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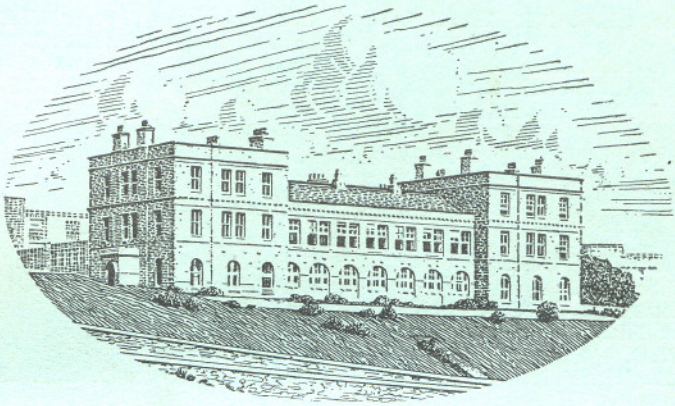

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Stanley Kemp.

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STANLEY WELLS KEMP

1882–1945

Stanley Kemp, Sc.D., F.R.S., Secretary of the Marine Biological Association of the United Kingdom and Director of the Plymouth Laboratory, died on 16 May 1945 at the age of 62. His death at the height of his power has come as a most grievous blow to both marine science and zoology in general.

It was typical of his character that he hated anything in the nature of exaggeration; knowing how strongly he felt this, I must be particularly careful in the use of words, yet, to give a true impression, the fact must be recorded that so many on first hearing of it used the word disaster to describe the effect of his loss upon our science. We all felt it as a calamity; he was our undisputed leader. Before becoming Director at Plymouth he had organized and led the expeditions of the *Discovery* Investigations, the greatest oceanographical enterprise since the voyage of the *Challenger*. At the time of his death he was the inspiration of so many plans, not only for the development of the Plymouth Laboratory emerging from the blast of bombardment, but for the future of home and empire fisheries and of oceanography in general. His sound judgement will be equally missed in the councils of pure zoology.

I have stressed first our sense of the loss of a great leader—but he was also a great friend, beloved by so many and by all who served under him.

Future generations might wonder what was the secret of his outstanding position: his scientific publications were in the main in a somewhat restricted field of zoology, he was not a writer of books and he always shunned publicity. We, his contemporaries, and particularly those who served under him, know what it was: it was not an autocratic power but an exceptional capacity for a most energetic devotion to the task in hand, the example of which compelled all his followers to action. There was no parade of this unselfish devotion, no Dedication to Duty atmosphere; he just went full steam ahead carrying everyone with him: as someone aptly said, 'he put through the big and difficult jobs without any fuss or heroics'. Kemp's lasting monument will be the great series of *Discovery Reports* (now in volume XXIV with many more likely to come); the foundation of this work and so much of its achievement is due to his energetic planning and leadership, yet characteristically his name as author (and each time as joint author) appears on only three of the *Reports* so far issued. He was the spirit behind it all, filling his time with making perfect the many sides of organization and so willing to give the kudos of authorship to all his staff. How in his modesty he would hate to hear all this said! I can almost hear him now replying to a speech I made in his praise at a dinner when he left the *Discovery* Directorship to become Director at Plymouth; instead of the thanks I had expected for my words, with a pretence at scorn but with a

The plate is from a photograph taken by Dr J. H. Welsh of Harvard University, who has kindly given permission for its reproduction.

twinkle in his eye for my benefit, he dismissed them as: 'This nauseating eulogy.'

With this introduction I will now attempt to sketch his life, and in doing so acknowledge much information kindly provided by his friends. He was born on 14 June 1882, the son of Stephen Kemp, F.R.A.M., who was an eminent pianist and Professor at both the Royal Academy and Royal College of Music. He was educated at St Paul's School and Trinity College, Dublin. A keen naturalist from early youth, his first love was entomology: a love indeed he never lost; it was a great joy to him that his daughter Belinda followed in his footsteps in this, and he once confided to me that it gave him particular pleasure because it provided him with an excuse for once again indulging in the delights of butterfly hunting. With her I believe he collected all the British butterfly species, and later turned to beetles. But to return to his youth, his gift for organization was evident from early days: he paid his small sisters a farthing for each caterpillar they brought him! Water beetles and dragonflies were a particular interest. As a schoolboy he built an aquarium on perhaps a somewhat ambitious scale at the top of the house, but alas, when filled, the water pressure proved too much for its sides; it came asunder and the flood penetrated to every floor below.

At Trinity College, Dublin, Kemp had a distinguished University career graduating in 1903 with a 1st Senior Moderatorship (Gold Medal) in Natural Science, with Zoology as his special subject.

His very active life may now be divided into four distinct phases: in the Irish fishery service from 1903 to 1910; as a zoologist in India from 1910 to 1924; Director of the *Discovery* Investigations from 1924 to 1936; and Director of our Plymouth Laboratory from 1936 to the time of his death.

Kemp was appointed Assistant Naturalist in the Fisheries Branch of the Department of Agriculture and Technical Instruction of Ireland as soon as he had graduated in 1903. At this time E. W. L. Holt, then Scientific Adviser to the Fisheries Branch, was organizing a series of cruises with the fishery cruiser *Helga* (later called the *Muirchu*) to explore the life of the continental slope to the west and south-west of Ireland from 300 to 1000 fathoms. In this work Kemp took a prominent part, gaining a thorough practical knowledge of marine zoology and oceanographical methods. From this experience he contributed the valuable section on the equipment of yachts for marine investigations in Fowler's well-known volume, *Science of the Sea*. His first zoological paper was on the echinoderms of the coast of Galway and of the deeper water to the west, but it was the decapod Crustacea, particularly the *Natantia*, that claimed his main interest, and in these he has always been our leading authority. In this period he was the author of a series of papers in the *Scientific Investigation Reports* of the Irish Fisheries: 'The occurrence of the genus *Acanthephyra* in the deep water off the west coast of Ireland' (1905); 'Macrura from the west coast of Ireland' (1906); 'Decapoda' (1907); 'The Decapoda *Natantia* of the coasts of Ireland' (1910), containing detailed figures of all

known Irish species; 'The decapods of the genus *Gennades* collected by H.M.S. *Challenger*' (1909); 'The Decapoda collected by the *Huxley* from the north side of the Bay of Biscay in August' (1910); and 'Notes on the Photophores of decapod Crustacea' (1910). The magnificent collections of deep-water life made later under his leadership on the R.R.S. *Discovery* and the R.R.S. *Discovery II* are in no small measure due to his early experience of work over the Irish continental slope. For some few years before his death he was advocating and eagerly looking forward to taking part in a renewed investigation of this deep-water fauna to the west of Ireland; this he had hoped to organize soon after the war. He felt strongly that this field, so rich in interesting problems and relatively so near at hand, was worthy of a much closer attention by our marine biologists; it is to be hoped that it may not be long before his lead may be followed.

In 1910 Kemp accepted the appointment of Senior Assistant of the Zoological and Anthropological Section of the Indian Museum, which was later, in 1916, reconstituted as the Zoological Survey of India. Here he took up again the study of the Crustacea, continuing the work begun by Mr J. Wood Mason and Colonel A. W. Alcock on the Indian Decapoda. During his fourteen years in India he wrote a series of seventeen papers under the title of 'Notes on decapod Crustacea in the Indian Museum' (1910–1925). Other crustacean papers were his 'Notes on Asiatic species of the Crustacea *Anostraca* in the Indian Museum' (1911); 'An account of the Stomatopoda of the Indo-Pacific region' (1913); 'The pelagic Crustacea Decapoda of the Percy Sladen Expedition in the *Sealark*' (1913); 'On a collection of stomatopod Crustacea from the Philippine Islands' (1915).

It was an excellent policy of the Indian Museum, and later of the Zoological Survey of India, that its officers should spend a part of every year studying and collecting animal life in the field. Kemp made many such expeditions. In 1911 he visited the Kumaon Lakes in the lower ranges of the Western Himalayas at altitudes ranging from 3600 to 6400 feet. In November of the same year he accompanied the Abor Expedition to the region where Assam and Tibet meet on the north-east of India. It was on this expedition that he discovered a species of a new genus of peripatus which he described under the name of *Typhloperipatus williamsoni*.

In 1913 and 1914 he visited the extreme south of India, making collections around Pamban and Rameswaram Islands and on the mainland at Mandapam and Kilakarai; also in 1914 he assisted Dr Annandale in an investigation of the Chilka Lake in Orissa.

In 1915 Kemp was collecting on the tropical coral reefs of the Andaman Islands, where the wealth of the fauna made a great impression on him, and later in the same year he visited the Sundarbans to investigate the life of the Matlah River and Gangetic Delta.

He became Superintendent of the reconstituted Zoological Survey of India in 1916. He was for a time on war work in which he took a prominent

part in an investigation to see if the water-snails of India could become infected with the larvae of the parasitic trematode *Schistosoma* (*Bilhartzia*). Since many Indian soldiers returning from service in the Middle East were suffering from schistosomiasis, it was feared that they might introduce the disease into India, where it was hitherto unknown. Fortunately none of the Indian snails was found to become a carrier of the larvae. In 1918 he made an expedition with Dr Annandale into Seistan and Baluchistan. It would indeed take a large book to describe his many and varied activities during his period in India. Here I must be content merely to give some indication of his remarkable and tireless energy as a field worker, and conclude it with but a reference to two other expeditions: another visit to the coral reefs of the Andaman Islands in 1921 and an outstanding exploration of the Siju Cave in the Garo Hills of Assam in 1922. The results of these many expeditions are, like most of his Indian crustacean papers, published in the volumes of the *Records* of the Indian Museum.

In 1924 he was offered and accepted the Directorship of the *Discovery* Investigations. Before leaving this Indian section of his life, there are other important events to record apart from his zoological activities. In 1913 he married Miss Agnes Green, a daughter of that very remarkable man, the Rev. William Spotswood Green, C.B., whose versatility enabled him to be a country rector, a world traveller and the first climber of Mount Cook in New Zealand, an author of books on mountains and glaciers, and in addition Government Inspector of the Irish Fisheries (Kemp's former chief). The daughter of so active a father became the wife of an equally energetic husband, and her understanding of his passion for work contributed in no small measure to his great achievement. So many of us know what a very happy partnership they made, and have enjoyed such a kind and generous hospitality at their home.

In the same year as his marriage he received two honours: he was elected a Fellow of the Asiatic Society of Bengal (a select fellowship limited to fifty) and also a Fellow of Calcutta University. In the Asiatic Society, which he had joined as a member in 1910, he became Honorary Librarian in 1916 and Member of Council in 1917; during these years he performed a great service to those doing research in Calcutta by compiling a catalogue of all the serial scientific publications in the twenty libraries of the city, giving references to more than 3000 volumes. When on leave in 1919 he was granted the degree of Sc.D. by his old university, Trinity College, Dublin.

Now came the period of his greatest achievement when he returned in 1924 to become the first Director of Research in the *Discovery* Investigations. It was in the spring of that year that I first met him; I had had the great privilege of becoming his Chief Zoologist at the same time. I shall never forget the evening I spent with him at his London hotel after we had both been appointed: the first of so many happy nights (and days) of eager planning and discussion, the first meeting with so great a friend. 'Dr Kemp was tall and

finely built with a quiet but most powerful manner; this was combined with a sense of humour and a gift for genuine friendship. No finer leader and no better companion for a long and lonely voyage in Sub-Antarctic waters could be imagined.' I have quoted from the obituary notice in *The Times* (18 May 1945); it is I think a perfect description of him.

There may be little need to outline in detail the aims of the *Discovery* work, which must be familiar to every reader; yet it may be fitting to give space to some actual quotations from 'The Objects of the Investigations', written by Kemp himself as an introduction to Volume 1 of the *Discovery Reports* published in 1929. They will remind us vividly of the scale upon which he planned; while these were the authorized plans of the *Discovery* Committee, I am sure they would acknowledge them to be largely *his* plans.

The proposal to send a scientific expedition to Antarctic waters was initiated by Mr E. R. Darnley, Chairman of the present Discovery Committee, rather more than ten years ago. The proposal had in view the systematic exploration of all the economic resources of the Dependencies of the Falkland Islands, but the main reasons for it are to be traced to the very rapid development of the whaling industry in those Dependencies, and to the fears which arose that this industry, like others formerly existing in both northern and southern hemispheres, would prove shortlived. For this reason the investigations undertaken bear mainly on the bionomics of the whales upon which the industry is based. The desirability of executing coastal surveys in the interests of the vessels which navigate these dangerous and largely uncharted waters was also realized....

The main object of the work was thus to obtain further information on whales and on the factors which influence them....

It was realized at the outset that a great deal of valuable information could be obtained by examination of whales brought in by whale-catchers. The precise identification of the common southern rorquals could not be regarded as definitely settled, for though it was generally recognized that the Blue and Fin Whales of the southern ocean closely resembled those to which the same names had been applied in the north, the possibility that the southern forms might represent a distinct race could not lightly be dismissed. Some might think this a question of purely zoological interest, but it must be pointed out that it has a very definite bearing on the economic aspect of whaling. If the rorquals in the south can be shown to be racially distinct from those which live in the north some degree of isolation of the two stocks may be inferred, and conversely, if no such distinction exists, some intermixture of these stocks is rendered probable. In dealing with migratory animals such as whales accurate knowledge on this point cannot fail to be valuable. It may set a limit to the area through which the southern stock ranges, and it will inevitably be of importance in studies of migration. This problem of the racial identity of southern whales is being attacked mainly by statistical methods.

In the economic study of any mammalian stock there are certain elementary facts which must be thoroughly understood before progress can be made. Among the more important are the rate of growth, the age at sexual maturity, the time of pairing, the period of gestation, the number at a birth, the length of the suckling period and the nature of the food. In whales most of these facts are less easily ascertained than in other mammals and the information already available was very deficient. By special anatomical investigation it is, however, possible to obtain results which will throw much light on such questions, and the Committee consequently decided to build a laboratory at South Georgia....

But work on shore, no matter how intensively it is undertaken, can only give solutions to some of the problems which are involved. It requires to be supplemented by observations at sea, and the principal reason for such research is the necessity for a thorough study of the environment of southern whales. Experience has shown that the hydrological and planktonic methods employed by the International Council for the Exploration of the Sea have been productive of valuable results in the north-east Atlantic and it could not be doubted that equally good results would follow their application in the south. Whaling, like most fisheries, fluctuates greatly from season to season, and the cause of these fluctuations are to be sought in changes in the environment. The food of southern rorquals is now known to consist exclusively, or almost exclusively, of large Euphausian crustaceans, which themselves feed mainly on diatoms. On analogy with conditions ascertained in the north, the seasonal abundance of the Euphausians on the whaling grounds of the Dependencies will be preceded by a period of great reproductive activity in the phytoplankton. The phytoplankton in its turn is dependent on the physical and chemical constitution of the water, and it is to hydrological, and ultimately perhaps to meteorological conditions, that the fluctuations in the whaling industry are to be ascribed.

So much could be inferred from the scientific work which had been done in the north, but much special investigation in the south was needed before theory and fact were brought into accord. The life history of the Euphausian which forms the main food of whales was unknown and no information existed on its relations with the other constituents of the plankton. Knowledge of the southern phytoplankton was limited almost entirely to the specific identification of the various species, and data on the water movements and general hydrology of the south were wholly deficient.

It was accordingly decided to equip a vessel for oceanographic research in southern waters. The *Discovery*, originally built for the National Antarctic Expedition, 1901–3, of which Captain (then Lieut.) R. F. Scott was leader, was purchased and refitted for her new work, and in July 1925, with the consent of His Majesty the King, she was commissioned as the Royal Research Ship *Discovery*....

It is in these investigations that the *Discovery* has been primarily engaged during a commission which lasted two years, but before she left this country the Committee foresaw that the work was likely to be more than a single square-rigged vessel could undertake and that certain other lines of research were beyond her power....

Whales are well known to be migratory animals.... In the economic study of whales it is of the utmost importance that we should have fuller and more accurate knowledge of these migrations.... It is, for obvious reasons, more difficult to mark whales than fish, but as a result of experiments made before the *Discovery* sailed on her first commission, a practicable method was discovered....

In considering the design of a second ship for investigations in the south, the Committee attached great importance to this question of whale-marking. A vessel of comparatively high speed was necessary, built generally on the lines of a whale-catcher, but it was recognized that she would also be required to assist in routine work on plankton and hydrology, and it was also considered desirable that she should carry a full-sized otter trawl for the exploration of certain areas in the Dependencies which might prove commercially profitable.

These varied requirements have been successfully met in the Research Steamship *William Scoresby*. This vessel is named after the celebrated whaling captain, whose *Account of the Arctic Regions*, published in 1820, may be regarded as the first scientific contribution to the study of whaling. The *William Scoresby* was launched at Beverley on December 31, 1925....

The examination of the plankton conditions on the whaling grounds was already an important part of the programme of the *Discovery*, and in deciding what use might be made of occasions for work of a less obviously practical nature it was natural to

consider an extension of these operations. The more strictly economic results were to be sought in the upper layers of the water, and work at greater depths, while it might also prove to have practical value, would without doubt result in a material increase in our knowledge of the biology of southern waters. When opportunity permitted, plankton nets, up to $4\frac{1}{2}$ metres in diameter of mouth, were accordingly used at all depths, and by this means a large amount of valuable material has been accumulated during the two years of the first commission.

An examination of the bottom fauna was evidently less relevant to the main purpose of the work, and it was decided that deep-sea trawling, which necessarily involves a great expenditure of time, could not be undertaken. The *Discovery* was, however, supplied with a 40 ft. otter trawl and dredges, to be used in shallow water when circumstances allowed. The weather in the south is frequently unsuitable for off-shore work, and on a number of occasions the rich bottom fauna of the sheltered coastal waters of the Dependencies has been explored....

The above are but fragments broken from the grand sweep of his conception of what the *Discovery* Investigation should be. The long line of bulky volumes to which this was the introduction show how this great man had the power to convert his conception into accomplished reality. The fact that Scott's famous old *Discovery*, chosen for the work before Kemp was appointed, proved unsuitable for the wide ocean traverses necessary for a full realization of his plans did not discourage him. After the first commission Kemp set to work with renewed enthusiasm to lay down the requirements for the *Discovery II*. The new full-powered steamship sailed on her first commission, again under Kemp's leadership, in 1929: she is acknowledged by all to be the finest research ship ever built. 'After the experience gained in voyages extending over nearly ten years it would be difficult to devise any major improvements', writes Dr Mackintosh who succeeded Kemp as Director in 1936.[1] If it was unfortunate for the stocks of whales that, with the development of pelagic whaling ships, the fishery spread to all the waters round the Pole, it was a gain for oceanography. In the later years the work of the *Discovery II* was extended to cover the whole of the Southern Ocean, bringing back immense collections of plankton and hydrological data from her circumpolar voyages; it is now likely that we know more of the physics, chemistry and planktonic biology of these waters than of any other ocean in the world.

Countless memories come to mind of the months of planning for the first voyage. The old *Discovery*, bought by the Committee from the Hudson's Bay Company in whose service she had sailed since Scott parted with her, was found on a closer examination to require a great deal more reconstruction than was first anticipated; many of the timbers of the hull itself had to be replaced. All hope of sailing in the autumn of 1924 vanished, and it was not until the late summer of the following year that she was completely ready. Trying as were these delays to all of us eager to be off, every moment of the time was spent in preparation.

Kemp, with his ship's scientific staff of four, all worked in a room, none too large, at the top of the Colonial Office. There were J. E. Hamilton, naturalist

[1] *Nature*, Vol. CLVI, p. 42, 1945.

to the Falkland Islands Government, who had just returned to England to join the expedition, the late E. Rolfe Gunther then fresh from Cambridge, H. F. P. Herdman from Belfast, and myself. What a room that was: charts of the ocean, plans of the ship, samples of all kinds of gear filled it to overflowing. There we worked out every detail of the ship's scientific equipment and laboratories. The Marine Station too was designed and equipped to be sent out in advance in 1924 to be erected in South Georgia. With it sailed the shore party: N. A. Mackintosh, J. F. G. Wheeler, L. Harrison Matthews and A. J. Clowes to await our arrival in the South. From all this which might have been confusion, Kemp with his admirable blended qualities of tact, understanding and firmness, distilled an ordered progress. While we each had our different jobs to do, he supervised and discussed every smallest detail. The many new devices of plankton net design, opening and closing mechanisms, etc., described in Volume I of the *Discovery Reports* were invented in that room. Each was drawn to scale on squared paper, discussed, redesigned and redrawn perhaps several times before finally being passed for construction. All the different kinds of log books with their various headings and columns for the entry of hydrological and plankton data, also the many kinds of labels with spaces for the different entries, were evolved after much deliberation and the testing of various kinds of paper in sea water. Nothing was left to chance. It was this attention to small but vital points that contributed so much to the subsequent success in the field. In Kemp we saw the vision and imagination of the planner of a great enterprise combined with a remarkable grip of detail.

I am dwelling on these early days of *Discovery* history not for the history itself, so much has happened since, but to try and illustrate in different ways the qualities of our leader. The ship's reconstruction was hurried towards the end in an attempt to reach the South for the opening of the Antarctic summer season. We sailed from Portsmouth in July 1925 intending to carry out tests off the Bay of Biscay with the new deep-water echo-sounding gear then in its infancy, and to return to let the technical experts land in Falmouth before finally heading south. It proved to be a test of more than the echo gear; by good fortune, as it turned out, we struck a summer gale of unexpected violence in the Bay. The hurried final work on many of the fittings and hatchways were tested and found faulty and leaking as heavy green seas thundered on the decks and sent at times cascades of water into the cabins below. But for this gale we might not have had such a test till we were in the roaring forties of the Southern Ocean. We returned to lie in the river at Dartmouth for two months while she was made perfect. During these two months we saw a Kemp we had not seen before: Kemp the craftsman, the cabinet-maker.

In the former hurry to get the ship to sea so many of the details of laboratory fittings we had carefully designed and specified had not materialized; the essential little table racks for tubes and bottles to prevent breakage in a rolling ship, shelves and brackets to hold this and that upon the walls, racks for whale-

marking guns and many other such things were urgent needs. Under Kemp's guidance we all became workers in teak. His products, beautifully dovetailed and fitting to perfection, might have come from the hands of a Chippendale; they were superb. Mine I always maintained had a certain rustic charm about them: an artistic (if unintended) asymmetry. Cabinet-making—carpentry I'm sure he would call it in his modesty—was a hobby all his life, and Mrs Kemp has told me how the workshop was always quite the most important room in the house. He had made his daughter Belinda a beautiful desk complete with secret drawer; it perished along with all the family belongings in the Plymouth blitz.

Kemp was a demon for work of all kinds; he never seemed to tire. Some people have said, 'Did you not get on each other's nerves during the long tedious voyages out of sight of land for many weeks at a time?' The answer is that we never had time to get on each other's nerves—and the time went all too quickly and was never tedious. If we were not working routine hydrographic and plankton stations, as so often we were, then at intervals the larger nets were lowered to great depths to explore the bathypelagic life; the sorting into groups, writing colour notes of fresh specimens, preservation and labelling of the very varied contents of the hauls kept us busy. Whenever we had time to work in shallow water—perhaps when prevented by storms from work in more open sea—then we used the dredge or small trawl. The amazing richness of the benthic fauna of the sub-Antarctic seas has to be seen to be appreciated, I have known a single morning's dredge haul in the Brandsfield Straits keep us occupied all day and half the night in making sure we had found everything worth taking. There can never have been a more enthusiastic collector than Kemp; he showed us how collecting should be done. First we sorted out for separate preservation all the larger forms—the sponges, coelenterates, polychaetes, molluscs, polyzoa, echinoderms, ascidians, etc., in great variety—treating some before fixation with this narcotic, some with that, to give the best result for later systematic or morphological examination. The polychaetes for example were narcotized, and then one by one laid out in flat trays on blotting paper while they were fixed in a shallow layer of weak formalin and then transferred to spirit in separate tubes. Some specialists asked us to preserve material for them in particular ways: Professor Graham Cannon, for instance, was keen on certain crustacea fixed in Dubosc (we always kept a special pot in the laboratory labelled 'Cannon fodder'). Then we turned to deal with collections caught in little fine nets which Kemp (following Holt's example) had cunningly fixed to the back of the dredge or trawl to catch the host of small crustacea stirred up and passing through its meshes. Next we sieved the sand, gravel or mud for the tiny forms which might easily have been thrown away. Then had we finished?—dear me no! Kemp could extract much more from the haul and from his team working like blacks. He then showed us how by splitting open fragments of crumbling rock, kelp roots and bits of coral, what an assemblage of small burrowing forms of life were to be

found in unexpected places. What a zoological education it was. I've said we worked like blacks—but we were not driven, we were compelled by his example and enthusiasm. If we stopped for a moment's relaxation, on he went, tireless, sometimes into the early hours of the morning. The large *Discovery* collections in the British Museum are products of Kemp's zeal. No one could make people work so willingly as he did.

The charming Victorian vignettes which form the tail pieces in some of the *Challenger Reports* caused us no little amusement. We compared ourselves—Kemp always leading, hauling on ropes, grovelling among the contents of the trawl, bespattered with mud and looking like a gang of pirates—with the elegant immaculately dressed naturalists of the *Challenger* who stood by with an almost nonchalant air while the common sailors soiled their hands in picking out the contents of the dredge. No doubt those *Challenger* pictures were the products of an armchair artist's imagination—but at times we used to wonder, and it was always a good joke.

When we were working routine stations—a long vertical series of water-bottle and plankton samples followed by towed nets—at intervals of ten miles, we were indeed pressed for time. Hardly had we got one lot of samples safely bottled and labelled and logs written up before we were on the next station. It was continuous work broken only by hurried meals. I've never met anyone who could eat a good meal so quickly as could Kemp; we could never keep pace with him! Down we dashed to feed—usually before we had finished our first course he had got through his second and was up once more on the job on deck.

With Kemp so much work led not to dullness; it was always work with gusto. He combined this passion for getting the most out of whatever he had in hand with a rich sense of humour. He sang most beautifully and was a devoted admirer of Gilbert and Sullivan. On Saturday nights we usually had a ward-room sing-song gathered round the piano while our old Chief Engineer (the late Commander W. A. Horton, R.N.) hammered the keys. Kemp's songs from his extensive repertoire from the Savoy operas were always the high lights of the evening, and he brought out the Gilbertian fun to the full; but perhaps our favourite was his rendering of 'My old Shako', called for again and again when, in later London reunions, we lived once more those happy nights of friendship. His joy at the merriment of those occasions was as great as that of the youngest of us; he was always with us by the piano joining in the choruses and contributing as much to the fun of the evening as anyone. In vivid memory I can see him helping the most junior scientist to impel the reluctant Third Officer to give 'The Fishermen of England', or see him enjoying the 'I belong to Glasgow' of our incomparable Scots comedian (Andrew Porteus, Second Engineer and later Chief), and those hilarious ditties from the Week-end Book. He had the capacity for the enjoyment of people, so long as they were honest and unpretentious.

He had both a keen musical and artistic sense. He followed the attempts

that several of us made to sketch in water colours with a kindly interest and encouragement. He was himself a real artist with the camera. He did not take many photographs, but those he took were superb not only in technical excellence, bringing out a wonderful range of delicate light and shade, but in their viewpoints carefully chosen to give pictures of perfect composition. His series of polar studies showing the mountainous regions of Graham Land and the Palmer Archipelago must rank high among examples of landscape photography.

Kemp's modesty might almost be considered a fault. When he had to speak in public on the work of the *Discovery*, he was so anxious not to give the false impression that we were heroic explorers suffering the hardships and dangers of the great terrestrial polar journeys of Scott and Shackleton, that he tended to go too far in the opposite direction of overstressing what he liked to call the relatively prosaic nature of our undertaking. He so hated anything that hinted of glamour and the sensational, that few laymen on hearing him speak of the enterprise he had so largely planned and carried into effect realized its true scientific importance or the greatness of the man who spoke.

He was elected a Fellow of the Royal Society in 1931 and served on the Council in 1935 and 1936. In the latter year he was awarded the Victoria Medal of the Royal Geographical Society.

To the staff of the *Discovery*, and to those who like myself had left it to take up other work, the news of Kemp's resignation from the Directorship to follow Allen at Plymouth came as a blow. Of course he was right. He had built up the *Discovery* Investigations into their great oceanographical position and he was leaving them in excellent hands. Plymouth meant so much not only to British marine biology: Allen like Kemp had built up our institution into one of world-wide importance. Kemp was *the* man to follow him.

He became Director of our Plymouth Laboratory in 1936. Of his work here I cannot write as I have done for his *Discovery* period, from the inside, but I know from my visits and talks with friends on the staff that he has inspired the same spirit of endeavour, loyalty and friendship that we knew in the *Discovery*. He was the beloved Director of both.

At Plymouth, Kemp's task was somewhat different from that of directing his great expeditions. The *Discovery* Investigations are a supreme example of planned research: a plan with many different parts but all interlocking to form a closely integrated whole. Plymouth, while undertaking some investigations having a more direct economic bearing, is essentially a home of 'pure' research where many different lines of independent enquiry are being pursued by the various members of the staff; it is too the Mecca of British zoologists going there to carry out their particular private researches. Kemp maintained this tradition. As did Allen before him, he had the faculty of developing a genuine interest in the widely different fields of work going on. He always tried to see how he could help each worker towards better facilities and equipment if such were possible.

His keen interest in some of the major problems being studied at Plymouth was well shown in his Presidential Address to the Zoology Section of the British Association at its Cambridge meeting in 1938.

Because I was never working at the Laboratory at the time of Kemp's directorship, I have thought it would be fitting to quote from two who were with him. I asked one member of the permanent staff, Mr F. S. Russell who has succeeded him in office, and then one who was a visitor at Plymouth on special work, Dr F. Gross, to give me in a few words their impression of Kemp as Director.

Mr Russell writes as follows:

When Stanley Kemp came to the Plymouth Laboratory to take control very few of us knew more of him than his name and reputation. In a very short time, however, his personality made itself felt and we soon realized that we had in our new Director a great leader of men. We quickly found that he was a man of most determined character, with pronounced ideas of his own, yet he was always willing to listen to others' views and if convinced would give full credit and whole-hearted support. He had greatness of character with a forthright and generous manner, and his lovable nature quickly endeared him to all. His was that rare charm of manner which made you feel when talking with him that you were his only interest. You felt that his thoughts were all for the welfare of others, and he would spare no effort to get the best for everyone.

He could not hold with niggardly ways and almost ruthlessly cleared the boards to make things clean, simple and straightforward.

On coming to Plymouth Kemp took over a scientific staff already in being, and throughout his remaining years there was no change in this staff. All were well content to remain under him. Only three years had elapsed when war broke out and many of his staff became scattered on war service. He therefore had little time to influence the scientific activities of the Laboratory. But it was already evident that his mind was wide enough to realize the value of the Plymouth tradition. Essentially a faunistic biologist himself, he had not previously had very much contact with the work of a more experimental nature which plays so important a part at Plymouth. Yet he quickly realized the value of these researches and, far from attempting to divert the staff into more orthodox biological channels, he was only too anxious that all facilities should be given in such work.

It is, however, certain that given the necessary time his impress on the Plymouth work would have been very marked. With his wide experience of faunistic investigations and oceanographic research he was aiming at carrying the work of the Laboratory further afield to embrace the larger area of the mouth of the English Channel and the Continental Shelf. His hope must certainly have been that the marine biology so typical of Plymouth and oceanography so typical of his 'Discovery' should flourish side by side.

During the war years the researches at Plymouth were necessarily greatly reduced by the absence of so many of the staff. Kemp made every effort to assist and develop any marine biological work that might prove useful in the war effort. In this he was concerned mainly with algal researches, much of which he directed from Plymouth. He was also very actively engaged in planning for the future and he devoted much time and thought to the development of Colonial Fisheries Research. In this his very wide experience and his knowledge of India and the Colonies proved of great value. Even to the end, although a very sick man, he carried on with his plans for the future with indomitable courage and tenacity.

His duties as Director and his many outside activities left him little time for his own researches, yet he snatched what moment he could to continue his studies on deep sea prawns, representatives of the group which was his chief life interest.

In a very short time after his arrival at Plymouth Kemp set to work on a much needed extension scheme. For some years past the Laboratory had been overcrowded during the summer months. The cubicles and tanks in the main building were out of date and needing repair. The job was tackled in a manner typical of the man, and great thought was given to making the most of the space available. The finished result was that the main Laboratory gained an additional floor and had well-fitted working rooms throughout, with clean-lined and up-to-date tanks and a museum for type specimens. There is much there to remind us of Kemp the craftsman. The woodwork and fittings were most carefully chosen and the rooms equipped with furniture of useful and pleasing design. In addition to this extension a much needed cleaning up and simplification of existing installations such as the engine room, heating appliances and so on was undertaken, and throughout could be seen his desire for general improvement and modernizing of equipment to reduce unnecessary labour.

It was to all of us a great tragedy that the war came just when this work was completed and Kemp never saw the new accommodation really filled under peace-time working conditions. Members of the Plymouth staff appreciate working in surroundings both workmanlike and pleasing which they owe to him.

The Plymouth Laboratory and the welfare of his staff were always foremost in our Director's mind. He had great plans for the future and during the darkest hours planned for the renovation and rebuilding of the Laboratory. We only wish that he were here to-day to carry us all through the difficult times created by the war.

Dr Gross writes:

I gladly give you my impression of the late Dr Kemp. I was fortunate enough to be working at the Plymouth Laboratory from 1935–1937, i.e. during the transition period when the directorship passed from Dr Allen, that great and benevolent man, to Dr Kemp. From my first contact with him my impression was that of a great personality, possessed of boundless energy and organizing ability, and a rare grasp of problems however far outside his own field of work they may have been. I was greatly impressed by his vigorous interest and keen appreciation of the necessity for modern equipment for work of experimental nature. I remember that on more than one occasion, when I outlined to him a piece of research for which the facilities of the Laboratory were not adequate, understanding was rapidly turned into action, interest into energetic support. He had the broad outlook, tact and judgement which made him a great director, inspiring all workers at the Laboratory with a team spirit and a sense of purpose which, but for the outbreak of war, would have enormously enhanced the progress of marine biological research in this country.

Those who were present on the night of the bombardment are agreed that the reason the Laboratory was not completely destroyed by fire was largely due to Kemp's unselfish action in letting his own house burn while he devoted all his energies to preventing the fire from spreading through to the rest of the building. This means all the more when we know what a home lover he was and what a sacrifice he made. He was a collector of beautiful antique furniture, old clocks, and rare oriental carpets chosen with great discrimination. He and Mrs Kemp lost everything. Not only did he lose all his books—he lost all the material and manuscript notes of a work on the *Discovery* deep-water decapod Crustacea he had been engaged on for many years.

It seemed to me appropriate that there should be in our *Journal* a record of what happened in the bombardment, and I thought that no better place for it could be found than appended to this tribute to our great friend. Mr D. P. Wilson, who was with Dr Kemp through that night, has kindly provided me with a graphic account of what took place. He feared it was too long and gave me leave to cut it as I thought fit—but I feel sure all will agree that it should be given in full as follows.

It was just getting dark on the evening of 20 March 1941 when the alert sounded; the time was about 8.30 p.m. Previously there had been many alerts and a number of sharp raids on Plymouth—the Laboratory had once had many windows broken—but there had been nothing in the nature of a 'blitz'. Coventry and other cities had suffered, but so far Plymouth was relatively untouched. As we hurriedly grabbed our equipment and gathered in the entrance hall, there is little doubt we all hoped this was just another quiet alert. We were soon disillusioned by a burst of heavy firing, the sudden appearance of parachute flares and of hundreds of incendiaries strung out along almost the whole length of Staddon Heights. For some weeks past the Laboratory had arranged a nightly rota of fire guards from amongst the staff to reinforce Dr Kemp and his family and the resident caretaker, Mr A. G. Butler. The guards this night were Mr E. Latham and myself; also in the building at the time were Dr N. K. Panikkar, Dr Mary W. Parke and Miss N. G. Sproston. As soon as it became evident that the enemy meant business Dr Kemp ordered the ladies down to the shelter, which had during the first days of the war been constructed in the lower part of the tunnel leading to the foreshore. Barely had they gone before heavy bombs were crashing into the town not far away, and more and more incendiaries were at this time making a fierce glare in the direction of Sutton Harbour. I remember Dr Kemp telling us a funny story, but of what it was about I have not the slightest recollection, my attention being fixed on other things, though I do remember pretending to laugh when he came to what must have been the funny part. As we stood outside watching the incendiaries on Staddon he remarked how pretty they looked. Showers of shrapnel sent us back into the entrance hall with the remark that the guns hadn't taken long to get going—'quick work', said Dr Kemp. A flare was hanging low over the Citadel, lighting up the whole of the Laboratory buildings in the ghastly manner peculiar to enemy flares. The roar of an aircraft mingled with the piercing rattle of machine guns aimed at the flare, there was a rushing sound as of corn sheaves blowing in the wind; in a moment incendiaries were bursting into flame all over the Hoe. It was obvious that the main bunch had missed us but there might be an odd straggler somewhere in the building. There was nothing to be seen round the front, so rushing through the Receiving Room, led by the Director, we made for the back. As he reached the door to the quadrangle he shouted, 'Get back, there is something coming.' Immediately was heard the familiar whine, getting louder; it was ours! Before we could move there was a heavy thud on the ground outside, followed at once by a blinding flash and a terrific blast which threw us to the ground in a heap. There is no doubt had we been outside at that moment many of us, if not all, would have been killed; the quick decision to keep us inside had saved us from anything worse than a severe shaking. The bomb had struck only eighty feet from the Receiving Room door and right outside the Director's kitchen window; it had only just missed penetrating the building. As we were picking ourselves up we were blown down again by blast from another bomb which had struck a grassy bank not far from the front door. When finally we did reach our feet we were already ankle deep in water flooding from burst aquarium tanks. Dr Kemp was soon back with the news that the largest tank and some others had gone and that conger eels and other fish were in the passage-ways, but we must leave them. He sent us on various missions to look for incendiaries; on my way back from mine—a quick agonizing survey of the first and second floors of the

main building where everything was a shambles strewn with broken glass—I met him coming up the stairs with a stirrup pump which he flung to me whilst he returned for another. He had from outside seen a fire in the back bedroom at the top of his house, everywhere else was clear. We hurried through the main laboratory to be delayed for a moment by the door from his office to the house; it was closed and jammed by a great pile of books which had fallen from shelves alongside, and could not be opened. Luckily the door panels had been blown out, so scrambling over the books we squeezed through into the house and ran up the stairs to the top floor. We found a blazing furnace with flames leaping out of the door. The blast from the bomb had wrecked the room thereby enabling the incendiary to start a big fire at once. We were two men with two stirrup pumps and a few buckets of water, attempting the impossible: the intense heat evaporated the jets almost before they had passed through the doorway and they made no difference at all. Whilst we sweated at the pumps the others were endeavouring to rig a hose from the water main outside; not until it was rigged did they find that there was no pressure, the second bomb having severed the pipe leading to the Laboratory. Upstairs we were running short of water for the pumps and Dr Kemp turned on his bath taps, but only the hot water was running. We took to throwing buckets of water on to the fire, though we could not get within more than a few feet of the door. The intense heat was already setting alight to woodwork on the landing and it was obvious that we could not hope to put out the fire unaided. In this dilemma he went to telephone for help, whilst Panikkar, who had now arrived, assisted with the pumping as we tried to hinder as much as possible the progress of the flames. The telephone was dead—the wires were down. Despatching Latham to get help, if he could, from the Citadel the Director returned to call us down from the top floor, for we were already in danger of being cut off by fire on the stairs. We continued to fight, as well as we could, from the first floor, dipping buckets of sea water from tanks in the main laboratory and spilling much of it in scrambling over the books in the office and in passing the buckets through the broken door panels. We wanted at this stage to save some of Dr Kemp's belongings but he insisted on continuing our efforts to delay the flames. He was prepared to let his own property go if only the fire could be kept from the other buildings. There was a good chance of doing this if we could prevent the fire passing the doorway between his office and the main laboratory. A thick stone wall isolated the house from the rest of the building except for the access afforded by this doorway; the merciful absence of wind encouraged our hopes. Back and back we were forced until by the time Latham returned from his hazardous mission to tell us that a squad of soldiers was on its way with a motor pump (he had met them coming, for our plight had been seen by the military) we were back almost into that strategic doorway itself. It was then that the most terrifying incident occurred. At the time Dr Kemp was holding the nozzle of a hose near the jammed and broken door between his office and his house; I also was well inside the office with another nozzle, somewhere near the middle spraying water on to the far wall. Latham, just inside the main laboratory was pumping. Panikkar and Butler had, I think, at that moment gone to meet the soldiers. Suddenly there was a noise overhead and a warning shout from the man at the pumps, 'Look out, the ceiling is coming down'. With a roar and a shower of blazing debris the whole fire fell about us. A great flaming beam and a smouldering mound of red hot ash lay between where Dr Kemp had been and myself. Half-blinded and choking from the fumes I was at that moment certain he was underneath. I had to kick myself free and run over the top of the mound to get out. There was no answer to my yell of 'Dr Kemp'. Latham left the pumps and dashed into the fire in the direction of where he had been. He too vanished, and still scarcely able to see I seemed at that harrowing moment to be left alone powerless to help, without even a tool to dig into the smoking ash which buried the hoses of our stirrup pumps and, as I supposed, him. After what seemed an age, but which could only have been two or three minutes at most, his voice and Latham's were heard calling from the ground outside and the

nightmare was over. By great good fortune the main fall of debris had just missed us both and he had made his escape by his own stairs, where Latham found him staggering down with his grandfather clock over his shoulder. He said he might as well take something out of the house with him and he had picked up the clock on his way. On getting outside his first thought was for his parrot and he rescued it just in time. Luckily the cage had been placed near the dining-room window and could be reached from outside.

The further proceedings can be told briefly. The men from the Citadel were soon throwing powerful jets of sea water from our reservoirs on to the flames, one hose being directed through that all important doorway inside the building. Except for acting as guides our work for the moment was over. We were exhausted and could do little more. What it must have meant to a man of Dr Kemp's age is better left to the imagination. Throughout it all he was a magnificent inspirer of courage; he was cool, calm and collected. It seemed almost a privilege to crouch on the floor with him each time a bomb whined down near by, some very close into the Citadel behind, or just missing our roof to crash on to the foreshore below. Often that night we must have been a target in the bomb-sights of the enemy.

