bottom mid-river; therefore the former position would be more dangerous to organisms affected by rate of fluctuation.

At low-water mark the fluctuation was high—from 16 to 30°/₀₀ in about 4 hr.; this was followed by a high, relatively steady salinity (over 30°/₀₀) for 4 hr.; then as sudden a drop as the original rise in another 4 hr. The osmotic changes to which an organism would be subjected are thus considerable, i.e. *ca.* 10 atm. in 4 hr.

The data given in Fig. 2 are for a specific day—May 24 1937, but considering the height of the tide, the rainfall and other factors, they cannot be very far short of normal winter conditions. The series for June 3 (see Table I) must approximate to summer conditions. Fluctuation may be a little less than on June 3 during drought, but it will be appreciably greater than on May 24 during a winter spate. Some indication of the maximum and minimum salinities for the season in question may be gained from Fig. 3 and data given on pp. 538–9. The effect of these positional fluctuations on the horizontal up-river penetration of marine organisms will be discussed in a later paper.

SEASONAL SURFACE VARIATIONS IN SALINITY

In an investigation of the fauna and flora of the mid-river buoys it was found necessary to have some idea of the surface salinities in mid-river. They were taken at a depth of 1 ft. (0·3 m.). At high and low water of spring tides samples were regularly taken at three positions in the estuary (Table II) and supplemented by open-sea observations taken at the same time. At spring tides the maximum and minimum salinities (river-flow and wind being normal) may be expected since it is at this time that the sea advances and recedes farthest in any estuary.

Saltash No. 15 Mooring Buoy (6 km. from mouth), and Drake's Island, No. 1 Mooring Buoy (− 2·5 km. from mouth), were taken always at exactly high and low water; Breakwater, No. 1 Mooring Buoy,* within 90 min. on either side of the tide on the few occasions on which the times of collection did not coincide

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* Position outside the area covered by the map of the estuary: it is well out in Plymouth Sound, 2 km. due S. of the W. end of Drake's Island.

TABLE I. SALINITY ‰ AT VARIOUS POINTS ON THE ESTUARY BED

At hourly intervals between High Water (H.W.) and Low Water (L.W.)

	Mean low-water mark of spring tides		Mid-tide mark		Mean high-water mark of spring tides			
State of tide	Devon bank	Cornish bank	Devon bank	Cornish bank	Devon bank	Cornish bank	Bottom mid-river	Date
L.W.	16–17	17–18	...	...	...	...	24	May 24 1937
+1	19–20	18–19	...	...	...	...	25	
+2	22–23	19–20	...	...	...	...	27	
+3	26–27	26–27	25	20–21	...	...	28	
+4	29–30	29–30	29–30	29	27–28	26	30	
+5	30–31	30–31	29–30	29–30	28–29	26–27	31	
H.W.	30–31	30–31	30–31	30	29–30	28–29	31	
−1	30–31	30–31	30	30	29–30	27–28	31	
H.W.	31–32	32	30–31	31–32	29–30	31	32·5	June 3 1937
−1	31–32	32	30–31	31–32	29–30	31–32	32	
−2	31	31–32	30–31	31–32	29–30	30	32	
−3	30–31	31	29–30	30–31	...	...	31·5	
−4	29–30	29–30	...	...	...	...	30	
−5	28–29	28	...	...	...	...	29·8	
L.W.	26–27	27	...	...	...	...	29·9	