As we gathered in the tunnel shelter after midnight when it was all over we were a sorry sight, filthily begrimed and burnt. The ladies themselves had experienced many moments of real danger, and of physical discomfort as when the aquarium water flooded down through the tunnel after the bursting of the tanks, but they had borne it all, and their terrible anxiety as to what was happening above, with great fortitude. Now they bandaged our burns and there were some lighter moments as when it was discovered that one member of the party was carrying around a pound or two of congealed lead on the back of his mackintosh. The lead had come from the flat roof and Dr Kemp had himself received a sprinkling of the molten metal on his head. His burns were treated with methyl violet and for the next few days his hair was rather a beautiful colour, much, we think, to his inward annoyance.

Dr and Mrs Kemp and their daughter had lost their home and almost all their possessions. It was amazing how little outwardly they showed it although within they must indeed have felt bitter. All the treasures of a lifetime were gone. We were all amazed, I think, how before the ashes had barely cooled Dr Kemp was already planning for the future, the future of the Laboratory, not his own. As we began the long depressing task of clearing up the mess he was already dreaming of a link between the eastern ends of the south and north buildings. How impossible and unlikely of fulfilment it seemed in those days when we were out night after night watching the searchlights and the bursting shells. How likely it seemed that another bomb would destroy everything. As it was, only the vigilance of the fire guards saved us from several fires started by incendiaries on succeeding nights, and a time-bomb which fell almost into the crater left by the first bomb was a menace to the building for several days. Throughout it all the Director kept his faith, and his vision of the future broadened into the fine plans for reconstruction and extension which he has left. As one who had the privilege to work with him on those plans I know the boundless energy and hard thinking which went into their making at a time when so many of us could barely see our way from one day to the next. Whilst for us the immediate present was the most pressing concern he was reaching out to a future when the storm would have passed and men once again could think in security.

Kemp with his great and buoyant spirit showed little trace of the strain he had been through and, as Wilson has just told us, was full of his plans for the future of our Plymouth Laboratory; but few of us can doubt that the strain of that night undermined his strength and brought on the illness that took him from us. Mrs Kemp and his daughter Belinda will know how deep is the sympathy of all the members of the Association for them.

A. C. HARDY

THE TRIRADIATE AND OTHER FORMS OF *NITZSCHIA CLOSTERIUM* (EHRENBERG) WM. SMITH, FORMA *MINUTISSIMA* OF ALLEN AND NELSON

By Douglas P. Wilson

Naturalist at the Plymouth Laboratory

(Text-figs. 1–9)

CONTENTS

Introduction

The diatom forming the subject of these notes was first isolated by Allen & Nelson (1910); it has been kept in culture for over thirty years. Owing to the ease with which it may be cultured this particular species of *Nitzschia* has proved of great value for experimental work on diatom physiology, and it has been of no less value as a food for marine larvae in captivity, enabling much embryological work to be accomplished. From the Plymouth Laboratory subcultures have been distributed to many research institutions in this country and abroad; in some places stocks are still maintained. It is the policy of the Plymouth Laboratory always to have available healthily growing stocks which may be drawn upon at any time by workers throughout the world.

It is surprising that with this widespread use so little appears to be known about the general natural history of the species in culture, especially as regards morphology and reproduction. When the Plymouth stocks came into my

care interest in these problems was stimulated by the facts that the majority of the cells presented a three-rayed or triradiate appearance, and that the normal or fusiform cells seemed to be dying out. It was evidently desirable to re-establish cultures of the normal form, especially as the triradiate seemed to be an unsatisfactory shape for larval mouths and gullets. Knowledge was also needed of the relationship of the triradiate to the normal cell, as was also a better understanding of the sequence of events in the stock cultures. To some extent this has now been achieved and, although there is much still to seek, these notes are presented as a partial solution of the many problems raised by this remarkably variable species.

Types of Cell

In general three main types of cell are to be observed: the normal, the triradiate and the oval.

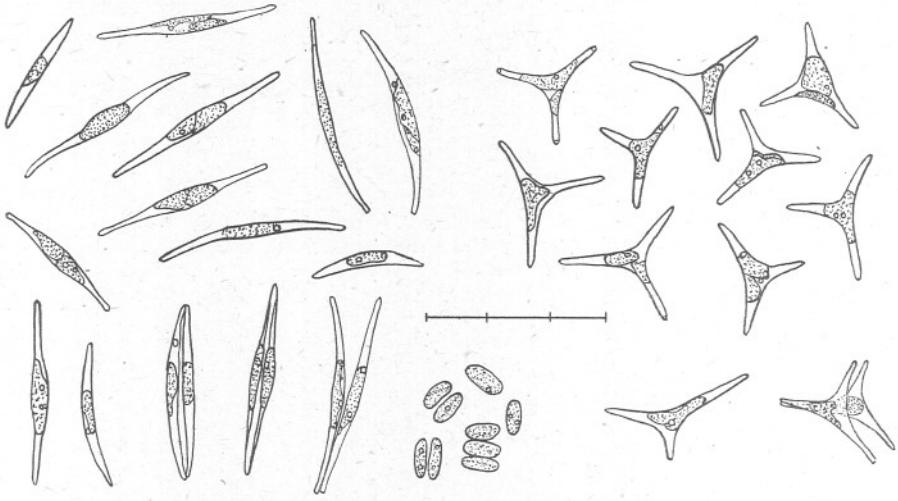

Fig. 1. *Nitzschia closterium* forma *minutissima*. Typical normal, triradiate and oval cells from different cultures drawn on various dates. Division stages are included and one short-armed triradiate is shown. Each division of the scale represents 10 μ.

The Normal Cell. This is a spindle-shaped almost fusiform cell, straight or more usually slightly curved, 25–35 μ long, though sometimes shorter. It is rare to find cells longer than 35 μ. Approximately the middle third of the spindle is swollen, each end tapering off to a rounded point (Fig. 1). It will be necessary to refer very frequently to these tapering prolongations, the rostra, rostral prolongations, beaks, horns, etc., as they are variously called by diatomists. They are, of course, prolongations of the valves and are not true spines. In what follows they will be referred to as 'arms'. The swollen central portion contains, in addition to the nucleus, the chromatophores, one to two, which in a dim light expand into and down the arms. Besides the chromato-

phores, more especially in old cultures in which growth has ceased, are to be seen one or more refringent globules stainable with Scarlet Red and evidently of a fatty nature. At the bluntly rounded and often slightly swollen extremities of the arms there is frequently an appearance as of polar nodules. This may, however, be an optical effect due to overlap of the valve ends; the effect sometimes disappears with increased magnification. The individual valves are exceedingly difficult to make out, but in very old cultures, with all the protoplasmic contents contracted, the valves tend to separate and can then be seen (Fig. 3 B, *a*). The girdle pieces seem to be much thinner than the valves. In healthy cells the girdle pieces are so closely apposed that in transverse section—sections have been cut as thinly as 2μ—the cell wall under the highest powers gives the appearance of a complete uninterrupted ring. I have not been able to satisfy myself that I have seen any of the usual valve markings of the Nitzschioideae, the keel and canal raphe or the carinal dots, although my optical equipment resolved all the usual test diatoms with the single exception of *Amphipleura pellucida*. Only in some gently incinerated specimens mounted in Sirax (a medium of high refractive index) were to be seen what might possibly be the keel and raphe with some slight suggestion of carinal dots, but it was impossible to be certain of the identity of the structures seen; they might very well have been artifacts. This species of *Nitzschia* is minute, and its size is a great handicap on all observations concerned with structural details and also makes the handling of individual cells a task of considerable difficulty.

The Triradiate Cell. This closely resembles the normal except that it has three arms instead of two. The three angles enclosed by the arms are rarely equal and there is much variation between individuals. On the whole the arms are shorter than those of the normal form, being 6–8μ long in good-sized specimens as compared with about 10μ long in the normal. They are often unequal in length. Whilst there may occasionally be three chromatophores one to two is the usual number. It would be interesting to know how the keel and raphe, if present, are arranged, but it has not been possible to make them out. Some incinerated specimens mounted in Sirax showed what might have been these structures running between the bases of two of the arms and ignoring the third, but this appearance could have been caused by folds due to collapse of the cell wall and they were not visible in all specimens.

The Oval Cell. This cell has no arms, and as the name suggests is roughly oval in shape. It is about 8μ long and 3–4μ broad, almost the whole of the space inside the cell wall being taken up by the chromatophores of which there are one or two. At each end there is sometimes a refringent globule which appears to be a product of photosynthesis. The cell wall is of the same appearance and thickness as that of normal and triradiate cells, and presumably is made up of valves and girdle pieces although these have not definitely been distinguished.

The Triradiate Cell at Plymouth and Elsewhere

During the long period from first isolation until 1936 the stock cultures at Plymouth were under the care of the then Director, the late Dr E. J. Allen, who with the late Mr E. W. Nelson had made the original isolation from the sea. Dr Allen told me (in 1942) that although he had seen occasional triradiates in his cultures they were never, to his knowledge, very numerous. However, Mr Clifford Dobell writes to inform me that he remembers that in the winter of 1910–11 he had occasion to examine some old exhausted cultures which Dr Allen had himself left at the Royal College of Science, South Kensington, during the previous summer, and he was surprised to find 'that they all contained enormous numbers of "triradiate" forms the like of which I had never seen previously'. Thus triradiates were present, and could become numerous, in the early days of the cultures and are not a product of a long-continued artificial environment. Dr F. Gross remembers often noticing them in the Plymouth cultures whilst they were in his care for a short period in 1936–7. In the summer of 1939, when my own attention was first attracted to the problem, triradiate cells accounted for over 90% of those present. The cultures were perfectly healthy and not noticeably contaminated with bacteria or other organisms. Later on these stocks became almost completely triradiate, although by the summer and autumn of 1941 normal cells were once more fairly abundant. The history of this period is studied in detail below.

Similar happenings to those at Plymouth have taken place elsewhere with cultures originally derived from Plymouth stocks. Some account of the stock cultures at Hull and their comparison with those at the Plymouth Laboratory has already been published (Wilson & Lucas, 1942) and will be more fully discussed later in this paper. From Woods Hole, Massachusetts, Dr Bostwick H. Ketchum informs me that his *Nitzschia* cultures had been derived from Plymouth about 1930, and that when he started work on the species in 1934, 5–10% of the culture consisted of triradiate forms. In that year he succeeded in isolating a single normal cell, and in cultures grown from it no reoccurrence of the triradiate had been observed as late as the summer of 1941. The original culture containing the triradiates was lost. Also in America, Barker (1935) records experimental work on *Nitzschia* cultures originally derived from Plymouth and mentions 'distinctly oval cells and cells shaped like a three-pointed star' but does not figure them. In order to obtain bacteria-free cultures he grew the diatom in a succession of plates of solid agar, finally inoculating liquid media after elimination of the bacteria. From an examination of the agar plates he found that 'all three cell shapes are interconvertible'. In successive plates oval cells became more numerous and 'after the fifth transfer only oval-shaped cells could be found. When these cells are inoculated back into liquid media there is a gradual reversion during several transfers to spindle-shaped cells. The oval cells do not entirely disappear. The star-shaped cells have never yet reappeared in their original abundance. They can be

observed only rarely in a dense culture and represent not more than one cell out of 100,000. These observations demonstrate clearly that these variously shaped cells of *N. closterium* belong to a genetically pure line.' I am indebted to Prof. A. C. Hardy for calling my attention to this reference after I had already made substantially the same observations using liquid media.

Methods

The cultural methods of Allen & Nelson (1910) and of Gross (1937) were followed. The stock cultures were always grown in the former's 'Miquel sea water', the 'Erdschreiber' formula of the latter being employed only for special experiments. There is in practice a little difference between the two media in that the Erdschreiber contaminates more readily with other organisms; cells grown in it are, in general, slightly larger and better formed than those in the traditional Allen-Miquel sea water.

Some single cells were picked out with fine pipettes under a high-power dissecting microscope, but they proved too minute for much work to be done in this way. It was more practicable to select small clusters of cells of the same type, especially ovals which tend to agglomerate, and more cultures were started from such clusters than from single cells. It was relatively easy to make certain that such a cluster contained only one type of cell, for it could be examined on a slide under a cover-glass with a high-power objective, subsequently being washed through several changes of sterile media. Single cells treated in this way were nearly always lost in the process.

Another method of separating types of cell was greatly to dilute a drop of the appropriate culture and then to inoculate sterile media in shallow Petri dishes. After a few days clusters of cells would be found scattered over the bottom of the dish, each cluster derived from the growth of a single cell. A cluster of the type needed was then removed with small risk of contamination from neighbouring clusters. The drawings were made with a camera lucida. They are merely outlines which do not convey the transparent delicacy of the living cells.

Clone Cultures

In July 1939 a single triradiate cell was, after several attempts, successfully isolated into a watch-glass of Erdschreiber. It grew quickly, giving rise to a small group of triradiate cells and to none of any other kind. These cells were transferred to a small flask of Erdschreiber, and from this some days later a large flask of Allen-Miquel sea water was inoculated, so establishing a clone of triradiates which has been regularly subcultured ever since. In what follows this clone will be referred to as Series III.

About the same time one of several attempts to isolate a single normal cell was successful, and from it, in a similar manner, a clone of normal cells was obtained. This clone was divided into two series of subcultures, Series I and Series II, which were ever afterwards kept separate. A slight difference of

treatment marked their inception. Some minute flagellates had been observed in the Erdschreiber in which the single original cell had grown, and therefore, whilst Series I was inoculated directly into a large flask of Allen-Miquel sea water, the initial cells of Series II were washed for a minute or so in a dilute solution of iodine in sea water. The flagellates were thereby killed, but the only observed effect on the diatoms was to check for a few days their growth as compared with Series I. In the latter series the flagellates soon died out, probably because the Allen-Miquel sea water was an unsuitable medium for them.

The subsequent history of the clone cultures will be discussed in detail later. Here it is sufficient to state that for some months, though regularly subcultured, they remained fundamentally true to type, except that oval cells were produced. This was true not only for healthy actively growing subcultures, but also for old exhausted subcultures kept for several months after finishing their growth. Some of these old cultures eventually became heavily infected with bacteria, flagellates and moulds before they were finally discarded.

It was in July that the clone cultures were first formed, and it was in the following January that the first regular normal cells were seen in Series III and the first regular triradiates in Series I and II, although some hint of their coming appearance had been noted as early as the end of October. At that time a few triradiates each with one or two reduced arms had been observed in Series III, whilst in the clone normal series a dividing three-cornered oval was seen in one culture. In the old infected cultures some misshapen cells could be found, but it did not appear that these were producing cells of the alternate form and it did not seem that overcrowding or unhealthy conditions were initiating a change-over from one type of cell to the other. It had at one time been thought that the triradiate might be a product of unhealthy cultural conditions, but this was not supported by observation.

The first normal cells in Series III and the first triradiates in Series I and II were very rare, especially in Series II, where it was often impossible to find any during the first two years. The proportion of normal cells to triradiates in Series III increased much more rapidly than did the proportion of triradiates to normals in Series I and II. Thus an estimation in June 1941 showed that in Series III (see Table V) 1·2% of the cells were normal, a proportion that had by November that year increased to 40%. In June 1941 Series I showed (Table V) much less than 1% of the cells triradiate, whilst in Series II none appeared in the count. However, by February the proportion in Series I had risen to 5·4% and thereafter steadily increased. In Series II a significant proportion appeared about the same time and also increased, though much more slowly. Figures showing the subsequent changes in the proportions are set out in Table V.

Formation of the Oval Cells

In practically all cultures are to be found the armless oval cells already described. They are most abundant on the bottom and sides of the flask, adherent in sheets, sometimes mixed with armed cells of both sorts. They secrete a mucus-like substance which stains deeply with methylene blue. When examined on a slide they show, if obtained from a healthy growing culture, gliding movements over the substratum and a group of cells soon scatters. Normals and triradiates show similar movements.

Oval cells derive, by division, from armed cells of both kinds. Stages in their production are often common in the cultures, and typical ones are shown

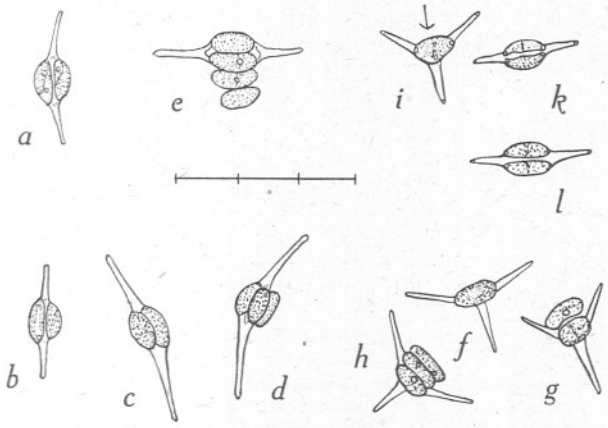

Fig. 2. Stages in the formation of oval cells from normal and triradiate cells. *a–c*, formation from normal cells; *d*, *e*, more than two ovals arising from one normal; *f–h*, formation from triradiates, including multiple oval formation; *i*, a stage in the formation from a triradiate cell which is drawn again at *k* as viewed in the direction of the arrow; *l*, another cell viewed as in *k*. The cells are from various cultures on different dates. Each division of the scale represents 10 μ.

in Fig. 2. Details of the process are not clear; the behaviour of the nucleus and of the cell wall during division have not been made out in spite of considerable effort directed to that end: the structures are too minute to be seen clearly in detail. It seems that ovals are merely the product of division stages in which only one of the two daughter cells retains the arms. An armed cell about to give rise to an oval becomes very swollen in the central chromatophore region prior to division, and at the same time probably shortens in overall length. At any rate such cells are in general shorter than the longer cells in a culture. The oval frequently adheres for a time to the armed cell, often itself dividing so that two or more ovals all attached to a single armed cell is by no means an uncommon sight. It may be that the armed cell itself continues to bud-off ovals; this is suggested by finding groups of cells such as those shown in Fig. 2, *e*, where with two ovals already outside the frustule the valves are distended by two ovals still within. It is unfortunate that attempts to grow

the diatom in cavity slides or in hanging-drop cultures, with a view to following the divisions of individual cells, met with no success. However, the different stages found in the cultures leave no doubt that oval cells are produced from armed cells by some form of direct division.

The conditions under which oval-cell production is initiated are not completely known. At one time it was thought that their most common occurrence on the bottom and sides of a flask indicated that contact with a substratum stimulated their formation, but cultures grown on a shaking apparatus, which ensured that no cell was allowed to sink and rest, produced them no less readily. In these shaken cultures the oval cells were scattered throughout the culture, both singly and in little clumps, the clumps containing armed cells as well. The ovals in the shaken cultures were very numerous; it should be noted that they were grown rather quickly in a good light. Overcrowding does

Fig. 3. A. Oval cells from a culture where ovals were multiplying rapidly to form more ovals. The cells showed slight elongation and the chromatophores did not completely fill them. The globules were products of photosynthesis and the cells were moving about actively. B. Cells from an old exhausted culture with much contracted chromatophores. *a* and *b*, normal cells, in *a* the valves have moved apart; *c*, oval cells embedded in a mucilaginous substance; *d*, free oval cells. The scale represents 10 μ.

not appear to be a contributory factor in oval production because they frequently occur in sparse and actively growing cultures. On the whole they appeared more readily in Erdschreiber than in Allen-Miquel sea water, though there were exceptions to this. This might indicate that good cultural conditions are favourable to their production. They appear more definitely in cultures set in a good light, such as that near a north window, and they may be absent, or almost absent, in cultures grown in a dimmer light. This observation was confirmed by a series of simple experiments. It was significant to find that in cultures placed well back from a north window, and grown without disturbance, ovals were markedly abundant in patches on the sides of the flasks away from the window where the light had focused by refraction through the convex fronts. There seems little doubt that a good light (but not direct sunlight which is distinctly harmful) is essential for active oval production, and that in a relatively dim light few, or none, are formed.

It will be remembered that Barker's cultures in solid agar (see p. 238) after the fifth transfer contained only oval cells. This may indicate that a solid

medium is unfavourable to the production of elongated valves, but *Nitzschia* grown in agar in this laboratory (by Dr S. P. Chu, to whom I am indebted for some of his material) showed no special tendency to oval production and the cells were fully normal in shape. Perhaps Barker's results were due as much to good lighting conditions as to anything else.

Oval cells divide and give rise to more ovals. This sometimes goes on for a long period, and small clusters of ovals isolated to fresh media will often produce vast numbers of oval cells with a complete absence of armed forms. The ovals may, however, be slightly elongated and the chromatophores not quite so tightly packed as in newly formed ovals (Fig. 3A). This may continue through several stages of subculturing. Oval cells thus cannot be mistaken for resting spores, although in old exhausted cultures (Fig. 3B) they secrete thick mucus-like coats, deeply stainable with methylene blue and gentian violet, and in this condition remain dormant for a long time until supplied with fresh media.

Development of the Oval Cells

Clusters of oval cells have several times been isolated and grown in fresh media. The experiments fall into two groups of which the first concerns ovals removed from the clone triradiate (Series III), some details of which will now be given.

In eight experiments small clusters of oval cells were removed from subcultures of Series III and placed in fresh media. Each cluster and the drop of medium containing it were most carefully examined to ensure that only oval cells were present. Six of these clusters eventually produced normal cells and no triradiates; one other produced normals and triradiates in about equal numbers; the remaining one produced a few triradiates among a very large number of normals. In all the experiments the ovals multiplied before and after producing armed cells. In the first experiment, made in March 1940, fully sized normals were produced within a week. The second experiment, when roughly equal numbers of normals and triradiates were produced, was made in the following July; armed forms did not appear for about a fortnight when the ovals, as described later, gradually grew arms (Table II, Series 'U'). The remaining six experiments were made simultaneously in November 1940 (Table I, Series 'T'). In these, apart from slight elongation, the ovals multiplied in the armless condition through several stages of subculturing until June and July 1941 when armed cells first appeared in three of them, the flasks constituting the other three experiments having been lost by enemy action during the preceding March, at a time when they contained ovals only.

In addition to the foregoing experiments in which oval cells were definitely isolated from all other kinds some tests were made in which the clusters of ovals, picked out from Series III, contained a few triradiates as well. No normals were present in these clusters. In seven such tests, made in April and May 1940, the cultures resulting from a week's growth of the clusters all contained normal cells, together with triradiates and many more ovals than

were in the original clusters. In three tests the normals were 35μ long within the week, in the other four they did not exceed 25μ after 3 weeks. In several of these tests many very small triradiates in process of development from ovals, as described below, were observed.

The second group of experiments concerns oval cells which had been isolated from clone normal cultures. In five experiments, in November 1940 (Table I, Series 'N'), small clusters of three or four oval cells each were placed in freshly sterilized media. It was known definitely that no armed cell was present. Within 3 weeks one of these experimental cultures had given rise to many more ovals and to normal cells 30μ long. The other four cultures produced at first ovals only through several stages of subculturing. One of them became heavily infected by bacteria and was thrown away, whilst one other was lost by enemy action in March 1941. The two remaining cultures contained only oval cells until the end of the following May when some of the ovals began to elongate to form normals. By the end of July these normals were mainly 20–25μ long. No triradiate had as yet been seen amongst them, but a month later a few three-cornered oval cells and a few small triradiates were observed. In later subcultures occasional triradiates were seen, but were very rare until the autumn of 1942 when some increase in the abundance of this type occurred.

Prior to the five experiments just recorded four less precise tests had been made in May 1940. Small clusters of ovals from a clone normal culture had been separated into small flasks. Each cluster contained some armed cells as well. In a week there were to be seen transition stages between oval and normal cells; there had also been a great increase in the numbers of ovals and normals present. These cultures were kept for 4 weeks and then discarded; during that time no triradiate cell was seen although a special search was made for them.

From all the experiments it is clear that oval cells, however derived, multiply by binary fission and sooner or later develop arms. These are generally only two in number, the resulting frustule being normal in shape. There is generally no special tendency for oval cells derived from triradiates to grow three arms, and thus a triradiate culture will in course of time come to contain normal cells. Much less frequently do some ovals develop three arms to become triradiate, but only a very small proportion usually does so, whether the ovals be derived originally from triradiate or from oval cells. In my experience Series 'U' was exceptional in producing almost as many triradiates direct from ovals as normal cells from ovals. At present it is not possible to suggest any special condition or set of conditions which might be regarded as a predisposing or causative factor, or factors, in inducing the development of more than two arms. Always when triradiates have arisen from ovals many more normal cells have been produced in the same culture at the same time. Neither is it known why sometimes there is a long period between isolation of ovals and their subsequent development of arms—the ovals in the meanwhile multiplying abundantly—whilst at other times fully developed normals appear

almost immediately. The type of culture-medium used does not seem to have an influence on this. It may, however, be significant that long delay has in the main been associated with the short dull days of winter, whilst rapid outgrowth of arms has generally, but not invariably, taken place in the spring and summer. Daily duration and intensity of light, and perhaps temperature, may thus be suspected of some influence in this respect. To test this some simple experiments were made but the results were inconclusive. Rigid control of temperature, intensity of light and duration of lighting will be necessary before these physical factors can be ruled out as ineffective.

The enlargement of the oval cell to the full-sized armed form does not involve auxospore formation. In all the cultures I have examined and of all the innumerable cells I have seen there has been nothing that in any way

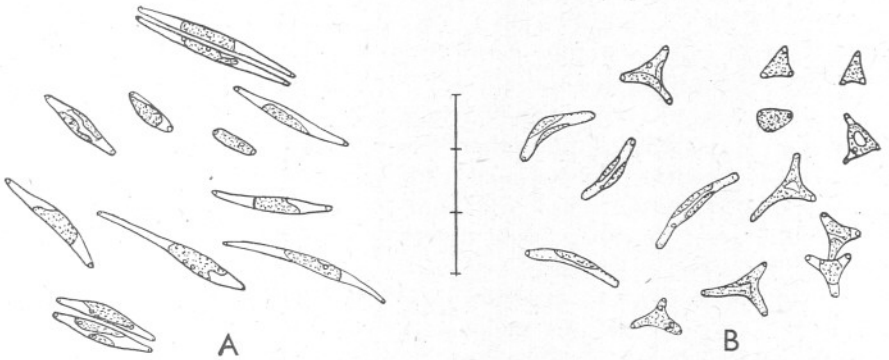

Fig. 4. A. Stages in the production of normal cells by elongation from ovals which had themselves originated in a clone normal culture (Series II). Two division stages at differing lengths are shown. B. Cells developed from ovals which had been removed from a clone triradiate culture (Series III). In addition to cells elongating to form normals there were many three-cornered ovals and small triradiates formed from them. Some of the small triradiates were dividing and a division stage is included in the lower right-hand corner of the figure. Each division of the scale represents 10μ.

resembled an auxospore. The arms merely grow out from the oval at each end —in other words the oval elongates—or from three corners if a triradiate is being formed. They appear to grow out steadily and not in sudden jumps. In a culture in which cells are actively elongating (Fig. 4A) all sizes are to be seen between oval cells and fully, or nearly fully formed cells with long arms. Fission stages at any size are common (Fig. 4 A, B); it thus appears that as elongation proceeds division takes place regularly whatever the length reached.

The oval cell is tightly packed with the chromatophores; often at each end a refringent globule is to be seen, as already described. As elongation begins a space forms at each end between the chromatophores and the cell wall. When globules are present they usually remain close beside the chromatophores, but at the apical ends of the cells there is often an appearance as of polar nodules. As a rule elongation through the transition stages is fairly

rapid, although it may take several days. The final length reached is very variable; it has already been recorded how in some cultures 30–35μ was reached by a large number of cells in a week or so, whilst in other cultures it took longer to reach even 25μ. Cultures in which the maximum cell length reached during the first relatively rapid lengthening is 25μ or thereabouts generally show a slow increase in maximum length from subculture to subculture during succeeding months. This process will be discussed in the next section.

This growth in length of the cells is quite unlike that normally associated with diatom frustules where strong silicification of the cell wall is generally held to preclude size increase which is brought about, when needed, by auxospore formation. In the *Nitzschia* of these cultures silicification is at best extremely weak, the cell wall dissolving entirely in acids, quickly so when the acid is used hot. Incineration on a cover-glass after washing away the salt water by fresh will, if carefully performed, yield fairly clean valves, but even by this method the cell wall is destroyed almost as soon as the softer contents. The valves, moreover, are quite pliable and can be bent without fracturing. It may be that what silicification there is is mainly confined to the valves and that the thinner girdle pieces are even less strongly armoured. Under these circumstances there can be little hindrance to growth of the cell wall, and this may well account for what would otherwise in a diatom be regarded as a remarkable method of growth.

It should be noted that a number of species of diatoms have been reported as having lost their siliceous skeletons in culture, this being followed by variability in cell shape. Wiedling (1941) discusses some of these observations and reports on one of his own on *N. Kützingiana* var. *exilis* Grun., where the skeleton disappeared after the normal form had been cultivated for many years. However, none of these instances appears exactly comparable with the *Nitzschia* of the Plymouth cultures in which light silicification seems to be the normal condition. Specimens of the same species from the hatching tank at Charsaig (see p. 265) dissolved in hot mineral acids to leave no trace as do the culture ones, though perhaps a little less readily. These naturally occurring specimens were thus very lightly silicified, and there is therefore no adequate reason to suppose that long years of culturing are primarily responsible for the light silicification of cultured cells. A species of *Nitzschia*—which is possibly *N. closterium* (Ehr.) W. Sm. and which is discussed below (p. 263)—common in dredgings and in aquarium tanks likewise readily dissolves in acids which leave intact the valves of other diatoms treated with them at the same time.

It is probable that the usual conception of size decrease with successive division does not hold for all diatoms, and that when silicification is weak, or where special structural features permit—as in *Eunotia pectinalis* var. *minor*, where the curvature of the girdle allows new valves to be formed as big as the parent ones (Geitler, 1932)—multiplication may take place with constant apical length, or even with increase in length, though such instances are likely to

be rare, the *Nitzschia* of the Plymouth cultures being one of these. Recently Wiedling (1943) has briefly discussed the general problem of size variation in diatoms, mentioning his own observations on various species of *Nitzschia*, particularly *N. subtilis* var. *paleacea* Grun., *N. Kützingiana* Hilse and *N. palea* var. *debilis* (Kg.) Grun., where growth with constant apical length was sometimes observed.

Variation in Length of the Normal Cell

In these studies the maximum cell length is used as a standard of measurement. Since cultures contain all sizes down to ovals the determination of the average cell length would have been preferable; the time and eyestrain necessary to make sufficient measurements would, however, have been out of all proportion to the value of the results obtained. It was found that the maximum length was fairly quickly determined, for it was only necessary to measure a number of the longest cells seen, and the figure obtained did give a fair indication of the cell size of the culture. The maximum length is usually shown by only a small percentage of the cells present, but a big proportion are generally just a few microns shorter. Very occasionally an exceptional cell considerably longer than the common maximum would be encountered, but they were so rare that they have been ignored for present purposes. There are nearly always a number of cells of all lengths between that of the maximum and that of the ovals, but ones much shorter than the maximum were in general in small proportion.

There does not appear to be any great variation in maximum cell length during the growth of a subculture from the time when it is first inoculated until growth ceases. This has been checked from time to time during the growth of typical subcultures. There has, however, been noted a slight increase in maximum length during the growth of a subculture belonging to a series in which the maximum was steadily increasing. The increase from subculture to subculture is generally of the order of 1μ when measurements are made at equivalent growth stages; similarly with any decrease that takes place. More rapid changes occur from time to time. Tables I and II record changes in maximum length in those cultures for which records have been kept; all of them began as a few isolated ovals, except that with the 'A' series a few triradiates, but no normals, were present as well. It will be noted that the records for the 'A' series cover a period of 3 years during which there were twenty-two subcultures, whilst for the 'T' and 'N' series the records cover 2½ years and they were subcultured fifteen times. The 'A' series was always grown in a 1 l. flask, the 'T' and 'N' series in wide-necked flasks holding about 120 c.c. Both types were only half-filled with culture medium, as is the usual practice. In the smaller flasks growth came more or less to a standstill—owing to exhaustion of nutrients—2 or 3 weeks before subculturing; all the flasks, large and small, were subcultured together. The large flasks were always subcultured shortly before or after attaining maximum density. Cells were measured, alive or after preservation in formalin, a little while before this

TABLE I. VARIATION IN MAXIMUM LENGTH OF NORMAL CELLS IN CULTURES GROWN FROM OVAL CELLS

Date	Sub-cultures nos.	Maximum lengths in experimental cultures: Series 'T' I	II	III	IV	V	VI	Series 'N' I	II	III	IV	V
19. xi. 40	1	Oval	Oval	Oval	Oval	Oval	Oval	Oval	Oval	Oval	Oval	Oval
3. xii. 40	1	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	,,
10. xii. 40	1 and 2	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	30 μ
16. xii. 40	1 and 2	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	30 μ
8. i. 41	1 and 2	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	,,
4. ii. 41	2	,,	,,	,,	,,	,,	,,	—	,,	,,	,,	,,
26. v. 41	3	—	—	,,	—	18 μ	,,	—	20 μ	15 μ	—	—
23. vii. 41	4	—	—	24 μ	—	27 μ	20 μ	—	22 μ	25 μ	—	—
25. viii. 41	5	—	—	29 μ	—	30 μ	24 μ	—	25 μ	27 μ	—	—
11. ix. 41	6	—	—	26 μ	—	26 μ	—	—	27 μ	27 μ	—	—
10. xi. 41	7	—	—	26 μ	—	26 μ	26 μ	—	25 μ	25 μ	—	—
2. i. 42	8	—	—	27 μ	—	28 μ	26 μ	—	28 μ	28 μ	—	—
10. iii. 42	9	—	—	27 μ	—	26 μ	27 μ	—	27 μ	28 μ	—	—
20. v. 42	10	—	—	28 μ	—	28 μ	29 μ	—	28 μ	29 μ	—	—
30. vi. 42	11	—	—	29 μ	—	30 μ	27 μ	—	27 μ	29 μ	—	—
11. viii. 42	12	—	—	28 μ	—	30 μ	26 μ	—	29 μ	30 μ	—	—
11. ix. 42	13	—	—	29 μ	—	31 μ	26 μ	—	29 μ	31 μ	—	—
20. i. 43	14	—	—	29 μ	—	32 μ	25 μ	—	26 μ	31 μ	—	—
20. ii. 43	15	—	—	29 μ	—	29 μ	25 μ	—	26 μ	30 μ	—	—
22. iii. 43	16	—	—	30 μ	—	30 μ	26 μ	—	26 μ	29 μ	—	—
3. vi. 43	17	—	—	29 μ	—	29 μ	25 μ	—	25 μ	29 μ	—	—

density was reached, and the figures are mainly for cultures at the end of their growth. Occasionally, as already mentioned, cells were measured during earlier growth stages as a check on results.

It will be seen from the figures that there is a definite, usually slow, change in maximum length over a period of several months. The general cell size of the cultures reflected these changes, those with a high maximum containing a large proportion of long cells, the reverse, of course, being true for those with a low maximum. The differences were sufficiently distinct to be readily noticeable, to an experienced eye, without actual measurement. There is no correlation with the seasons, and size may increase in one series whilst decreasing in another. All the flasks stood side by side and there could have been little difference between one and another.

The figures given for the 'A' series, which covers the longest period, are the most interesting. The normal cells in the culture originated from ovals which were removed with a few triradiates from Series III in May 1940. It will be seen that an initial rapid increase in maximum length was followed by a slower increase until February 1941 when cells 32 μ long were measured. In that month normal cells 29 μ long were common and the smallest seen, apart from some ovals, were about 26 μ long. This subculture, No. 'A' 9, was lost by enemy action, and the series was restarted by subculturing again from the old 'A' 8 subculture which partially survived in the shattered remains

TABLE II. VARIATION IN MAXIMUM LENGTH OF NORMAL CELLS IN CULTURES GROWN FROM OVAL CELLS

Series 'A'			Series 'U'		Series 'A' (*cont.*)		
Date	Sub-culture no.	Maximum length	Sub-culture no.	Maximum length	Date	Sub-culture no.	Maximum length
8. v. 40	1	Oval	—	—	26. v. 41	9*a*	28 μ
13. v. 40	1	"	—	—	23. vii. 41	10	26 μ
17. v. 40	1	16 μ	—	—	25. viii 41	11	21 μ
27. v. 40	2	21 μ	—	—	15. ix. 41	12	21 μ
13. vi. 40	3	25 μ	—	—	4. xi. 41	13	23 μ
24. vi. 40	4	27 μ	—	—	2. i. 42	14	24 μ
10. vii. 40	—	—	1	Oval	7. iv. 42	15	26 μ
19. vii. 40	—	—	1	"	20. v. 42	16	27 μ
24. vii. 40	5	29 μ	1	15 μ	30. vi. 42	17	29 μ
31. vii. 40	—	—	1	23 μ	11. viii. 42	18	29 μ
9. viii. 40	6	29 μ	—	—	11. ix. 42	19	28 μ
20. viii. 40	—	—	2	25 μ	20. i. 43	20	27 μ
28. viii. 40	7	30 μ	—	—	20. ii. 43	21	25 μ
11. ix. 40	7	30 μ	2	26 μ	22. iii. 43	22	25 μ
13. xi. 40	8	30 μ	3	27 μ	3. vi. 43	23	28 μ
4. ii. 41	9	32 μ	4	28 μ			

of its flask. The new subculture, 'A' 9*a*, showed a decrease in size, and this decrease continued until by August and September 1941 only short cells, most of them less than 20μ long, were present. There followed a slow lengthening for nearly a year, followed by a slight shortening, with the last measurement in June 1943 showing again an increase in maximum size. Similar changes in length have been observed in the clone normal cultures, Series I and II and in other stock cultures, but the data for these are not so complete and are therefore not given.

The interpretation of the 'A' series is complicated by the presence throughout of a considerable proportion of triradiates which at certain times, as will be shown later, gave rise to some normals by a process of losing one arm. However, as normals so produced appear always to be small, shorter than about 25μ, their production probably does not affect the picture to any appreciable extent. This complication does not arise in the 'T' and 'N' series where triradiates were always rare and where similar fluctuations in length of the normal cells were observed.

In diatoms a decrease in the general cell size through successive divisions is followed as a rule by a sudden increase brought about by auxospore formation. In these *Nitzschia* cultures auxospores have never been seen, and when an increase in maximum cell length takes place it is always slower and more gradual than would be likely if normal auxospores were produced. It seems probable that the cells, being so lightly silicified, merely grow in length in the ordinary manner of a plant cell, material being added to the cell wall as required. Perhaps slow shrinkage can also take place by absorption.

When a *Nitzschia* cell divides, one of the daughter cells always looks to be slightly shorter than the other, as is usual for a diatom. Once they have

separated, however, there seems to be no reason why the shorter should not enlarge slightly; if this should happen the general cell size of a culture would be maintained, or even raised. Auxospores would thus not be needed by this species and it may well be they are never formed.

Allen & Nelson (1910, p. 462) noticed no appreciable diminution in size in their cultures over a period of 2 years, although the total growth observed was enormous. Unfortunately, they do not appear to have made any measurements or they might possibly have found some slight changes. They also do not appear to have noticed any variation in the size of the cells in any one culture, as has been a common feature in my cultures, the direct descendants of theirs. My findings are in agreement with their conclusion that 'the theory of gradual decrease in size with successive generations cannot be generally applied'.

The triradiate does not readily lend itself to measurement, but there is little doubt that it undergoes similar size changes. Cultures with predominantly large triradiates and others with mainly small ones have frequently been noticed.

The Formation and Behaviour of Triradiate Cells in Culture

It has been shown how triradiate cells may arise in cultures of the normal form by the development of three-cornered ovals. It is not known how an oval cell becomes three-cornered, but it is definite that such cells are infrequent. It follows that in any pure culture of normals triradiates are likely to put in an appearance sooner or later. For long periods, as in the 'T' and 'N' series of my experiments, and presumably also in the Plymouth stock cultures whilst under the care of Dr Allen, these triradiate cells may be present in very small numbers only to be found by special searching. If there be any physical and chemical conditions favouring their appearance these are still to be discovered; some preliminary experiments on growing cultures of pure normal cells under varying light intensity gave only negative results. It should be noted that triradiates first appeared in Series I and II (clone normal) whilst they were being kept at a constant temperature of 12° C., as they had been since they were first formed. It was not until after enemy damage to the controlled temperature chambers in March 1941 that these cultures were subject to the temperature changes of an ordinary room. There is also no evidence whatever that exhaustion of nutrients, or the presence of moulds or bacteria, has any effect in bringing about triradiate production. In old infected pure normal cultures many misshapen cells may be found, especially in the thick mass at the bottom of the flask, but these are multitudinous in form, and though some of them have three or more bent and uneven arms no regular triradiate has been seen amongst them. Subcultures made from such masses have never yielded triradiate cells; they have given rise to normals only. There is thus no reason to suspect that the presence of triradiates is an indication of bad cultural conditions.

There has been little to suggest that normal cells ever become triradiate by growing out a third arm, although the opposite process of a triradiate becoming normal by gradually eliminating one arm is of common occurrence. Nevertheless, a very few normals, two or three out of many hundreds of thousands of normals seen during the last few years, have had one arm bifid in a manner suggesting that the process is not impossible and that it may occasionally take place. However, there is no doubt that as a general rule triradiates arise from normals only through the intermediary of oval cells.

The notable increase in recent years of the numbers of triradiates in the Plymouth stock cultures and in cultures elsewhere (see p. 238) cannot yet be fully explained. It might be that from time to time strains of triradiates arise which have a higher division rate than that of the normal cells in the same culture. The result of mixing cells from the clone triradiate with cells from a clone normal was therefore likely to be interesting, and accordingly the following experiment was carried out.

In June 1941 triradiates from Series III and normals from Series II were mixed in about equal proportions, about 5 c.c. of a well-grown subculture of each being used. The mixture was estimated—by counting a thousand cells—to be 51·5% triradiate. Two 1 l. flasks containing Allen-Miquel sea water were inoculated from this mixture; these were designated Series IVA and Series IVB. From then on they were regularly subcultured, and from time to time estimations were made of the percentage triradiate; these results are recorded in Table III. For each estimation at least five hundred cells were counted, nearly always several hundreds more. In the earlier estimations usually between a thousand and fifteen hundred cells were counted. The sampling error of the percentages given is of the order of 1·0. It will be seen that the proportion of triradiates present increased in both series by some 20% during the first month and thereafter rose steadily though more slowly, until by February 1944 over 90% of both series consisted of triradiates.

In April 1942 two additional series of cultures were begun in order to test the effect of changing the medium. Similar sized flasks containing Erdschreiber were inoculated from Series IVA and IVB and subcultures were continued in this medium. The figures (Tables III) show that in Series IVA there was a preliminary slight fall in the percentage triradiate, followed by a steady rise some months later. In Series IVB there was merely a check, followed by an almost steady rise, although as in Series IVA the percentage triradiate never quite catches up with that in the Allen-Miquel sea water. The Erdschreiber thus appears in these cultures to be slightly more favourable to the normal cells, mainly perhaps owing to the initial fall or check in the numbers of triradiate when the change-over from the other medium took place. In any event the effect is slight. It has already been remarked (p. 242) that there is often a tendency for oval cells to be produced more readily in Erdschreiber than in Allen-Miquel, and this tendency has sometimes been noticeable in these Series IV cultures. As ovals develop more often into normals than into

TABLE III. VARIATION IN THE PERCENTAGE TRIRADIATE OF MIXED CLONE CULTURES OF TRIRADIATE AND NORMAL CELLS AND THE PERCENTAGE OF THE TRIRADIATES WITH SHORTENED ARMS

		Series IVA				Series IVB				Series IVC	
		Allen-Miquel		Erdschreiber		Allen-Miquel		Erdschreiber		Allen-Miquel	
Sub-cultures made	Date counted	Tri-radiate	Short-armed	Tri-radiate	Short-armed	Tri-radiate	Short-armed	Tri-radiate	Short-armed	Tri-radiate	Short-armed
13. vi. 41	13. vi. 41	51·5	—	—	—	51·5	—	—	—	—	—
13. vi. 41	11. vii. 41	70·6	—	—	—	73·6	—	—	—	—	—
24. vii. 41	24. vii. 41	—	—	—	—	—	—	—	—	7·0	—
19. vii. 41	20. viii. 41	74·7	—	—	—	76·1	—	—	—	—	—
24. vii. 41	20. viii. 41	—	—	—	—	—	—	—	—	10·3	—
28. viii. 41	27. ix. 41	74·0	—	—	—	77·0	—	—	—	10·5	—
8. x. 41	4. xi. 41	73·2	8·0	—	—	77·4	—	—	—	12·6	—
26. xi. 41	9. i. 42	77·0	—	—	—	79·1	—	—	—	17·3	—
4. ii. 42	1. iv. 42	78·0	—	—	—	81·1	—	—	—	20·4	—
16. iv. 42	7. v. 42	81·5	2·3	75·8	2·9	82·4	1·1	81·2	1·2	—	—
29. v. 42	30. vi. 42	—	—	—	—	84·7	1·7	85·6	2·9	—	—
2. vii. 42	18. viii. 42	82·8	2·1	75·0	2·6	88·7	1·6	86·8	3·5	41·2	0·0
26. viii. 42	2. x. 42	83·8	1·1	74·9	4·8	89·5	1·4	86·3	6·4	42·8	2·5
14. x. 42	25. xi. 42	82·2	1·9	68·4	4·1	89·1	1·9	78·7	3·8	48·2	0·9
21. xii. 42	20. ii. 43	87·9	0·1	72·9	1·9	90·4	0·6	84·9	2·5	54·4	0·7
24. ii. 43	31. iii. 43	88·8	0·2	77·5	1·6	91·7	0·6	83·8	1·0	55·7	1·4
21. iv. 43	3. vi. 43	91·3	0·5	77·9	2·1	92·3	1·5	86·4	1·4	61·3	1·7
7. vi. 43	15. vii. 43	91·6	0·3	85·0	0·7	91·7	4·3	88·5	1·9	68·7	2·7
6. viii. 43	17. ix. 43	92·0	2·3	88·7	3·6	93·0	4·8	88·0	4·2	80·4	5·3
6. x. 43	15. xi. 43	92·6	1·4	90·3	3·8	90·9	3·5	90·2	4·1	81·1	6·4
17. xii. 43	19. ii. 44	95·3	0·8	91·9	2·2	92·8	2·1	90·8	2·1	—	—

triradiates, those cultures producing most ovals are likely to have a higher percentage of normals, other things being equal.

More striking even than in the Series IVA and IVB cultures is the great increase in abundance of triradiates in another mixed culture where the initial percentage triradiate was much less. This series, IVC, was begun in July 1941 with a mixture of Series II with Series III in such proportions that the mixture was 7% triradiate. Table III shows that from the first there was a steady increase in the proportion triradiate, until by November 1943 over 80% of the culture consisted of these cells.

In these experiments the triradiates evidently grew more strongly, that is, had a higher division rate, than the normal cells mixed with them. It has already been suggested (p. 251) that this is what had happened in the Plymouth and other stock cultures during the years when the triradiate type of cell seemed to be ousting the normal. This phenomenon can thus be explained on the assumption that from time to time in cultures of the normal cell there are produced ovals from which arise more vigorously growing triradiates. It may well be that some strains have more vigour and a higher division rate than others, and that it is only when a vigorous strain appears that any great increase in the number of triradiates is to be noticed. Thus a number of cultures derived from Plymouth stocks some years ago and kept apart by other workers

(e.g. the cultures kept at the Plymouth Technical College by Miss F. A. Stanbury, who obtained her material from Dr Allen in 1929) have produced few or no triradiates. Something similar appears to have happened in my own 'T' and 'N' experiments in which triradiates were very rarely seen for 4 years, after which they suddenly became very common in four out of the five series of subcultures. In the fifth they were less numerous. The early subcultures kept at the Royal College of Science (see p. 238) which produced such an abundance of triradiates not long after separation from the early Plymouth stocks may have produced a particularly vigorous and fast-growing strain of triradiate shortly after the separation had taken place. It may also be that a strain will weaken in vitality after a period of years.

Short-Armed Triradiates and the Production of Normal Cells from them

In most cultures containing triradiates a number of the latter are usually to be found with one arm considerably shorter than the other two (Fig. 5B) or with one long and two short arms when the cell has a Y-shaped appearance. In some

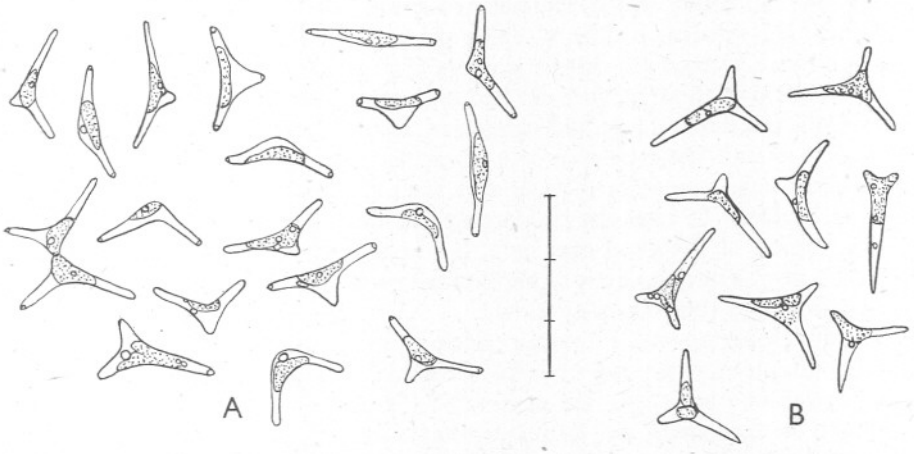

Fig. 5. A. Short-armed triradiates and normals produced from them. All were drawn from Series III on 10 December 1941 from the subculture of 8 October 1941 (see Table IV). B. Various types of short-armed triradiates from different cultures. Each division of the scale represents 10 μ.

cultures, as in the clone triradiate during the first 3 months of its growth, such cells are absent or are very rare; at other times they may be common, and all degrees of shortening are to be observed from scarcely at all to the shortest arm being nothing more than a slight swelling on the other two (Figs. 5A, 6*c*). The question arises whether these forms are abnormalities or whether they are stages in the conversion of triradiates into normals. It has already been mentioned (p. 251) that there is no definite evidence of the converse

process taking place, although with such a variable species it cannot be maintained that it would never happen.

These short-armed triradiates first came prominently to notice in the autumn of 1941. It was in the summer of that year that the regular stock cultures, numbered respectively 569 and 589, had become almost entirely triradiate and the clone Series III was still almost pure triradiate. During the following autumn all three series of cultures produced a great number of normal cells, thereby completely altering their composition and general appearance. At this time very large numbers of short-armed triradiates, of all degrees of shortening (Fig. 5A), were to be seen in the cultures, and there can be no doubt whatever that these had been derived from ordinary triradiate cells. Far too few normals had been in the cultures previously for there to be any possibility that the short-armed triradiates were normals in process of acquiring third arms. There can likewise be little hesitation in accepting the interpretation that these triradiates were converting to normal by a process of gradually shortening one arm until it was finally eliminated. Large numbers of normals had appeared, and there was no special reason to suspect at this time that they had been derived directly by the development of oval cells. The latter were no more frequent than usual, whilst short-armed triradiates were relatively abundant.

Whilst this process had been taking place in the Plymouth cultures similar changes were going on in cultures kept at Hull by Dr C. E. Lucas. For several years previously the Hull cultures had undergone changes closely parallel with the Plymouth ones. They had originated from Plymouth stock sent to Hull about 1930 and have been grown there independently ever since. A few triradiates were noticed in 1932, and by 1934 they may have formed about 1% of the cultures. In 1936 the proportion had risen above 50%, reaching 97% by the spring of 1939 and over 99% by the summer of 1941. In addition to these cultures a sample of my clone triradiate was sent to Hull in February 1940 and maintained there since that date.

In November 1941, Dr Lucas noticed in all his cultures a sudden increase in the numbers of normal cells present. At that time he was unaware of happenings at Plymouth. He made a rough analysis on 18 November, subcultured on the 29th of that month and again on 16 January 1942, and counted both sets of subcultures early in February 1942. His results are shown in Table IV. If these figures are compared with those for the Plymouth stock cultures and clone triradiate (Series III) for the same period (Table V), it will be seen how closely they correspond, the greatest divergence being shown by

TABLE IV. PERCENTAGE TRIRADIATE OF HULL CULTURES

	June 1941	February 1942	
		Subculture of 29. xi. 41	Subculture of 16. i. 42
Standard culture	>99·0	62·0	59·0
General culture		64·5	63·0
Clone triradiate		68·2	70·7

the clone triradiate culture which had most recently been divided between the two places. As at Plymouth at this time short-armed triradiates were frequent in the Hull cultures and there seems to be no doubt as to the method of change. The later history of the Hull cultures is discussed below.

In both the Plymouth and Hull cultures during the period of change (and subsequently at Plymouth whenever short-armed triradiates were common) there were normal cells which were much more curved than usual, they were indeed bent (Figs. 5A, 6 *a*, *b*). It seems certain that such cells represent two arms of a triradiate after final disappearance of the third arm. In most triradiates no two arms lie along the same straight line, although this is sometimes seen. Presumably the bend ultimately straightens out; this is confirmed by finding a division stage (Fig. 6*e*) in which one of the daughter cells is bent and the other almost straight. Bent normals are definitely associated with short-armed triradiates, and they are not seen in cultures where the latter do not occur.

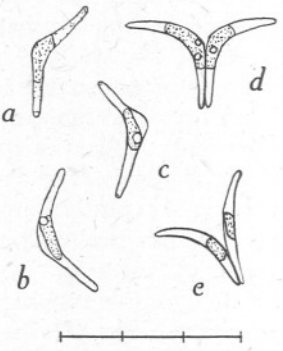

Fig. 6. *a*, *b*, *c*, types of 'bent' normals produced from triradiate cells by the loss of one arm; in *c* the base of the third arm is still present; *d*, bent normals dividing; *e*, a division stage in which one of the daughter cells has straightened out. Each division of the scale represents 10 μ.

There remains the possibility that a dividing triradiate will sometimes produce a pair of daughter cells in which one will lack the third arm or be provided with only a stump of it, whilst the other is fully triradiate. Of the many thousands of division stages I have seen, none has fitted this description, but Dr Lucas tells me that he has seen one such. Thus at best this type of division must be extremely rare and the direct production of normals by this method equally rare. In the many division stages of short-armed triradiates which have been seen there has been little difference in size or shape between the daughter cells, although one of the two does sometimes show a perceptible reduction in length of the short arm as compared with the other.

The close correspondence in behaviour of the Plymouth and Hull cultures is very puzzling. With a view to hearing whether similar events had taken place elsewhere a short account has already been published (Wilson & Lucas, 1942) calling attention to the facts. Some interesting letters were subsequently received from other workers but none had to report a similar phenomenon, though there are good indications that something of the sort happened in Edinburgh. When in 1937 Dr Gross left Plymouth for that city he took with him samples of our stock cultures. For a short period they were grown in Allen-Miquel sea water as at Plymouth, but the medium was soon changed to Erdschreiber. Dr Gross informs me that during the summer of 1940, whilst they were temporarily in charge of Dr J. E. G. Raymont, the cells were almost all triradiate, but that by February 1942 (when he kindly sent me samples)

they were almost all normal with only a few triradiates amongst them. The change-over was not observed, but it seems likely that it took place earlier, as well as more completely, than at Plymouth. The use of Erdschreiber may have had some influence on this, but in view of the experiments described above, and the difference in subculturing practice between Hull and Plymouth where nevertheless results were so similar, one cannot regard this as furnishing a satisfactory explanation.

Since the constant-temperature apparatus was damaged by enemy bombing in March 1941 the Plymouth cultures have been kept in an unheated room exposed to the ordinary daylight and temperature variations of a north window. The cultures in Hull are kept under similar conditions. It seemed possible therefore that some seasonal fluctuations might occur in the cultures, indeed, that to some extent the close correspondence between the Hull and Plymouth cultures might be related to the seasons as being a common factor for both places. The Plymouth cultures were thus watched with this end in view; it was, unfortunately, not possible to refer back to cultures earlier than 1941, as practically all preserved material was lost during the air raids of the spring of that year.

The cultures investigated were the regular Stocks 569 and 589, the clone triradiate Series III, the clone normals Series I and II, the mixed Series IVA and IVB, and the Series 'A'. In every instance estimations were made of the percentage of triradiates with shortened arms, only those cells being counted in which the shortening was really definite. The amount of shortening varied from just definitely perceptible to the arm having almost entirely disappeared. The results are shown in Tables III and V alongside the percentage triradiate, which was estimated at the same time.

Over a period of 3 years it can be seen that the percentage of short-armed triradiates increases, almost without exception, in October and November of each year (in the 'A' series the maximum was in July 1942), with sometimes at the same time a corresponding fall in the percentage triradiate, or if not an actual fall often a check in the rate of increase of the percentage triradiate. In no instance, however, was the phenomenon as marked as in November 1941. The most striking figures are for the Stocks 569 and 589 and for the clone triradiate Series III, but the same trend is to be observed, though to a lesser extent, in the mixed cultures of Series IV, being more marked in the Erdschreiber cultures than in the Allen-Miquel sea water. It is well shown in the figures for the clone normal cultures Series I and II, although here the triradiates were present in very small numbers, especially at first, and the percentage figure is in each case based on only a few individuals and therefore is not so accurate. The 'A' series is an exception to the general picture in that maximum shortening occurred earlier in 1941 and 1942, in September and in August respectively, although in 1943 the maximum was reached in November.

From these results it seems permissible to conclude that whilst some arm reduction may take place at any time during the year there is a definite tendency

TABLE V. THE PERCENTAGE TRIRADIATE OF PLYMOUTH CLONE AND STOCK CULTURES AND OF SERIES 'A' AND THE PERCENTAGE OF THE TRIRADIATES WITH SHORTENED ARMS

Sub-cultures made	Date counted	Series III		Stock 569		Stock 589	
		Triradiate	Short-armed	Triradiate	Short-armed	Triradiate	Short-armed
3. iv. 41	8. vi. 41	98·8	—	99·3	—	98·6	—
15. vii. 41	26. viii. 41	87·7	6·6	—	—	—	—
28. viii. 41	15. ix. 41	77·2	7·8	—	—	—	—
8. x. 41	7. xi. 41	60·0	21·8	62·6	21·1	66·4	17·7
8. x. 41	10. xii. 41	59·9	13·1	—	—	—	—
27. xi. 41	17. ii. 42	60·3	13·3	61·6	11·3	64·7	—
16. iv. 42	7. v. 42	62·0	6·0	60·9	6·8	66·7	5·6
16. iv. 42	28. v. 42	62·8	6·4	62·6	7·9	65·2	5·5
29. v. 42	30. vi. 42	64·9	7·1	62·3	8·3	68·4	5·9
2. vii. 42	29. viii. 42	63·4	6·5	62·3	8·7	66·0	9·9
26. viii. 42	10. ix. 42	64·5	8·1	61·9	9·9	65·1	10·8
26. viii. 42	2. x. 42	64·5	10·7	62·3	11·8	64·9	10·6
14. x. 42	25. xi. 42	65·4	11·4	59·4	14·3	62·0	11·6
14. x. 42	16. xii. 42	64·0	7·7	58·9	9·0	64·3	6·9
20. xii. 42	20. ii. 43	67·4	2·6	64·5	3·8	67·5	3·8
24. ii. 43	31. iii. 43	73·6	2·7	71·2	3·3	69·6	3·7
21. iv. 43	3. vi. 43	67·1	3·2	64·7	5·4	71·5	4·9
7. vi. 43	15. vii. 43	70·7	5·1	72·7	3·7	69·3	6·2
6. viii. 43	17. ix. 43	79·2	8·5	73·6	10·9	60·9	15·0
6. x. 43	15. xi. 43	75·5	11·0	72·8	13·1	58·0	15·8
17. xii. 43	19. ii. 44	76·8	2·5	78·0	3·2	62·2	6·1
10. v. 45	13. viii. 45	90·5	1·6	91·8	4·2	77·1	2·6

Sub-cultures made	Date counted	Series I		Series II		Series 'A'	
		Triradiate	Short-armed	Triradiate	Short-armed	Triradiate	Short-armed
24. vii. 40	9. viii. 40	—	—	—	—	46·4	13·6
3. iv. 41	8. vi. 41	0·2	—	0·0	—	—	—
20. v. 41	23. vii. 41	—	—	—	—	61·0	8·6
15. vii. 41	26. viii. 41	—	—	—	—	60·7	11·5
28. viii. 41	15. ix. 41	—	—	—	—	44·0	18·7
8. x. 41	7. xi. 41	Very few	—	Extremely few	—	—	—
27. xi. 41	2. i. 42	—	—	—	—	40·6	9·5
27. xi. 41	17. ii. 42	5·4	—	A few	—	—	—
16. iv. 42	7. v. 42	—	—	—	—	49·5	11·3
16. iv. 42	28. v. 42	6·0	9·0	3·0	37·5	—	—
29. v. 42	30. vi. 42	10·4	13·6	3·3	69·2	—	—
2. vii. 42	29. viii. 42	9·1	14·1	4·8	34·0	55·9	13·5
26. viii. 42	10. ix. 42	14·1	15·8	5·7	46·4	—	—
26. viii. 42	2. x. 42	13·8	10·0	4·9	41·3	59·1	11·1
14. x. 42	25. xi. 42	20·6	5·8	3·6	25·0	60·5	4·4
20. xii. 42	20. ii. 43	22·8	2·5	5·8	21·0	68·7	3·0
24. ii. 43	31. iii. 43	34·6	2·9	6·7	11·4	73·5	3·3
21. iv. 43	3. vi. 43	43·0	7·0	8·4	14·6	76·5	2·6
7. vi. 43	15. vii. 43	50·0	12·0	10·4	20·4	81·0	4·8
6. viii. 43	17. ix. 43	55·2	14·6	17·6	24·7	80·3	7·0
6. x. 43	15. xi. 43	59·1	13·6	18·9	16·6	79·2	8·9
17. xii. 43	19. ii. 44	62·6	3·8	27·8	9·9	81·2	4·4
10. v. 45	13. viii. 45	74·8	3·4	67·7	2·0	—	—

for the process to be most active during the late autumn. It is then that triradiates with mere stumps of a third arm and sharply bent normals are more frequently seen than at any other time of the year. Such stages are, on the whole, most infrequently seen in the spring.

The existence of a regular seasonal change of this nature makes it a little less difficult to understand the close correspondence between the Hull and Plymouth cultures, at least as far as time of year is concerned. It is still not clear why in 1941 the change should in both places, and in so many cultures, have been of such great magnitude, and at the moment there is no rational explanation to offer.

A regular yearly cycle suggests that either light or temperature, or both, are causative factors. A few simple experiments devised to test this gave inconclusive results, perhaps because the experimental conditions were not sufficiently rigid. As regards light, duration of day seems likely to have more effect than mere variation in intensity.

Experiments with Low Salinity

The species having been recorded from the Baltic (see p. 264), it was decided to see what would be the effect of growing the species in a medium of lowered salinity. It was found that in mixtures of Allen-Miquel sea water with distilled water growth was good at all concentrations up to 50% distilled water.

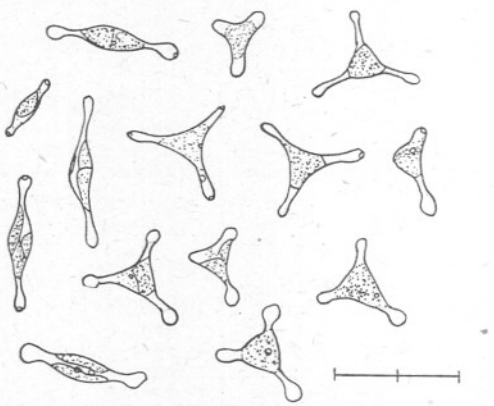

Fig. 7. Normal and triradiate cells with swollen extremities from cultures grown in a mixture of one part of normal Allen-Miquel sea water to three parts of fresh water. Each division of the scale represents 10 μ.

There was some growth even with only 25% Allen-Miquel sea water. When the mixture contained only 5% of the latter no growth was visible. Thus the species can live and grow at salinities much lower than that of normal sea water, but not in fresh, or almost fresh, water.

An interesting feature of these experiments was the relatively large number of cells, both normal and triradiate, with much swollen tips to the arms. Some extreme, although common, examples are shown in Fig. 7. Other cells had

swellings intermediate between these and normal cells, in which the enlargement of the tip is only just perceptible. It must be noted, however, that swollen tips are not confined to cells grown at lowered salinities but occasionally have also been seen in ordinary Allen-Miquel solutions, though not as commonly. The fact that they were present in the Allen-Miquel controls to these salinity experiments suggests that lowering the salinity merely accentuates a tendency to form swollen tips and is not in itself a primary causative factor. In connexion with this subject Hustedt (1930, p. 158) has mentioned that he found a size increase in marine diatoms with reduced concentration of the medium.

Cruciform Cells

The experience with lowered salinity serves to emphasize the great variability of cell form in this species, a variability that can rarely be attributed to some obvious condition of the environment. Cells of odd shape are not uncommon in most cultures, and from time to time even four-armed cells are seen; these

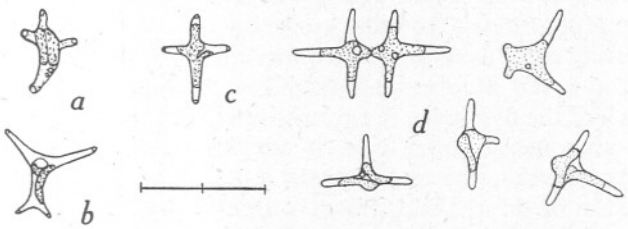

Fig. 8. Cruciform cells. *a*, *b*, irregular types; *c*, regular cruciform cell; *d*, a group of cruciform cells with one arm reduced; a division stage is shown in which the shortened arm of one daughter cell is a little smaller than that of the other. Each division of the scale represents 10 μ.

in healthy cultures about which there is nothing noticeably unusual. They are generally irregular in shape; two specimens are drawn in Fig. 8 *a*, *b*. It is possible that for a time their descendants remain four-armed, but of the irregular cells division stages have not been observed. The shape is probably unstable, and it is likely that they die out or quickly revert to a smaller number of arms. Slides containing specimens have often been washed off into culture medium, but the shape has never been found again in the ensuing growth, even after much searching. As the cells were always noticed when under a cover-glass and when using a high-power objective it was not possible to pick them out individually.

It has already been mentioned that in February 1942 Dr Gross sent to me samples of the cultures he maintained at Edinburgh. They had been derived from Plymouth stocks in 1937. From one of these samples two subcultures were started, one in Allen-Miquel sea water and one in Erdschreiber; they were maintained for a considerable period. They continued mainly free from triradiates although a few were always present in both media. In January 1943, during a routine examination, there was noticed in these cultures, and

more frequently in the Erdschreiber culture, cells in the form of a perfect cross (Fig. 8*c*), not an irregular four-armed structure like those mentioned in the preceding paragraph. In general, one arm was slightly longer than the other three, which were equal. The finding of several of these cells, all exactly alike, seemed to indicate that the type was relatively stable reproducing true to type. This was confirmed when they increased somewhat in abundance during the next few weeks and dividing pairs were seen. In April the first of a series of attempts to obtain the form in pure culture was made. Some of the culture containing crosses was diluted down with a large volume of sterile Allen-Miquel sea water and placed in Petri dishes in a north window. After some days clusters of cells were visible to the naked eye. The majority of the clusters had grown from single cells and were all of one type. It was just possible to distinguish the type with a $\frac{2}{3}$ in. objective and to find a few clusters which consisted entirely of crosses. They were picked out with fine pipettes and transferred to sterile media in small flasks. It was impossible to avoid picking up cells of other types with the crosses, but the latter nearly always formed a big proportion of the cells thus selected for further growth. Ten days after inoculating eight flasks in this manner three showed no signs of crosses, but five did so in fair numbers, although less than half the cells were of this type. In each of the five flasks the crosses were very similar in form; between flasks there was some variation, those in one flask, for instance, having shorter and stumpier arms than the crosses in the others. Three of these flask cultures were selected to be diluted and strewn in Petri dishes as before, the resulting clusters this time being, of course, more frequently cruciform, and were more readily picked out without admixture with other types. In spite, however, of repeated attempts a pure culture of crosses was never obtained, although on several occasions it was practically certain that nothing but crosses had been picked up by the pipette, except possibly for ovals mixed with, and probably produced from, the crosses. All the cultures started in this way with crosses and perhaps a few ovals soon had a big proportion of triradiates and normals, often of small stunted varieties which had probably arisen by reversion from the crosses, either directly or through the formation of oval cells. Cruciform cells with one, or even two, arms shortened have been seen (Fig. 8*d*) and suggest that this is one way in which they may change back to the triradiate or to the normal condition. Cruciform cells producing ovals have also been seen. The best cultures obtained were about 50% cruciform and this figure was not improved on. Indeed, in some series successive subcultures have shown a considerable diminution in the proportion of crosses present. The cross is evidently less stable in form than the triradiate, although it keeps its shape through what must be a very large number of generations.

By early 1945 in one series of cultures cruciform cells had become very rare and they showed signs of dying out altogether. In another series they were still frequent, but normal and triradiate cells were more numerous; in a third series cruciforms were very common although not so abundant as the other types.

It is not easy to suggest how cruciform cells originate. They probably arise from oval cells which become four-cornered, in the same way that triradiates arise from three-cornered ovals. Such four-cornered ovals have not been seen, though this is hardly surprising as they must be very rare indeed. There seems to be no obvious explanation of why oval cells should occasionally become four-cornered.

The appearance of true cruciform cells was not confined to the cultures obtained from Dr Gross, although in them they were much commoner. Cells of identical appearance were seen very rarely in four other series of cultures from early 1943 until the end of that year; they had not previously been observed. The cultures in which crosses were seen, sometimes only one or two cells in each series, were Stock 589, Series II, Series III, and Series IV C. They were also seen again in May 1945, in Stock 569 and Series III. There is no question of contamination between these cultures or between them and those from Edinburgh; the cells must have arisen independently in each. In these cultures they never increased in abundance as they did in the cultures from Edinburgh; they probably died out as they have not been seen lately. It seems strange that crosses should have appeared in several cultures all about the same time. The cultures were all standing side by side subjected to the same temperature and lighting conditions, but one flask contained Erdschreiber as the medium, the others Allen-Miquel sea water. On the whole it does not seem satisfactory to attribute the occurrence of the crosses to physical or chemical conditions unless it be that all-round good cultural conditions are favourable to the production and survival of aberrant shapes, as they may well be. The cross is evidently a moderately stable form that now and again appears, though rarely, and in good cultural conditions can survive. The appearance of a very few specimens in several separate cultures in 1943 and again in 1945 must be regarded as coincidences.

Frustules with more than four arms have not been seen.

Nomenclature

The diatoms used in these experiments were all derived from the original cultures of Allen and Nelson. The stock series 589 has been traced back through Dr Allen's notes to a Petri dish inoculated on 5 December 1907 with plankton from outside the Sound. Stock series 569 does not occur in his notes and is probably derived from a flask of 589 in which the middle figure, written on the flask with a glass-marking pencil, had become partly rubbed away and later interpreted as a 6 when it was subcultured at some time before the cultures came into my keeping. There appears to have been no addition to the cultures from the sea, since the species was isolated before Allen and Nelson's 1910 paper was published.

The species was identified by Nelson (private information from Dr Allen) and the name *Nitzschia closterium* W.Sm. forma *minutissima* was given by him.

As he quotes no authority for the forma it is not clear whence he derived the name; it may have been suggested by some then recent systematic papers. Mereschkowsky (1901), for instance, discussing these difficult diatoms abandoned the name *closterium*, splitting the forms included under it into two new species which he called *Nitzschiella tenuirostris* and *N. gracilis*. Of the former, which corresponds most closely to what is generally regarded as *Nitzschia closterium*, he had several varieties, one of which, *Nitzschiella tenuirostris* var. *parva* Mer. forma *minutissima* is a minute diatom, 35–40μ long. His figure of it shows a more swollen central portion and finer arms than those of our cultured species. Of his *tenuirostris* as a whole he remarked that the striae and carinal dots are invisible. Peragallo & Peragallo (1897–1908, p. viii) discussed this classification of Mereschkowsky's without reaching any definite conclusion, but in the text of their systematic part they recorded *closterium* Ehr. as a variety of *N. longissima* though in the legend to their plate LXXIV they give it specific rank.

My own impression is that whilst the *Nitzschia* of these cultures is very close to *N. closterium* (Ehr.) W.Sm., it may well be specifically distinct, but that with our present inadequate knowledge of this extremely difficult group the possibility cannot be excluded that it is merely a 'phase' of that species in the sense in which Hendey (1937) uses the term. For the time being it may continue to be distinguished as forma *minutissima* in Nelson's sense until such time as the genus is thoroughly revised.

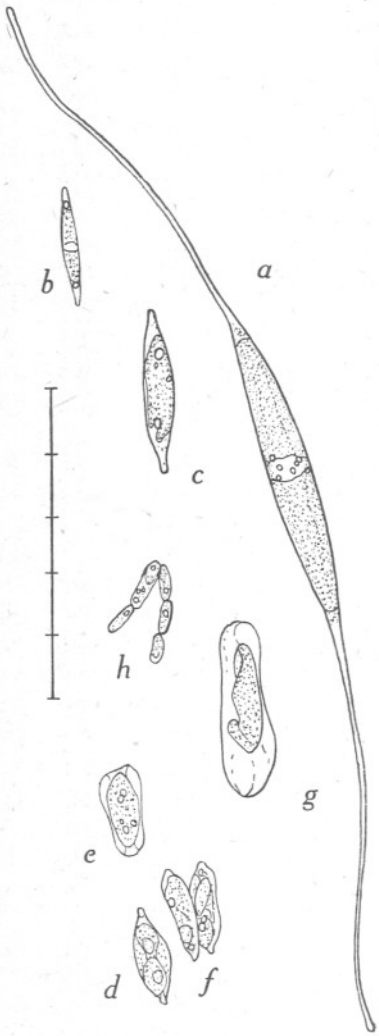

Fig. 9. *Nitzschia* (? *closterium* (Ehr.) W. Smith) from an aquarium tank. *a*, frustule from aquarium tank; *b*, *c*, reduced frustules after culturing; *d*, an 'oval'; *e*, *f*, division stages of 'ovals'; *g*, a large type of 'oval'; *h*, a string of small oval types. Each division of the scale represents 10μ.

Some notes on *N. closterium* as it appears in the literature are relevant to this discussion. Ehrenberg (1840) described and figured as *Ceratoneis Closterium* n.sp. a diatom about 100μ long which he obtained in the North Sea at Cuxhaven and elsewhere. His figure of three cells was copied closely (except as regards colouring) by Pritchard (1852). Smith (1853) described

and figured as *Nitzschia Closterium* n.sp. what is apparently the same organism. He indicated a species about 160μ long with definite striae (? carinal dots). Except for the striae, which I have not seen, his species resembles a *Nitzschia* common in Plymouth dredgings and which lives abundantly in some of our shallow tanks. A particularly fine specimen is shown in Fig. 9*a*, but the arms are often much shorter than this and curved in one direction only. Another figure of what seems to be the same species is given by Lebour (1930, fig. 176, p. 212). I disagree with the statement that 'it is the form used commonly by Dr Allen...for culture', in spite of the fact that the size she gives approaches, although it is considerably longer than, the cultured form. I have never seen a cultured *Nitzschia* in which the arms are so slender along their whole length and so markedly differentiated from the central part containing the chromatophores. Moreover, the manner in which the chromatophores are drawn in this figure agrees with the dredged and tank-living form much more closely than with the cultured type. The question arises, is the latter a modification of the former brought about by culturing?

To answer this question specimens from the aquarium were isolated into Allen-Miquel sea water and grown in the usual way. There was a marked tendency for the arms to shorten relatively and the cells to become dwarfed (Fig. 9 *b*, *c*), but the frustules never came to resemble those of the regular cultures, the chromatophores especially differing in appearance. Cells even resembling ovals were produced (Fig. 9 *d–h*) but they varied in size and were always distinctly different from ovals of the stock species, although they divided in a similar manner. Moreover, the aquarium species would not give dense cultures as does the stock species, indicating that its requirements as to *p*H, etc., are not the same. Nothing resembling a triradiate was seen in these cultures of the aquarium form which seems to be very close to Smith's *N. Closterium*, and may indeed be the same species although the striae he mentions have not been seen. Van Heurck (1896) regarded Smith's species as a variety of *N. longissima* (Bréb.) Ralfs and gives the length as 260–320μ. He remarked that 'the carinal dots are only visible with difficulty. It requires an excellent immersion objective to distinguish them clearly.... It was probably the carinal dots that Prof. Smith described as indistinct marginal striae.' Peragallo & Peragallo (1897–1908), as we have seen, also regarded *closterium* as a variety of *N. longissima*; they said that the striae are invisible, and give the length as 26–140μ. Their figure (pl. LXXIV, fig. 15) resembles the aquarium form more closely than the culture species. Karsten (1899) shows a figure (fig. 177) of *N. closterium* W.Sm. which resembles the aquarium species; he regards it as distinct from *N. longissima* (Bréb.) Ralfs, ascribing to it a length of 50–84μ. Gran (1905) copies Karsten's figure and more or less his description. Hendey (1937) describes a species resembling the aquarium form with a length up to 80μ. His figures do not suggest the cultured form. Hart (1942, p. 292) comments on the ubiquity and variability of the same species and mentions a very minute phase from the Antarctic 'which in fresh samples can often be

seen to form chains of from three to twelve frustules'. Lucas (1940) has remarked on the association with *Phaeocystis* of a very slender variety of *N. closterium* 'at times so slender as almost to suggest the possibility of another species'. I have examined some of his material which he kindly sent at my request. His slender form seems to be nearer to the culture type than to the aquarium type but is on the whole longer (40–70μ) than the former and also differs from it in the clearer separation of the chromatophores, in which respect it resembles the latter. Dr Lucas tells me that he has not observed triradiates in his North Sea material.

The only reference in the systematic literature which can fairly confidently be ascribed to the same species as that of the culture form is by Karsten (1905). His figure closely resembles the normal cell of the cultures. He identifies it as *Nitzschia* sp. and says it is like *closterium* but considerably smaller. It has two chromatophores and is about 23μ long.

The Triradiate in Nature

As *Phaeodactylum tricornutum* n.g., n.sp., Bohlin (1897) has described and illustrated the triradiate form of *Nitzschia*. For this reference I am greatly indebted to Prof. Fritsch's unique knowledge of algological literature. Bohlin's description and figures of his *Phaeodactylum* agree in all particulars with the triradiate of the cultures, even to his chemical tests which I have repeated. Bohlin was puzzled as to the affinities of his organism and considered, on the basis of the chemical reactions of the cell and the plane in which it divides, that it stood near to the diatoms. He also considered that his *Phaeodactylum* might possibly be identical with *Cerasterias raphidoides* forma *tridens* (Reinsch, 1867). Unfortunately, I have not been able to see a copy of Reinsch's work but it may be that Bohlin is mistaken because *Cerasterias* Reinsch (now included in *Tetraëdron* Kützing) is a genus of freshwater green algae. Bohlin's specimens appeared in cultures of another organism (*Brachiomonas*) which he had obtained from rock pools on some Baltic islands near Stockholm. The triradiate was evidently removed from the pools along with the much more abundant *Brachiomonas*, but a period of time was necessary for it to multiply in the culture before it became sufficiently numerous to be noticed. Nevertheless, this can be regarded as a record of the occurrence in nature of the triradiate.

In a later paper Bohlin (1902) stressed the similarity between his *Phaeodactylon* (as he now spelt it) and *Centronella Reichelti* Voigt, a triradiate freshwater alga, and proposed that Voigt's genus *Centronella* be suppressed and that his species be known as *Phaeodactylon Reichelti*. However, as I have shown, *Phaeodactylon* is the triradiate form of a *Nitzschia*, with which genus *Centronella* Voigt does not appear to be related. This seems clear from a study of Voigt's original paper (1902) and from Krieger (1927), who figures and describes two species of *Centronella* and gives several references not quoted

here. Krieger regards *Centronella* as a diatom but Fritsch (1935, p. 607) considers that this is doubtful.

So far I have not myself succeeded in obtaining the triradiate direct from the sea, but Dr Mary Parke informs me that it was frequent in water samples from the Irish Sea off Port Erin, together with the normal form, sometimes being more abundant than the latter. There was no possibility of there being a mistake in identification because she was familiar with it in *Nitzschia* cultures derived from Plymouth. It has also been abundant in Loch Craiglin, Argyllshire, where it has been observed frequently by Dr S. M. Marshall and by Dr F. Gross. Dr Marshall kindly sent me a sample of the surface water from the Loch, and I was able to assure myself that the triradiates occurring there are identical in every respect with those in the cultures. It is perhaps noteworthy that the Loch is the scene of fertilization experiments, the water being treated with artificial fertilizers. There is, however, no reason to suppose that the presence of artificial fertilizers is necessary for their existence, although they may very well produce conditions favouring its multiplication.

Not far from Loch Craiglin, at Charsaig on the Atlantic coast of Argyll, is a fish-hatching tank which is filled from time to time with water from the open sea. Dr Marshall informs me that early in 1945 it was fertilized with phosphate and nitrate and that *Nitzschia* was observed in it. It later was emptied, washed down and refilled with water from the open sea, but not fertilized apart from the excretions of two hundred or more plaice kept in it and fed on mussels. About a fortnight after refilling, Dr Marshall noted that it was a thick soup of *Nitzschia*, both normal and triradiate, and she very kindly sent a preserved sample to me (mid-July 1945). The *Nitzschia* presumably came from the sea, for at no time had a culture been added to the water in the tank.

The sample from the fish-hatching tank was of great interest; never have I seen so great a variation in cell shape. The normals were anything from straight to curved into an almost complete ring, the ends of the arms sometimes almost meeting; often the arms were bent in opposite ways to form an S-curve. The triradiates, which were extremely plentiful, varied very greatly also. All stages of arm reduction were to be seen; sometimes only a mere trace of the third arm remained. Cells with all three arms complete often had them bent at varying angles. No culture has ever shown such great diversity amongst its cells, but apart from this these *Nitzschia* from Charsaig agreed closely with the culture forms, except that possibly the arms were a trifle longer and a little more slender. There is no doubt they were the same species. From these observations from nature, few as they are, we cannot but conclude that the triradiate is a natural phase in the biology of the species.

Conclusion

The species of *Nitzschia* forming these cultures shows a degree of variability in shape which is surprising even for diatoms, and the different shapes have varying degrees of stability, the normal and triradiate in particular retaining

their respective characteristics through many generations without passing one into the other. The cruciform is relatively less stable although it too will continue to multiply for a long period of time, though a fair proportion of the daughter cells appear to revert readily to one of the other types. The oval shape is often an intermediate stage between the other shapes, although they are not dependent on it for passing one into the other. Apart from the influence of light in stimulating the production of ovals nothing concrete is known as to there being any physical or chemical character of the environment capable of initiating these changes, although the marked autumnal tendency of the triradiates to shorten and lose one arm suggests that light, either intensity, or perhaps more likely length of day, is not without some influence. Nothing is known as to the relation of any of these changes to a sexual method of reproduction, which has not been seen in this species.

The comparatively great stability of some of the shapes raises some interesting reflections. If these shapes were to become fixed in the sense that they no longer changed one into another, and if each continued to multiply its own kind, there would arise forms entitled to be regarded as so many species. However, until we have more complete information, especially as to any sexual phases there may be, it is not possible to assess the degree of probability of this happening in the future.

A very interesting example parallel to the triradiate *Nitzschia* is recorded by Conger (1939) from the Crystal Lake, Wisconsin, where *Fragilaria construens* was found in tremendous abundance stratified in several middle layers of the bottom deposit, a high proportion being completely triangular or triradiate in shape. Dr Conger has very kindly sent me some of his material; in it can be found all stages in complete transition from the regular form of the species, elongate with swollen median portion, to completely triradiate forms, the intermediate stages showing a gradual bulging out of one side until a complete third arm (in the sense that this term has been used for *Nitzschia*) is produced. It is, of course, impossible to say whether these are stages in the production of a third arm or in its gradual disappearance. Many of the stages can be seen in the photomicrograph reproduced in Conger's plate 1, fig. 1.

With regard to the abundance of *Fragilaria* in the lake deposits Conger remarks: 'it shows that there must have been a considerable period at some time in the history of the lake when its waters "bloomed" for many successive years with this form. The presence in these particular samples of a high preponderance of mutant and abnormal forms of this species is also strongly suggestive of a radical transition stage in the history of the lake when conditions were not always too favourable, though this is in itself a variable species which may partially account for these mutants.' It seems to me equally likely that the production of the mutants may have been stimulated by conditions exceptionally favourable to the species at the time when it became so completely dominant. In the same way the production of triradiate *Nitzschia* in abundance may be an indication of conditions especially favourable to the multiplication

of the species and the survival of aberrant forms. It has been shown by experiment that under good conditions triradiates can multiply more rapidly than normal cells, and the same seems to be true to some extent of cruciform cells. Thus certain strains of aberrant forms, under good conditions such as those of constant culturing, are better able to compete for nutrients than the more normal forms and to overtake them. When conditions are unfavourable normal forms are better able to survive than aberrant ones.