TABLE II. HIGH- AND LOW-WATER SURFACE SALINITIES AND TEMPERATURES AT SPRING TIDES

Samples taken at 1 ft. (0·3 m.) below surface

		Breakwater No. 1 Mooring Buoy		Drake's Island No. 1 Mooring Buoy		Saltash No. 15 Mooring Buoy	
Date 1937	State of tide	Salinity ‰	Temp. °C.	Salinity ‰	Temp. °C.	Salinity ‰	Temp. °C.
Jan. 16	H.W.	...	...	...	...	14·0	...
	L.W.	...	...	19·5	...	7·6	...
Jan. 29	H.W.	34·9	8·9	32·7	8·9	18·2	7·0
	L.W.	29·7	8·1	28·1	8·9	15·6	8·5
Feb. 15	H.W.	34·0	9·85	32·7	9·6	24·6	9·5
	L.W.	31·7	9·8	29·8	9·5	12·9	10·5
Mar. 1	H.W.	30·7	8·4	31·1	8·5	18·9	6·5
	L.W.	32·0	8·95	25·6	7·6	10·8	6·5
Mar. 19	H.W.	26·9	9·4	26·4	9·0	26·4	8·0
(Saltash, Mar. 16)	L.W.	26·6	9·0	25·3	9·1	19·3	7·25
Apr. 1	H.W.	34·5	9·2	32·5	8·4	26·4	7·0
(Saltash, Mar. 30)	L.W.	33·6	9·2	31·1	8·6	15·3	6·5
Apr. 14	H.W.	33·8	10·4	31·1	10·0	28·2	9·5
	L.W.	33·4	10·6	29·9	10·8	15·4	11·5
Apr. 29	H.W.	33·7	10·8	33·7	11·2	29·1	11·0
	L.W.	33·4	11·3	33·3	12·1	23·8	12·0
May 14	H.W.	33·6	11·1	33·4	12·1	29·7	13·0
	L.W.	32·5	12·1	31·8	12·0	23·8	13·2
May 28	H.W.	33·5	13·1	33·4	13·2	28·3	18·0
	L.W.	33·1	14·1	32·5	14·4	21·3	20·0
June 11	H.W.	34·1	14·1	32·0	14·2	30·5	16·0
	L.W.	32·5	16·1	31·8	16·1	28·7	17·5

with high and low water. When samples were not taken on the exact date of springs, they were taken when the tide was still of spring magnitude according to the tide-table.

At a position about half a mile above Hamoaze Buoy No. 15 the following differences in the salinity of the surface layers were noted:

	Salinity (‰) difference between					
	Surface and 0·9 m.			Surface and 1·8 m.		
Date	Max.	Min.	Mean	Max.	Min.	Mean
May 24	1·9	0·0	0·59 ± 0·22	3·4	0·0	1·55 ± 0·50
June 3	1·1	0·0	0·24 ± 0·14	1·2	0·0	0·41 ± 0·16

These figures are a summary of conditions at hourly intervals from high to low water. It has been pointed out farther back that the data for May 24 may be taken as (roughly) representative of a condition not far short of normal winter condition, and that of June 3 as normal summer. The differences from the surface salinity are small in the first two metres and almost negligible in the first metre. Moreover, the differences between the salinity at the surface and the depths mentioned become less and less on proceeding seaward, till in the Sound, under the worst winter conditions, they are practically non-existent.

Fig. 3 and Table II show the fluctuation in salinity at 6 hr. intervals at each position. There is a fluctuation gradient increasing up-river from the seaward end of the estuary. Not only does the fluctuation increase in range in the up-river direction, but it also moves down in the scale of salinities—both high- and low-water salinities become less (as might be expected) and the low-water salinity decreases to a greater extent than the high-water salinity. The fluctuation is very great at Saltash.

The greatest and least *differences* between the mid-river surface salinity at high water and the succeeding low water are:

	Greatest difference	Least difference
Saltash	12·8‰ (9·0 atm.)	1·8‰ (1·5 atm.)
Drake's Island	5·5‰ (3·5 atm.)	0·2‰ (—)
Breakwater	5·2‰ (3·5 atm.)	0·3‰ (—)

Figures in brackets are the resulting changes of osmotic pressure (corrected for temperature at the prevailing salinities).

The lowest low-water and the highest high-water salinity recorded during January to June, 1937, are (‰): Saltash, 7·6 and 30·5; Drake's Island, 19·5 and 33·7; and Breakwater, 26·6 and 34·9.

Here we have discussed spring tides as most likely to produce maximum and minimum salinity; but high and low values may sometimes be produced during neaps depending on the rainfall and wind.

October 1936 was an exceptionally dry month and although rainfall increased towards the end of the month it was still below average. During the last week of the month a daily observation of surface salinity at high water and low water was made (Fig. 4) at Weirquay. There is an indication of greater fluctuation at springs than at neaps; and even in dry weather the fluctuation is very great. Fluctuation is greater and has a longer duration of incidence on a buoy than at a corresponding point intertidally (extreme low-water mark excepted).