That the suggestion just advanced may be true is partly confirmed by changes in cultures which have stood neglected over a long period of time. Dr Lucas has recently informed me that after 1941 the Hull cultures were irregularly subcultured until the spring of 1943, and then, owing to pressure of other work, entirely neglected for over two years. When in the summer of 1945 steps were taken to revive them the subcultures made from them showed a striking decrease in the percentage triradiate, especially when compared with corresponding Plymouth stocks which had been regularly subcultured and kept growing through the same period. The difference in August 1945 is expressed in Table VI, and is especially striking for the clone triradiates and

TABLE VI. PERCENTAGE TRIRADIATE OF HULL AND PLYMOUTH CULTURES, AUGUST 1945

Hull	% triradiate	Plymouth	% triradiate
Standard stock	2·74	Stock 569	91·8
(7 weeks later)	1·26	Stock 589	77·1
(subculture from last)	0·94		
Clone triradiate		Clone triradiate,	
(subculture from a 1942 culture)	2·7	Series III	90·5
(subculture from a 1943 culture)	32·3		
(subculture from a 1943 culture)	22·2		
Clone normal	00·0	Clone Normal:	
		Series I	74·8
		Series II	67·7

normals, which were parts of the same clones kept respectively in Hull and Plymouth. It is possible that the great decrease in the percentage triradiate when subcultures are made from old exhausted cultures is due to some extent, at all events, to the gradual death of all kinds of armed cells and the survival only of ovals enveloped in a thick 'mucilaginous' coat. Such ovals, in a resting condition, are to be seen in old exhausted cultures and were abundant in these old Hull cultures, samples of which I was able to examine alive and to revive for myself with substantially similar results to those obtained at Hull. On adding fresh media resting ovals begin to divide again, and like all ovals eventually produce mainly the normal type of cell. It will be noted that the Hull subculture made from a 1942 culture of the clone triradiate had fewer triradiates in it than those made from a 1943 culture of the same clone.

In general it seems true that good cultural conditions are more productive of triradiates than bad or indifferent conditions, but there are exceptions.

A possible explanation of some of these exceptions has already been advanced (p. 252), where it was suggested that strains of varying virility may arise, and that when a strong strain of triradiate appears in a culture it increases in abundance relative to the normal cells. An exception not readily explained, on the supposition that triradiates are most likely to become abundant under good cultural conditions, is the finding by Dobell (see p. 238) of large numbers of triradiates in old cultures left at the Royal College of Science. These triradiates also seem to have become abundant in an unusually short period of time, a matter of about six months only; perhaps there were already some in the cultures which Dr Allen took with him to London in that summer of 1910. So long after the event it is no longer possible to make certain on these points.

Finally, there remains the possibility that in some strains of triradiate there is a greater tendency than usual to shorten the third arm, and that thereby a higher percentage than usual pass back into the normal condition. Something of this nature appears to be indicated by the figures for Series I and II (Table IV), where of the relatively small numbers of triradiates present a high proportion were short-armed, especially in Series II, and in correspondence with this it was long before triradiates in these cultures became at all common. When they did become common the proportion of short-armed cells to those fully triradiate was much less than it had been before.

It would be ungracious to conclude without recording the great interest the late Dr E. J. Allen, F.R.S., took in the earlier stages of this work and the benefit I derived from discussion with him. My grateful thanks are also due to the late Director, Dr Stanley Kemp, F.R.S., whose interest and encouragement were so helpful during the difficult years of the war. Correspondence with Dr C. E. Lucas at Hull has also been particularly stimulating. Other acknowledgements are made in the text.

Summary

1. The natural history in culture of the species of *Nitzschia* originally isolated from the sea by Allen & Nelson (1910) and grown at Plymouth and elsewhere ever since has been studied. It is shown that three main types of cell exist: normal with two arms (rostra), triradiate with three arms and ovals with none. Both normals and triradiates produce ovals by division, and the ovals so produced can multiply to form further ovals, or can grow either two or three arms, generally two, to form normal or triradiate cells.

2. Ovals are more readily produced under good lighting conditions than under weak illumination.

3. The cell wall is very lightly silicified, and the cells, unlike those of most diatoms, can elongate without auxospore formation. The maximum, and with it apparently the average, cell size of successive subcultures is variable.

4. When triradiates are present they may, and frequently do under good cultural conditions, multiply faster than normal cells and finally may almost

completely dominate the cultures. Now and again a proportion of the triradiate cells shorten one arm and gradually pass, during successive divisions, into the normal condition. There is a greater tendency for this process to take place in the autumn than at any other time. There was a notable instance in November 1941 when several cultures at Plymouth and at Hull simultaneously produced normals by this method on an extensive scale.

5. There is evidence that under unfavourable cultural conditions triradiates tend to be eliminated.

6. A cruciform type of cell has appeared occasionally in several cultures, but it has not been possible to obtain pure cultures of it, for the type appears to be somewhat unstable and readily reverts to the other forms. It has, however, persisted for a long time and for very many generations.

7. It is shown that the triradiate type occurs in nature, and there is no reason to suppose that it is an abnormal form due to culturing.

8. The nomenclature is discussed and it has been decided for the time being to retain the name Allen and Nelson originally gave to it, although there is a possibility that it is a species separate from *Nitzschia closterium* (Ehr.) W. Smith.

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THE SIZE OF DIATOMS

II. FURTHER OBSERVATIONS ON *RHIZOSOLENIA STYLIFORMIS* (BRIGHTWELL)

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(Plate V and Text-figs. 1, 2)

Since the appearance of Part I of this paper (Wimpenny, 1936), the measurement of diatom cell diameters has been continued and extended, rather special attention having been paid to *Rhizosolenia styliformis*, with which species this account is concerned. The unit of measurement (*ca* 4μ) and the technique used is the same as that outlined in Part I.

Through the kindness of the late Dr Stanley Kemp, F.R.S., Dr N. A. Mackintosh and the late Mr J. O. Borley, I have been able to examine material from the *Discovery* Expedition. Similarly, I am indebted to Mr Vedel Tåning for sending me samples collected by the *Dana* in the Atlantic, and to Miss Molly Mare (Mrs G. M. Spooner) for the loan of collections she had examined in connexion with the mackerel investigations made at the western entrance of the English Channel under the auspices of the Marine Biological Association. From the North Sea and Atlantic I have also received samples and information from Dr R. S. Clark, Dr J. B. Tait, Dr S. Gibbons and Miss H. Ogilvie of the Scottish Fishery Board. Finally, valuable material from the Antarctic was collected for me by Lt.-Commander S. Brooks from the whaling ship *Svend Foyn* during the season 1937–8. To all these sources I make my grateful acknowledgements.

The data have been condensed in Table I, where the mean diameter for each sample is shown. The recorded frequency distributions from which the various means have been obtained, together with the individual measurements, are being deposited at the Laboratory of the Marine Biological Association, where they will be available for examination by those interested.

The necessity of sorting the material into different varieties has not made it possible to obtain from it as much information as was first hoped, and all that can be said of the present collections is that there may be characteristic life cycles for the species type of this diatom in different places. The establishment of these life cycles, their meaning in terms of cell division and the effects of external agents, such as temperature and salinity, on cell diameter must remain the goal of future investigations. A similar extension of the work will be necessary in respect of the varieties and for the final elucidation of the taxonomic position.

TABLE I. LIST OF STATIONS, POSITIONS, DATES, TEMPERATURES AND SALINITIES AT OR NEAR 20 M., MEAN DIAMETERS (IN UNITS OF *ca* 4μ), NUMBER OF DIATOMS MEASURED AND FORM

(The following abbreviations are used to indicate the ships concerned with the various collections: *George Bligh*, *GB*; *Onaway*, *O*; *Explorer*, *E*; *Discovery*, *D*; *William Scoresby*, *WS*; *Dana*, *Da*; and *Svend Foyn*, *SF*.)

St.	Lat.	Long.	Date	$T°$ C. at 20 m.	$S°/_{oo}$ at 20 m.	Mean diam.	No. measured	Form
			Shetland and Faeroe areas					
*E*1	59° 23′ N.	0° 23′ W.	18/4/31	5·93	35·29	9·3	100	Not separated
*E*2	59° 30′ N.	1° 33′ W.	10/5/31	7·03	35·19	8·5	100	,,
*E*3	60° 06′ N.	0° 48′ W.	15/4/32	7·08	35·36	10·2	100	,,
*E*4	60° 45′ N.	0° 42′ W.	31/8/32	11·72	35·25	7·8	100	,,
*E*5	58° 21′ N.	0° 04′ W.	21/5/33	8·51	35·09	7·3	100	Var. *oceanica*
*E*6	60° 07′ N.	0° 45′ W.	7/6/33	9·18	35·37	9·5	100	Not separated
*E*7	61° 01′ N.	1° 29′ E.	30/5/34	8·52	35·37	8·4	100	,,
*E*8	60° 44′ N.	2° 28′ E.	19/4/35	7·75	35·35	9·8	100	,,
*E*9	61° 05′ N.	2° 10′ W.	14/6/36	9·52	35·39	6·9	100	Var. *oceanica*
*E*10	59° 21′ N.	3° 45′ W.	26/8/37	—	—	8·4	100	Not separated
*E*11	61° 02′ N.	7° 50′ W.	3/7/38	—	—	9·6	100	*Type
,,	61° 02′ N.	7° 50′ W.	3/7/38	—	—	8·45	100	*Var. *semispina*
,,	61° 02′ N.	7° 50′ W.	3/7/38	—	—	7·28	100	*Var. *oceanica*
*E*12	60° 01′ N.	1° 12′ E.	27/3/39	—	—	8·98	100	†Type
GB–Mc10	48° 20′ N.	6° 40′ W.	South-west of British Isles 18/4/39	10·95*	35·44*	7·82	100	Type
GB–Mc17	49° 06′ N.	9° 05′ W.	19/4/39	10·90*	35·44*	7·37	100	,,
GB–Mc23	50° 01′ N.	10° 18′ W.	20/4/39	10·88*	35·53*	7·70	40	,,
GB–Mc25	49° 36′ N.	9° 30′ W.	21/4/39	10·80*	35·50*	7·57	35	,,
GB–Mc6	48° 05′ N.	7° 53′ W.	3/6/39	12·48*	35·57*	8·17	100	,,
GB–Mc8	48° 58′ N.	8° 45′ W.	3/6/39	11·45*	35·40*	8·34	50	,,
GB–B2	56° 21′ N.	1° 10′ W.	Firth of Forth Swirl area 21/5/32	7·23	34·70	8·8	50	,,
GB–D12	55° 42′ N.	1° 17′ W.	30/6/32	11·84*	34·77*	10·0	100	,,
GB–B19	55° 40′ N.	0° 25′ W.	13/5/33	8·26	34·93	14·6	100	,,
GB–G3	56° 03′ N.	0° 38′ W.	23/5/36	8·69	34·79	8·5	100	Var. *oceanica*
GB–C10	55° 26′ N.	4° 42′ E.	East Dogger area 22/5/33	8·06	34·71	19·9	100	Type
GB–F7	55° 52′ N.	4° 23′ E.	23/5/35	8·14	35·00	16·3	100	,,
GB–Q12	54° 50′ N.	5° 44′ E.	20/11/36	10·40	34·65	20·3	100	,,
GB–F21	56° 53′ N.	6° 38′ E.	2/5/37	6·08	34·79	17·3	100	,,
GB–B9	57° 40′ N.	4° 52′ E.	Off southern coast of Norway 12/5/33	7·28	35·08	8·1	100	Var. *oceanica*
GB–G15	57° 30′ N.	4° 10′ E.	26/5/36	7·42	35·12	8·2	100	,,
O–20/2	54° 24′ N.	1° 22′ E.	South-west Dogger Swirl area 22/9/32	13·81	34·43	13·9	100	Type
GB–J12	53° 20′ N.	2° 40′ E.	27/10/32	11·75	34·23	16·6	100	,,
GB–J19	54° 10′ N.	5° 27′ E.	28/10/32	12·28	34·15	15·4	100	,,
GB–J22	53° 45′ N.	4° 02′ E.	29/10/32	11·89	34·72	17·6	100	,,
GB–J32–0 m.	54° 07′ N.	2° 03′ E.	31/10/32	10·74	34·49	15·9	100	,,

* The type, var. *semispina* and var. *oceanica*, occurred at this station in the following proportions: 61, 20 and 19.

† The type only was measured at this station, but both the varieties occurred there. Var. *oceanica* however did not occur in the random sample of 30 mentioned on p. 280.

TABLE I (*cont.*).

St.	Lat.	Long.	Date	*T*° C. at 20 m.	*S* °/₀₀ at 20 m.	Mean diam.	No. measured	Form
South-west Dogger Swirl area (*cont.*)								
GB–J32–20 m.	54° 07′ N.	2° 03′ E.	31/10/32	10·73	34·52	15·5	100	Type
GB–C20	54° 19′ N.	2° 49′ E.	23/5/33	10·72	34·90	17·5	100	,,
GB–G27	53° 27′ N.	2° 14′ E.	19/6/35	12·38	34·76	14·3	100	,,
GB–N5	53° 52′ N.	1° 02′ E.	24/9/35	14·66	34·72	12·9	300	,,
GB–N6	54° 08′ N.	1° 37′ E.	24/9/35	14·96	34·75	12·9	100	,,
GB–N12	54° 36′ N.	1° 42′ E.	26/9/35	13·52	34·57	13·5	100	,,
GB–O13	53° 24′ N.	1° 34′ E.	4/10/35	13·98	34·77	13·1	200	,,
GB–O15	54° 03′ N.	1° 36′ E.	5/10/35	14·40	34·73	12·8	100	,,
GB–O16	54° 13′ N.	2° 26′ E.	5/10/35	13·80	34·64	12·6	100	,,
GB–O34	54° 35′ N.	1° 48′ E.	9/10/35	12·98*	34·59*	13·4	100	,,
GB–P11	54° 30′ N.	3° 34′ E.	24/10/35	11·41	34·85	13·2	200	,,
GB–P14	53° 45′ N.	4° 37′ E.	25/10/35	12·33	34·62	13·5	100	,,
GB–P21	53° 15′ N.	2° 21′ E.	26/10/35	11·69	34·71	13·3	100	,,
GB–Q24	53° 44′ N.	4° 09′ E.	9/11/35	11·73	34·79	13·1	100	,,
GB–Q26	54° 05′ N.	4° 31′ E.	11/11/35	11·58	34·84	12·8	100	,,
GB–R3	54° 55′ N.	3° 18′ E.	23/11/35	9·90	34·65	12·9	100	,,
GB–R15	54° 00′ N.	1° 47′ E.	25/11/35	9·40	34·59	12·7	100	,,
GB–G39	53° 43′ N.	2° 58′ E.	31/5/36	9·26	34·39	13·5	100	,,
GB–J17	54° 00′ N.	3° 01′ E.	8/8/36	14·39*	34·66*	22·2	100	,,
GB–P22	53° 33′ N.	3° 49′ E.	3/11/36	11·38	34·59	19·4	100	,,
GB–Q18	54° 25′ N.	2° 06′ E.	21/11/36	8·88	34·65	20·2	100	,,
GB–Q30	53° 36′ N.	2° 01′ E.	22/11/36	9·70	34·66	18·3	100	,,
O–IV/F6	54° 32′ N.	1° 37′ E.	24/2/37	4·59*	34·80*	16·1	100	,,
O–VI/F6	54° 33½′ N.	1° 35½′ E.	23/4/37	6·48*	34·76*	16·8	100	,,
GB–H19	54° 21′ N.	0° 38′ E.	7/6/37	9·01	34·51	11·4	100	,,
GB–L30	54° 10′ N.	3° 03′ E.	7/8/37	14·22*	34·65*	19·4	100	,,
GB–L31	54° 04′ N.	2° 13′ E.	7/8/37	16·14*	34·83*	20·6	100	,,
GB–M10	54° 59′ N.	1° 30′ E.	12/10/37	13·36	34·62	18·5	100	,,
GB–M11–0m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·93*	20·6	100	,,
GB–M11–27m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·66*	19·7	100	,,
GB–M11–55m	54° 32′ N.	0° 49′ E.	12/10/37	12·66*	34·65*	20·2	100	,,
GB–M15–0m	54° 19′ N.	0° 40′ E.	13/10/37	13·06*	34·58*	19·2	100	,,
GB–M15–27m	54° 19′ N.	0° 40′ E.	13/10/37	12·94*	34·58*	20·2	100	,,
GB–M15–55m	54° 19′ N.	0° 40′ E.	13/10/37	12·93*	34·58*	20·3	100	,,
GB–M16	54° 23′ N.	1° 00′ E.	13/10/37	13·22	34·65	19·65	100	,,
GB–M16–0m	54° 23′ N.	1° 00′ E.	13/10/37	13·24*	34·61*	19·7	100	,,
GB–M16–18m	54° 23′ N.	1° 00′ E.	13/10/37	13·22*	34·65*	19·6	100	,,
GB–M16–36m	54° 23′ N.	1° 00′ E.	13/10/37	13·22*	34·59*	19·6	100	,,
GB–M17	54° 29′ N.	1° 19′ E.	13/10/37	14·05	34·75	18·7	100	,,
GB–M18	54° 33′ N.	1° 39′ E.	13/10/37	13·56*	34·69*	17·35	100	,,
GB–M19	54° 33′ N.	1° 58′ E.	13/10/37	13·48*	34·71*	17·3	100	,,
GB–M21	53° 56′ N.	0° 37′ E.	14/10/37	13·77	34·74	19·5	100	,,
GB–M23	53° 51′ N.	1° 43′ E.	14/10/37	14·07	34·87	19·3	100	,,
GB–M24	54° 07′ N.	2° 25′ E.	14/10/37	14·36	34·85	18·8	100	,,
GB–M26	53° 26′ N.	2° 11′ E.	15/10/37	14·39	34·16	19·2	100	,,
GB–M37a–0m	54° 07′ N.	2° 21′ E.	17/10/37	14·18*	34·85*	19·3	100	,,

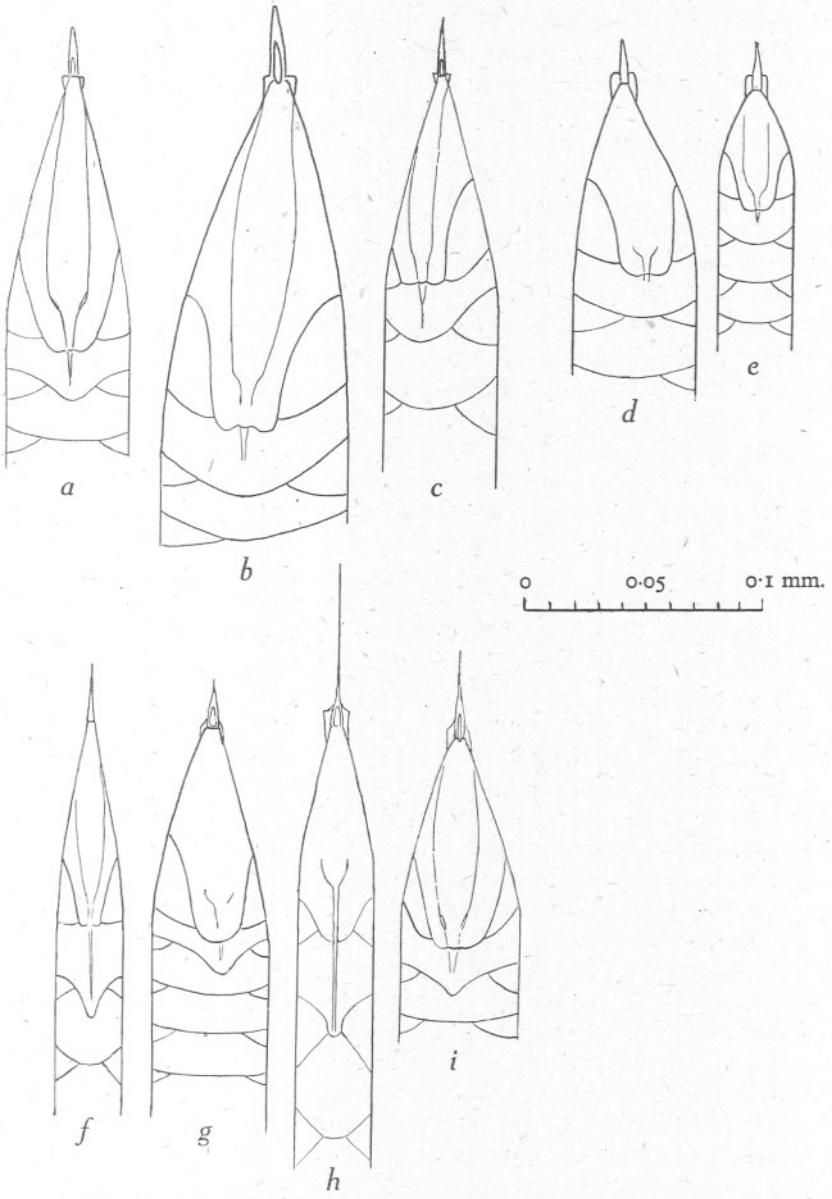
TABLE I (*cont.*).

St.	Lat.	Long.	Date	$T°$ C. at 20 m.	$S‰$ at 20 m.	Mean diam.	No. measured	Form
			South-west Dogger Swirl area (*cont.*)					
GB–M37a –18 m	54° 07′ N.	2° 21′ E.	17/10/37	14·10*	34·86*	18·9	100	Type
GB–M37a –36 m	54° 07′ N.	2° 21′ E.	17/10/37	13·84*	34·86*	19·45	100	,,
GB–N13	53° 35′ N.	2° 57′ E.	28/10/37	13·48	34·33	19·2	100	,,
GB–N16	54° 00′ N.	4° 21′ E.	29/10/37	13·76	34·48	19·2	100	,,
GB–N25	54° 25′ N.	2° 56′ E.	30/10/37	12·99	34·84	20·2	100	,,
GB–N29	53° 48′ N.	3° 40′ E.	30/10/37	—	—	18·5	100	,,
GB–P1	53° 32′ N.	2° 20′ E.	28/11/37	9·60*	34·41*	18·4	100	,,
GB–D/F6	54° 33′ N.	1° 40′ E.	28/2/38	5·37*	34·86*	17·8	100	,,
GB–E/F5	54° 31′ N.	1° 23′ E.	13/3/38	5·97	34·86	17·4	100	,,
GB–P11	53° 20′ N.	2° 29′ E.	22/10/38	—	—	17·3	100	,,
GB–P13	54° 00′ N.	2° 34′ E.	23/10/38	13·34	34·76	17·65	100	,,
GB–P18	54° 27′ N.	2° 11′ E.	24/10/38	11·48	34·58	17·6	100	,,
GB–P27	55° 18′ N.	1° 5′ E.	25/10/38	10·44	34·83	15·6	50	,,
GB–Q8	55° 16′ N.	4° 6′ E.	11/11/38	10·67	—	17·5	100	,,
GB–Q16	56° 49′ N.	6° 38′ E.	13/11/38	11·84	34·83	16·4	100	,,
				$T°$ C. at	$S‰$ at			
St.	Lat.	Long.	Date	20 m.	20 m.	Mean diam.	No. measured	Form
			Antarctic					
*WS*67	53° 19′ 00″ S.	45° 16′ 00″ W.	20/2/27	3·64	33·80	8·5	50	Var. *oceanica*
*WS*70	51° 58′ 00″ S.	55° 42′ 00″ W.	22–3/2/27	7·14	34·08	9·4	50	,,
*WS*472	59° 42′ 30″ S.	58° 01′ 00″ W.	12/12/29	−0·26	33·99	14·3	50	,,
*WS*520	52° 25′ 00″ S.	61° 20′ 00″ W.	27–8/2/30	6·33	34·11	8·4	100	,,
*SF*10	60° 04′ 00″ S.	10° 25′ 00″ W.	24/2/38	−0·40	—	6·7	50	,,
*D*161	57° 21′ 20″ S.	46° 43′ 30″ W.	14/2/27	1·43	33·80	4·1	100	Var. *semispina*
*D*496	53° 17′ 45″ S.	35° 56′ 00″ W.	19/11/30	−1·10	33·91	4·2	100	,,
*WS*472	59° 42′ 30″ S.	58° 01′ 00″ W.	12/11/29	−0·26	33·99	6·2	100	,,
*SF*7	56° 45′ 00″ S.	2° 41′ 00″ E.	27/12/37	−1·20	—	4·1	50	,,
*SF*10	60° 04′ 00″ S.	10° 25′ 00″ E.	24/1/38	−0·40	—	4·8	100	,,
			Tropical Pacific					
*WS*706	5° 37′ 30″ S.	83° 58′ 00″ W.	23/7/31	19·49	35·12	5·6	100	Var. *semispina*
*WS*707	5° 37′ 30″ S.	84° 31′ 30″ W	23/7/31	20·42	35·16	5·1	100	,,
			Tropical Atlantic					
*Da*4007	18° 22′ N.	18° 14′ W.	15/3/30	18·46	35·80	4·4	50	Type

* Depth nearest to 20 m. or that shown at left of column, except that temperatures and salinities were taken at 30 m. and 50 m. for *GB*–M15–27 m. and 55 m., at 20 m. and 30 m. for *GB*–M16–18 m. and 36 m., and at 20 m. and 40 m. for *GB*–M37a–18 m. and 36 m.

RHIZOSOLENIA STYLIFORMIS AND ITS VARIETIES

The application of biometric observations to material of *Rhizosolenia styliformis*, collected beyond the area dealt with in the first part of this paper, made it abundantly clear that the specific name had been regularly applied to more than one form (Text-fig. 1). It therefore became necessary for me to attempt



Text-fig. 1. Type and varieties of *Rhizosolenia styliformis* from different sources. *a*, Type from southern North Sea (St. 4, Cruise N, 24/9/35); *b*, Type from southern North Sea; *c*, Type from semi-tropical Atlantic (St. 4007, *Dana*, 15/3/30); *d*, var. *oceanica* from west of Faeroes, 3/7/38; *e*, var. *oceanica* from Antarctic (St. 10, *Svend Foyn*, 24/1/38); *f* and *g*, var. *semispina* from tropical coast of East Pacific (St. 707, *William Scoresby*, 23/7/31); *h*, var. *semispina* from Antarctic (St. 10, *Svend Foyn*, 24/1/38); *i*, var. *semispina* from west of Faeroes, 3/7/38.

an identification of the forms I have distinguished in order to compare like with like. The somewhat confused taxonomic position revealed in the sections that follow has involved, among other things, a future consideration as to whether the species originally established as *R. styliformis* can properly be separated from *R. hebetata*.

Rhizosolenia styliformis (Brightwell)

Brightwell, T., 1858. *Quart. Journ. Micr. Sci.*, Vol. VI, pp. 93–5, pl. V.
Hustedt, F., 1930. *R. styliformis* var. *longispina*. 'Die Kieselalgen', Rabenhorst's *Kryptogamen Flora*, Bd. VII, p. 586, fig. 334.

The type of the species has been figured by Brightwell who established it from observations made on specimens taken from a tunicate attached to an oyster shell dredged from the 'Silver Pit' south of the Dogger Bank, on others found as inclusions in the bodies of *Noctiluca* collected near Gorleston and from guano taken from Callao. Brightwell writes of boiling his material in acid, and for this reason, doubtless, his figures do not show the lateral wings at the base of the apical spine to which I attach considerable importance for purposes of diagnosis. Nevertheless, the shape of the valve or calyptra resembles that form which I have found to occur alone and with great uniformity throughout the southern North Sea south of latitude 56° N. This type-form is also similar to that figured by Hustedt as *R. styliformis* var. *longispina*, except that the apical spine may be either drawn out into a fine process or blunt, the two different conditions being sometimes seen at opposite ends of the same cell.

The type is characterized by its considerable size, the fact that its valves are nearly straight-sided, and the possession of right-angled wings, which arise along the valve near its point, but end at, or very near, the origin of the eccentrically placed terminal spine (Text-fig. 1*a*, *b*, *c*). These characters are found in all individuals from the southern North Sea, where, in the area near the south-west patch of the Dogger Bank, the species occurs regularly in its greatest profusion. Outside this area, the shape and position of the wings show variability. Samples from the western end of the English Channel and to the south-west of the British Isles nearly resemble those of the southern North Sea, but a few individuals occur in which the wings end above or below the origin of the apical spine, and the wing margins may not be quite right angled. In the Scottish material from the northern North Sea and Faeroe-Shetland areas, the proportion of these aberrant cells may be considerable, and instances in which the wings arise above the origin of the spine are particularly numerous. Of these latter individuals a certain number are to be found in which the position and even the shape of the wings is intermediate with that to be described for the variety *semispina* in the next section, and there is no doubt that the two forms are linked by a chain of morphological intermediates. Finally, in some of the smaller cells among the population taken at *Dana* St. 4007 in the subtropical Atlantic, wings are lacking.

In view of the fact that other workers have made little or no discrimination between the type and the varieties a distributional picture is difficult. From the material I have so far examined I can vouch for the presence of the type, occasionally in abundance, on the east side of the Atlantic from about 30° to 60° N. latitude, but nowhere else. Gran (1902) has recorded *R. styliformis* from the Norwegian Sea between Jan Mayen and the Norwegian coast, but the shape of the apical wings given in one of his figures suggest to me that the form found was probably not the type but my variety *oceanica*. The species has frequently been recorded from the Antarctic. However, in many of these samples, I think the organism concerned is the variety to be described below as *semispina*. It is also possible that there may have been confusion with *R. curvata* Zacharias, the shape and relation of whose wings and terminal spine are identical with that of the type I have just dealt with, so that it would not be possible to decide between the two species were only short terminal fragments available. Karsten (1905, p. 96) gives *R. styliformis* as occurring in the Antarctic, but he considers it to be a variety (*Valdiveae*) apparently synonymous with Brightwell's var. *latissima* and Castracane's *R. polydactyla* (Castracane, 1886). This larger form is now generally given specific status under the last name.

R. styliformis var. *semispina* (Hensen) Karsten

Karsten, G., 1905. *R. semispina*. *Wiss. Ergebn. Deutsche Tiefsee Expedition auf den Dampfer 'Valdivia'*, 1898–99, Bd. II, Pt. II, Lief. 1, p. 96, pl. X, figs. 4, 4*a* and 4*b*.

? Bailey, J. W., 1856. *R. hebetata*. *Amer. Journ. Sci.*, p. 5, pl. 1.

? Hensen, V., 1887. *R. semispina*. *Ber. Kom. der deutsches Meeres*, p. 84, pl. V, figs. 39*a*, *b*.

? Gran, H., 1902. *R. hebetata* forma *semispina*. *Fauna Arctica*, Bd. IV, p. 527, pl. XVII, figs. 11, 12.

Cupp, E., 1943. *R. styliformis* var. *longispina* Hust. *Bull. Scripps Inst. Oceanog.*, Vol. 5, No. 1, p. 87, fig. 488 and fig. C (5).

This second form of the species I have found to be very widely distributed. Like the type, the conical valves have rather straight sides ending in an eccentrically placed spine. The spine may be either blunt or drawn out into a fine process. Below its origin there arise on either side wing-like membranes which terminate some way up the spine. These wings commonly present an obtuse angle at their outer edge and are not rounded; they may, however, be absent altogether from some of the smaller individuals taken in warm water. Intercalary plates are numerous and arranged in two rows. The middle part of the first intercalary plate at the opposite side of the cell to the eccentrically placed spine (i.e. the 'ventral' side), is produced into a tongue extending some distance back into the next intercalary plate (Text-fig. 1 *f*, *g*, *h*, *i*).

In this variety I have classed examples from the Scottish collections in the northern North Sea and Atlantic, from the west coast of South America (*WS* 706 and *WS* 707 of the *Discovery* collections) and from the Antarctic (*Discovery* and *Svend Foyn* material). Transitional forms linking this variety to the type and found in the Scottish material have already been described in

the previous section. My richest collections came from the Antarctic and in these specimens the tongue of the first intercalary plate is often very pronounced, the spine ends in a long fine process and the thick-walled cells show little variation (Text-fig. 1*h*). I have also found the variety in a number of preparations in the British Museum collections to which the authorities of the British Museum of Natural History most courteously gave me access. Below I give particulars of those examples in which it is possible to give a locality.

Slide no.	Legend	Habitat
7,987	Ascension Island per *Buccaneer*, 1886	Ascension Island
14,336	Coll. Temp. et Perag	Côtes Equatoriales d'Afrique
15,262	*R. styliformis* Tempere et Perag. Coll. Deby	Mediterranean
21,334	*R. styliformis*. St Helena from Salps	St Helena
31,060 31,061 31,063	Arafura Sea, surface Coll. Comber	Arafura Sea
31,064	Antarctic surface	Antarctic surface

From such distributional records as are available, the general impression to be gained is that the form favours water near the coast or in continental slope areas, and that it finds its optimum in cold water at high latitudes in the Antarctic.

The examples of this variety taken in the Antarctic are identical with those reported for the same area as *R. semispina* by Karsten. The variety has also been recorded as *R. styliformis* in the *Discovery Reports*. Under the title *Rhizosolenia styliformis* var. *longispina* Hustedt, Cupp figures the characteristic apical wings of the variety under discussion and the tongued first intercalary plate. It is described as 'Oceanic' and 'found off California and in Gulf of California'.

The identity of the form with that described by Karsten as *R. semispina* Hensen raises a taxonomic complication in that Hensen's *R. semispina* does not possess the characteristic lateral wings, nor does he give any record or figure showing the median tongue of the first intercalary plate. Furthermore, the apical spine and the neighbouring part of the valve are very much thicker and there is little doubt that Hensen's Baltic specimens are similar in form and structure to the fragments taken from the sea bottom off Kamschatka and figured and described by Bailey as *R. hebetata*. Gran places Hensen's *R. semispina* as *R. hebetata* forma *semispina*, but in descriptions and figures of Gran's form the apical wings and median tongue of the first intercalary plate do not appear. It has already been said that some of the smaller specimens of the variety here described have been found to lack the apical wings when found in warmer habitats. In the event of the cell diameter being reduced, it is quite possible that the median ventral tongue of the first inter-

calary plate might disappear. These changes would bridge the gap between the variety under discussion and the northern hemisphere forms described by Bailey, Hensen and Gran. If this chain of intermediates is established, the variety I describe as *R. styliformis* var. *semispina* and the type species itself would become varieties of the species *R. hebetata* Bailey, as this name would take precedence over Brightwell's *R. styliformis*.

R. styliformis var. *oceanica* var. nov.

Peragallo, H., 1892. *R. styliformis. Le Diatomiste*, p. 111, pl. XVII.
Van Heurck, 1896. *R. styliformis. A Treatise on the Diatomacae.*
Gran, H., 1902. *R. styliformis. Rep. Norw. Fish. Mar. Invest.*, Bd. II, No. 5, pp. 36–9 and 173–5, pl. I, figs. 1–9.
Hustedt, 1930. *R. styliformis.* 'Die Kieselalgen' in Rabenhorst's *Kryptogamen Flora*, p. 584, fig. 333.
Cupp, E. E., 1943. *R. styliformis. Bull. Scripps Inst. Oceanog.*, Vol. 5, No. 1, p. 87, fig. 48 *Aa*.

The form which I am calling var. *oceanica* has been described or figured as the type by the authorities just given above. The valves slope somewhat convexly to the eccentrically placed terminal spine. The latter is distinguished by the possession of rounded wings which run on either side from its base often for half its length (Text-fig. 1*d*, *e*). There are numerous intercalary plates arranged in two rows and the plates and valves are seldom very stoutly made. There is hardly ever any trace of the tongue-like process of the first intercalary plate which is so pronounced a feature of the variety *semispina*. Wherever I have found this form, the diagnostic value of its characters have remained sharp and clear presenting no intermediates with any other.

I have recognized this variety in the Antarctic material of the *Discovery* Expedition, in Scottish Fishery Board collections made in the Atlantic near the Faeroes and in the following slides of the British Museum of Natural History.

Slide no.	Legend	Habitat
13,067	Cl. a. M. Diat. 308	Sea of Behring
26,013	In mare H. L. Smith (452)	58° N., 32° W.
26,753	Types of Synopsis des Diatomees Belge Van Heurck	—
28,039	Coll. O'Meara	Davis Strait, 7/8/1871, lat. 45°, long. 53° 43′
28,074	Coll. O'Meara	Atlantic, lat. 58°, long. 32°
31,057	Coll. Comber	Arafura Sea, surface
7,345	P. Oberg (Cleve)	Atlantic, 10/6/1870, lat. 58°, long. 32°

It also appears in figures of Gran's collections (*loc. cit. supra*) made in August and September 1900 in the Norwegian Sea between Jan Mayen and Norway and near Bear Island, and in a figure of *R. styliformis* stated by Cupp to be 'oceanic' and 'sometimes fairly numerous' off California. So far as they go, these occurrences, taken together with my own observations, suggest a more oceanic distribution than that indicated for var. *semispina* or the type and it appears to find its optimum conditions in cold, temperate or polar water.

When the Scottish material was first measured, the fact that several varieties of the species existed was not yet appreciated. However, in view of later work giving the distribution just outlined and also because it had a strictly limited southward distribution in the North Sea, it appeared possible that its abundance relative to the other varieties of the Faeroe-Shetland area might afford an index of oceanic inflow. For this reason, although no serious big-scale effort has been attempted, I have been through the twelve Scottish stations given in Table I and have found the proportion of *oceanica* individuals in random samples of 30. These I give below:

St. no.	Date	*Oceanica* individuals	St. no.	Date	*Oceanica* individuals
1	8/4/31	1	7	30/5/34	30
2	10/5/31	4	8	19/4/35	8
3	15/4/32	12	9	16/6/36	29
4	31/8/32	3	10	26/8/37	27
5	21/5/33	30	11	3/7/38	6
6	7/6/33	17	12	27/3/39	0

These proportions suggest that the variety was relatively more abundant in the period 1933–7 than in 1931–2 and 1938–9. The reports of the Scottish Fishery Board (1932–9) indicate that the period 1931–7 was one during which an unusual influx of Atlantic water entered the northern North Sea and in these circumstances my figures hold out the hope that a more complete examination of the Scottish collections might yield interesting results.

At two stations in Scottish waters the variety was found to be forming auxospores which arose at right angles to the parent cell in the way I have observed them to do in the type. I give below some of the circumstances of their occurrence.

Position	59° 44′ N., 1° 10′ W.	60° 02′ N., 7° 50′ E.
Date	23/6/35	3/7/38
T° C. at 20 m.	8·77	9·71
S °/$_{oo}$ at 20 m.	35·38	35·41
Diameter of parent	24μ	24μ
Diameter of auxospore	76μ	44μ

The forms I have described may be separated by the following dichotomous key:

A. Wings angular.
   a. Wings usually form right angles and do not extend beyond base of apical spine. Inner edge of first intercalary plate often shows trace of tongue-like projection. — *R. styliformis*
   b. Wings form obtuse angles and extend along apical spine. Inner edge of first intercalary plate generally produced into pronounced tongue-like projection. — *R. styliformis* var. *semispina*

B. Wings rounded. — *R. styliformis* var. *oceanica*

Diameter measurements of *Rhizosolenia styliformis*

All the biometric observations on the species given in my earlier paper (Wimpenny, 1936) and those for the southern North Sea, the western entrance of the English Channel, the semi-tropical Atlantic and certain stations of the north and central North Sea and the Faeroe-Shetland area, set out in Table I of this account, may be referred to the type of the species. The material from the semi-tropical Atlantic consisted of one station only and will not be further discussed at the present stage.

The increase in cell diameter, due to the formation of auxospores producing a new population and the continuous diminution due to fission, has been mentioned on pp. 38 and 39 of Part I of this paper. What was considered to be the newly-formed auxospore generation and the original parent stock were then shown to exist side by side in the southern North Sea. It was also pointed out that larger cells are favoured in the south and east of this area, and it was suggested that temperature may have exerted a selective effect.

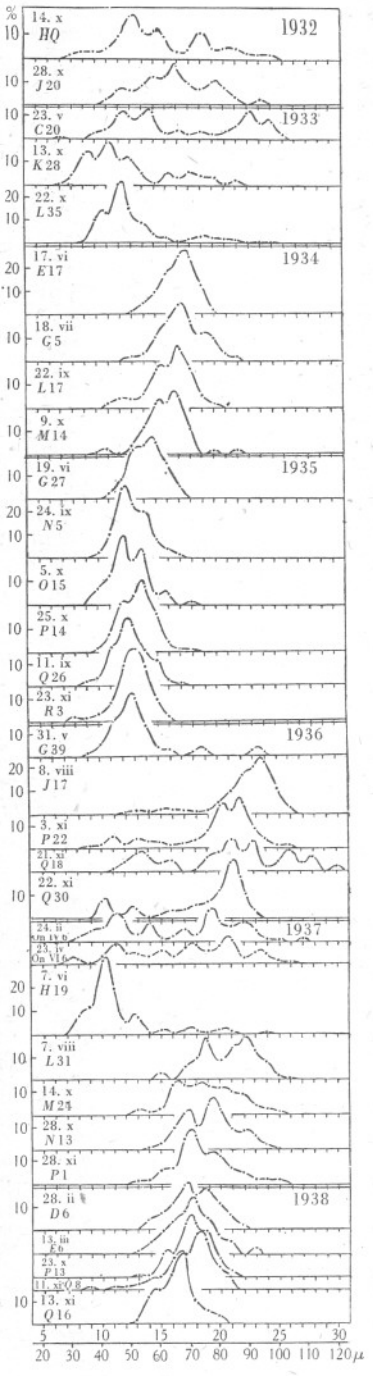
In Text-fig. 2 I have plotted the numbers at different diameters for a series of representative samples of the type species taken through various seasons of 1932–9, mainly from the south-west Dogger Bank Swirl area of the North Sea. It will be seen that the narrow original parent stock of 1932–3 had disappeared by 1934 and that the wide newly-formed auxospore generation recurred each year at a steadily diminished diameter until 1937 when it also disappeared. Before its extinction, however, it must be noticed that there was a relative revival in the winter of 1936–7 and in June 1937 which may have had its origin in some external factor such as temperature or salinity. Individuals of this latter generation (Pl. V) measuring 60μ in diameter attached to an auxospore of 120μ diameter and of 40μ attached to an auxospore of 90μ were found in September (St. 5, Cruise N) and October (St. 11, Cruise P) 1935 respectively. Among the cells of the October samples there were also a considerable number with scars showing that auxospores had been attached to them. The size of generation resulting from this formation of auxospores, first evident in 1936, was comparable to that found in 1932–3, when the species was also represented by two size generations. From mid 1937 until the observations ended the species was again represented by a unimodal population consisting of individuals of the most recent generation. These observations show that on this occasion a period of three to four years elapsed between the production of auxospore generations in the southern North Sea.

In this same area there is another internal factor which might be conceived to affect cell-diameter in these diatoms. This is the regular occurrence of microspores whenever a big flowering arises (Pl. V). Microspores were particularly numerous in the autumn and towards the end of the annual period of abundance. Their appearance is that of clear disc-shaped bodies bearing on their surfaces little extruded spheres of chromatic matter and

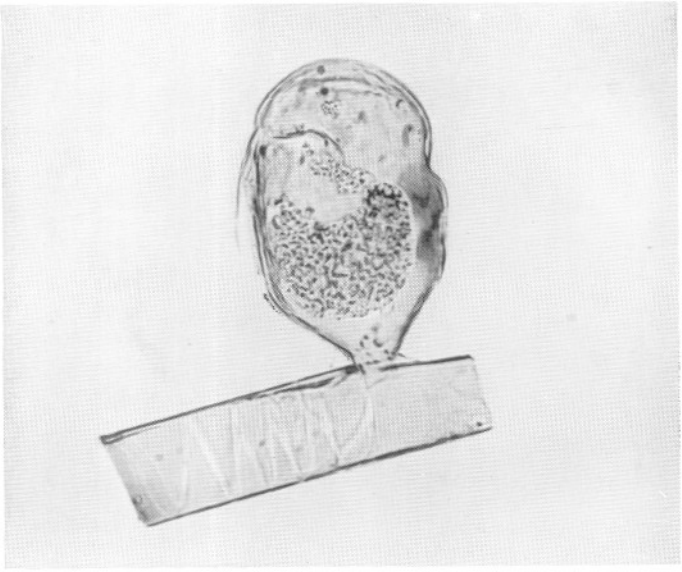
is similar to that reported for many other species of diatom. I have only to add in respect of *R. styliformis* that I have observed the disc-shaped bodies to become fusiform and exhibit amoeba-like movement. Whereas Gross (1937) appears to think microspores a morbid or parasitic phenomenon, Karsten (1905, pp. 107–12) has described them as the agents of sexual reproduction in *Corethron* and, more recently, Braarud (1939) has found that they unite and may produce normal cells in *Chaetoceras*.

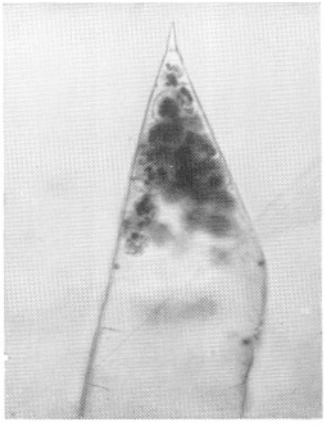
From such evidence as is available, therefore, it seems likely that microspores represent a method of sexual reproduction. However this may be, it is clear that unless cells derived from microspores immediately took up the size of microspore producers the steady size diminution ending in the production of auxospores that has just been recorded would not have been apparent.

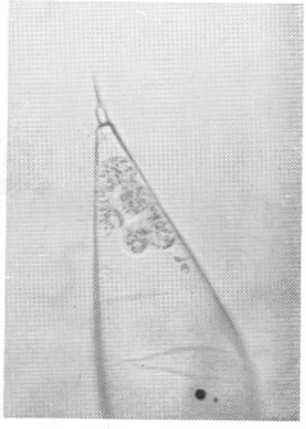
Passing through an intermediate stage in the Firth of Forth Swirl area, the individual cells of the species were much narrower in the northern North Sea and Faeroe-Shetland area than they were in the southern North Sea. No discrimination between the varieties and type of the species was made when several of the northern North Sea and Faeroe-Shetland samples were measured, but a subsequent examination showed the type to be present in most of them. The populations were unimodal in size distribution with the exception of E 6 in 1933. Of the two modes here, however, it was found on re-examination that the smaller one was caused by the variety *oceanica*. The largest cells from this area were found early in the year, a minimum being



Text-fig. 2. Frequency distributions for cell diameters of *Rhizosolenia styliformis* taken from *George Bligh* and *Onaway* stations made between 1932 and 1938 in the south-west Dogger area of the North Sea, except Q 8 and Q 18, which were in the north-east Dogger area. Percentages are given on the ordinate and the diameter measurements are shown as arbitrary units along the abscissa, the corresponding values in μ being given below this.







Photomicrographs of *Rhizosolenia styliformis* Brightwell, ×215. Above: auxospore in process of formation (St. 5, Cruise N, 1935). Below: parts of cells containing microspores, from southern North Sea material.

reached in July and August, the last months in which my material showed the species is to be found in any numbers in these waters. There was, therefore, no steady fall in diameter extending over several years, but an annual diminution and a regeneration of size evident each spring. In these circumstances it appears likely that auxospore formation is annual, a state of affairs in sharp contrast to that taking place in the southern North Sea.

Still smaller individuals were represented in six samples of the type taken at the western approaches to the English Channel in the summer of 1939 (Table I). These samples were also unimodal and included one individual of 20μ diameter taken in the April collections and found to be forming an auxospore. In the June samples one or two individuals were found with diameters between 60 and 76μ. It seems likely that these represented an auxospore generation formed in April, and this appearance of the large auxospore-produced cells in the same season as their generation, taken together with the fact that the populations were even narrower than those from the Faeroe Shetland area, suggests that the process of auxospore formation takes place at a shorter interval than in the North Sea.

While it is clear that more sampling, and some *in vitro* work which was contemplated before the war, will have to be carried out before any useful picture of the external and internal factors controlling the size of this diatom can be produced, the present work sets certain problems for further elucidation.

For instance, it has been pointed out in the preceding paragraphs that in the winter of 1936–7 and early summer of 1937, there was a relative recovery in the narrower generation. This occurred at a season of low temperature and high salinity, and it remains to be shown whether either temperature or salinity is capable of affecting the normal waning of an older and narrower generation when the population is bimodal. In 1935 and 1936 the origin and development of a new wide generation took place when the salinity in the area had begun a fall which continued until 1937–8 (Wimpenny, 1944). Did a lowering of the salinity play any part in the origin and survival of the new wide generation? Again the populations of the species type are successively narrower as one proceeds from the southern North Sea, through the Firth of Forth Swirl and Scottish areas to the western entrance of the English Channel. These districts constitute a progression of increasing salinities and the question arises as to whether the salinity has any significant relation to the diameters of the various populations.

Another question concerns the cell-wall. Is its thickness affected by the supply of silica and the conditions under which it is laid down? It is easy to see that the cell-walls of cold water diatoms are thicker than those of warmer water and there may be similar seasonal and local differences. Variations in the thickness of the cell-wall would obviously affect the number of cell divisions equivalent to a given diminution of diameter.

I have put these questions in order to show that their solution will be necessary before one can hope to estimate the age, number of divisions and

effect of nutrient salts on a population of *R. styliformis* as a result of considering differences in diameter. At present the chief use that can be made of these frequency observations is to help to identify populations by the noting of similar relative distributions of diameter frequencies. Useful evidence on these lines has already been obtained and more may confidently be expected to result from future work.

Summary

1. Diameter measurements of *Rhizosolenia styliformis* from the Antarctic, the subtropical Atlantic and Pacific Oceans and from the North Sea and neighbouring waters have made it appear necessary to set up two varieties, *oceanica* and *semispina*, in addition to the type of the species *R. styliformis*. The type as I describe it has been called var. *longispina* by Hustedt, but elsewhere it has often been figured as the var. *oceanica* of this paper. Var. *semispina* is synonymous with the form represented by Karsten as *R. semispina* Hensen. It differs from *R. semispina* as drawn by Hensen and its synonym *R. hebetata* forma *semispina* Gran, but is thought likely to be linked by intermediates. If this is so *R. hebetata* may have to be extended to include and suppress *R. styliformis*, as var. *semispina* is linked to the type by intermediates. Var. *oceanica* has no intermediate forms and, if *R. hebetata* is to be extended, this variety should be established as a separate species.

2. Var. *oceanica* is absent from the southern North Sea and appears to be an indicator species related to oceanic inflow.

3. Auxospore formation was observed for the type in the southern North Sea in 1935 and biometric observations suggest that a period of 3–4 years elapsed between the production of auxospore generations in that area. Outside the southern North Sea for the type, measurements give no indication of auxospore generations occurring at intervals exceeding a year. While auxospore formation has been seen in var. *oceanica* from the Shetlands area samples of June 1935 and July 1938, this phenomenon has not been observed for var. *semispina*.

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THE UTILIZATION OF ORGANIC PHOSPHORUS BY PHYTOPLANKTON

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The rate at which phosphorus and nitrogen are used by plants, returned to the water and again utilized, is a direct measure of the fertility of the sea (Harvey, 1942, p. 233). A knowledge of the processes of the cycle of such changes is important for the study of marine productivity. The nitrogen cycle has received much attention and much work has been done (Cooper, 1937; Harvey, 1940), but little is yet known about the cycle of phosphorus. The present investigation is intended to clarify a few of the processes in the phosphorus cycle.

Phosphorus in the sea is known to occur in living organisms, in particulate and dissolved organic material, and as dissolved inorganic phosphorus (of which only orthophosphate is known to be present). Phosphorus in living and particulate material becomes eventually dissolved in water as organic or inorganic phosphorus, and the dissolved organic phosphorus can turn into inorganic phosphorus through various agencies. It is only the dissolved phosphorus that can be used directly by plants, and it is generally assumed that only phosphate is being absorbed and utilized by plants in the sea. We have practically no knowledge of the other forms of phosphorus that can be utilized by marine plants. Harvey (1940) has demonstrated that phytoplanktonic diatoms may utilize ammonium nitrogen in preference to nitrate nitrogen, and that they can also utilize some organic substances, such as urea and uric acid, as sources of nitrogen. It is of interest to know whether they can use phosphorus from sources other than orthophosphate. In the following experiment parallel cultures were made with orthophosphate, pyrophosphate and phytin supplied as sources of phosphorus with a view to finding out whether diatoms can utilize the last two as effectively as they utilize orthophosphate. Phytin was chosen as it has been considered a stable organic phosphorus compound of plant origin.

Exp. 1. Sea water collected from the mouth of Plymouth Sound early in April was enriched with potassium nitrate giving a nitrogen concentration of 2000 mg./m.^{3} with an iron concentration of 50 mg./m.^{3} added in the form of ferric citrate. The original content of phosphate phosphorus in the sea water was 7 mg./m.^{3} Flasks of 500 c.c. capacity were used, each containing 300 c.c. of the enriched sea water. Phosphorus compounds were supplied giving a phosphorus concentration of 150 mg./m.^{3} In culture A, KH_2PO_4 was used; in B, $Na_4P_2O_7$; and in C, phytin ($C_{12}H_{22}O_{44}P_{10}Ca_7Mg$). These cultures were

aerated by bubbling a stream of filtered and washed air through them and equally illuminated by daylight, as they were kept on a rotating table in a north window. Duplicate cultures of B and C (B*d* and C*d*) were stored in the dark in order to check up the change of the phosphorus compounds which is not due to the growth of diatoms.

There was an increasing growth in both cultures A and C during the first 3 days, when the density of the growth, which consisted mainly of *Phaeocystis* with some chains of *Skeletonema costatum*, was about the same. The growth in A then stopped, while in C it was still increasing up to the fifth day. The increase was purely due to the increase of *Phaeocystis*, there being no further increase of *Skeletonema costatum* cells after the third day. There was no significant growth in culture B during the whole period.

In the sample B*d*, kept in the dark, a part of the amount of pyrophosphate was found to be turned into orthophosphate, 64 mg./m.^{3} of orthophosphorus being found, including 7 mg./m.^{3} present in the original sea water, after 27 days, and 70 and 95 mg./m.^{3} after 34 and 124 days respectively. In culture C*d* some of the added phytin changed to phosphate while kept in the dark. In some other similar storage experiments all the phosphorus in phytin was liberated as orthophosphate in 20 days in the dark, while in yet others it took 4 months.

Distilled water, to which had been added 10,000 mg. pyrophosphate phosphorus per cubic metre, gave a colour corresponding to 10 mg./m.^{3} of orthophosphorus 5 min. after adding the reagents when estimated with the Denigés-Atkins method (Atkins, 1923). The intensity of the colour increases much more rapidly than in the standard sample within this short period. This indicates that pyrophosphorus turns into orthophosphorus very quickly once the reagents are added. In another 5–10 min. the colour increased to an intensity matching the colour of 16–19 mg. of orthophosphorus per cubic metre. About half an hour after the addition of reagents the colour started decreasing. Full colour developed within 5 min. in the standard. The orthophosphorus content in the pyrophosphate solution before adding the reagents must therefore be much less than 10 mg./m.^{3} The rate at which pyrophosphate turned into orthophosphate in the presence of the reagents, as judged by the change during the interval from 5 to 10 min. after the addition of the reagents, was round about 0·02 mg./m.^{3}/sec., though the rate is slightly decreasing. The rate must be greater within 5 min. after adding the reagent. Therefore the orthophosphate in solution, before the addition of the reagent, should have been not more than 4 mg./m.^{3}; and no more than 0·04% of the calculated amount of phosphorus in the stock solution of pyrophosphate was in the form of orthophosphate. The conversion of pyrophosphate to orthophosphate is purely a chemical reaction in such weak solutions.

It seems clear from this experiment that pyrophosphate does not support any growth of *Phaeocystis* and *Skeletonema*. The amount of orthophosphate liberated into the culture together with the original amount in the sea water

(7 mg./m.^{3}) did not support enough growth to be easily seen on visual inspection. The orthophosphate in culture A (157 mg./m.^{3}) was depleted in 3 days. Phytin can support longer and larger growths of *Phaeocystis* than phosphate does when the amount of phosphorus is the same. This seems to show that the growth of this alga, just as that of some blue-green algae, is encouraged by the presence of organic substance.

Exp. 2. In order to ascertain the effect on the growth of *Skeletonema costatum* when phytin or orthophosphate is supplied as a source of phosphorus, and to make sure whether phosphorus can be utilized by this diatom from pyrophosphate, the above experiment was repeated with sea water which contained *Skeletonema costatum* as the dominant organism. The orthophosphate concentration in the original sea water was 15 mg./m.^{3} Three sets of cultures, A, B and C, were enriched with potassium nitrate, ferric citrate and phosphorus compounds as in Exp. 1. Two hours after the sea water was enriched, analysis of orthophosphate gave the result shown in Table I.

TABLE I. INITIAL PHOSPHORUS CONCENTRATION IN CULTURES SUPPLIED RESPECTIVELY WITH KH_2PO_4, $Na_4P_2O_7$ AND PHYTIN

Cultures	P sources	Amount of P added mg./m.^{3}	Original ortho-P in sea water[1] mg./m.^{3}	Ortho-P found mg./m.^{3}
A	KH_2PO_4	150	15	163
B	$Na_4P_2O_7$	150	15	16
C	Phytin	150	15	42

[1] Salt error corrected.

The cultures started with 146 cells of *Skeletonema costatum* per c.c., some *Thalassiosira decipiens*, a few cells of *Coscinodiscus excentricus*, and a very few colonies of *Phaeocystis Pouchetii*. There was little growth in culture B, while in cultures A and C there was a continuous and nearly similar increase until the fourth day when the number of cells of *Skeletonema costatum* was 5100 (A) and 5800 (C) per c.c. The diatom cells retained their healthy appearance the next day and were evenly distributed in the culture. Henceforth they began to sink to the bottom of the culture while *Phaeocystis* started a remarkable increase in C. On the seventh day nearly all the diatom cells settled on the bottom of the flask. *P. Pouchetii* flourished only in culture C, and its growth in cultures A and B was very poor.

The result of this experiment confirms that of Exp. 1. *Phaeocystis* grows much better when the culture is supplied with phytin than when it is supplied with orthophosphate. It also shows that *Skeletonema* grows well when either of these two phosphorus compounds is supplied as a source of phosphorus, but not when pyrophosphate is the only phosphorus compound supplied.

It was not clear why *Skeletonema* stopped growing in culture C when the medium was still suitable for the growth of *Phaeocystis*. In order to make sure that there was no shortage of silicate for the growth of diatoms, sodium orthosilicate was added in the following experiment.

Exp. 3. Sea water from Plymouth Sound was enriched as in the previous experiments, but with further addition of 20 parts per million of SiO_2 in the form of sodium orthosilicate. The sea water contained phosphate, 8 mg. P/m.^{3} *Skeletonema* seemed to be the only alga present. Growth of *Skeletonema* was fully developed on the fourth day in cultures A (orthophosphate) and C (phytin), while the growth in B was poor. The growth stopped and the diatoms started to sink to the bottom in cultures A and B, when the orthophosphate left in cultures A, B and C was 4, 3·5, and 2·4 mg. P/m.^{3} respectively. The growth finished in C the next day. The result of this experiment is shown in Table II. *Phaeocystis* did not develop in culture C in this experiment. It would seem that it did not exist in the sea water used. The end of growth of the diatom in cultures A and C seems to be caused not by the lack of silicate, but by the deficiency of available phosphorus. The fact that both phytin and orthophosphate can support much better growths of *Skeletonema* than pyrophosphate, is again confirmed by this experiment. Phytin supports longer periods of growth of *Skeletonema*, when it is the only alga growing in the culture, than orthophosphate.

Exp. 4. In this experiment the sea water was first enriched as in Exp. 3, and then sterilized by heating up to 95° C. and maintaining at this temperature for 20 min. 278 cells of *Nitzschia closterium* were inoculated from a unialgal culture into each 100 c.c. of the culture. The growth was fully developed in 4 days and, as shown in Table III, was good in all the cultures including those to which pyrophosphate was supplied as the only source of phosphorus. The sea water used was filtered through a Berkefeld candle with the filtration apparatus as described by Allen & Nelson (1910, p. 432), and the original content of orthophosphate in the filtered sea water was 5 mg. P/m.^{3}

This experiment, however, provided no evidence which showed that *Nitzschia* cells can use pyrophosphate, because more than half of the pyrophosphate was turned into orthophosphate after heating at 95° C. for 20 min. Phytin was used by *Nitzschia* as a source of phosphorus as effectively as by *Phaeocystis* and *Skeletonema* in the preceding experiments. The liberation of orthophosphate from phytin, when phytin is added to sea water, is partly effected by biological reaction. All the phosphorus in phytin added to a sea-water sample used for the above experiment was turned into orthophosphate after the sample was stored in the dark for 20 days. When a similar sample was heated to 85° C. before storing in the dark, only 53 out of 150 mg./m.^{3} (i.e. about one-third) of the phosphorus in the amount of phytin added turned into orthophosphate, while in distilled water 66 out of 150 mg./m.^{3} (i.e. a little less than one-half) of the phosphorus in phytin was turned into orthophosphate after storing in the dark for 20 days. It would seem, therefore, that phytin in such a low concentration is partly decomposed in sterile solution into orthophosphate, and that the rate of this chemical process is greater in distilled water than in sea water. When the *Nitzschia* cells in the unialgal culture were filtered off through filter paper (Whatman No. 541)

TABLE II. GROWTH OF *SKELETONEMA COSTATUM* IN KH_2PO_4, $Na_4P_2O_7$ AND PHYTIN

Cultures	P compounds	Initial conc. of P, mg./m.³	4 days	5 days		6 days	
					Ortho-P		Ortho-P
A	KH_2PO_4	158	Growth fully developed, very good	Growth stopped, and sedimented	4·0 mg./m.³	Sedimented	3 mg./m.³
B	$Na_4P_2O_7$	158	Poor	Do.	3·5 mg./m.³	Sedimented	2 mg./m.³
C	Phytin	158	Growth fully developed, very good	Rate of growth much decreased, cells beginning to sink	2·4 mg./m.³	Sedimented	6 mg./m.³

TABLE IV. GROWTH OF *NITZSCHIA CLOSTERIUM* IN BACTERIA-FREE CULTURES WHEN PHOSPHORUS WAS SUPPLIED IN DIFFERENT FORMS

Cultures	P compounds	Initial ortho-P mg./m.³	Initial no. cells per c.c.	9 days		11 days		13 days		18 days		20 days	
				Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.
Set A	Ortho-P	208	860	3·0	454,000	2·5	844,000	2·0	845,000	2·0	845,000	2·0	845,000
Set B	Pyro-P	9	860	10·0	72,000	3·0	224,000	2·5	594,000	2·0	844,000	2·0	544,000
Set C	Phytin	45	860	2·5	632,000	2·5	734,000	2·0	836,000	2·0	1,122,000	2·0	1,122,000

TABLE III. GROWTH OF *NITZSCHIA CLOSTERIUM* WHEN PHOSPHORUS WAS SUPPLIED IN DIFFERENT FORMS

Cultures	P added mg./m.³		3 days no. of cells	4 days no. of cells	Ortho-P left mg./m.³
1	Ortho-P	150	15,500	85,000	21
2	Ortho-P	150	16,000	100,000	20
3	Pyro-P	150	11,000	56,000	9
4	Pyro-P	150	10,000	58,000	6
5	Ortho-P and pyro-P	75 75	13,150	80,000	13
6	Ortho-P and pyro-P	75 75	14,150	80,000	10
7	Phytin-P	150	20,000	40,000	38
8	Phytin-P	150	22,000	118,000	35

and the filtrate was inoculated into the culture medium containing phytin, all the phosphorus in phytin was also turned into orthophosphate after the sample was stored in the dark for 20 days. If one-third of the amount of orthophosphate liberated is due to pure chemical reaction, two-thirds must be due to the effect of bacteria, as there were no *Nitzschia* cells in the sample.

Good growth was obtained in unialgal cultures of *Skeletonema costatum* and *Nitzschia closterium* when glycerophosphoric acid, sodium nucleinate and lecithin were supplied singly as a source of phosphorus. These organic phosphorus compounds, however, were also found to be broken down into orthophosphate in the presence of bacteria in the sea water.

It was advisable therefore to experiment on bacteria-free cultures so that the reaction due to bacteria might be avoided. Hence a bacteria-free culture of *Nitzschia closterium* forma *minutissima* was made, starting from single cells isolated from the unialgal culture. The method used is described in another paper (Chu, 1946).

Exp. 5. Half a c.c. of the bacteria-free culture of *Nitzschia* containing 430,000 cells was inoculated into each of the 500 c.c. cultures in Berkefeld filtered sea water which had been enriched with 2000 mg./m.³ of nitrate nitrogen, 2 mg./m.³ of iron in the form of citrate, 2000 mg./m.³ of SiO_2 and 200 mg./m.³ of phosphorus supplied in different forms in different sets of cultures. The media were sterilized the day before inoculation by heating at 95° C. for 15 min. The stock solutions of phosphorus compounds were sterilized at 95° C. for 15 min., and the required amount, containing 0·1 mg. of phosphorus, was added to each 500 c.c. of the medium just before the latter was inoculated with bacteria-free *Nitzschia* cells. The sources of phosphorus are KH_2PO_4 in culture set A, $Na_4P_2O_7$ in set B, and phytin in set C, each set containing four duplicate cultures. One culture from each set was kept in an incubator at 22° C. after adding 1% of sterilized peptone. The stock solution of peptone was sterilized by autoclaving for 1 hr. at 20 lb. pressure. Boiling for half an hour is not enough to kill bacterial spores, as bacteria growth occurred in the peptone solution so treated after having been kept in the incubator at 22° C.

The phosphorus content in phytin, as estimated by first wet ashing with sulphuric acid and perhydrol and then treating with the acid molybdate reagent (allowing for the amount of acid already present), was found to be the same as that calculated from the formula $C_{12}H_{22}O_{44}P_{10}Ca_7Mg$. When the stock solution of phytin (1 mg. P in 1 c.c.) was diluted 10 times, 0·14% of the total phosphorus was found to be in the form of orthophosphate. The phosphorus content of pyrophosphate was also found to be the same as shown by the formula $Na_4P_2O_7$, and when the stock solution (1 mg. P in 1 c.c.) was diluted 10 times, 0·0075% of the total phosphorus was found to be in the form of orthophosphate. The content of orthophosphate phosphorus, as estimated just before the inoculation of the cultures, is recorded in Table IV. The phosphate phosphorus content of the original sea water used was 7 mg./m.^{3}

One culture of each set was put on a revolving table, so that equal illumination was assured, while the other two cultures of each set were put near a north window. Noticeable growth was observed in culture sets A and C. In set B, the cultures showed no significant growth during the first 7 days, and only a slight growth was observed after 8 days; but the growth was increasing rapidly afterwards.

There was no growth of bacteria in the cultures kept in the incubator. Sterilized peptone was added to one of the illuminated cultures (20 days old) from each set, which were then incubated at 22° C. No growth of bacteria occurred.

Duplicate cultures of sets B and C were kept in the dark as a check to ascertain the amount of orthophosphate formed from pyrophosphate and phytin. 48 mg./m.^{3} of orthophosphate were found in sample B (pyrophosphate) and 71 mg./m.^{3} of orthophosphate in sample C (phytin) in 20 days. Therefore 39 (18%) and 26 (13%) mg./m.^{3} of orthophosphate were liberated from pyrophosphate and phytin in samples B and C respectively during this period. If the same amounts of orthophosphate were liberated in the illuminated cultures, it would seem that most of the phosphorus consumed was in the form of pyrophosphate in B and organic phosphorus in C. However, the delay of the growth in the cultures in set B evidently shows that pyrophosphate cannot, at least, be utilized as effectively as orthophosphate; then the later rapid growth in these cultures seems to show that more orthophosphate was liberated at that time, probably in some way due to the presence of the increasing number of cells in the cultures. The initial rapid growth in cultures of set C, which is about the same as in those of set A, shows that the phosphorus from phytin can be used as effectively as orthophosphate.

Exp. 6. In this experiment glycerophosphoric acid was used as a source of phosphorus (400 mg./m.^{3}). The sea water was first enriched with nitrate, ferric citrate, and silicate as in the previous experiments, and then sterilized and inoculated with *N. closterium* (700,000 cells in each 500 c.c. culture) from a bacteria-free culture. A parallel set of cultures was made using orthophosphate. This experiment was carried out in daylight during December

TABLE V. GROWTH OF BACTERIA-FREE CULTURES OF *N. CLOSTERIUM* IN GLYCEROPHOSPHORIC ACID (A), AND IN ORTHOPHOSPHATE (B). (AVERAGE OF TWO CULTURES FROM EACH SET. ORIGINAL ORTHOPHOSPHATE CONTENT WAS 6 mg./m.³)

Cultures	Sources of P	Inoculum cells per c.c.	Total P mg./m.³	Initial ortho-P mg./m.³	7 days		13 days		24 days		39 days	
					Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.
A	Glycerophosphoric acid	1400	406	12	25	2,460	0	112,500	0	685,000	0	2,120,000
B	Orthophosphate	1400	406	406	190	3,840	90	129,500	0	500,000	0	2,100,000

TABLE VI. GROWTH OF *N. CLOSTERIUM* IN BACTERIA-FREE CULTURES SUPPLIED WITH SODIUM NUCLEINATE (SET A, P = 200 mg./m.³) AND ORTHOPHOSPHATE (SET B, P = 200 mg./m.³). ORIGINAL ORTHOPHOSPHATE PHOSPHORUS CONTENT IN THE SEA WATER USED WAS 5 mg./m.³

Cultures	Sources of P	Initial ortho-P mg./m.³	Inoculum	5 days		8 days		11 days		21 days		38 days	
				Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.	Ortho-P mg./m.³	No. of cells per c.c.
Set A	Nucleinate	5	15,300	4	50,400	0	218,000	0	370,000	0	360,000	0	360,000
Set B	Orthophosphate	205	15,300	180	48,000	5	390,000	3	686,000	2	1,980,000	0	1,980,000

and January, and the growth was much slower because of the rather poor illumination. Table V embodies the result of this experiment.

When 400 mg./m.^{3} of phosphorus as glycerophosphoric acid were added to the sea water used, 1·6% of the phosphorus was found to be in the form of orthophosphate. Very slight or no increase of orthophosphate was found after autoclaving. In the duplicate cultures with inoculum, which were kept in the dark for 10 days, no more than 5% of the phosphorus was turned into orthophosphate. Therefore the phosphorus from glycerophosphoric acid must be used for the main bulk of the growth in cultures of set A. The growth in this set of cultures was more or less the same as that in cultures of set B supplied with orthophosphate. This indicates that glycerophosphoric acid can be used as a source of phosphorus as good as orthophosphate for the growth of this diatom. The diatom cells in cultures of set A were found to be able to divide as many as nine times when no orthophosphorus was detectable in the culture.

Exp. 7. This experiment was carried out in the hope of finding out whether sodium nucleinate can be used as a source of phosphorus in bacteria-free cultures of *N. closterium*. This compound is very stable and no change into orthophosphate occurred after it was added to the sterilized enriched sea water and kept for 5 days. As can be seen from Table VI, which embodies the growth in cultures of set A (average of three cultures) using sodium nucleinate as a source of phosphorus and that in cultures of set B supplied with orthophosphate, very little growth was obtained when nucleinate is supplied. It is clear that sodium nucleinate cannot be used as a source of phosphorus by this diatom.

Exp. 8. Lecithin was tried in cultures in a similar way as in the above experiment. No growth was obtained when it is supplied as the only source of phosphorus, and evidently it cannot be used by *N. closterium* in bacteria-free cultures. It is very stable, and very little, or none at all, is turned into orthophosphate in sterilized sea water.

It is clear from the above experiments that in bacteria-free cultures the marine diatom *N. closterium* forma *minutissima* can utilize phosphorus from some organic compounds such as phytin and glycerophosphoric acid, though not from some others such as lecithin and nucleic acid. The latter have been reported as utilizable sources of phosphorus for higher plants (Stoklasa, 1896; Schreiner, 1923). Further investigation is needed as to why they cannot be utilized by this diatom. In order to find out whether the phosphorus dissolved out from marine algae can be effectively utilized by this diatom in bacteria-free cultures, the following investigation was made.

Exp. 9. Square pieces were cut off from fresh fronds of *Laminaria saccharina* collected near low-water mark (about 1 year old), and the blade surface was dried with blotting paper and weighed. Then they were dried in an oven at 100° C. until there was no further decrease in the weight. The water content of the fronds was found on the average to be 84% of the fresh weight. The

total phosphorus as estimated by wet ashing with sulphuric acid and perhydrol after the method used by Cooper (1934, p. 756) varies from 0·3 to 0·4% of the dry weight in different plants and different parts of the fronds. The amount of total phosphorus in the fresh fronds collected from a craft was much larger, being 1% of the dry weight.

When extracted with distilled water in a hot water bath for 24 hr., 8·2% of the total phosphorus was dissolved out into the solution, 2% being in the form of orthophosphate and 6·2% in the form of organic material, while 80% of the total phosphorus of the moribund fronds, which had been kept in the laboratory tank for a week, was found to be soluble as orthophosphorus.

Parallel bacteria-free *Nitzschia* cultures were made in Berkefeld filtered sea water, which was enriched with nitrogen, iron and silica as in previous experiments. In one set of cultures (A) the phosphorus was supplied as orthophosphate, and in another set (B) it was supplied as hot-water extract of fresh *Laminaria* fronds, the phosphorus added in both sets of cultures being in all 400 mg./m.^{3}

The resulting growth of cultures in set B was as good as that in set A. As only 2% of the phosphorus in the *Laminaria* extract added to cultures of set B was in the form of orthophosphate, it may be assumed that the phosphorus used by *Nitzschia* cells in these cultures was mainly in the organic form.

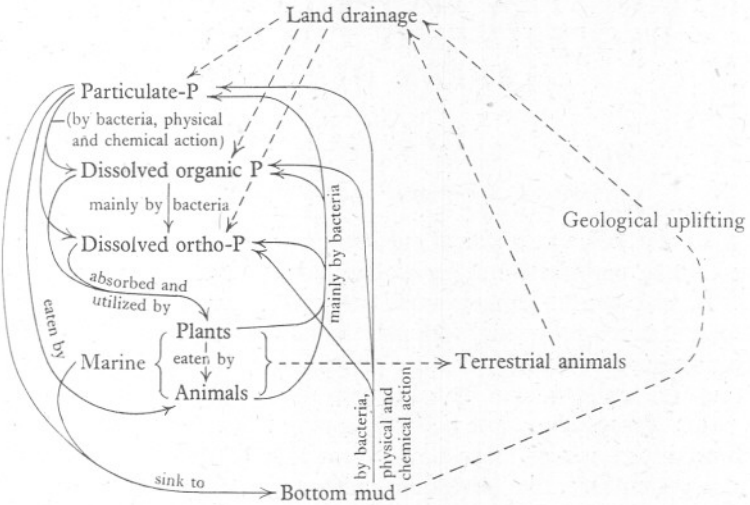
Summary and Conclusion

Cultural experiments were made with marine organisms in enriched crude sea water and in bacteria-free cultures with the phosphorus supplied in different forms. It was found that pyrophosphate cannot be utilized as a source of phosphorus as effectively as orthophosphate by the organisms cultured, i.e. *Phaeocystis Pouchetii*, *Skeletonema costatum* and *Nitzschia closterium*. Growth of *Phaeocystis Pouchetii* was a little better and lasted longer when phytin was supplied to natural sea water as a source of phosphorus than when orthophosphate was supplied. Phytin can also support a growth of *Skeletonema costatum* and *Nitzschia closterium* as good as, or a little better than, orthophosphate.

The organic phosphorus compounds used in these experiments were found to be broken down into orthophosphate in natural sea water. In bacteria-free cultures phytin and glycerophosphoric acid can be effectively used as such by *Nitzschia closterium* forma *minutissima* as a source of phosphorus, while sodium nucleinate and lecithin can not be effectively used as such. The organic phosphorus dissolved out from the blades of *Laminaria* can also be utilized by this diatom as effectively as orthophosphorus.

It would seem, therefore, that not only the dissolved orthophosphate as generally assumed, but the dissolved organic phosphorus in the sea may also be absorbed and utilized by plants. Thus the change of the dissolved organic phosphorus in the sea may follow two courses, (1) turning into orthophosphate

and (2) being absorbed and utilized by living organisms; and the essential feature of the phosphorus cycle would be as in the following diagram.



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NOTE ON THE TECHNIQUE OF MAKING BACTERIA-FREE CULTURES OF MARINE DIATOMS

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There is a great demand for algal cultures in studying morphology, cytology, ecology, cellular pathology and physiology, identification of species, and biotic interaction, and also in feeding small animals in culture for various studies. It is hoped that the following note may be of some use to those who want to start making pure cultures of marine phytoplankton organisms.

Bacteria-free cultures can be obtained directly by washing diatom cells (Chu, 1942; Pringsheim, 1921, 1936, 1937) with frequent change of the medium used for washing. It is, however, advisable to obtain first a flourishing crude unialgal culture, the 'persistent culture' of Allen & Nelson (1910), as a preparatory measure for making bacteria-free cultures. The bacteria-free culture of *Nitzschia closterium* forma *minutissima* used in my experiments (Chu, 1946) was isolated from a subculture from Allen's persistent culture. Diatom cells were first inoculated into the artificial sea water made with pure inorganic chemicals as described below, and cultured in low temperature and high-light intensity. The absence of dissolved organic substance in the medium, the high-light intensity and the low temperature are factors which are very effective in reducing bacterial growth. The cultures were artificially illuminated at night and exposed to bright daylight whenever possible, but not to direct sunlight. They were kept at 10–12° C. by means of running water, and were aerated by compressed air which was filtered through sterilized cotton-wool. Subcultures were made when the rate of multiplication was at its maximum (usually during the third day after inoculation). The inoculum was about half a million cells in each 500 c.c. culture. After several successive subcultures the number of bacteria was greatly reduced. Distinct bacterial growth was still obtained when inoculation from one of the sixth subcultures was made either in nutrient sea-water broth or on nutrient sea-water agar. When a drop from this sixth subculture was examined under oil immersion, however, no bacterium could be detected on the surface of some of the *Nitzschia* cells. Selected single healthy *Nitzschia* cells from this subculture were washed through drops of Berkefeld filtered or artificial sea water, five separate drops being contained in each sterilized Petri dish and a new sterilized micropipette used for each drop. Twenty-five drops were found to be quite sufficient to get rid of the bacteria, each drop containing approximately 0·1 c.c. The micropipettes and the Petri dishes (with well-fitted lids) were sterilized

beforehand, and the sterilized sea water was added before it was used for washing.

The washed diatom cells were then inoculated (five cells on to each agar plate or into each 10 c.c. of liquid media) into the following media:

(1) Artificial sea water (10 c.c. in each of the 150 × 16 mm. pyrex test-tubes. If no bacteria-free cultures could be obtained from the washed diatom cells, more successive subcultures would be made from this culture in order to reduce the bacterial number still further).

(2) Nutrient sea-water broth (consisting of dextrose, sodium acetate, Difco beef extract and peptone, each 0·1 %, in artificial sea water, or Berkefeld-filtered sea water enriched with $NaNO_3$, Na_2HPO_4, $Na_2SiO_3.9H_2O$, and Fe-citrate, 50, 5, 10, and 0·5 parts per million respectively), 10 c.c. in each 150 × 16 mm. Pyrex test-tube.

(3) Sea-water agar (1·5 % agar in artificial sea water with the amounts of nitrate, phosphate, silicate and citrate doubled, or in Berkefeld-filtered natural sea water enriched with $NaNO_3$, Na_2HPO_4, $Na_2SiO_3.9H_2O$, and Fe-citrate, 100, 10, 20, and 1 parts per million respectively).

(4) Nutrient sea-water agar [1·5 % agar in artificial sea water with the amounts of nitrate, phosphate, silicate and citrate doubled (or Berkefeld-filtered natural sea water enriched with $NaNO_3$ 100, Na_2HPO_4 10, $Na_2SiO_3.9H_2O$ 20, and Fe-citrate 1 parts per million) further enriched with dextrose, sodium acetate, Difco beef extract and peptone, each 0·1 %].

Bacterial growth occurred only in one of the five nutrient agar-plate cultures (medium 4), while the other four plate cultures proved to be bacteria-free. There was no bacterial growth in any of the cultures in nutrient broth (medium 2) or on sea-water agar plates (medium 3). When 1 c.c. from a culture in medium 1 (artificial sea water) was inoculated on a nutrient agar plate, no bacterial growth developed. Subcultures were made on nutrient agar slant from each of the cultures which were without evident bacterial growth, and these were then incubated in the dark at room temperature (20–22° C.). All of these except one proved to be bacteria-free. Hereafter one of the sub-cultures inoculated from one of the bacteria-free nutrient agar plates has been subcultured successively in nutrient agar slants.

This nutrient sea-water agar (medium 4) has been proved to be very suitable for keeping bacteria-free cultures of marine diatoms. It is good for bacterial growth, and any contamination will soon become visible from the colonies developed. At the same time it is also good for the growth of marine diatoms. When there is no need for the diatom to grow rapidly, slant cultures, before reaching the maximum growth, may be removed from good illumination to some distance from a north window where the light is not strong (100–200 f.c. for a large part of the day), and subcultures may be made once every 3–6 months. They can also be stored in a large glass jar covered with a cotton pad.

The quality of the nutrient agar differs with the method of preparation. The method used was as follows. 15 g. of the agar fibre (B.D.H.) is put into a

flask, 500 c.c. of tap water added, and the level of the water marked on the flask. The agar is then washed with running tap water for 1 day and with distilled water for another day. After returning the washed agar into the marked flask, the artificial or enriched Berkefeld-filtered natural sea water is added to the mark. This is autoclaved (at 20 lb. pressure for 5 min.) separately with the nutrient solution which consists of

	Parts per million		Parts per million
Dextrose	2000	Na_2HPO_4	7·5
Sodium acetate	2000	$Na_2SiO_3.9H_2O$	15
Peptone	2000	$FeC_6H_5O_7.3H_2O$	0·81
$NaNO_3$	75		

in 500 c.c. of artificial or enriched sea water. When the autoclave is opened after the pressure has dropped to zero, the aqueous agar, while still hot, is decanted and mixed with the nutrient solution. The mixture is poured into sterilized test-tubes or Petri dishes before they cool below 45° C. If contamination is suspected the agar tubes and plates are sterilized in a steamer for 20 min. If the nutrient agar is not prepared satisfactorily and the diatom fails to grow, the agar plates and slants can be improved by being impregnated each with 4 c.c. of clear sterilized soil extract which is poured over the agar surface and is absorbed by the agar.

A small droplet (containing about 50 cells) from the fifth preparatory subculture in artificial sea water was inoculated, without further washing, on the agar surface (medium 3). Besides a large colony of *N. closterium*, which was mixed with bacteria, several small colonies also developed later, some distance apart from the large mass of growth. These small colonies were formed from single cells which had moved away from the mother colony. The bacterial growth in the large colony was not obvious, but when it was subcultured into media 2 and 4, bacterial growth was obtained. Subcultures from two of the small colonies were, however, proved to be bacteria-free. This shows that when the diatom cells moved through the agar, the bacteria on them were pushed off. Thus for motile diatoms this provides another method for obtaining bacteria-free cultures.

Before inoculating on to the nutrient agar, bacterial growth can be further reduced by first inoculating on to the silica gel, which can support good growth of diatoms but not bacteria. It was prepared according to Pringsheim's method (1926, p. 301) by mixing equal volumes of diluted HCl (sp.gr. 1·1) and diluted water-glass (sp.gr. 1·08). These were diluted to the required specific gravity with the help of a hydrometer. The acid-silicate mixture was poured into Petri dishes up to a depth of about 3 mm. The silicic acid formed set as a gel, and when the gel was well hardened the plates were washed, first in running tap water for 2 days or more until free from acid, and then several times in distilled water. The plates were then drained, covered with 5 c.c. of the artificial sea water for 24 hr., put in an oven at 60° C. until the surface was fairly dry, and sterilized in a steamer for an hour.

Five washed diatom cells were inoculated separately on the same silica gel plate, and subcultures made successively from the very edge of the largest colony developed until a culture was obtained which is proved to be bacteria-free when inoculated on to the nutrient agar. Sometimes small colonies were formed apart from the mother colony by single cells moved away from it. More than half of the subcultures inoculated from such small colonies proved to be bacteria-free.

The lids of Petri dishes used for making silica gel and agar plates must fit well in order to avoid contamination from the air. After inoculation the lids are fastened tightly against the dishes with an adhesive paper strip. For the inoculation during the process of making bacteria-free cultures, a micropipette as used for washing is found to be more suitable than a platinum wire, as the former can pick up cells from the margin of the colony with less disturbance to the rest of the colony where bacteria may be abundant. The platinum wire is, however, more convenient for making inoculations from bacteria-free cultures.