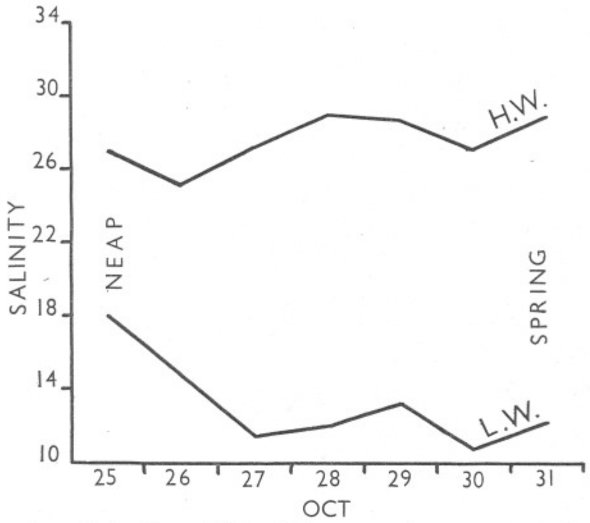

Fig. 4. Daily surface salinity °/₀₀ at high and low water from neap to spring at Weir quay.

The regular sampling of surface salinities was carried out from January to June 1937, but five other spring tide observations were taken during October, November and December 1936 (see Fig. 3).

Rainfall and Salinity

Since rainfall influences salinity, the average total monthly rainfall from October 1936 to September 1937 is also given in Fig. 3. These values have been compiled from data supplied by the Cornwall Rainfall Association from eight stations distributed in the Tamar Valley area. Unfortunately the normal average for the area is available for one only of these eight stations, namely Egloskerry; this, for lack of better, has been included in Fig. 3 as illustrative of the normal average. Rainfall was extraordinarily high in the winter of 1936–7. Mr A. Pearse Jenkin, secretary to the Association, notes that at Redruth in Cornwall the rainfall for the first four months of 1937 was practically equal to the normal fall for the first eight months of the year.

On comparing the rainfall curve with the salinity curves in Fig. 3 it will be seen that there is a noticeable lag between excessive rainfall and salinity depression. That the salinity curves are irregular is explained by the fact that wind and tidal height affect water movement also. For instance at point *X* (Fig. 3) salinity at low water is higher than might be expected taking tidal height and rainfall into account—it ought to have been at least 5°/₀₀ lower. Water movements in the Tamar Estuary are affected by winds from about S.S.W. through S. to S.E. tending to pile water up-river; and winds from the opposite directions tending to push water down-river. At the point *X*, which was on March 19 1937, the Plymouth Meteorological Report gives:

March	Wind direction at 9 a.m.	Velocity at 9 a.m.	Greatest velocity during preceding 24 hr.
18	S.S.W.	25 m.p.h.	49 m.p.h.
19	S.S.W.	18 „	45 „
20	S.E.	12 „	32 „

Thus the high salinity recorded at low water was due to the tide being prevented from flowing out to its fullest extent, even though it was a 5 m. tide. The effect of a continued southerly wind is to prevent the ebb flowing completely out of the estuary basin and to pile up the next flow still farther. If river level, tidal height and wind were known, other anomalies could be explained.

OTHER SURFACE AND BOTTOM RECORDS OF SALINITY

Many samples were taken in the estuary of the River Tamar during the course of other work; these are not easily tabulated, but the following is a brief summary, from over 100 records, given in round figures for the sake of clarity; they are included for the use of other workers in this series. When considering mud-dwelling animals, it must be remembered that the salinity of interstitial water is always higher, usually much higher, than that of the overlying water (Tees Survey, 1935; Reid, 1930, 1932). For depths at the various stations see Part I of this series.

Hamoaze near the outlet of St John's Lake (1·5–2 km. from mouth).

In a normal winter the surface salinity at low water varies from 34 to 20°/₀₀; while at high water it varies from 35 to 30°/₀₀. Bottom salinity is generally well over 30°/₀₀ at all states of the tide. In the exceptionally rainy months of January and February 1937, high-water salinities such as 14, 18 and 24°/₀₀ were recorded at the surface. In a normal summer, salinities are not much below open sea condition, and the lowering at low water is naturally much less than in winter.

Saltash (6·8 km. from mouth).

Fig. 3 and Table II give records of surface salinity in all sorts of conditions of spring tide, rainfall and wind, summer and winter. Fig. 1 and Table I, which refer to a station midway between Saltash and Neal Point, gives bottom and intertidal values in what might almost be taken as normal summer and winter conditions. The only other records available for Saltash are bottom salinities for the months of October, November and December of 1936 when the rainfall was only a little below the normal for winter: high water, 30–35$^{\circ}/_{\circ\circ}$; low water, 25–32$^{\circ}/_{\circ\circ}$.

Neal Point (9 km. from mouth).