The artificial sea water was first used when the author was working in the Marine Station at Millport during 1942. It proved to be satisfactory for the growth of a number of marine diatoms, such as *Asterionella japonica* Cleve & Möller, *Biddulphia mobiliensis* (Bail.) Grun, *Chaetoceros didymus* Ehr., *Coscinodiscus excentricus* Ehr., *Ditylium Brightwelli* (West) Grun, *Fragilaria striatula* Lyngb., *Nitzschia seriata* Cleve, *Rhizosolenia alata* Brightw., *Streptotheca thamensis* Shrubs., and *Thalassiothrix longissima* Cleve & Grun. Its composition is largely based on the combination of ions in sea water as suggested by Lyman & Fleming (1940) and Thompson & Robinson (1932).

Artificial sea water

	Parts per million		Parts per million
NaCl	23,477	$Na_2SiO_3.9H_2O$	10
$MgCl_2$	4,981	$Al_2(SO_4)_3$	3
Na_2SO_4	3,917	$BaCl_2.2H_2O$	0·09
$CaCl_2$	1,102	$RbHCO_3$	0·34
KCl	664	$MnCl_2$	0·2
$NaHCO_3$	192	$LiNO_3$	1
KBr	96	$FeC_6H_5O_7.3H_2O$	0·54
H_3BO_3	26	$CuSO_4.5H_2O$	0·4
$SrCl_2$	24	KI	0·06
NaF	3	As_2O_3	0·03
$NaNO_3$	50	$ZnSO_4.7H_2O$	0·01
Na_2HPO_4	5		

The last eleven chemicals listed above, were often dissolved in the following minor elements solution, 1 c.c. of which was added to 1 l. of the artificial sea water:

Minor elements solution

	Parts per million		Parts per million
$Na_2SiO_3.9H_2O$	10,000	$FeC_6H_5O_7.3H_2O$	540
$Al_2(SO_4)_3$	3,000	$CuSO_4.5H_2O$	400
$MnCl_2$	200	KI	60
$BaCl_2.2H_2O$	90	As_2O_3	30
$RbHCO_3$	340	$ZnSO_4.7H_2O$	10
$LiNO_3$	1,000		

Variation of the concentration of any of the major constituents over a certain range makes no important difference to the growth in this medium. The concentrations of nitrate and phosphate are those within the range supporting optimum growth of the marine diatoms studied, but well below the concentrations which have definite prohibiting effects on the growth. Good growth has been obtained by adding a little *Laminaria* ash, and omitting the last ten salts. A piece of *Laminaria* frond is first ashed, and then dissolved in weak HCl and neutralized with NaOH before use.

Another medium, which proved to be very helpful in obtaining crude but flourishing unialgal cultures, was used in the early stages of making the bacteria-free culture of *Nitzschia seriata* Cleve. It consists of a layer of baked sea-mud powder which is covered by a layer of natural sea water, or the above artificial sea water, in test-tubes of convenient size with a capacity of about 25 c.c. The idea was derived from the works of Jacobsen (1910) and Pringsheim (1921 and later works), who succeeded in obtaining subcultures in soil and water. The bottom mud collected from Plymouth Sound was dried, pulverized, wrapped in a layer of linen or filter paper (preferably Whatman No. 541), about $1\frac{1}{2}$ in. in length, fitted into the bottom of test-tubes which were then plugged with cotton-wool and sterilized in an electric oven at 120° C. for half an hour. Then the sterilized natural or artificial sea water was poured into the tubes up to about $1\frac{1}{2}$ in. over the mud powder block. The whole preparation, pulverized dry mud covered with liquid in cotton-wool-plugged test-tubes, can also be sterilized at once by autoclaving at 15 lb. pressure for half an hour, or by steaming in a steamer for 3 or 4 hr. If unialgal culture only is ultimately required, but not a bacteria-free culture, the steaming sterilization is preferable, as it sometimes results in a better growth for certain organisms. A crushed grain of wheat or barley put into the mud sometimes improves the growth. If too much acid comes into solution from the mud, the addition of a little lime or calcium carbonate into the mud block is advisable. This mud solution can be used for culture the day after it is sterilized. It often provides a good growth for starting the process of making bacteria-free cultures.

It is important that the inoculum into this mud solution should contain no other alga than the one required. Single diatom cells can easily be isolated from a fresh sample collected from the sea, free from other organisms except bacteria, by the washing method described above. Washing through only ten drops of water is often enough for this purpose. It is advisable to make several such crude cultures, some inoculated with only a single washed cell, while a few others with five or more washed cells, in case some of the washed cells may fail to multiply or some of the mud solution preparations may contain something inhibiting growth. The selected cells for isolation must be healthy. The size of the chromatophore and the intensity of its colour can be of great help in judging the healthiness of diatom cells.

This method is found to be one of the safest to get the alga required

from the sea into culture. From this mud solution culture, a large inoculum, about 50 or more cells per 10 c.c. of medium, can be sown into the artificial sea water, and then one can proceed to make bacteria-free cultures as described above for *N. closterium* forma *minutissima*.

Both isolation of single cells and inoculation of subcultures can be carried out in a convenient isolating chamber (Chu, 1942) within which a suitable flame is available. The following device, however, has also been used and proved to be convenient and effective in avoiding contamination during the processes of making subcultures, as well as inoculating culture series in experiments and taking samples from them for examination. The apparatus used consists of a basin containing hot water which is heated either on a hot plate or by inserting an electric heater into the water; a Bunsen burner fixed on the edge of the basin, and provisions to hold the pipette, and cotton-wool plugs if required, over the hot water. As the cotton-wool plug is removed from the culture flask or tube, its neck is passed into the Bunsen flame. When a portion of the culture is being taken from or added to the flask or tube, it is held over the steam bath. The sterilized pipette used is suspended over the steam bath throughout the operation. When samples are removed from the flask to sample tubes, the latter are placed in a container which is put into the steam bath. Hence throughout every phase of the operation the apparatus and samples are protected from infection by the rising steam. The method is easy and simple, and yet very convenient and effective; it could be used in any laboratory.

As mentioned before, the absence of organic matter in the artificial sea water, strong illumination and low temperature are the effective factors in reducing the bacterial growth in the preparatory cultures. When artificial illumination is used, the electric light should pass through a screen of cold water before reaching the cultures (Chu, 1942) in order to eliminate the heat effect and reduce the infra-red radiation. A 1000 W. lamp is to be recommended (though a 500 W. lamp will also serve the purpose), and the cultures could be hung just outside and about 1 in. apart from the bell jar holding the water where a light intensity of no less than 30,000 metre-candles can be obtained. The temperature should be as low as conveniently possible. A low temperature of 8° C. was found to be more satisfactory than higher temperatures. The rate of multiplication of bacteria decreases with decreasing temperature in this region, but low temperature was found to have no unfavourable effect on the growth of diatoms.

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THE ESTIMATION IN SEA-WATER SOLUTIONS OF MICRO-QUANTITIES OF MERCURY IN THE PRESENCE OF COPPER BY MEANS OF DITHIZONE

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Introduction

With the development of leaching methods (Ketchum, Ferry, Redfield & Burns, 1945; Harris, 1945) for the study of anti-fouling compositions and the increased interest in the toxicity of copper and mercury to marine organisms, it has become desirable to have a moderately rapid method for the estimation of mercury in the presence of copper ions. Frequently, in these solutions, the copper is in large excess; commonly, leachates contain from 300 to 900 μg. of copper and up to 50 μg. of mercury per litre of sea water. Mercury in the absence of copper may be readily estimated in these concentrations by the use of dithizone, and the tentative curves of Wichmann (1939) suggest that it is completely extracted even at *p*H 2·0. However, according to these curves copper is also partially extracted at this acidity. The two most recent methods for the determination of mercury by dithizone in the presence of copper are those of Laug & Nelson (1942) and Reith & van Dijk (see Sandell, 1944). The former workers separate the mercury from the copper by shaking an acid potassium bromide solution with the mixed dithizonates. The mercury is thereby transferred to the aqueous phase and is determined by a mixed colour method after bringing the *p*H of solution to 6·0. The method of Reith & van Dijk is much longer and involves regulated extraction of the mixed dithizonates. In addition, Hubbard (1940) has separated the two metals with a dithizone technique by shaking the combined dithizonates with sodium thiosulphate solution; the mercury is transferred to the aqueous phase and after destruction of the thiosulphate with permanganate and of the latter with hydroxylamine, the mercury may be estimated in the aqueous layer. The method outlined below is simpler; it depends upon the slow rate of reaction of a *chloroform* solution of dithizone with copper and the complex forming action of potassium cobalticyanide with copper salts.

General

The mixed colour method has been used, transmittancies being determined with the Spekker Photoelectric Absorptiometer using blue-green filters (Ilford 603) and a 1 cm. cell.

The experimental work has been carried out in a darkened room and all transmittancy measurements made as rapidly as possible after extraction. This precaution is particularly necessary when working with mercury solutions, for the decomposition of the mercury dithizonate seems to be catalysed by the presence of small traces of copper salts. The instrument is usually set at 0·700 against pure chloroform; the differences between the drum reading for the dithizone blank and the unknown is, over the range used, directly proportional to the mercury content of the solution. Such a procedure is more reliable when working over long periods (since the instrument may be reset for each reading of the unknown) than the alternative of setting the instrument against the dithizone blank at the beginning of the series and leaving it so set. Using the strength of dithizone and volumes given below, 10 μg. of mercury per litre corresponds approximately to a difference in the drum reading of 0·025. Assuming that the drum may be read in the lower regions to 0·003 (one-quarter of a division) the accuracy of the method cannot be greater than $\pm$ 1–2 μg. of mercury per litre. When using the Spekker Absorptiometer it has been the practice to set the instrument and then rapidly take an approximate reading of the unknown. The instrument is then reset and, with the shutter closed, the drum is moved into the previous position. The unknown is now placed in position and the final adjustment of the drum made rapidly. All these precautions are necessary when working with concentrations indicated, i.e. 5–50 μg. of mercury per litre. With the method outlined below manipulative losses are, however, negligible. A working curve is constructed using mercuric chloride in sea water.

Concentrations are expressed throughout in μg. or mg. per litre of solution finally extracted.

It must be stated that strict adherence to the volumes indicated is essential, i.e. 100 ml. solution and 10 ml. dithizone. The amount of mercury present in the 100 ml. of solution actually extracted is 1–10 μg.

The sea water was freshly collected for each day's work, and filtered before use.

Reagents

Nitric acid—A.R. 25 % v/v.

Hydroxylamine hydrochloride—A.R. 4 % aqueous solution.

Dithizone—this is purified by repeated extraction with ammonia (see Sandell, 1944). The stock solution (1 g./l.) is stored in a refrigerator and is diluted 40–50 times just before use, giving a final strength of approximately 20 mg./l.

Chloroform—B.P. grade.

Potassium cobalticyanide—freshly prepared solution containing 10 g. per 100 ml. distilled water.

The Stability of Dithizone in Chloroform Solution

In view of the difficulties experienced by some workers, the stability of the reagent during long runs of mercury determinations in sea-water solutions

has been checked. In many months' work no significant trouble has been experienced when using the conditions outlined above. Thus in fifty determinations taken at random from a fortnight's work, some taken morning and afternoon with the same solution, some being blanks and others from solutions containing copper and mercury both together and alone, the determinations being carried out in triplicate or duplicate (and in part by two observers), the variation in Spekker reading of replicates was equivalent in three instances to 2 μg. mercury per litre and in the remainder to 1·0 μg. mercury per litre. The *p*H of the extracted solutions varied from 1·56 to 4·87 (glass electrode). No change was found in the strength of dithizone taken direct from the burette during a morning's work.

The Rate of Extraction of Copper by Dithizone Solutions

Wichmann's tentative curves (1939) suggest that copper is not completely extracted until a *p*H of 5·0 is reached. Greenleaf (1942) has pointed out that copper is more difficult to extract at *p*H 2·0 with dithizone (carbon tetrachloride solution) than other metals, and that the amount of copper extracted is related to the amount of dithizone in excess; extraction was complete with no excess dithizone at *p*H 2·0 and almost complete at *p*H 1·0 with 100 % excess dithizone. Laug & Nelson (1942) also noticed that copper is extracted only slowly by chloroform solutions of dithizone at *p*H 1·0. Sandell (1937) states that using carbon tetrachloride solutions of dithizone the extraction of copper (3–20 μg.) is complete with 30–40 sec. vigorous shaking. However, using a working curve of pure copper sulphate the results were low.

It would appear from the foregoing that copper is much more rapidly removed as dithizonate when a carbon tetrachloride solution of the reagent is used. The use of chloroform solutions in an attempt to eliminate the interference in the extraction of mercury seemed, therefore, to be more promising.

That the rate of extraction of copper by chloroform solutions of dithizone is slow, even when large amounts of copper are present, is indicated by Table I. In all these experiments the volumes of sea water and reagents used were

Table I

Sea-water solution at *p*H 1·43 ± 0·05. Total volume extracted 100 ml.

Time of shaking in min.	Spekker reading		
	3 mg. Cu/l.	6 mg. Cu/l.	15 mg. Cu/l.
1	0·418	0·410	0·350
2	0·402	0·357	0·293
4	0·355	0·345	0·227
10	0·297	0·210	0·077
15	0·247	—	—
25	0·158	—	—

similar to those when working with a solution containing 0–50 μg. mercury per litre final concentration. The procedure was as follows. Sufficient nitric acid was added to the copper solution in sea water, contained in a 250 ml. separating

funnel to bring the *p*H to the required value when the volume was made up to 100 ml. 1 ml. of 4 % hydroxylamine hydrochloride was then added and the solution shaken. 10 ml. of dithizone were added and the funnel shaken for a given time. After allowing the two layers to separate and inserting a roll of filter paper in the stem of the funnel, sufficient of the chloroform layer was run off to fill a 1 cm. cell and the transmittancy of the solution measured. The *p*H of the aqueous layer was then measured using the glass electrode.

In the above experiments the dithizone was clearly not in excess (it has been suggested that the formula for the dithizonate is $CuDz_2$, so that 30 μg. of dithizone are equivalent to about 3·7 μg. of copper). In the above, approximately 200 μg. of dithizone were present. However, even with excess dithizone and a higher *p*H value the copper is still extracted comparatively slowly by chloroform solutions of the reagent as is indicated by Table II.

TABLE II

Sea-water solution at *p*H 4·20 ± 0·09. Total volume extracted 100 ml. 7·5 μg. copper present per litre.

Time of shaking (min.)	Spekker reading
1	0·360
4	0·217
10	0·206
15	0·200

Table I indicates that even with 300 μg. of copper present and shaking for 1 min. the equivalent of only 1 μg. of mercury (assuming all the mercury to be taken up) would be extracted. The rate of extraction of copper with chloroform solutions is in marked contrast to that for carbon tetrachloride solutions of the reagent. The figures of Table III indicate the much more rapid rate of extraction even at comparatively low copper concentrations and low *p*H values.

TABLE III

Sea-water solution—dithizone in carbon tetrachloride. Total volume extracted, 100 ml.

Time of shaking min.	Spekker reading		
	*p*H 1·16		*p*H 2·80
	52 μg. Cu/l.	25 μg. Cu/l.	26 μg. Cu/l.
1	0·410	0·465	0·445
2	0·396	0·440	0·436
5	0·378	0·440	0·440

THE RATE OF EXTRACTION OF MERCURY

Before proceeding further it was established that shaking for 1 min. was adequate to ensure 'complete' extraction of the mercury. (By 'complete', nothing is assumed with regard to completion of mercury-dithizone reaction but only that equilibrium has been attained under the specific conditions.)

Using the above procedure the results given in Table IV were obtained, indicating that a shaking time of 1 min. is adequate.

TABLE IV

Sea-water solution. Total volume extracted 100 ml. 55 μg. mercury/l.

Time of shaking min.	Spekker reading		
		*p*H 1·20 ± 0·02	
	*p*H 1·42 ± 0·02	(*a*)	(*b*)
1	—	0·354	0·353
2	0·353	0·352	0·354
4	0·350	—	—
10	0·350	0·352	0·360

THE INTERFERENCE OF COPPER IN THE ESTIMATION OF MERCURY

The tentative curves of Wichmann suggest that the *p*H in the estimation of mercury should not be reduced below 1·0. Since the mercury can be extracted by 1 min. shaking at *p*H 1·2 (see above) the interference due to moderate amounts of copper was next investigated. With the procedure outlined the results shown in Table V were obtained.

TABLE V

Sea-water solution at *p*H 1·2. Total volume extracted 100 ml. 55 μg. mercury/l.

Copper added μg./l.	Mercury found μg./l.	Error (positive) μg./l.
0	55	0
290	55	0
570	58	3
860	58	3
1150	62	7
2300	63	8
6900	90	35

That the extent of this interference depends in some measure on the strength of the dithizone and possibly on the relative amounts of copper and mercury present is shown by the figures of Table VI, which were obtained using dithizone one-fifth the usual strength and only 11 μg. of mercury per litre.

TABLE VI

Sea-water solution at *p*H 1·20. Total volume extracted 100 ml. 11 μg. mercury/l.

Copper added μg./l.	Mercury found μg./l.	Error (positive) μg./l.
0	11	0
290	14	3
570	15	4
860	17	6
1150	17	6
2300	24	13
3450	29	18

It is clear that the interference with moderate amounts of copper is small and somewhat irregular.

The Cobalticyanide Method

The interference due to copper may, then, be reduced by the reduction in time of shaking and the acidity. Elimination of the residual interference would seem possible by a reduction in the copper concentration by means of a complex forming substance—stable in acid solution. Potassium cobalticyanide appears to fulfil these conditions and the following technique has proved satisfactory.

Procedure

To 92[1] ml. of the solution contained in a 250 ml. separating funnel add 2 ml. of nitric acid. After shaking add 1 ml. of hydroxylamine hydrochloride solution and repeat the shaking. Add 5 ml. of cobalticyanide solution, shake and allow to stand 10 min. Add 10 ml. of dithizone solution and shake for 1 min. at approximately four shakes per second. After the chloroform layer has settled, insert a roll of filter paper in the stem of the funnel, draw off the required volume of chloroform into a 1 cm. cell and determine its transmittancy immediately.

Results

The results of a series of mercury determinations in the presence of varying amounts of copper are shown in Table VII.

Table VII

Total volume extracted 100 ml. Concentration in μg./l.

Cu present mg./l.	1·0 Cu	5·0 Cu	5·0 Cu	6·9 Cu
Hg present μg./l.	22 Hg	11 Hg	55 Hg	55 Hg
Found Hg	22	11	53	55
	22	11	56	56
	22	12	55	55
	21	12	55	55
	22	10	—	55
	22	10	—	56
	24	—	—	—

Table VIII gives the results of the analysis of a series of solutions prepared by an independent worker, the copper and mercury contents being unknown to the analyst.

It should be noted that above about 1 mg. of copper per litre of solution the addition of the cobalticyanide produces a precipitate; this does not affect the estimation except in so far as it necessitates careful drawing off of the chloroform layer after the dithizone extraction. Occasionally a rather high return has been obtained when working at 1·0 mg./l. of copper, and this may be attributed to the difficulty of separating the small amount of precipitate

[1] This volume was chosen from a consideration of the intended application: the effect of changes in volumes of solution and dithizone on the method has not yet been studied.

TABLE VIII

Total volume extracted 100 ml. Concentration in μg./l.

Cu present	Hg present	Hg found
1150	47	48
3450	99	99
6900	71	71
0	99	98
6900	25	24
4600	47	47
500	33	34
500	88	89
1000	59	62

formed under these conditions. In one run when this was experienced, a further addition of 500 μg. was made to an aliquot portion *after* the addition of the cobalticyanide so that a distinct precipitate was then produced; the positive error was then eliminated.

It need hardly be emphasized that dithizone technique requires care and experience. The results quoted above were obtained after considerable experience and continuous work on the present method. However, using the method as outlined above, the results shown in Table IX were obtained by an analyst without previous experience of the procedure.

TABLE IX[1]

Sea-water solution at *p*H 1·20. Total volume extracted, 100 ml. Concentrations in μg./l.

Hg present	Cu present	Hg found	Error
11	0	10	−1
30	1250	31	+1
36	5000	32	−4
41	1250	42	−1
50	310	49	−1
52	3000	50	−2
60	940	60	0
65	6300	65	0
74	630	72	−2
88	3750	87	−1
91	1000	89	−2
103	930	105	+2

[1] Acknowledgement is made to Dr Stubbings of the Metallurgical Laboratory, Emsworth, in whose department the results quoted in the table were obtained.

THE ESTIMATION OF COPPER AND MERCURY

It may, on occasions, be desirable to determine the copper and mercury in the same solution, and the method given below may then be used.

Reagents

As for the mercury estimation with the following additions:

Citric acid—25 % w/v in distilled water.

Ammonium hydroxide—(A.R.) sp.gr. 0·880.

Sodium diethyldithiocarbamate—0·1 % filtered aqueous solution.

Procedure

The mercury is first estimated after the addition of cobalticyanide, as already described.

Draw off all the remainder of the chloroform-dithizone layer after the mercury estimation. (Any interfacial scum should be left.) Add 5 ml. chloroform and shake for 15 sec. to remove any remaining dithizone. Allow the solution to stand for some time, during which the contents of the funnel should be gently swirled at intervals to collect together the drops of chloroform adherent to the sides of the funnel. Run off the chloroform layer and discard. Add to the contents of the funnel successively 5 ml. citric acid, 2 ml. ammonium hydroxide and 10 ml. of carbamate, shaking between each addition. Allow to stand 5–10 min. and then add 10 ml. chloroform (up to 0·5 mg. of copper per litre) or 20 ml. of chloroform (up to 1·0 mg. of copper per litre). Shake for 2 min., allow to settle and run off the required amount of chloroform layer into a 1 cm. cell. Measure the transmittancy with the Spekker set at 1·00 against pure chloroform. Violet filters (Ilford 601) are used.

Discussion

The method clearly depends on the inability of the added cobalticyanide to prevent the formation of the yellow complex with the copper reagent when the solution is made alkaline. That complete recovery of the copper was obtained in the presence of cobalticyanide after the addition of ammonia was shown by adding these reagents to solutions of copper sulphate whose copper content had already been determined by the carbamate method; the results are shown in Table X (appropriate 'blank' corrections have been made).

Table X

Total volume extracted 100 ml. Concentrations in μg./l.

Cu present, by carbamate method	Cu found after cobalticyanide-ammonia
124	124
248	250
620	630

Table XI

Total volume extracted 100 ml. Concentrations in μg./l.

Copper		Mercury	
Present	Found	Present	Found
500	510	33	34
320	320	99	99
155	143	55	57
670	675	88	Not determined
820	810	22	
995	990	66	

A working curve must be constructed for the 10 ml. and the 20 ml. volumes of chloroform. The copper solution for this must be taken through the whole procedure, otherwise a considerable error will arise due to the solubility of chloroform in water, for the final extraction is made from a solution saturated with respect to chloroform by the additions involved in the first part of the estimation (mercury). If this is not done an error of some 4% will be incurred.

Using this combined method, mixtures of copper and mercury were analysed, the amounts present being unknown to the analyst, with the results shown in Table XI.

The author is indebted to the Marine Corrosion Sub-Committee of the Iron and Steel Institute for permission to publish this work and to Professor J. E. Harris for his interest in it.

SUMMARY

1. A brief survey is given of the methods for the estimation of mercury by means of dithizone.

2. The precautions necessary in mercury estimations are outlined and the stability of dithizone in chloroform solutions shown to be satisfactory.

3. Data are presented on the rate of extraction of copper, from sea-water solutions, at low *p*H values with chloroform and carbon tetrachloride solutions of the reagent. Using the former solvent the rate of extraction of copper is shown to be slow, while mercury is rapidly extracted under the same conditions.

4. The use of potassium cobalticyanide in combination with a chloroform solution of dithizone has enabled a method to be developed which eliminates interference of copper in mercury estimations; with the procedure given, mercury in concentrations of 1 to 55μg/l. may be determined in the presence of copper concentrations up to 6·9 mg./l.

5. Copper may be determined in the same solution subsequent to the mercury estimation by the use of sodium diethyldithiocarbamate, after the solution has been made alkaline with ammonium hydroxide.

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THE GENITAL DUCTS OF *THEODOXUS*, *LAMELLARIA* AND *TRIVIA*, AND A DISCUSSION ON THEIR EVOLUTION IN THE PROSOBRANCHS

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(Text-figs. 1–7)

CONTENTS

INTRODUCTION

The prosobranchiate gastropods are divided into three orders, the Archaeogastropoda, the Mesogastropoda and the Stenoglossa. In the first of these groups the gonad is connected with the right kidney by a duct which is developed from the ovary, and the sex cells escape to the posterior end of the mantle cavity through the right ureter. The eggs are usually shed singly into the sea where fertilization occurs. In the Mesogastropoda and Stenoglossa the right kidney is not developed and the ovarian duct leads to a short and

narrow section of the genital duct which is typically ciliated, and may communicate with the pericardium by a gonopericardial duct and passes anteriorly to a long glandular tract running forwards to the mouth of the mantle cavity. This glandular section is incipient in the archaeogastropod *Calliostoma zizyphinum*. It is probably formed, as Thiele (1935) suggests, by an ectodermal intucking and will be referred to as the *pallial oviduct*, for it lies anterior to the opening of the original right kidney, and must be derived from the ectoderm of the mantle (Bourne, 1908; Giese, 1915). The short duct which links it with the ovarian duct will be termed the *renal oviduct*: in *Paludina* (= *Viviparus*), in which its development has been investigated (Drummond, 1903), it is formed from the vestige of the right kidney, and even in the highly specialized Stenoglossa it retains the connexion with the pericardium which is characteristic of the right and left kidneys of the archaeogastropods. Similarly, in the male system of the Mesogastropoda and Stenoglossa there can be distinguished a testis duct, which is connected to the posterior end of the mantle cavity by a *renal vas deferens*, and this in turn is followed by a *pallial vas deferens*.

The Neritacea, although grouped among the archaeogastropods, resemble the mesogastropods in the loss of the right kidney and in the development of a pallial oviduct and vas deferens. They also approach this group in that they produce egg capsules within which the young are nourished until they escape as a crawling form resembling the parent.

THEODOXUS FLUVIATILIS (L.)

The male

From the testis, which spreads over the surface of the digestive gland, the testis duct takes a sinuous course along the right side of the visceral mass to the posterior end of the mantle cavity. Except for its initial part this duct contains sperm and acts as a vesicula seminalis, which is much dilated in the coils overlying the posterior end of the prostate. The testis duct is continued into a much narrower ciliated conducting tube—homologous with the renal vas deferens of mesogastropods—which leads forwards beneath the posterior end of the prostate and up its left side to open into the lumen of the gland. The renal vas deferens is heavily loaded with black pigment granules contained in the ciliated cells, and is surrounded by a coat of circular muscles which constrict the lumen except at times when sperm are passed through it. The wall of the distended vesicula seminalis is grey, since its epithelium also contains black pigment granules, though the cells are not ciliated.

The lumen of the prostate is, except at the two ends, U-shaped in transverse section because of a downgrowth from the dorsal wall. Its walls are ciliated throughout, and between the ciliated cells lie gland cells and the ducts of subepithelial glands. There are two principal masses of these subepithelial secreting cells, the more posterior—the 'glande annexe' of Lenssen (1899)—

appearing as a pinkish mass in dissection and consisting of blind tubules. Some of these underlie the vesicula seminalis and open into the posterior wall of the prostate, whilst others spread forwards dorsally between the two limbs of the gutter-shaped lumen and around the left wall to open at the summit of the left limb. The vas deferens penetrates this mass, and its opening into the left wall, also near the summit of the left limb, is surrounded by the openings of these tubules. Where the opening occurs the cavity is slightly enlarged, and this region is referred to by Bourne (1908) as the thalamus—it comprises a larger chamber in other Neritidae. The glands which open into it Bourne terms the prostate, though it seems better to include all the glands opening into the lower or pallial part of the male duct under this name. The histology of the posterior mass is uniform throughout, the tubules being lined by large secreting cells, alternating with wedge-shaped ciliated cells. In the secreting cells the nuclei are round, basal and with a nucleolus, and in the vacuoles of the protoplasm are large spherules which in the fully elaborated state stain rather deeply with iron haematoxylin.

The second large subepithelial glandular mass comprising the prostate fills the gap between the limbs of the gutter anteriorly, projecting downwards as a ridge to invaginate the dorsal wall, though the ridge is free behind and not attached to the concave posterior wall of the duct. About half-way along the length of the prostate this gland ends against the left wall. The cells of which it is composed are filled with small spherules of secretion, protein in nature, and form an opaque white mass in the living tissue. The nuclei are basal, round and nucleolated.

A longitudinal strip of mucous cells, for the most part alternating with ciliated cells, runs parallel with the central glandular area and lines the dorsal edge of the gutter-shaped duct on each side. The wall along the dorsal edge is thrown into slight longitudinal folds, and it is between the folds on the left side that the vas deferens and tubules of the posterior gland open. Ventral to each mucous strip on the outer side is a second longitudinal tract of glands similar histologically to those of the central ridge; posteriorly the two tracts meet one another along the ventral wall. Some of the glands are subepithelial, others lie between the ciliated cells. Otherwise the ventral wall is composed of a simple columnar ciliated epithelieum with mucous cells.

Anteriorly the genital duct is gradually reduced in size and rotates through an angle of 90°, so that the ventral concave wall lies to the right, the left edge of the gutter becomes ventral and the right dorsal. The tracts of gland cells filled with protein spherules dwindle and are replaced by mucous cells. Towards the genital aperture, which lies in front of the anus and within the mantle cavity, the lumen of the duct is no longer crescentic in transverse section, but approximately rounded, and the wall has longitudinal folds.

Median to the base of the right tentacle and beneath the anterior edge of the mantle arises the penis which is dorso-ventrally flattened, stout proximally and tapering distally; a deep seminal groove lined by cuticularized epithelium

runs up the outer edge to the tip. The genital aperture is close to the origin of the groove, and in the intervening space there is a pronounced gutter in the overlying mantle. This is lined by mucous cells alternating with ciliated cells which produce a strong forward current and presumably direct the seminal fluid on to the penial groove.

The female

The anus (Fig. 1A, *a*) and oviduct (*oa*) open at the tip of a papilla near the mouth of the mantle cavity on the right side; ventrally and subterminally is the opening of the vagina (*va*). The vagina (*v*) is entirely separate from the oviduct and runs parallel with it and with the rectum (*rm*) along the right side of the mantle cavity. Posteriorly it leads into the bursa copulatrix (*b*), whilst from its right wall arises a receptaculum seminis (*re*) which passes back ventral to the bursa to the limit of the mantle cavity. Not far from its origin the receptaculum gives off a duct (*dr*) which is at first narrow and coiled and then, before opening into the posterior end of the glandular oviduct, broadens into a small vestibule (*ve*). Except for the complete separation of the vagina from the oviduct the female system agrees in its general outlay with that of the mesogastropods—a proximal ovarian duct, with an epithelium resembling that of the ovary, is followed by a narrow thin-walled section—presumably a renal oviduct—which, in turn, leads into a wide glandular pallial oviduct, and into the inner end of this opens a receptaculum seminis. Moreover, as in the mesogastropods, the glandular section, which occupies the length of the mantle cavity, comprises an albumen gland followed by a bilobed capsule gland.

The ovarian duct runs forward from the ovary and passes for a short distance beneath the capsule gland where it joins the narrow, thin-walled, ciliated duct, which leads back to open into the albumen gland. The albumen gland is divided into dorsal (Fig. 1A and B, *d*) and ventral (*av*) lobes, the ventral one forming a small pouch partly embedded in the posterior tip of the right lobe of the capsule gland (*r*). Near the anterior end of this pouch the thin-walled oviduct opens ventrally (Fig. 1B, *o*), and not far from this opening in a dorso-lateral position is a narrow communication with the much larger dorsal lobe of the albumen gland (*vd*). This lobe lies immediately above the ventral one, extending considerably farther forwards, and opens along its length into the capsule gland. At its posterior end the dorsal lobe is C-shaped in transverse section—the ventral wall overlying the right lobe of the capsule gland, and the concavity resting against the dorso-lateral wall of the ventral pouch of the albumen gland. The dorsal wall is at first separated from the left lobe of the capsule gland by a thin sheet of tissue, a forward extension of the posterior wall of the pallial oviduct (Fig. 1A and B, *p*); anteriorly, however, it spreads across to fuse with this lobe, and appears in dissection as the most prominent part of the gland—a yellowish and rather transparent mass which opens ventrally into the capsule gland. Near the anterior end of the albumen

gland the dorsal edges of the two lobes of the capsule gland, which have so far been separated from one another, approach and fuse, causing the lumen of the oviduct to be abruptly constricted at this point (Fig. 1 C).

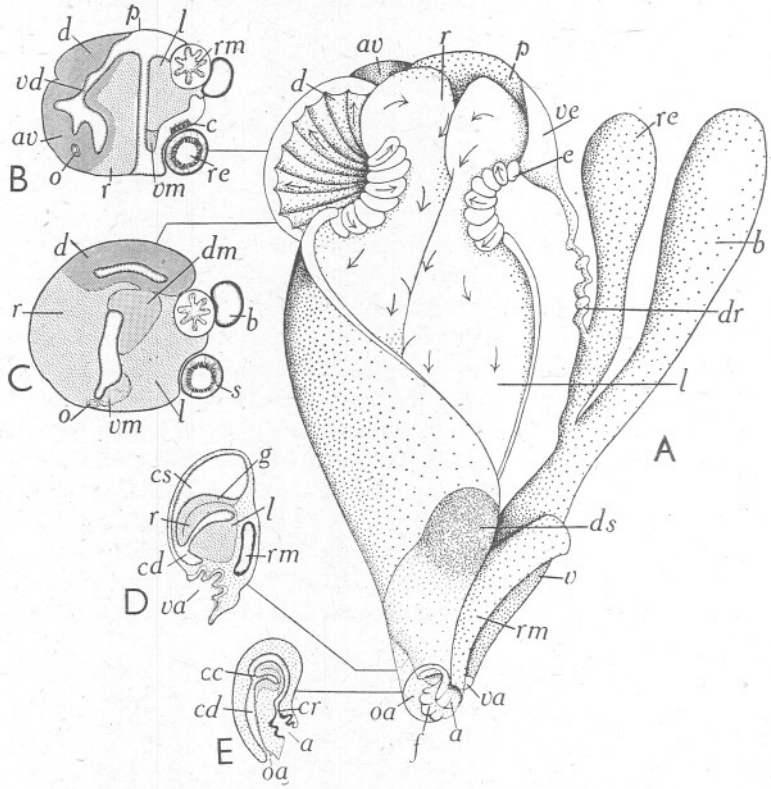

Fig. 1. *Theodoxus fluviatilis*. A, pallial oviduct seen from the dorsal surface, posterior end above. The bursa copulatrix and receptaculum seminis have been dissected away from the glandular oviduct, the dorsal lobe of the albumen gland opened by an incision along its right wall and the two lobes of the capsule gland separated mid-dorsally. Arrows indicate ciliary currents. ×43. B, C, D, E, transverse sections taken at the levels indicated. The bursa copulatrix and spermotheca are in their natural positions. ×30. *a*, anus; *av*, ventral lobe of albumen gland; *b*, bursa copulatrix; *c*, strip of tall columnar ciliated cells; *cc*, opening of crystal sac into capsule duct; *cd*, capsule duct; *cr*, opening of crystal sac into rectum; *cs*, crystal sac; *d*, dorsal lobe of albumen gland; *dm*, dorsal longitudinal strip of mucoid cells; *dr*, duct of receptaculum seminis; *ds*, diatoms and sand grains in posterior end of crystal sac; *e*, strip of glandular and ciliated epithelium spreading ventrally from albumen gland; *f*, flap of tissue acting as valve; *g*, glandular ventral wall of crystal sac; *l*, left lobe of capsule gland becoming ventral anteriorly; *o*, renal oviduct; *oa*, opening of pallial oviduct; *p*, posterior wall of pallial oviduct; *r*, right lobe of capsule gland becoming dorsal anteriorly; *re*, receptaculum seminis; *rm*, rectum; *s*, orientated sperm; *v*, vagina; *va*, vaginal aperture; *vd*, opening of ventral into dorsal lobe of albumen gland; *ve*, vestibule; *vm*, ventral longitudinal strip of mucoid cells.

The ventral pouch of the albumen gland is strongly ciliated. The epithelial cells are separated by ducts of subepithelial glands. These are unicellular,

grouped in clusters lying at various depths, and bound together by a tenuous layer of connective tissue; from each cluster the ducts run parallel with one another to open into the lumen. Except for the dorsal wall the secreting cells of the pouch are of one type, their secretion spherules are small, stain lightly with iron haematoxylin and blue with azan, though they are unaffected by mucicarmine. Along the dorsal wall and surrounding the opening into the dorsal pouch is a strip of mucous cells, some lying within the epithelium. Around the periphery of this strip are a few cells in which the secretion appears bright yellow after the azan stain.

The epithelium of the dorsal pouch is also ciliated, though the cilia are short. Histologically this part of the gland is divisible into three regions. The largest comprises the dorsal wall in which each group of subepithelial glands contains mucoid cells alternating with cells filled with minute secretion droplets of a protein nature which stain deeply with iron haematoxylin. Along the right wall is a longitudinal band of mucous cells which is in contact posteriorly with the mucous strip of the ventral pouch through which the two parts of the gland communicate. The third histologically differentiated region consists of subepithelial and epithelial mucoid cells which, together with strongly ciliated cells, form the wall overlying the left lobe of the capsule gland. The ciliated and glandular epithelium spreads ventrally down this lobe (Fig. 1 A, *e*), and together with a similar area on the opposite lobe is responsible for directing the contents of the albumen gland into the capsule gland.

The posterior wall of the pallial oviduct (*p*), thin and somewhat muscular, encloses a small pouch, the 'poche de confluence' of Lenssen (1899). Into this on the left side opens the duct from the receptaculum (*dr*), on the right the posterior end of the dorsal lobe of the albumen gland, whilst anteriorly it communicates with the capsule gland. Eggs passed from the ovarian duct and embedded in albumen from the albumen gland are directed into the posterior end of the pallial oviduct, and here they are fertilized. On the ventral wall of the vestibule (*ve*) which terminates the duct from the receptaculum is a strip of tall columnar ciliated cells (Fig. 1 B, *c*) which is continued along the ventral wall of the 'poche de confluence' and up the median side of the right lobe of the capsule gland towards the albumen gland. To the opening of this gland the cilia direct the sperm. The tip of the left lobe of the capsule gland (*l*) overlies the opening of the vestibule into the oviduct, and its posterior and ventral edges are free to act as a valve which can regulate the flow of seminal fluid.

From its point of constriction at the anterior end of the albumen gland the lumen of the capsule gland gradually deepens as it passes forwards, and becomes crescentic in transverse section, with the concave inner surface of the right lobe (*r*) enveloping the convex inner surface of the left (*l*). The two lobes are separated dorsally and ventrally by a narrow strip of wall almost without glands. Anteriorly the lobes taper so that the lumen narrows again and the whole gland rotates through 45°, the original right lobe becoming dorsal, the

left ventral, and the intervening strips lateral. They both extend to the genital aperture near which the dorsal one is very thin (Fig. 1 D, *r*).

The capsule gland is lined by a columnar ciliated epithelium resting upon a basement membrane, beneath which in localized areas muscle fibres are developed. Over the thick lobes of the gland the membrane is pierced by ducts of the underlying secreting cells which are grouped as in the albumen gland. The typical secreting cells which comprise the two lobes, except at their anterior ends, produce a white or yellowish viscid fluid which in contact with water hardens to a horny substance. Within the gland cells the secretion is in the form of spherules which give the gland an opaque white appearance in living tissue; they stain a vermilion red with azan and deeply with iron haematoxylin, displaying the same staining reactions as similar spherules in the capsule gland of the Stenoglossa (Fretter, 1941). Only the left lobe of the gland has mucoid cells, and these constitute, first, a ventral longitudinal strip of epithelial and subepithelial glands (Fig. 1 B and C, *vm*) which extends from the posterior tip of the left lobe to half-way along its length, and, secondly, a much shorter though deeper area situated dorsally (Fig. 1 C, *dm*) immediately in front of the albumen gland. The cilia on the walls of the gland beat towards the genital aperture and mix the two types of secretion from the left lobe of the capsule gland; the effect of this mixing can be traced in the structure of the egg capsule. Anteriorly, as the lobes of the gland narrow, the typical secreting cell is replaced by another type of gland; the replacing cells in the ventral lobe are filled with large droplets, irregular in outline, which stain more deeply with iron haematoxylin and are purple-red after azan; the replacing cells in the dorsal lobe are similar to this, but their spherules are minute. The secretion from this anterior region of the capsule gland is more fluid than that produced posteriorly though of a similar nature.

The muscles of the gland are responsible for moulding the egg capsule. They are developed not only beneath the ciliated lining, but also in the connective tissue which separates the groups of underlying glands. Two especially pronounced bands of circular muscles underlie the epithelium, one around the narrow lumen anterior to the albumen gland enabling this space to be still further reduced, the other towards the tapering end of the gland near the point at which the histology of the lobes is changed. The intervening portion of the gland is about as long as it is deep, and it is probably here that the capsule is, for the most part, constructed. Beneath the narrow strips of epithelium which separate the two lobes of the capsule gland are circular muscles, and radial fibres from these narrow walls penetrate the connective tissue between the nearby groups of glands; a few also occur elsewhere in the thickness of the lobes.

The most unusual feature in the reproductive system of female Neritidae is the crystal sac, the function of which has been described by Andrews (1935). It lies at the anterior end of the oviduct, the blind posterior part resting against the left side of the dorsal lobe of the capsule gland just above the

rectum (Fig. 1 A, *ds*). Anteriorly the sac spreads over the convex surface of this lobe and so envelops its outer wall. At the anus the crystal sac opens into the dorsal wall of the rectum (Fig. 1 E, *cr*) from which it collects faecal scraps. In *Theodoxus* these consist of diatom cases, small sand grains and sponge spicules; in *Nerita* Andrews (1935) states that the sac collects spherules which have come from the liver. The contents of the sac are used to reinforce the wall of the egg capsule and for this purpose are passed into the oviduct.

Towards the female aperture, and level with the opening of the vagina, the thin right wall of the capsule gland gradually expands outwards and ventrally to form the short terminal region of the oviduct, which may be termed the capsule duct (Fig. 1 D and E, *cd*). The crystal sac spreads over the dorsal lobe to its right side and opens along the length of the dorsal wall of the capsule duct (Fig. 1 E, *cc*); anteriorly the sac is open to the exterior. In *Theodoxus* the crystal sac always has a supply of diatoms and sand grains stored in its posterior end, where the wall is muscular and not ciliated (Fig. 1 A, *ds*). The anterior part does not appear to be used for storage, but to conduct particles from the rectum to the blind end of the sac and thence to the oviduct; for this purpose the epithelium is ciliated. The anterior part of the ventral wall which overlies the dorsal lobe of the capsule gland is also glandular (Fig. 1 D, *g*). The gland cells, which resemble those of the underlying lobe of the capsule gland, secrete a sticky fluid in which the particles are entrapped as they leave the crystal sac and are conducted to the capsule duct (*cd*). The capsule duct is very muscular and is lubricated by mucous cells scattered between the ciliated columnar cells which direct the capsule towards the genital opening. This opening is separated from the anus by a projecting flap of tissue (Fig. 1 A, *f*), a downgrowth from the anterior tip of the ventral lobe of the capsule gland, which can be folded over the anus and the adjacent opening of the rectum into the crystal sac, acting as a valve which directs contents of the rectum into the sac.

Only a few structural and histological details need be mentioned in connexion with the copulatory ducts of the female system. The epithelium of the bursa copulatrix (*b*) and the vagina (*v*) is ciliated and glandular. The gland cells, which are club-shaped with rounded distal ends and spherical basal nuclei, have large irregularly shaped secretion spherules, colourless in the living state, staining blue with azan and lightly with iron haematoxylin. Beneath the epithelium is a considerable layer of circular muscles, which, in the vagina, penetrate the characteristic longitudinal folds of the wall. After copulation the bursa contains large numbers of unorientated sperm, which are transferred later to the receptaculum seminis, though there is usually a surplus retained in the bursa. No gland cells occur in the receptaculum (Fig. 1 A and B, *re*); to its walls are attached orientated sperm with their tails embedded in the epithelium (Fig. 1 C, *s*). The passages from the receptaculum into the vagina, and into the receptacular duct (Fig. 1 A, *dr*), are each surrounded by a sphincter and strongly ciliated. The sperm are passed along the

duct by peristalsis as well as by the action of cilia. Towards the distal end of the duct originates the ventral strip of tall columnar cells (Fig. 1B, *c*) which passes through the vestibule (Fig. 1A, *ve*) to the 'poche de confluence'. Except for its ventral wall the vestibule has a covering of squamous epithelium.

The egg capsule

An account of the egg capsules of the Neritidae is given by Andrews (1935) who studied their structure in eight species including *Theodoxus fluviatilis*. He found that all conformed to the generalized plan (Fig. 2A) in which the shape is that of a flattened spheroid made up of two approximately equal halves sutured together (*s*) around the equator; one half, the base, is fixed to the substrate and rises up to form part of the side wall of the capsule, the other, the lid (*l*), is strengthened by particles from the crystal sac (Fig. 2B, *p*) and is lifted off when the young escape—the base of the used capsule remains attached to the substrate for some time (Fig. 2A, *b*). The walls are of tough conchiolin, white to straw colour, lined internally by a homogeneous membrane enclosing an albuminous fluid in which the eggs float. Andrews states that the capsule is produced by the lower part of the oviduct, but he did not study the structure of this and consequently can give no suggestions as to the local manufacture of the various parts of the egg case.

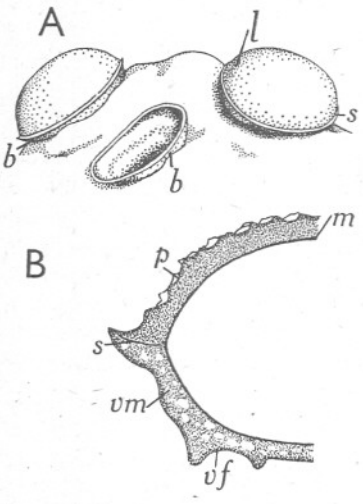

Fig. 2. *Theodoxus fluviatilis*. A, egg capsules on a stone. The young animal has escaped from one capsule and the base remains. ×25. B, part of a V.S. through a capsule. ×96. *b*, base; *l*, lid; *m*, membrane; *p*, particles from crystal sac; *s*, suture; *vf*, viscous outer layer; *vm*, vesicles filled with mucus.

Sections of the egg capsule of *Theodoxus* suggest that the thick outer wall is formed by secretion from the bilobed capsule gland, since both have the same composition and staining properties. The lid of the capsule is homogeneous in texture, and so differs from the base, in the substance of which there are vesicles filled with mucus (Fig. 2B, *vm*). It may be assumed that since the capsule is made up of two approximately equal parts, and since the capsule gland is bilobed, we have, as in the Stenoglossa (Fretter, 1941), one lobe of the gland responsible for forming one-half of the capsule. In *Theodoxus* these lobes differ histologically: in the left there are patches of mucous cells, the secretion from which is mixed with the conchiolin secretion. It follows that probably this left lobe secretes the base of the capsule, whilst the right produces the uniform secretion for the lid.

The periphery of the egg capsule is approximately circular in outline, and here the lid and the base are fused together. The diameter is roughly equal

to the length of the oviduct between its constriction at the anterior end of the albumen gland (Fig. 1C), and the tapering anterior end at the locus of the band of circular muscles which underlies the ciliated epithelium; the depth of the oviduct between these two points is equivalent to its length. It seems probable that the wall of the capsule is secreted within these limits, whilst the fertilized eggs embedded in albumen are detained here. If this be so then the suturing of the two sections, produced by the right and left lobes, is brought about by the anterior and posterior limiting bands of subepithelial circular muscles, and by the muscles underlying the narrow dorsal and ventral walls.

Microscopic examination of the capsule wall shows that on the outer surface is a very thin layer of secretion which has a slightly different staining property from the rest of the wall (Fig. 2B, *vf*), and is similar to the viscid fluid produced by the anterior tips of the capsule gland. This would be coated around the capsule as it passes anteriorly, and here, with the rotation of the oviduct, the future lid of the capsule would be dorsal and the base ventral. Towards the genital aperture the capsule projects laterally into the terminal capsule duct, and on to its upper wall are poured the contents of the crystal sac which are then pressed to the sticky outer covering (*p*). This similar covering over the ventral wall serves for attachment to the substrate. The method by which fixation is accomplished has not been observed. In female animals a semicircular muscular flap of tissue projects from the body wall immediately beneath the genital opening, and this may act as an ovipositor. No such structure has previously been described in any of the Neritidae. When the capsule is laid it contains over seventy eggs, but of these only one attains full development and comes to occupy the entire space within the capsule walls, hatching as a miniature of the adult.

LAMELLARIA PERSPICUA (L.)

The male

The male genital duct of *Lamellaria perspicua* closely resembles that of the stenoglossan *Nassarius reticulatus*. A short distance from the gonad the testis duct is thrown into deep coils and acts as a vesicula seminalis, which is distended with sperm throughout the year. The wall is composed of a columnar ciliated epithelium, and beneath the basement membrane circular muscles are developed. The vesicula seminalis leads forwards immediately beneath the body wall on the right side of the viscera, and on approaching the mantle cavity is delimited by a sphincter which surrounds the very short renal vas deferens. Anteriorly the histology of the genital duct changes abruptly, and throughout the rest of its course the epithelium is ciliated and glandular; the glandular part subserves the function of a prostate. The gland cells, alternating with wedge-shaped ciliated cells, contain colourless spherules which dissolve readily on fixation. Their nuclei are round and basal, whilst those of the ciliated cells are elongated and lie in the mid-region of the cytoplasm. The

cilia arise from basal granules and to these are connected intracellular fibrillae. The tubular prostate traverses the mantle cavity on the right side and reaches the base of the penis. Posteriorly, near its origin, it gives off a short duct which opens into the right posterior corner of the mantle cavity; a corresponding structure has been figured for *Buccinum* (Fretter, 1941). In this duct the cilia are longer than elsewhere; the opening into the mantle cavity is surrounded by a sphincter. As in *Nassarius reticulatus* and *Buccinum undatum* it is probable that the duct functions as a safety valve which allows the escape of sperm and secretion into the mantle cavity. At the base of the penis which lies behind the right tentacle the genital duct enters the haemocoele and, turning abruptly back on its course, it passes towards the posterior end of the mantle cavity, and then leads forwards again by a circuitous route and runs through the penis. These coils lie on the right side of the oesophagus, just beneath the body wall; they are surrounded by a layer of circular muscles which may attain considerable thickness.

The penis is relatively enormous and is equivalent in length to the pallial oviduct, through which it is inserted during copulation. It is laterally compressed like the lumen of the oviduct, and from the ventral surface, at about a quarter of its length from the extreme tip, there arises a flagellum which is traversed by the genital duct. The flagellum extends well beyond the tip of the penis, the ventral edge of which is deeply grooved anterior to its origin. The free edges of this groove, lubricated by the secretion of epithelial gland cells, may embrace the base of the flagellum and steady its position when, during copulation, seminal fluid is being passed from its filamentous tip into the fine ducts of the spermotheca of the female. As the genital duct passes through the penis its lumen decreases in size until in the flagellum it has the dimensions of a fine capillary tube through which the sperm are conveyed by peristalsis assisted by cilia. Near the genital opening the epithelial gland cells of the duct are gradually replaced by ciliated cells.

Lebour (1937) states that the echinospira larvae of *Lamellaria perspicua* are found in the plankton in all stages of development throughout the year, which suggests that breeding may occur in any month. This is supported by the fact that there is no marked seasonal reduction in the glands of the genital ducts. The maximal breeding occurs in spring and summer.

The female

From the ovary, which spreads over the visceral mass, the ovarian duct, with an epithelium resembling that of the gonad, leads forwards on the right side of the viscera to the posterior end of the mantle cavity. Here the epithelium changes and becomes columnar and ciliated and the duct turns abruptly dorsalwards to open into the glandular oviduct. The ciliated section is the renal oviduct (Fig. 3, *ro*); its walls are folded longitudinally and are surrounded by a coat of circular and longitudinal muscles.

The pallial oviduct, in which the egg capsule is formed, extends along the right side of the mantle cavity and comprises an albumen gland (*ag*) which receives the renal oviduct, a capsule gland (*pc*, *dc*, *vc*, *ac*), and a capsule duct (*cd*) which opens anteriorly on a papilla (*ga*). The albumen gland lies ventral to the posterior lobe of the capsule gland, and along its posterior wall open the ducts of six diverticula which constitute the receptaculum seminis (*s*, *dr*), their openings closely approximated. Each duct, lined by columnar ciliated epithelium and surrounded by a sphincter, leads to a small sac (*s*) which is not ciliated and contains throughout the year unorientated sperm. During copulation the sperm are deposited directly into the receptaculum by the

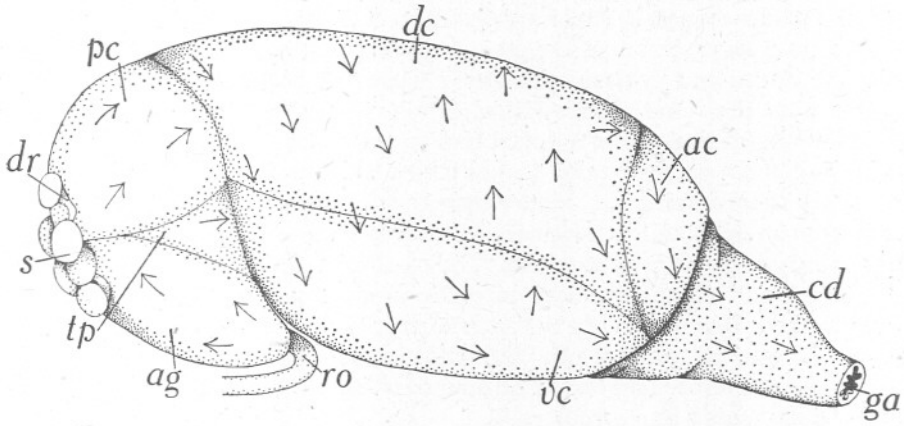

Fig. 3. *Lamellaria perspicua*. Oviduct seen from the right side. Arrows indicate ciliary currents on the inner side of the wall of the right lobe of the pallial section; those on the left are similar. × 13. *ac*, mucoid cells forming anterior tip of capsule gland; *ag*, albumen gland; *cd*, capsule duct; *dc*, subepithelial mucoid cells; *dr*, duct of diverticulum of receptaculum seminis; *ga*, genital aperture; *pc*, posterior lobe of capsule gland; *ro*, renal oviduct; *s*, end sac of diverticulum of receptaculum seminis; *tp*, triangular patch of gland cells; *vc*, ventral region of capsule gland with uniform secreting cells.

flagellum of the penis: the penis flattened from side to side, passes through the lumen of the capsule gland, which is also laterally compressed, and because of the ventral insertion of the flagellum this comes into contact with and may penetrate the ducts of the diverticula to discharge the seminal fluid.

The albumen gland and the capsule gland are lined by columnar ciliated cells, and their walls, especially laterally, are thickened by subepithelial gland cells. These are arranged in tightly packed bundles lying at various depths, and the long ducts run parallel with one another to open between the ciliated cells. A fairly precise indication of the main groups of gland cells can be made out from a study of living material, and is indicated in Fig. 3. In a transverse section of the albumen gland nearest the renal oviduct two types of secreting cells may be recognized though the boundaries between the areas which they occupy are not visible externally. One type constitutes the dorsal

half of the gland, which underlies the ventral wall of the capsule gland, and the other the ventral half. In the former the secretion spherules stain lightly with iron haematoxylin; in the latter they are smaller and stain more deeply. This second type spreads up the posterior wall of the pallial oviduct to beyond the point of entry of the receptaculum and comes into contact with the posterior lobe of the capsule gland (*pc*). In living material this lobe is distinguished by its pink colour. Its cells are filled with small droplets which are purple after methylene blue intra-vital staining, are slightly affected by mucicarmine and stain lightly with iron haematoxylin. Ventral to this pigmented lobe, and wedged between it and the albumen and capsule glands, is a small triangular patch of gland cells (*tp*), which is distinguished by its opaque whiteness and in which spherules stain deeply with iron haematoxylin.

In a transverse section of the capsule gland the lumen appears as a vertical slit, the dorsal and ventral walls being narrow and comparatively thin, the lateral ones deep and thick. Histologically the main part of the gland is divided longitudinally into a dorsal region composed of subepithelial mucoid cells (*dc*), and a ventral region (*vc*) in which the secreting cells are filled with regularly shaped spherules, longer than they are broad, staining deeply with iron haematoxylin and red with azan, the cells resembling histologically those of the capsule gland of Stenoglossa. The two types of secretion are passed into the lumen and mixed by ciliary currents, producing a viscid fluid which can be drawn out into fibrils. At the anterior tips of the right and left lobes of the gland the mucoid cells are of a different character and respond more readily to the mucicarmine stain (*ac*). The boundary between capsule gland and duct (*cd*) is surrounded by mucous cells.

In the thickness of the wall of the albumen and capsule glands there are muscle fibres developed in the connective tissue binding together the groups of gland cells; they are especially numerous dorsally and ventrally. Circular muscles are also present in the layer of connective tissue which surrounds this part of the oviduct. By means of these muscles the lumen may be enlarged and become tubular.

The capsule duct is lined by columnar ciliated cells and surrounded by a very thick layer of circular muscles; no gland cells are present.

The egg capsule

The egg capsules of *Lamellaria perspicua* which are sunk in the tissues of compound ascidians (*Leptoclinum*, *Polyclinum*, etc.) are common between tidemarks around our coasts. The capsule is described and figured by Ankel (1935). Each is pot-shaped, with a rounded base, and measures approximately 2 mm. high and 3 mm. across the broadest diameter, and tapers slightly towards the circular opening which is filled with a plug made of concentric layers of a rather transparent material. Only the plug, surrounded by a low rim of capsule wall, is exposed at the surface of the ascidian, and it is frequently so transparent that through it may be seen the contents of the capsule

—many unshelled eggs, yellow in colour, floating in an albuminous fluid. The wall of the capsule is divided into approximately equal halves by a suture which runs down its length and is continuous through the substance of the plug bisecting its concentric layers. Externally the wall has a fibrillar appearance, the fibrillae running in a circular direction. There is also a thin inner layer to the wall which completely surrounds the albumen, and so is continuous beneath the substance of the plug. The dimensions of the capsule correspond to those of the lumen of the capsule gland. In its general lay-out the egg capsule thus resembles those of *Nucella* (Ankel, 1937; Fretter, 1941). Since there is a fairly close resemblance between the female genital ducts of these two molluscs it is probable that the method of formation of the egg capsules is similar. I have never observed a capsule in the process of manufacture in *Lamellaria*, but the following conjecture seems most probable. The eggs are passed down the ovarian duct in considerable numbers—according to Ankel 1000–3000 are contained in one capsule—and in the albumen gland they are embedded in a nutritive fluid. On to the eggs are poured sperm from the receptaculum seminis and fertilization occurs. The eggs embedded in albumen are then directed into the capsule gland and retained there whilst the capsule wall is secreted. The thin inner layer of this wall, which is continuous round the egg mass, may be derived from secretion poured into the lumen of the gland prior to the entry of the egg mass and invaginated by this mass as it passes into the capsule gland. Around this layer is then deposited the outer coat, the thicker part of the capsule wall. One half of this is produced by each lobe of the gland and the dividing suture lines correspond to the thin dorsal and ventral walls of the gland. The transverse fibrillar appearance of this outer layer is undoubtedly due to the blending of the protein secretion from the ventral half of the capsule gland with the mucoid secretion of the dorsal half, the mixing being effected by the action of the predominantly transverse ciliary currents of the epithelium. In *Nucella* the plug is produced by the posterior lobes of the capsule gland, and this probably occurs in *Lamellaria* too, since the plug is of a different consistency from the rest of the wall. The substance for the plug would be driven into the open end of the capsule by cilia and muscular action. At the opposite end of the capsule gland whilst the case is being formed the lumen is closed off from that of the duct by the sphincter which surrounds this part.

Lamellaria, unlike the Stenoglossa, possesses no ventral pedal gland for the final moulding and deposition of the egg case. With the aid of the radula the mollusc bites small round holes in the compound ascidian and places therein a capsule, but the exact method by which this is accomplished is unknown: it may be a function of the foot aided by the anterior pedal mucous gland. The capsule is embedded vertically in the test of the ascidian so that only the plug projects slightly from the surface, and around this the test thickens to form a protecting rim.

Trivia monacha (da Costa) and *T. arctica* (Montagu)

The male

Fig. 4 displays the essential features of the male genital ducts of *Trivia monacha*. The testis duct leads from the gonad, which is situated on the columellar side of the visceral mass, towards the right posterior corner of the mantle cavity. Except in its initial part it forms a deeply coiled vesicula seminalis (*vs*) of which the epithelium is ciliated. The cilia are often difficult to detect in sections. Beneath their basal granules the cytoplasm contains spherules which stain blue with azan and deeply with iron haematoxylin. Frequently a number of amoebocytes are seen between the epithelial cells and among the sperm, but it is uncertain as to whether they absorb effete sex cells as in the oviduct of the female. The vesicula seminalis passes into the renal vas deferens (*rd*), a short, narrow and more muscular duct which communicates with the prostate by a papilla. Sperm are only contained in the renal vas deferens during copulation, and then they are passed rapidly through the duct by peristalsis aided by the action of the thick coat of cilia which covers its walls. The prostate (*pr*) is a roomy pouch extending along the right side as far as the opening of the mantle cavity; in transverse section its lumen appears as a deep dorso-ventral slit. The epithelium is glandular and ciliated cells are wedged between the distal ends of the gland cells, alternating regularly with them. The gland cells are tall, particularly in the lateral walls, and are of two kinds. In the more plentiful, which is also the larger of the two, the cytoplasm is filled with secretion spherules of a considerable size, which tend to dissolve in acid fixatives; both they and the rather fibrillar cytoplasm stain blue with azan and lightly with iron haematoxylin. The nuclei are large, lying towards the bases of the cells, and each contains two or three prominent nucleoli. In the second type of gland the spherules are small and so numerous that there appears to be little intervening cytoplasm, and the nucleus is hidden; these spherules stain bright red with azan and black with iron haematoxylin. Such glands are most common in the anterior edge of the prostate; some occur in the epithelium of the posterior wall, and fewer laterally. The epithelium rests upon a basement membrane beneath which is a layer of connective tissue containing muscle fibres.

The papilla through which the sperm are emitted from the vas deferens opens at the posterior end of the ventral wall of the prostate. Immediately in front of its opening the gland communicates with the mantle cavity by a longitudinal slit (*ls*)—an opening which in *Lamellaria* lies at the end of a short duct. Cilia direct the sperm through the gland, but they beat away from the slit; the lateral lips which border it are covered by a columnar ciliated epithelium, and normally embrace one another to keep the prostate closed.

From the anterior end of the ventral wall of the prostate arises the narrow ciliated tube (*cd*) which runs up the right side of the head to the penis (*p*). It is of uniform diameter throughout. Among the ciliated cells which line it are

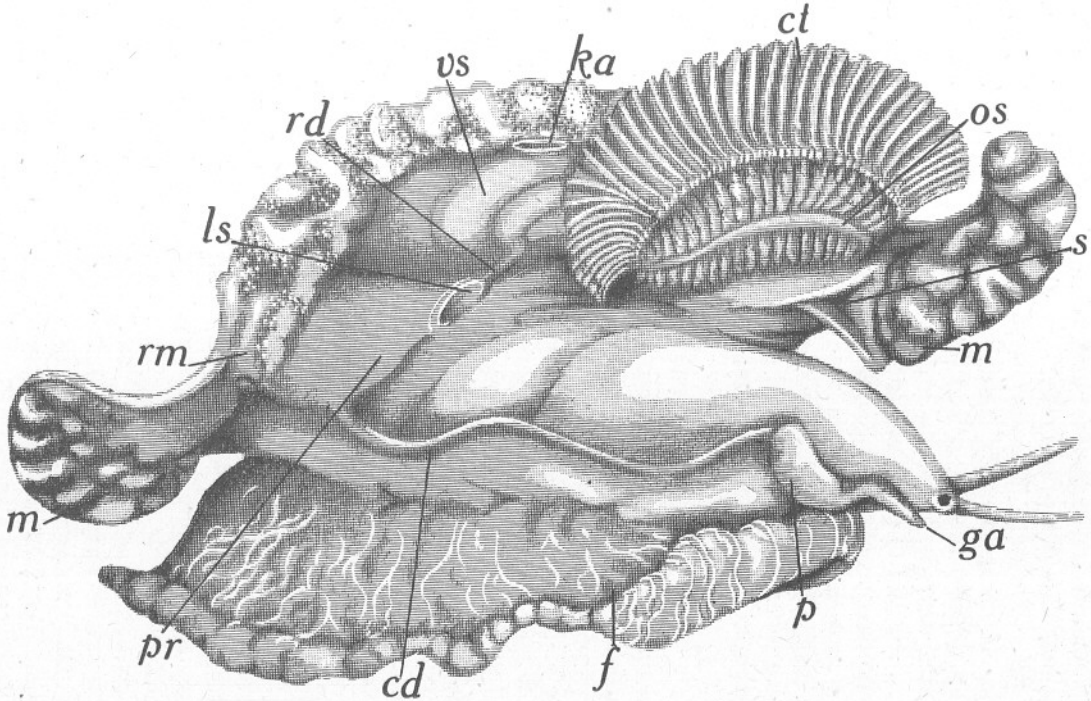

Fig. 4. *Trivia monacha*. Dissection to display the male genital duct; the mantle cavity has been opened along the right side. × 10. *cd*, ciliated duct leading from prostate to penis arising from antero-ventral corner of gland; *ct*, ctenidium; *f*, foot; *ga*, genital aperture; *ka*, kidney aperture; *ls*, longitudinal slit in ventral wall of prostate; *m*, mantle; *os*, osphradium; *p*, penis; *pr*, prostate; *rd*, renal vas deferens; *rm*, rectum with overlying hypo-branchial gland; *s*, siphon; *vs*, vesicula seminalis.

scattered gland cells of a different nature from those already described—the cytoplasm, which is filled with minute spherules, stains blue with azan, whilst the spherules are purple; the glands are unaffected by mucicarmine and stain but lightly with haematoxylin. In the ciliated cells the cytoplasm contains small yellowish granules which are most numerous beneath the basal granules from which the long cilia arise; these cilia may attain a length exceeding twice the height of the epithelium. The duct is surrounded by a thick layer of circular muscles which assist in the transmission of the spermatozoa to the penis. The duct through the thin cylindrical penis is similar in histological detail, except that towards the genital aperture (*ga*) gland cells are lacking. Here the duct is reduced to the dimensions of a fine capillary tube.

The male reproductive system of *Trivia arctica* is constructed on the same plan as that of *T. monacha*, and between the two there is close correspondence in histological detail. The outstanding point of difference, and the only one that need be mentioned, is in the size and shape of the penis—in *T. arctica* it is larger and assumes a broad leaf-like shape.

The female

The ovarian tubules, which lie between the lobes of the digestive gland, converge towards the anterior ventral surface of the visceral mass on the right side, and here join one another to form a short ovarian duct with an epithelium resembling the gonad. The epithelium becomes ciliated as the duct merges into the renal oviduct (Figs. 5A and B, *ro*), which is a muscular tube lined by thickly ciliated columnar cells. The renal oviduct opens into the albumen gland (*ag*), which is a differentiation of the posterior end of the pallial oviduct and is connected to the receptaculum seminis. Anterior to this gland is the bilobed capsule gland (*rc*, *lc*) constituting the anterior part of the pallial oviduct and possessing, as in most mesogastropods, deep and thick lateral walls, and narrow and thin dorsal and ventral walls. The genital aperture is not terminal, but is a longitudinal slit along the greater length of the ventral wall (*f*).

The relationship between the albumen gland and the receptaculum seminis is the chief point of difference between the two species of *Trivia*. In *T. arctica* the receptaculum takes the form of six large diverticula which open separately into the albumen gland (Fig. 5B, *dr*), so that the arrangement corresponds with that of *Lamellaria perspicua*, except that in *Trivia* the albumen gland is constricted off from the capsule gland along the dorsal part of its anterior wall. In *T. monacha* the receptaculum is a spherical sac (Fig. 5A, *rs*) lying above the albumen gland, which has the appearance of a thick duct leading from the receptaculum to the capsule gland.

Trivia monacha (da Costa)

The epithelium of the renal oviduct is folded longitudinally and surrounded by a coat of circular muscles. The muscles increase in thickness to form a

sphincter around the papilla by which the duct opens into the pallial oviduct. Proximal to this opening a bunch of branching diverticula (Fig. 5 A, *bd*) leads from the renal oviduct to end blindly in the tissues of the digestive gland. The diverticula contain sperm which are orientated in the lower proximal parts

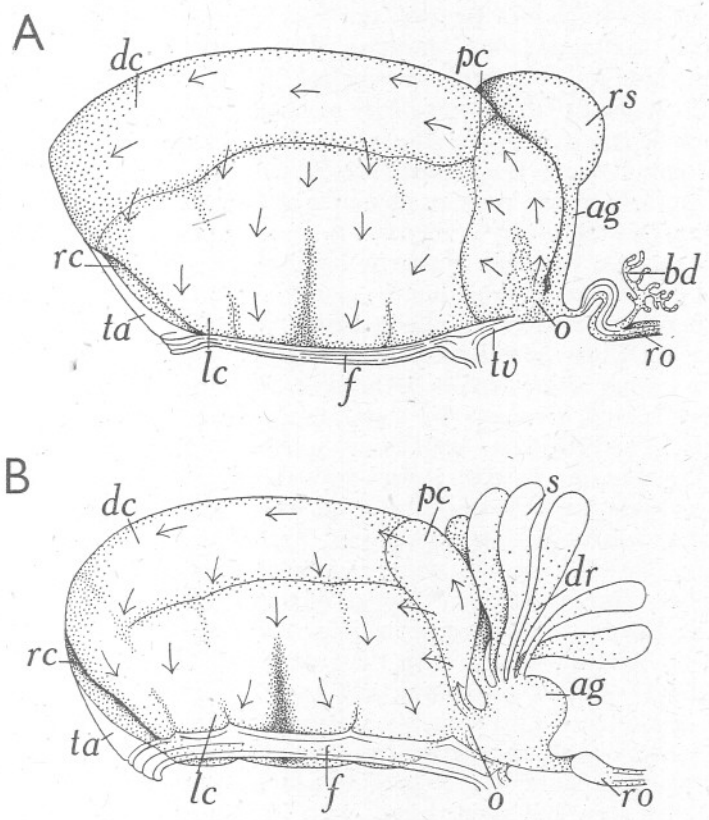

Fig. 5. A, *Trivia monacha*. Oviduct from the left side. ×24. B, *Trivia arctica*. Oviduct from the left side. ×30. Arrows indicate ciliary currents on the inner side of the wall of the left lobe of the pallial section; those on the right are similar. *bd*, branching diverticula from renal oviduct; *f*, ventral wall forming flange over genital aperture; *lc*, left lobe of capsule gland; *o*, position of opening of albumen into capsule gland; *rc*, right lobe of capsule gland; *rs*, receptaculum seminis; *ta*, thin anterior wall of capsule gland; *tv*, thin ventral wall of capsule gland. Other letters as in Fig. 3.

of the tubules, their heads embedded in the ciliated epithelium, whilst in the distal ends the sperm lose their orientation and their heads appear shorter. Their ultimate fate is ingestion by amoebocytes, which invade the blind ends of the tubules in large numbers and there devour and digest the effete sex cells. It is probable that these sperm enter the renal oviduct when ripe eggs are liberated from the ovary. The excess sperm which are not used in

fertilization are trapped here and lodge in the diverticula, in which they orientate themselves and remain healthy for some days.

The epithelium which lines the receptaculum seminis is thrown into deep and somewhat irregular folds. It is composed of ciliated cells, the cilia arising from basal granules from which intracellular fibrillae run through the superficial layer of cytoplasm. Beneath the fibrillae the cytoplasm is vacuolated, the vacuoles containing small granules. If animals be dissected immediately after copulation it is found that the seminal fluid fills the receptaculum, which suggests that the tip of the penis may reach as far as the base of this pouch. This is made possible by the position and size of the female aperture. The sperm orientate themselves immediately after deposition, pushing their heads into the epithelium, and perhaps obtaining nourishment from it. Occasionally a few may become totally embedded in the cytoplasm, when they are contained in vacuoles and later appear to be digested.

In the epithelium of the albumen gland tall secreting cells alternate with wedge-shaped ciliated cells. The secreting cells are of two kinds—mucous cells and unicellular gland cells filled with colourless spherules of protein, which are contained in vacuoles in the cytoplasm, tend to dissolve on fixation, and after the iron haematoxylin stain are a dense blue-black, as is also the cytoplasm. This glandular epithelium spreads around the opening to the receptaculum and up its ventral wall for a short distance.

In the capsule gland the thickness of the wall is due to tightly packed groups of secreting cells underlying the ciliated epithelium, which is penetrated by their ducts. Various types of glands are present and their secretions are mixed by the ciliary currents to form the wall of the egg capsule. The posterior tip (*pc*) of the gland is opaque white in living material, and is distinctly marked off from the anterior part. Along the ventral wall is the opening of the albumen gland (*o*), and the secreting cells from this extend dorsally for a short distance as a tongue separating two different groups of glands, one anterior and one posterior, which together constitute the posterior tip. The posterior group of glands is composed of cells containing spherules which are a bright crimson after azan and stain deeply with iron haematoxylin, whilst in the anterior group the spherules are very small, stain pale blue with azan and lightly with mucicarmine and iron haematoxylin. It is probable that these posterior tips, as in the Stenoglossa, form the plug of the egg capsule. If this be so then the rest of the gland must be responsible for forming the capsule wall. In fresh tissue the capsule gland is characteristically pigmented—from the genital aperture a strip of deep brown runs dorsally up each lateral lobe, and on either side of this strip the walls are yellow in colour. The grouping of the various types of subepithelial gland cells is as follows. The thin dorsal and anterior walls of the capsule gland are bordered on each side by mucous or mucoid cells, the former running forwards for a short distance from the posterior tip and also surrounding the anterior end of each lobe, the latter occupying the intervening area. Ventrally two other types of gland cells occur.

In one of these the secretion spherules stain very faintly with haematoxylin and pale blue with azan. These cells spread dorsally from the genital aperture to occupy a semicircular area; among them are a few epithelial and sub-epithelial mucoid cells. This area is surrounded on the side away from the genital aperture by the second type of gland which, except for mucoid cells, constitutes the remainder of each lobe, and in histological detail appears to be identical with the secreting cells of the ventral half of each lobe of the capsule gland of *Lamellaria*. The mucoid cells along the dorsal border run ventrally between these secreting cells in two areas, one towards the anterior and the other towards the posterior end of the genital aperture.

Beneath the epithelium of the ventral wall of the capsule gland no glands occur. Posterior to the genital aperture the wall unites the two lobes and is pouched beneath each, so forming a ventral channel which is surrounded externally by a layer of circular muscles, and along which the penis is inserted during copulation. The passage is lubricated by intra-epithelial gland cells which are similar to those of the albumen gland, and are very numerous near the junctions of the ventral and lateral walls. In the region of the genital aperture the ventral wall forms a flange which is attached to the left lobe of the capsule gland and embraces the free ventral edge of the right lobe so as to close the opening. Anteriorly the lobes are separated by an epithelium which is composed almost entirely of mucous cells.

The musculature of the capsule wall consists of a circular layer which is developed in the connective tissue surrounding the gland externally, and of radial and circular fibres in the connective tissue which binds together the groups of glands in the neighbourhood of the dorsal wall.

Trivia arctica (Montagu)

The renal oviduct (Fig. 5B, *ro*) is lined by a columnar ciliated epithelium which is folded longitudinally. The duct opens by a papilla into the pallial oviduct and possesses no branching diverticula for the accommodation of sperm—a feature which appears to be peculiar to *T. monacha*. The epithelium of the receptaculum seminis is similar in both species: ciliated, and with spherules in the cytoplasm which may provide nourishment for the spermatozoa. In *T. arctica* each diverticulum of the receptaculum is surrounded by a thick layer of circular muscle which forms a sphincter around the duct, and which will eject the sperm lying orientated in the terminal sac on contraction. Only very infrequently do sperm become embedded in the cytoplasm of the epithelial cells.

The albumen gland is in the form of a spherical sac (*ag*), the ventral wall of which is produced posteriorly to meet the renal oviduct and anteriorly to the opening of the capsule gland. The epithelium of the dorsal part of the sac is thrown into deep folds as in *T. monacha*, and within the lumen unorientated sperm, an excess from the receptaculum, are present during the winter months when copulation occurs and egg capsules are produced. The epithelium

consists of ciliated cells, similar to those of the receptaculum except that the spherules in the cytoplasm are more resistant to fixatives, and two types of gland cells which resemble those of the albumen gland of *T. monacha*. The secreting cells are very numerous in the ventral part of the gland, especially near the opening of the renal oviduct and the capsule gland, but are sparse dorsally; a few may extend to the ducts of the receptaculum.

The capsule gland is built on the same plan as that of *T. monacha*, and since the histology is very similar no detailed account need be given. An essential difference between the two species is in the size of the genital aperture which in *T. arctica* extends as far back as the albumen gland—this may be correlated with the larger size of the penis in this species.

The egg capsule

The egg capsule of *T. monacha* is figured by Lebour (1931), and specimens laid in the tissues of the compound ascidian *Polyclinum* have been collected at Port Erin, dissected from the ascidian, sectioned and examined microscopically. The capsule is an erect vase-shaped structure, circular in transverse section, rounded at the base, and above the constricted neck at the opposite end it broadens to a tall funnel. A plug at the base of the funnel blocks the entrance and closes off the sac in which the eggs float in an albuminous fluid. The capsule is approximately 5 mm. high, the funnel accounting for two-thirds of this measurement, and 2·5 mm. is the diameter of the egg sac in its broadest region. The breadth corresponds to that of the capsule gland, though the height exceeds that of the gland; this, however, may be accounted for by the fact that the funnel is moulded to its final dimensions after the capsule has left the gland. The wall is of a light straw colour, somewhat transparent so that the orange-coloured eggs can be seen through it, and has a fibrillar texture; in all these features it resembles the secretion from the capsule gland. The fibrillae are for the main part circular in direction corresponding to the transverse nature of the ciliary currents which determine their alinement within the capsule gland. Two longitudinal lines of thickening can be traced over the smooth surface of the capsule wall, and these are placed so as to divide the capsule into approximately equal halves; the suture is continuous across the plug at the base of the funnel. Ankel (1935) states that neither the plug nor the longitudinal suture is present, and the latter was not figured by Lebour (1931): its presence shows that as in *Lamellaria* and the Stenoglossa (Fretter, 1941), the structure of the capsule reflects the nature of the capsule gland, within which one-half of the wall is secreted by each of the two lobes. The suture which divides the plug into two demarcates the limit of secretion produced by each posterior tip of the capsule gland.

Female individuals of *Trivia* may be distinguished from the male by the presence of a ventral pedal gland which appears as a pit in the mid-ventral

region of the sole, a short distance behind the anterior pedal mucous gland. If the animals be anaesthetized a small papilla surrounded by a deep groove is protruded from the pit. In *T. monacha* the gland is lined by columnar ciliated epithelium in which mucous and mucoid cells occur; these, however, are much fewer than in the surrounding epithelium of the foot. A layer of large unicellular glands underlies the epithelium, their long ducts opening between the ciliated cells. The secretion within the cells is in the form of spherules which stain lightly with haematoxylin. Beneath and between the subepithelial glands are groups of longitudinal muscle fibres which cause the protrusion and withdrawal of the papilla; when protruded the papilla is kept turgid by blood in the nearby sinuses. Since the gland is present only in females it is probably homologous with the ventral pedal gland of the Stenoglossa (Fretter, 1941) and is concerned with the deposition of the egg capsules. In the Stenoglossa the capsule is moulded within the gland, which then fixes it to the substratum. In *T. monacha* the capsule is sunk in a hole in the test of compound ascidians, the hole being excavated by the radula, and the funnel-shaped end projects from the surface of the test. The size and structure of the ventral pedal gland suggests that it is responsible for moulding this projecting part. After the capsule has been placed in the tissues of the ascidian the gland would then drive it into the hole, at the same time gripping the pliable projecting portion of the capsule wall and would fashion it into its final form. The size of the funnel thus formed is equal to that of the papilla which is protruded from the gland, and the characteristic out-turned rim of the funnel is of the same dimensions as the deep groove around the papilla. In *Lamellaria* no ventral pedal gland is to be found, and in connexion with this it is of interest to note that the capsule has no prominent rim projecting around the plug. The latter is surrounded by a thickening of the test of the ascidian—an attempt on the part of this animal to close the hole.

The embryos of *Trivia* develop to echinospira larvae before they leave the capsule. Their escape has not been observed, but empty capsules opened by the loss of the plug have been found. Perhaps the larvae produce an enzyme which loosens the plug and so enables them to quit the embryonic nursery and take up a planktonic life in the coastal waters.

The egg capsules of *T. arctica* are unknown though the larvae have been described by Lebour (1933). Since, however, the female genital duct and the ventral pedal gland are similar in both species, it is probable that there is a close resemblance in the structure of the capsules.

The glandular tissue of the female reproductive system—and this also applies to the male—is greatly reduced between the breeding seasons, that is, during autumn and winter for *T. monacha*, which has a more southerly distribution and which produces egg capsules in spring and summer, and during the summer for *T. arctica*, in which the breeding season extends from late autumn to early spring.

Discussion

Archaeogastropoda

In the archaeogastropods both right and left kidneys are developed: each opens into the posterior end of the mantle cavity by a short ureter, and communicates with the pericardial cavity by a narrow, ciliated renopericardial duct which arises near the base of the ureter. There is a single gonad which discharges into the right kidney by way of a gonadial duct, so that the genital products reach the mantle cavity through the kidney opening. The point of connexion between the gonadial duct and the kidney varies: in *Diodora*, *Puncturella* and the trochids (Fig. 7A) the gonadial duct (*gd*) opens into the renopericardial duct (*rp*), in *Patella* and *Haliotis* it opens into the kidney, and in the other Docoglossa into the ureter (for diagrams see Linke, 1933). In all cases the course taken by the genital products in passing from gonad to mantle cavity is through a composite duct, the proximal part of which is derived from the gonad and the distal part from the kidney, the latter varying somewhat in its constitution. The sperm and ova are directed through the mantle cavity by the exhalant pallial current, and fertilization is external.

The majority of the archaeogastropods are littoral. They either shed their eggs singly, and development to a free trochosphere or veliger stage takes place in the plankton, or embed them in a common gelatinous secretion forming egg masses or ribbons. From data given by Lebour (1937) it appears that in the latter forms the young may develop to a crawling stage within the protection of the common gelatinous covering. If the eggs are liberated singly each is surrounded by one or more protective coats described by Lebour as an inner albuminous layer and an outer jelly layer. Observations show that, at least in certain species, these investments are formed in the ovary and the oviduct can have little or nothing to do with their production. If ova be removed from ripe females of *Patella*, *Patina*, *Gibbula cineraria*, *G. umbilicalis* or *Monodonta* and placed in sea water, each is seen to be provided with an outer gelatinous layer which swells in contact with water, and, except in the two Docoglossa, a thin inner layer of albumen; in fact, the appearance of these eggs seems identical with those which have been obtained from the plankton and described and figured by Lebour (1937).

In *Gibbula* and *Monodonta* the female urinogenital aperture is, unlike that of the left kidney, provided with glandular rosette-shaped lips which are yellow or bright orange in the living animals (*l*). They are not developed in the male. There is some controversy concerning these glandular lips around the opening of the right kidney in the female: Randles (1904) describes them for *Gibbula* spp., and Frank (1914) for *Monodonta turbinata*, though Robert (1902) and Lamy (1928) state that in trochids which lay their eggs singly the glandular appendage is missing, and according to Gersch (1936) 'die Mundung des Ureters in die Mantelhöhle ist bei *Gibbula cineraria* und *G. tumida* durch eine in beiden Geschlechtern gleichmassig ausgebildete Ampulle

kenntlich'. Since the investments of the egg appear to be a product of the ovary or of the egg itself, the secretion from this gland in *G. cineraria*, *G. umbilicalis* and *Monodonta lineata* may merely be responsible for hardening the outer jelly coat, or, more probably, since it is wholly mucous, may augment the secretion from the hypobranchial gland and so assist in the entanglement of the egg stream within the mantle cavity. According to Gersch (1936) the hypobranchial gland secretes most actively during the breeding season, and he concludes that in *Gibbula tumida* it also produces the jelly in which the eggs are embedded, since in this species he finds no glandular appendage around the genital aperture. In *Pleurotomaria Beyrichii* an accessory gland around the female urinogenital aperture, similar to that of trochids, has been described by Woodward (1901).