In a normal winter, surface salinity at low water varies from about 7 to 26$^{\circ}/_{\circ\circ}$; while at high water it ranges from 12 to 29$^{\circ}/_{\circ\circ}$. Bottom salinity is from 24 to 32$^{\circ}/_{\circ\circ}$. Values as low as 4–7$^{\circ}/_{\circ\circ}$ have been recorded for low-water surface in January and February 1937. In a normal summer, high-water surface may be as high as 33$^{\circ}/_{\circ\circ}$.

Weirquay (13 km. from mouth).

In a normal winter, surface salinity at low water may fall to 1$^{\circ}/_{\circ\circ}$, and high water is quite commonly 23$^{\circ}/_{\circ\circ}$. Bottom salinity may be 16–25$^{\circ}/_{\circ\circ}$ at low water, though in excessively rainy periods it will fall much lower. In a normal summer, high-water surface salinity may reach 26$^{\circ}/_{\circ\circ}$.

Pentillie Quay (16·5 km. from mouth).

In a normal winter the surface salinity at low water ranges from less than 1$^{\circ}/_{\circ\circ}$ up to 5$^{\circ}/_{\circ\circ}$; at high water the surface is from 5 to 16$^{\circ}/_{\circ\circ}$. The lowest record from the bottom was 2$^{\circ}/_{\circ\circ}$, though the water may be almost fresh for a short time during a heavy spate. The normal summer surface salinity may reach as high as 24$^{\circ}/_{\circ\circ}$ at high water.

Percival (1929) also gives high-water surface salinities for a dry summer at all these stations.

Attention may here be drawn to the presence of a thin "skin" of practically fresh water on the surface at the upper stations for a short time immediately after an excessive downpour of rain.

Spate waters from the Plym affecting the Sound.

The Plym brings down large quantities of china-clay in colloidal form which give the water a milky appearance. If the wind is from the south, this clay water may be seen on the surface covering an area bounded by a line drawn through the north end of Rum Bay, No. 1 Mooring Buoy Drake's Island, and the bathing pool just below the Laboratory. On January 13 1937, a surface sample just inside this area had a salinity of 16·2$^{\circ}/_{\circ\circ}$ as compared with a salinity of 28·2$^{\circ}/_{\circ\circ}$ on the surface just outside the area (the two sampling stations about 30 m. apart near Drake's Island).

Temperature of the Surface Waters

Morning high-water and afternoon low-water temperatures for springs—at about 8 a.m. and 2 p.m. respectively—were taken fortnightly with standardized thermometers from January to June 1937 at 1 ft. below the surface (0·3 m.) at Saltash, Drake's Island and Breakwater in "mid-river" (Table II); temperatures were also taken at various positions in the open sea beyond the Breakwater. Fig. 5 contains only the Breakwater and Saltash average (between morning and afternoon) temperatures, for the sake of clearness.

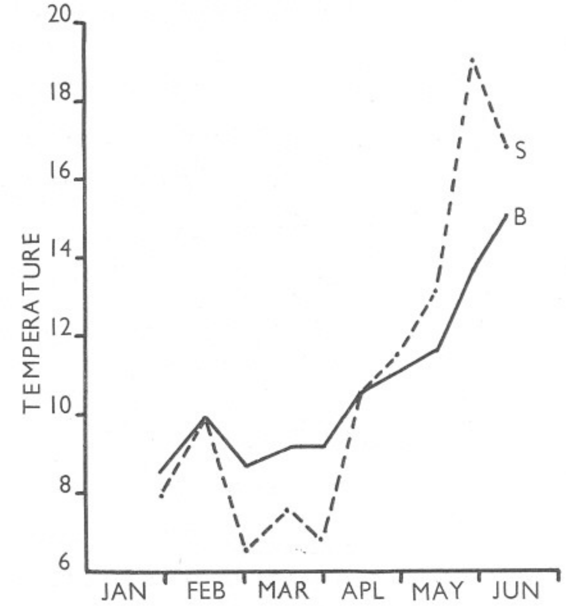

Fig. 5. Temperature (°C.) of surface waters at the Breakwater (*B*) and Saltash (*S*). This is the average between high-water (morning) and low-water (afternoon) temperature at 1 ft. depth (0·3 m.).

In the winter sometimes the morning and sometimes the afternoon temperature was the higher; in the summer the afternoon temperature was always the higher. The differences between morning and afternoon tend to be least at the Breakwater and greatest at Saltash; they vary from 0·0 to 2·0° C., and are greatest in summer.

Temperatures at Saltash were lower in winter and higher in summer than at the Breakwater (Fig. 5). Breakwater temperatures approximate to open sea temperatures; they show only a slight increase in range. Drake's Island records are similar to those at the Breakwater with a small increase in range; the bottom end of the range is lower—showing a decided tendency towards the Saltash condition. Thus we see a gradient from open sea to Saltash, with the smallest range in the former and the greatest in the latter.

The temperature records given are not to be taken as absolute maxima and minima for the period in question; they are intended only as an indication of the conditions prevailing. Maximum ranges recorded were:

Breakwater	8·1–16·1° C.
Drake's Island ...	7·6–16·1° C.
Saltash	6·5–20·0° C.

There must be violent fluctuation in temperature, at least in the marginal waters if not in mid-river, when on a hot day the water runs in over the exposed mud-flats. In mid-river, however, the greatest changes in a fortnight were: Breakwater, 3·0° C., May–June; Drake's Island, 2·9° C., May–June; and Saltash, 7·0° C., May. The temperature increases gradually from winter to summer. Day-to-day fluctuations in temperature were not measured.

Taken alone temperatures may have only a very small effect, but in conjunction with salinity their influence is much increased (cf. Huntsman, 1918) and this combined influence increases in the up-river direction. In estuaries farther north, such as the Dee in Aberdeenshire, very big fluctuations due to the mixture of the relatively warm sea water and large quantities of melted snow may be expected in winter; in such localities, low temperature might be of more importance as a limiting factor than in the Tamar.

HYDROGEN-ION CONCENTRATION

The Tamar draws much of its water from peat moor, but sea water is so well buffered that there was little evidence of acidity in the surface waters (at least in that section of the Tamar under consideration) on April 27 1937 when rainfall was of normal winter order, as shown below:

High water at 8 p.m. Samples from 1 ft. depth (0·3 m.). *p*H corrected for salt error.

Position	Time	*p*H	Salinity (°/₀₀)
Pentillie	12 noon	7·54	9·8
Saltash	6.40 p.m.	8·18	29·7
St John's Lake (Hamoaze end)	7.05 p.m.	8·23	32·4
Drake's Island	7.30 p.m.	8·15	33·9

No continuous survey of *p*H was taken.

Thanks are due to Dr H. B. Moore for help in collecting of cross-section samples.

SUMMARY

An attempt has been made to give the range and rate of fluctuation of salinity (and, to a lesser extent, of temperature) that organisms experience at various points on the bed of the lower Tamar Estuary and in the overlying water—especially near the surface. Such work until now does not seem to have been attempted. The following general facts emerge: On proceeding from high-water mark to low-water mark there is an increase in the range, rate and duration of fluctuation in salinity. Also the upper limit of the salinity range rises very slightly while the lower limit falls by a large amount, i.e. there is a more or less uniform gradient from high-water mark to low-water mark. Near high-water mark the fluctuation is less and of shorter incidence and is distributed over a higher level of the total salinity range (for the intertidal area) than near low-water mark. Owing to stratification, the farther down the intertidal area the (slightly) longer is the duration of the high salinities, especially in winter. At mid-tide mark the fluctuation is very similar to that on the bottom in mid-river, but is of twice the rate.

Conditions in the surface waters at 1 ft. depth (0·3 m.), as representative of the top metre at least, were also investigated at fortnightly intervals summer and winter. Samples were taken at springs as being most likely to give an indication of maxima and minima, though wind, tidal height and river level may on occasion combine to give maxima and minima at neaps. As the average salinity decreases up-river the range of fluctuation increases. While both high- and low-water salinities fall, the latter falls more rapidly.

Rainfall in the winter of 1936–7 was exceptionally heavy and there is a noticeable lag between excessive rainfall and depression of salinity.

Rather more scanty data of salinity at various other stations in the region under consideration in this series are given for the use of other workers in the series.

Temperature records for surface waters in summer and winter at springs show that on proceeding up-river (1) there is a slight daily fluctuation in mid-river, (2) there is an increase in the annual range, i.e. the farther from the sea the colder it is in winter and the warmer in summer.

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The Association was founded in 1884 at a meeting held in the rooms of the Royal Society of London with Professor T. H. Huxley in the chair. Amongst distinguished scientific men present on that occasion were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester, who was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £16,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Resident Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter and in September, and marine animals and plants are supplied to educational institutions.

Research work at sea is undertaken by the steam drifter "Salpa" and by a motor boat, which also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	*s.*	*d.*
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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