Diodora apertura and *Calliostoma zizyphinum* exemplify two methods by which gelatinous egg masses may be produced in the archaeogastropods. If eggs be removed from the ripe ovary of *Diodora* they are seen to possess both albuminous and jelly coats. Around the urinogenital aperture there are no glandular lips which might produce a secretion for cementing the eggs together as they are laid, but, according to Boutan (1885), this is accomplished by secretion from a 'glande annexe' developed on the wall of the female genital duct. The eggs coated with a thin layer of this secretion leave the urinogenital aperture and pass to the anterior end of the mantle cavity in a continuous stream; they are spread, usually on the under-surface of a stone, by means of the foot. The outer surface of each egg adheres to that of its neighbours and to the substratum, and an egg mass commonly one cell thick is thus formed. On the other hand, sperm from the male are passed through the apical opening of the mantle and shell and are discharged near the eggs when these are laid.

Calliostoma zizyphinum shows a more marked sexual dimorphism than any other gastropod so far mentioned. In the male the left and right kidney apertures lie level with one another at the posterior end of the mantle cavity, but in the female the right one is considerably farther forwards, since a glandular section is added which is assumedly derived from a closed off portion of the mantle and is built on the same plan as the pallial oviduct of the mesogastropods—lined by columnar ciliated epithelium, the lateral walls deep and thickened by tightly packed bundles of subepithelial gland cells, the dorsal and ventral walls narrow and comparatively thin. The secretion from this glandular section is of a uniform mucoid nature, and as the eggs are passed through it, each covered by an albuminous and gelatinous coat from the ovary, a further fluid of gelatinous consistency is poured over them and binds them into an egg ribbon. Thus in *Calliostoma* the oviduct is made up of (*a*) the ovarian duct, (*b*) part of the right kidney and its duct, and (*c*) a glandular duct derived from the mantle. This triple origin of the genital duct is the general plan on which that of higher gastropods, both male and female, is built. The more advanced nature of the genital duct in *Calliostoma* supports

Lebour's (1937) suggestion, based on the character of the spawn, that in the classification of the Trochidae the genus *Gibbula* should be regarded as more primitive than *Calliostoma* and not as more advanced as in Winckworth's classification (1932).

The aberrant freshwater *Theodoxus fluviatilis* is an archaeogastropod which approaches the mesogastropods not only in the loss of the right kidney and the right ctenidium, but also in the possession of genital ducts which are as complex as in any prosobranch, and which open alongside the anus at the mouth of the mantle cavity. Bourne (1908) suggests that the loss of the ctenidium in the Neritidae is correlated with the development of these accessory genital organs which occupy all the space on the right side of the mantle cavity. This, as in the mesogastropods, probably accounts for the loss of the right kidney. It seems more profitable to discuss the condition of the genital ducts of this genus with the mesogastropods.

Mesogastropoda and Stenoglossa

In the archaeogastropods the anal papilla is well back in the mantle cavity, though in front of the kidney openings. The faeces, bulky in such herbivorous forms, are elaborated in long coils of intestine, in the epithelium of which there are special glands for cementing together the discrete faecal particles (Graham, 1932). Here there is little fear of the compacted pellets disintegrating and fouling the mantle cavity as they are passed to the exterior by the exhalant pallial current. In the mesogastropods the rectum runs across the right side of the mantle cavity to open at its mouth, so that the faeces are discharged directly to the exterior and their elaboration need not be so complete. This new terminal section of the intestine, which brings the anus far forward to a more advantageous position, is probably derived from a folding over of the mantle wall. Running parallel with it is the oviduct which is longer than in *Calliostoma* and extends to the anus. This section of the oviduct which crosses the mantle cavity and frees the eggs directly to the exterior, must be comparable to the terminal part of the intestine and derived from the mantle. It is therefore referred to as the pallial oviduct, as distinct from the renal oviduct which precedes it. Most probably it first arose as a longitudinal groove with a ciliated epithelium similar to that of the mantle, in which case secreting cells producing a lubricant would be present. In no living gastropod does it persist in so simple a form, but the glandular element has been exploited, the walls thickened by addition of subepithelial secreting cells of various kinds, and the lips of the groove have fused to form a more or less spacious tube. From the genital aperture the egg mass, spawn or capsule may be directed on to an ovipositor as in *Littorina littorea* (Linke, 1933) or come under the manipulation of the foot by which it is deposited as in *Bithynia tentaculata* (Ankel, 1936), *Trivia* and the Stenoglossa (Fretter, 1941).

The forward migration of the anus and oviduct is not followed by that of the left kidney opening, except in specialized cases, e.g. the freshwater

genera *Viviparus* and *Valvata* which possess a long ureter opening at the mantle edge. The functional right kidney of the archaeogastropod is lost except for the vestige which forms that part of the genital tract linking the ovarian or testis duct with the mantle cavity; the original communication between the ureter and the pericardial cavity may persist.

The gonadial duct sometimes retains an epithelium resembling that of the gonad (Linke, 1933); its musculature is feebly developed as compared with that of the renal genital duct. In the male its lower part is coiled and functions as a vesicula seminalis, the epithelium of which may absorb effete sperm (*Littorina*, Linke, 1933; Stenoglossa, Fretter, 1941). The renal oviduct and vas deferens are for conduction: the epithelium is strongly ciliated and surrounded by a thick coat of circular muscles. In the female a gonopericardial duct may be present, and, if so, it arises between the ovarian duct and the renal oviduct resembling the latter histologically. This connexion with the pericardial cavity has never been described for the male, though in some genera in which it is well developed in the female it is represented in the male by dense strands of connective tissue passing from the origin of the vas deferens to the pericardium (*Littorina*, Linke, 1933; *Cremnoconchus*, Linke, 1935; *Ocenebra erinacea* and *Nassarius reticulatus*, Fretter, 1941). As such it first makes its appearance when the protandrous hermaphrodites *Calyptraea* and *Crepidula* develop female organs (Giese, 1915). The persistence of the gonopericardial duct in the female proves that it is at least no handicap in the functioning of the genital system, and its appearance in the female stage of *Calyptraea* and *Crepidula* may indicate that it serves some essential role. Its occurrence, however, in the male might be a serious disadvantage in allowing the escape of sperm into the pericardial cavity.

The male system

The evolution of the male genital ducts of the mesogastropods is parallel with that of the female. Since when the eggs leave the female aperture they are embedded at least in a thick gelatinous secretion or contained in a capsule, their fertilization must take place within the oviduct. For this purpose a pedal penis is developed behind the right cephalic tentacle of the male, and the male orifice is secondarily removed to the tip of the penis. In some the opening of the vas deferens is still at the posterior end of the mantle cavity, and the seminal fluid is directed forwards along a ciliated groove which runs across the floor of the cavity and up the right side of the head to the tip of the penis. Such a sperm-conducting groove, which functions as a closed tube, is present in *Littorina* (Linke, 1933) *Calyptraea chinensis*, *Crepidula unguiformis*, *Capulus ungaricus* (Giese, 1915) and species of *Cypraea* (Rau, 1934). In *Littorina* that section of the groove lying within the mantle cavity is bordered on each side by a glandular strip of tissue, the secretion from which is mixed with the sperm during copulation. This glandular area therefore functions as a prostate; its origin is similar to that of the pallial oviduct. Such

an open prostate is also present in *Turritella communis* in which the seminal groove ends at the opening of the mantle cavity and no penis is developed; the entry of seminal fluid into the female is probably effected by the inhalant pallial water current. In other mesogastropods and in the Stenoglossa the seminal groove is closed throughout its length. The prostate may form a wide sac-like portion of the duct lying within the mantle cavity, with subepithelial gland cells thickening the deep lateral walls and the narrow dorsal and ventral walls remaining thin. Or the prostate may be a narrow tube of about the same diameter as the rest of the male duct, with epithelial gland cells only; in either case the walls are ciliated. The former type of prostate occurs in the hydrobiids, *Assemania grayana* (Krull, 1935), *Trivia monacha*, *T. arctica*, *Ocenebra erinacea*, *Nucella lapillus* (Fretter, 1941) and *Cremnoconchus* (Linke, 1935); the latter in *Lamellaria perspicua* and *Nassarius reticulatus* (Fretter, 1941). *Ocenebra erinacea* and *Nucella lapillus* demonstrate the formation of a closed prostate from the open type of *Littorina*, for the ventral lips of the groove which fuse to form the tube retain the double layer of epithelium at the point of fusion. Moreover, the closure is incomplete at the posterior end so that a ventral slit-like communication with the mantle cavity is retained. A similar opening is also present in the prostate of *Trivia arctica* and *T. monacha*, whereas in forms in which the prostate is a rather narrow tube it may communicate with the posterior end of the mantle cavity by a short duct as in *Nassarius reticulatus*, *Buccinum undatum* and *Lamellaria perspicua*. The presence of this opening in the higher mesogastropods as well as in the Stenoglossa offers further support for the suggestion that it plays some important role, probably in providing a means of escape for seminal fluid, and so preventing the possible rupture of the genital duct which might occur if an animal were forced to withdraw into its shell during copulation when the duct is filled with seminal fluid.

The closure of the seminal groove and also the development of the prostate appear to have occurred independently in different genera. In the Hydrobiidae, which are among the more primitive mesogastropods, the vas deferens is closed throughout its length and a sac-like prostate lies within the mantle cavity (Krull, 1935), whereas in the more highly organized cypraeids the duct may be represented by an open groove and Rau (1934) describes no prostate along its course.

The male genital duct of *Theodoxus* follows the same general plan as that of the mesogastropods in so far as there is a testis duct, which stores sperm in its distal coils, a short renal vas deferens, a closed prostate extending the length of the mantle cavity and a penis. The arrangement of the glands in the prostate is, however, more elaborate. With a closed prostate it is customary to have a closed genital duct leading forwards up the side of the head to the male opening at the tip of the penis, but in *Theodoxus*, and in other Neritidae, the male opening is at the anterior end of the prostate. In the short space intervening between genital aperture and penis, in *Theodoxus fluviatilis*, the

flow of seminal fluid appears to be guided by a furrow in the overlying mantle.

In *Lamellaria* the portion of the male duct which lies anterior to the prostate has sunk into the haemocoele and lengthened so that it is thrown into deep coils. These lead to a large penis which is folded beneath the mantle when not in use, and through which the duct pursues a straight course to open at the tip of a flagellum. The reserve coils of the genital duct, which lie within the haemocoele, are drawn upon during copulation when the penis and the anterior end of the body are distended. This condition contrasts with that of the closely allied genus *Trivia* in which, as in other mesogastropods and the Stenoglossa, the genital duct remains embedded in the body wall—it is distended with it during copulation and retracts with it when the animal withdraws into its shell—and at the same time the duct through the penis shows a zigzag course which is straightened on the expansion of this organ. In the opisthobranchs and the pulmonates at least part of the vas deferens has separated from the body wall and lies within the haemocoele, so that the condition in *Lamellaria* approaches this.

The female system

The pallial oviduct of the mesogastropod and stenoglossan is elaborated for the reception and storage of sperm and for the production of secretions, both nutritive and protective, in which the eggs are embedded before they leave the genital duct. The glandular elements are fairly constant in their disposition—subepithelial gland cells are invariably grouped in clusters beneath the deep lateral walls of the duct, leaving the narrow dorsal and ventral walls relatively thin. This arrangement is similar to that which is common in the prostate. The glands surrounding the posterior end of the pallial oviduct constitute an albumen gland, whilst, anteriorly, around the greater length of the duct they form either a jelly gland, as in *Littorina* and *Lacuna*, which embed their eggs in a gelatinous secretion, or a capsule gland as in the majority of the mesogastropods and in the Stenoglossa, all of which produce egg capsules. In the viviparous prosobranchs—*Littorina rudis* (Linke, 1933), *Paludestrina jenkinsi* (Krull, 1935) and *Viviparus viviparus*—the jelly gland or capsule gland forms a thin-walled brood pouch. The capsule gland may be composed of various types of secreting cells and their secretions mixed by ciliary currents on the walls of the duct. A composite fluid thus produced comprises the wall of the egg capsule in *Calyptraea chinensis*, *Trivia*, *Lamellaria* and the Stenoglossa. In *Littorina* (Linke, 1933), in which each egg is shelled after it has received its albuminous coat, a shell gland lies between the albumen and jelly glands.

In *Littorina* and the Stenoglossa a bursa copulatrix (Fig. 7B, *b*) at the distal end of the pallial oviduct receives the seminal fluid from the penis. Fertilization takes place at the innermost end of the duct where there is a second pouch, the receptaculum seminis (*rs*), serving as a more permanent

storage place for the sperm. The spermatozoa reach the receptaculum by a channel along the ventral wall of the oviduct (*vc*), arched over by longitudinal folds of epithelium. In the Stenoglossa the receptaculum is produced into glandular diverticula which form an absorptive organ for unwanted sperm. The position of the bursa varies. In certain hydrobiids (Krull, 1935) it lies close to the receptaculum at the inner end of the ventral channel and the latter functions as a vagina into which the penis is passed. In *Paludestrina jenkinsi* the ventral vaginal channel is closed off from the oviduct giving two openings to the exterior, a vaginal pore and a birth pore. A somewhat similar condition is found in *Theodoxus* in which the vagina with its associated bursa and receptaculum is cut off from the pallial oviduct in an antero-posterior direction, the receptaculum retaining connexion with the innermost end of the pallial oviduct by a narrow, coiled fertilization duct. A further complication in the female genital system of these highly specialized Neritidae is found in the fresh water *Septaria* and *Paranerita* where there are three external openings, the additional one being that of the 'ductus enigmaticus' which lies between the vaginal pore and the birth pore. This duct would appear to be formed by a subdivision of the vagina, and Bourne (1908) suggests that it may serve to admit water into the sperm sac (=bursa copulatrix), or it may be a means of expelling waste matter.

In a number of mesogastropods only the receptaculum is developed: it is a dorsal outgrowth of the initial part of the pallial oviduct where the eggs are fertilized, and seminal fluid is either deposited directly into it by the penis or close to its opening. The receptaculum may be a simple sac as in *Capulus* (Giese, 1915) and *Trivia monacha*, or subdivided to form diverticula, six in *Calyptraea* (Giese, 1915), *Lamellaria* and *Trivia arctica*, three in *Crepidula* (Giese, 1915). The duct of each diverticulum is muscular and helps the uptake of sperm during copulation and their later ejection for fertilization. Since the penis is long enough to reach the receptaculum no longitudinal sperm-conducting channel is developed. Sections of *Calyptraea* show that along the ventral wall of the pallial oviduct, against which the penis lies during copulation, there is a narrow longitudinal strip of cubical cells which are neither ciliated like the epithelium elsewhere, nor underlaid by glands. It would seem that this line represents the point of closure of the pallial gonoduct in the transformation from the male stage with an open seminal groove to the female stage in which the lips of the groove have fused to form a closed duct.

The temporary storage of sperm in diverticula of the renal oviduct of *Trivia monacha* is an unusual phenomenon, though in *Cremnoconchus* (Linke, 1935) the receptaculum itself is a longitudinal tract along the renal oviduct, stretching from the gonopericardial duct to the pallial oviduct.

In *Turritella communis* the pallial oviduct is open along its entire length. It resembles the prostate of the male in that the lateral walls of the channel are deep, thickened by subepithelial gland cells, joined together dorsally and open to the mantle cavity ventrally. Along the free edge of the left wall is a

thin flange (Fig. 6, *f*) which may lie under the free ventral edge of the right wall and so form a functionally closed duct with an anterior aperture near the mouth of the mantle cavity. At the inner end of the pallial oviduct there are two pouches one on either side of the longitudinal glandular tract. The pouch lying against the right wall, near the columellar muscle, is the smaller of the two and acts as a receptaculum seminis (*rs*) which appears to receive sperm from the inhalant, pallial water current, the principal use of which is as a feeding current (Graham, 1938). The left pouch is embedded in the thickness of

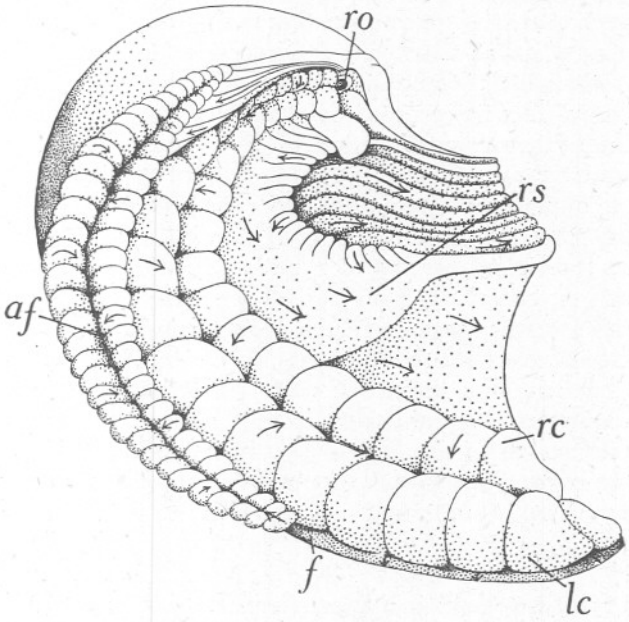

Fig. 6. *Turritella communis*. Upper part of the pallial oviduct. Arrows indicate ciliary currents. ×24. *af*, albumen gland and fertilization pouch; *f*, flange bordering ventral edge of left wall of pallial oviduct; *lc*, left wall of capsule gland; *rc*, right wall of capsule gland; *ro*, opening of renal into pallial oviduct; *rs*, receptaculum seminis.

the left wall (*af*), on the ventral edge of which it has a fairly extensive opening; anteriorly the lips of this opening fuse and are continuous with the flange bordering the free edge of the wall. In this second pouch the eggs appear to be fertilized and surrounded by an albuminous fluid. The lips of the pouch are mobile and may envelop the opening of the receptaculum for the collection of sperm and approach that of the renal oviduct to receive the eggs; both sperm and eggs have been found within it.

The open condition of the pallial oviduct of *T. communis* is certainly secondary and associated with the rigours of a ciliary food-collecting habit in a muddy situation. The mantle cavity must be isolated from the environment in order to avoid clogging of the gills, and this is effected by a curtain of tentacles

which surrounds the pallial opening (Graham, 1938). Should copulation be practised the introduction of the penis into the female aperture would impair this isolation. With an open pallial oviduct exposing the receptaculum the sperm may be transferred to the female by the inhalant water current obviating the necessity for a penis. The route by which the spermatozoa reach the receptaculum remains obscure. The animals are gregarious, and the spawning of large numbers will probably occur simultaneously. So far as is known no other living mesogastropod has a fully open pallial oviduct, and although the open condition in *Turritella* is secondary it represents the condition of an open glandular groove which in the course of evolution must have preceded a closed pallial duct. In the prostate of male mesogastropods, though not in the pallial oviduct of females, there is evidence of the method by which a closed duct has evolved from an open groove, first by the fusion of the epithelial of the free ventral edges of the groove (*Ocenebra*, *Nucella*) and then by the loss of these epithelia so that no trace of the line of closure can be found. It is no unreasonable assumption that the history of the pallial oviduct is similar, and, if so, then the reopening in *Turritella* has occurred along the same line as the original closure took place. In *Trivia* the female genital opening, which is ventral and not terminal as in other mesogastropods, and also the opening of the prostate in the male, probably represent points of incomplete closure of the duct. Posterior to the female opening there is a thin-walled channel along which the penis passes during copulation. This, and also the equivalent ventral channel leading to the receptaculum in other gastropods, correspond in position to the thin marginal strips which would border the free edges of a glandular channel as in *Turritella*, and are probably formed by the fusion of these lips.

The egg masses

The eggs of the mesogastropod and stenoglossan are rarely shed singly into the sea. They are always embedded in albumen provided by the initial part of the pallial oviduct, and then surrounded by a protective outer covering of varying thickness and consistency. Within these coverings the egg develops to a veliger or crawling stage; in no species is there a trochosphere. A great variety of spawn occurs reflecting variations in the histology of the glandular oviduct, and in the manipulation of the egg mass both within the duct and after it has left the genital aperture. In the spawn of *Littorina* and *Lacuna* (Hertling & Ankel, 1927) each egg is surrounded by albumen and is isolated from any companions first by a shell and then by a common mass of jelly in which all are embedded. From the pelagic capsules of *Littorina littorea* and *L. neritoides* veliger larvae are hatched, and from the fixed egg masses which are laid on weed either veligers, as in *Lacuna vincta*, emerge, or the young develop to the crawling stage and escape by biting their way through the jelly as in *Littorina littoralis* and *Lacuna pallidula*.

In other mesogastropods and in the Stenoglossa it is customary for the eggs

which are laid within any one capsule to share a common albuminous fluid and for the capsules to be attached. The thickness and composition of the capsule wall varies with the size of the capsule and the exposure to which it is submitted. In the rissoids (Lebour, 1937) the capsules are usually lens-shaped, little more than 0·5 mm. in diameter and with a wall which is tough, of inconsiderable thickness, and frequently quite transparent. Each is attached to the substrate by the flattened surface, and through a thin area in the centre of the upper surface the young break through on hatching. The eggs are individually enclosed in a delicate membrane and float together in an albuminous fluid. In most species the larvae hatch as veligers, but in *Cingula cingillus* and *C. semicostata*, which lay only one egg in each capsule, the young emerge in the crawling stage (Lebour, 1937). *Turritella* lays grape-like clusters of capsules each with a thread which fastens it to the substratum. The thread is a prolongation of the spherical wall of the capsule, which measures 0·6 mm. in diameter and is secreted around a group of eggs, in their albuminous covering, as it passes down the pallial oviduct. About ten or more capsules are laid in one cluster and their walls are thin and transparent so that the pinkish eggs are visible. In *Crepidula* and *Calyptraea* the delicate capsules are also stalked and fastened to a stone in clusters of about a dozen. Additional protection is given to the developing embryos by the parent covering the capsules with her body. Sections of the capsules of *Calyptraea* show that the outer covering is a composite secretion with an alveolar texture. A suture divides the wall into two equal halves, reflecting the bilobed nature of the capsule gland and demarcating the limit of secretion produced by each of its thick lateral lobes. Such a suture is a common feature of the egg capsules of prosobranchs being more pronounced in those with thicker walls. In the flattened spheroidal capsule of *Theodoxus* it is the line along which the wall breaks when the young mollusc escapes. The comparatively thick conchiolin wall of this capsule protects the embryo against the adversities associated with life in shallow streams and, as in all freshwater molluscs, the larval stage is suppressed.

Trivia monacha and *Lamellaria perspicua* lay spawn cases which are built on the same plan as those of the Stenoglossa, though they are less robust and not subjected to the same degree of exposure since the mollusc sinks them in the tissues of the compound ascidian on which it feeds. Each capsule is pot-shaped with a plug of mucoid material blocking the opening. The wall displays a fibrillar texture and is divided longitudinally into two equal halves by a suture, which also passes through the substance of the plug. As in the Stenoglossa the latter would appear to be secreted by the posterior tips of the capsule gland, a region of the pallial oviduct homologous with the shell gland of *Littorina*. In *Trivia* the rim of the capsule which projects above the surface of the ascidian is moulded by the ventral pedal gland of the female. Such a gland is also present in the Stenoglossa and serves to mould the egg case to its final form, harden it and fix it to the substrate.

The practice of embryonic cannibalism in the Stenoglossa has been described by Portmann (1925) for *Buccinum undatum* and *Nucella lapillus* and by Thorson (1935) for *Colus islandicus*. In these three species the most precocious embryos within a capsule devour their fellows and, thus supplied with nourishment, they develop to the crawling stage. Such cannibalism is permitted through the absence of a protective shell which in the Lacunidae encloses the egg together with its individual supply of albumen. According to Giard (1875) and Pelseneer (1911) nurse cells are also present in *Lamellaria perspicua*, though Ankel (1935) finds no evidence of such.

Although in the majority of prosobranchs the sexes are separate hermaphroditism occurs amongst the archaeogastropods and the mesogastropods. The hermaphrodite form may be protandrous, as in *Acmaea fragilis* (Willcox, 1898), *Crepidula fornicata* and *Capulus ungaricus* (Giese, 1915), the Scalidae (Ankel, 1926) and perhaps *Patella* (Orton, 1928), or it may be simultaneously male and female as in *Valvata*, *Pelseneeria stylifera*, *Velutina* and in all the Pyramidellidae (Ankel, 1936). In those groups which have evolved from the prosobranchs, the pulmonates and the opisthobranchs, the latter is the rule—the pallial genital duct is divided into sperm-conducting and egg-conducting regions, the former leading to the penis by which internal fertilization is accomplished, the latter being associated with massive glandular tracts which provide the albuminous and gelatinous coverings for the spawn. Egg capsules are not produced, but typically a number of eggs, each surrounded by its own portion of albumen, are embedded in a mass of jelly which is fastened to the substratum. The spawn may contain a large number of eggs which hatch as veligers, as in most tectibranchs and nudibranchs, or fewer and larger eggs which hatch as miniatures of the adult as in the Onchidiidae and pulmonates.

The pallial genital duct of the tectibranchs and pulmonates has separated from the mantle and comes to lie within the haemocoele. Apart from minor variations its fundamental plan, for such typical members of these as *Actaeon*, *Aplysia* and *Helix*, agrees remarkably with what has been described for the female genital duct of *Littorina* and the otherwise highly specialized Stenoglossa. To this same plan also conforms the hermaphrodite genital system of *Onchidella celtica*, a member of the Onchidiidae which may be regarded as an early offshoot from the main stem of the opisthobranchs (Fretter, 1943). In *Littorina* and the Stenoglossa (Fig. 7B) the pallial oviduct of the female is incompletely divided by internal longitudinal folds to give a spacious glandular channel (*c*), for the conduction of eggs and the manufacture of their protective coverings, and a narrow, ventral, thin-walled channel (*vc*) for the conduction of sperm from the bursa copulatrix (*b*) to the receptaculum seminis (*rs*); the short terminal part of the duct between the genital aperture and the opening of the bursa acts as a vagina (*v*). In *Actaeon tornatilis* (Fig. 7C), which is hermaphrodite, the pallial genital duct is similarly subdivided (Guiart, 1901). The sperm-conducting channel (*vc*, *vd*), separated from the oviduct by two

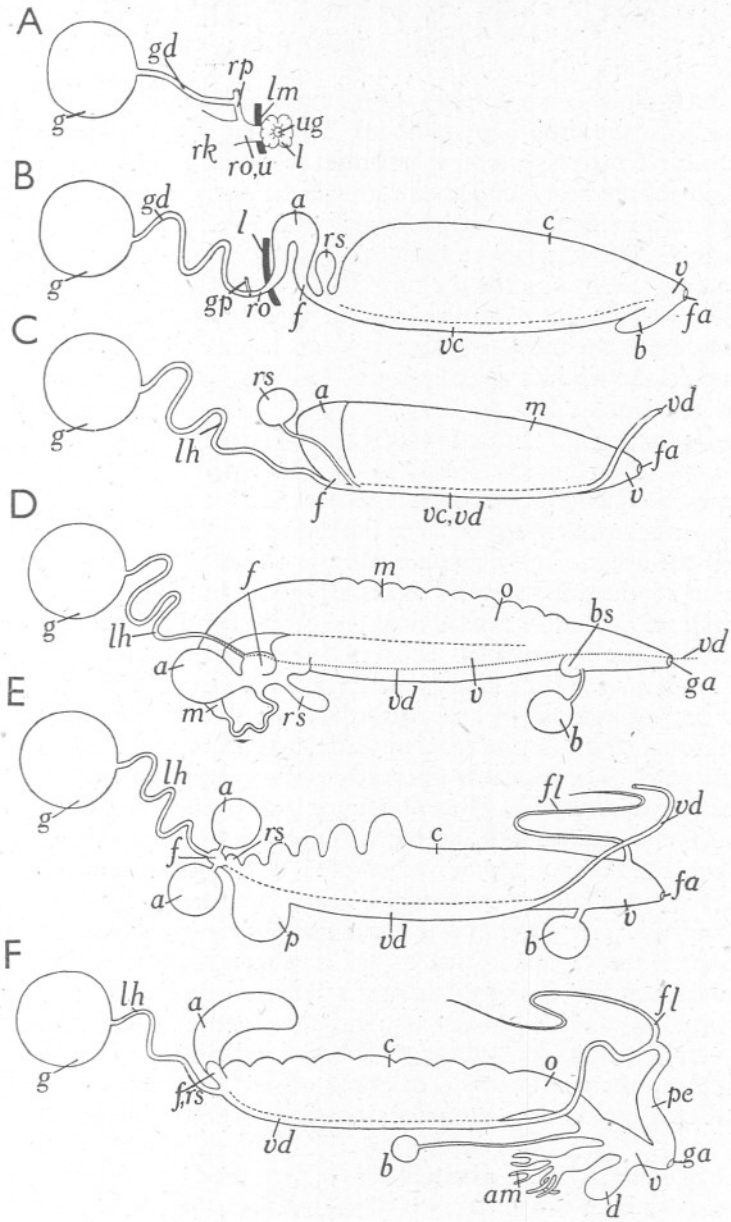

Fig. 7. Comparative diagrams of the genital ducts of: A, the Trochidae ♀; B, *Nucella* ♀; C, *Actaeon* ♀; D, *Aplysia* ♀ (after Eales); E, *Onchidella* ♀; F, *Helix* ♀. Broken lines represent incomplete separations between channels; the dotted line the vas deferens, an open groove throughout. *a*, albumen gland; *am*, additional mucous gland present in pulmonates; *b*, bursa copulatrix, commonly called spermotheca in D and F; *bs*, bursa seminalis; *c*, capsule gland, in F usually called female part of large hermaphrodite duct; *d*, dart sac; *f*, site of fertilization, in D, E and F a definite fertilization chamber; *fa*, female aperture; *fl*, flagellum; *g*, gonad; *ga*, common genital aperture; *gd*, gonadial duct; *gp*, gonopericardial duct; *l*, glandular lips; *lh*, little hermaphrodite duct of gonadial and renal origin; *lm*, inner limit of mantle cavity; *m*, mucous gland; *o*, oviduct; *p*, prostate; *pe*, penis; *rk*, right kidney; *ro*, renal oviduct; *rp*, renopericardial duct; *rs*, receptaculum seminis; *u*, ureter; *ug*, urino-genital aperture; *v*, vagina; *vc*, ventral sperm channel; *vd*, vas deferens.

longitudinal folds, communicates at its upper end with the receptaculum (*rs*) and also with the little hermaphrodite duct (*lh*); at its lower end, as it approaches the female aperture, it separates from the pallial genital duct, runs up the side of the head and passes through the penis to its tip. This tube (*vd*) has the sole function of a vas deferens, whilst the channel along the pallial genital duct appears to have a double role, that of a vas deferens and of a path for incoming sperm, since at the time of copulation sperm are introduced into it by the penis of the partner and from there they make their way to the receptaculum. No bursa copulatrix is developed. The subepithelial glands surrounding the oviduct are compacted to form an albumen gland (*a*) and a mucous gland (*m*).

In *Aplysia punctata* (Fig. 7D) the vaginal channel (*v*) and the vas deferens (*vd*) are two distinct tracts (Eales, 1921). The latter is the smaller of the two and arises as a longitudinal groove in the wall of the little hermaphrodite duct (*lh*), and runs forwards between the vagina on the one side and the mucous gland on the other. At their upper end the glandular oviduct separates from the sperm-conducting channels and is elongated and coiled, whilst along the mid-region of the pallial genital duct the three channels, oviduct, vagina and vas deferens, are incompletely separated from one another—three channels sharing a common wall. Towards the female aperture the vaginal channel and oviduct become completely one whilst the vas deferens retains its identity and passes through the aperture (*ga*), up the right side of the head and along the retractile penis. The vagina is associated with a receptaculum seminis (*rs*) at its inner end, and distally, where it merges with the oviduct, there is a second pouch (*b*) homologous with the bursa copulatrix of other gastropods. Eales refers to this second pouch as a spermotheca. It communicates with the vagina by a narrow canal, and at the junction of the two there is a glandular sac, the bursa seminalis (*bs*). Eales (1921) states that during copulation the penis may pass through the vagina so that its tip approximates to the base of the receptaculum, into which the sperm pass. 'There is always a certain amount of debris introduced with the sperms, and this, agglutinated by the secretion of the glands lining the wall of the bursa seminalis, is drawn up into the spermotheca, where it is either absorbed or discharged through the external aperture. No satisfactory evidence, however, has been obtained on this point.'

In the prosobranchs the albumen gland (Fig. 7B, *a*) comprises subepithelial glands surrounding the initial part of the pallial oviduct which is frequently the site of fertilization (*f*). In *Aplysia* and *Onchidella* these glandular elements are separated from the wall of the duct (Fig. 7D and E, *a*), the initial part of which is termed the fertilization chamber (*f*), and receives eggs from the little hermaphrodite duct (*lh*), sperm from the receptaculum (*rs*) and albumen from the associated gland.

In *Onchidella celtica* the little hermaphrodite duct (Fig. 7E, *lh*) is also functionally divided into two channels at its distal end. On approaching the

pallial genital duct the female channel separates from the male and opens into the fertilization chamber (*f*), whilst the male opens into the pallial vas deferens (*vd*). This separation is only for a microscopic distance. The oviduct and vas deferens unite again to form two relatively deep, parallel and glandular passages sharing a narrow, ciliated dorsal wall. Near its origin the vas deferens is dilated to form a pouch, the prostate (*p*), and the oviduct is produced into six diverticula along each of which the eggs must travel on their way to the genital aperture. The first, the smallest diverticulum, is the receptaculum seminis (*rs*) which overhangs the fertilization chamber. The sperm reach the receptaculum from the bursa (*b*), which is at the opposite end of the oviduct, by way of a ciliated tract along the thin and narrow wall which overlies the male and female passages. Thus, as in *Aplysia*, the incoming and outgoing sperm have separate tracts. Towards the distal end of the pallial genital duct, which owing to complete detorsion of the visceral mass is directed posteriorly, the vas deferens and the oviduct become separate tubes. The latter opens, by way of a vagina (*v*), into the much-reduced mantle cavity which is at the posterior end of the body between mantle and foot. The former is narrow, ciliated and non-glandular. It passes forwards along the right side of the body to reach the retractile penis which lies on that side of the head. The penis cannot be affected by the detorsion which brought the female opening to its posterior position; hence detorsion must be accompanied by the lengthening of the male duct. A flagellum (*fl*) which arises from the vagina, not far from the opening of the bursa, has glandular walls: it may be functionally equivalent to the bursa seminalis of *Aplysia*, the secretion from which is said to agglutinate waste matter from the genital tract. Such waste is frequently found in the bursa copulatrix giving it, as in *Aplysia*, a purple or pinkish hue.

In *Helix pomatia* the receptaculum seminis which receives the little hermaphrodite duct is also the fertilization chamber (Fig. 7F, *f*, *rs*). It is partly embedded in the albumen gland (*a*) from which it receives secretion. The pallial oviduct (*c*) and vas deferens (*vd*) are initially two channels along a single duct; distally they separate. The vas deferens passes to the retractile penis (*pe*) near which it is produced into a fine flagellum (*fl*) where spermatophores are formed. The glandular oviduct, which provides the calcareous coats for the eggs, passes to the vagina (*v*). From this there arises not only the bursa copulatrix (*b*) with its long connecting duct, but accessory structures specifically characteristic of snails—the dart sac (*d*) and mucous gland (*am*). The vagina and the penis open into a common genital atrium (*ga*), with an opening to the exterior far forwards on the right side.

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Summary

General mesogastropod structure

The reproductive ducts of male and female mesogastropods conform to the same plan. They may be divided into the following sections:

(1) a gonadial region forming in the male a seminal vesicle;

(2) a renal region which conveys the eggs and sperm over a very short distance to reach the posterior end of the mantle cavity;

(3) a glandular pallial region which passes to the mouth of the mantle cavity, and comprises an albumen gland, a capsule or jelly gland, a receptaculum seminis and a bursa copulatrix in the female; and a prostate in the male from which a narrow duct, also developed from a fold of epidermis, runs up the right side of the head to the penis.

Details of Trivia *and* Lamellaria

In *Trivia* and *Lamellaria* no bursa copulatrix is developed on the female duct. Owing to the lateral position of the female genital aperture in *Trivia*, and to the large size of the penis and its possession of a flagellum in *Lamellaria*, the sperm is deposited in contact with the receptaculum seminis which opens into the albumen gland at the inner end of the pallial oviduct. This is the site of fertilization. The egg capsules are the product of the pallial duct, each is basin or vase-shaped, filled with albumen in which numerous eggs float, and sealed with a plug at the external opening; their mode of formation would appear to be similar to that of the Stenoglossa. In both species of *Trivia* a ventral pedal gland moulds the capsule into its definitive shape and deposits it in the tissues of a compound ascidian.

Details of Turritella

In *Turritella communis*, a specialized mesogastropod, the male and female pallial ducts are open, bilobed tracts. No penis is developed in the male and the sperm are collected in the spermotheca of the female from the inhalant pallial water current. This open condition of the duct is secondary and is associated with the rigours of a ciliary feeding habit carried out in a muddy situation.

Details of Theodoxus

Theodoxus fluviatilis, although grouped amongst the archaeogastropods, has male and female genital ducts resembling those of the mesogastropods both in structure and function. In the female, however, the vagina is separate from the oviduct communicating with it only indirectly through a narrow tube which conducts sperm from the bursa copulatrix to the posterior end of the pallial oviduct. In the latter the lens-shaped capsules are produced, each with several eggs encased in a tough, resistant conchiolin wall. The lid of the egg case is reinforced with diatom cases and sand grains from the crystal sac, which collects these from the rectum and transfers them to the oviduct. From

each capsule only one individual emerges. In the male the prostate is of complex structure and extends to the genital aperture at the opening of the mantle cavity. Between the genital opening and the penis the seminal fluid passes along a gutter in the overlying mantle.

General archaeogastropod structure

In archaeogastropods in general the course of the eggs from the gonad to the mantle cavity is through a gonadial duct and the duct of the functional right kidney. The eggs are shed singly, their protective coats being a secretion either of the ovary or of the egg itself. Although a pallial section is normally absent, indications of its formation are found in *Gibbula* and *Monodonta* in the form of glandular lips surrounding the genital aperture and providing lubrication for the passage of the eggs, and in *Calliostoma* in the form of a short bilobed glandular tube which provides the gelatinous ribbon in which the eggs are embedded.

Comparison of mesogastropods, opisthobranchs and pulmonates

The evolution of the hermaphrodite genital ducts of the pulmonates and opisthobranchs from the female genital duct of their prosobranch ancestors would necessitate little structural modification: the development of sperm as well as ova in the gonad; the use of the ventral sperm channel of the pallial oviduct as a vas deferens, as well as a vaginal channel, and its extension forwards to a penis. Such a condition is found in *Actaeon*, *Aplysia*, and the abberrant opisthobranch *Onchidella celtica* and, with the addition of certain structures peculiar to snails, in *Helix*.

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A COMPARISON OF THE FEEDING MECHANISMS OF *CALMA GLAUCOIDES* AND *NEBALIOPSIS TYPICA*

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(Text-figs. 1–3)

Introduction

The feeding mechanism of the nudibranch *Calma glaucoides* (Alder & Hancock) has been described by Evans (1922) and that of the crustacean *Nebaliopsis typica* (Sars) by Cannon (1931) and myself (1943). *Calma* is seasonally relatively abundant in the coastal waters of parts of Europe where it is found attached to the eggs of certain fishes. It is known to feed exclusively on these eggs and young embryos. *Nebaliopsis* is a deep pelagic form from the Antarctic Ocean. It has been obtained only rarely and cannot be observed alive and in its natural environment. Two specimens were available for examination. Thus complete certainty about the diet is impossible. The external features and mouth parts were described by Cannon and the structure of these suggested that *Nebaliopsis*, like other known Nebaliacea, might be a filter feeder. Examination of the morphology of the gut and its contents indicates that this is very improbable. There is no mechanism for the sorting out of particles of different sizes such as is found in other filter feeders. The food passes into a blind sac and there is no apparent means by which the large quantities of indigestible material taken in when particles are filtered from the water indiscriminately might be evacuated. In addition to this negative evidence the food mass found in the large storage chamber of one specimen was completely homogeneous and structureless, its appearance in section suggesting coagulated yolk. It has therefore been suggested that *Nebaliopsis* feeds on fish eggs found floating in the deeper water layers. Some eggs were caught along with all the specimens of *Nebaliopsis* which have so far been obtained.

Both *Calma* and *Nebaliopsis* have evolved certain peculiar characteristics in which they differ from their nearest relatives and which may be functionally associated with this specialized type of food. Thus these two species, one a mollusc and the other a crustacean, provide an interesting example of parallel adaptation.

As both species have already been described in detail the descriptions and diagrams given here are intended only to clarify the comparison which follows.

I wish to thank Prof. H. Graham Cannon, F.R.S., for drawing my attention to *Calma* and for his criticism and advice.

CALMA GLAUCOIDES

Calma feeds on eggs of various species of shore living fish, which are laid on the sea floor in coastal waters. Once the eggs have been found *Calma* crawls on to them and, according to Evans, sticks tightly by means of its 'face' which 'fits like a hood over the egg'. It sucks a part of the egg membranes into its mouth by the action of the powerful retractor muscles of the buccal mass (Fig. 2, A, B, *ret*). These muscles enlarge the buccal cavity and at the same time draw the jaws out laterally while the retractor muscles of the odontophore draw the radula diagonally upwards and backwards. The ridges on the lips and oral hood grip the slippery surface of the egg while the jaws are brought together by bands of muscle which stretch between them on their ventral sides, connecting them together along the whole of their length except in the region of the mouth (Fig. 2 B, *vent*). Muscles interwoven with the retractors serve to keep the biting edges of the jaws tilted towards the mouth (Fig. 2, A, B, *j.m*). Simultaneously the radula is lowered to meet the jaws and may be protruded out of the mouth. This movement is caused by the transverse muscles which stretch between the two sides of the odontophore (Fig. 2 A, *t.o*). Thus the three sharp biting edges come together and nip the egg membranes between them. Pressure is exerted by the oral hood (Evans, 1922) and the contents of the egg are sucked through the slits into the capacious stomach or 'gastric sac' from which diverticula run into the cerata. Here storage, digestion and absorption take place. There is no anus. Little indigestible waste material is present, the amount depending on the stage of development of the embryos eaten, and the residue from the meals accumulates slowly, the 'fine brown granules' being compressed into a mass which does not mix with the next meal. Apparently this accumulation is never sufficient to inconvenience the animal.

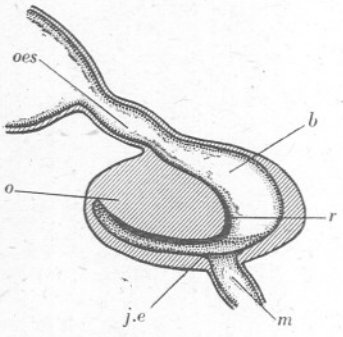

Fig. 1. *Calma*. Diagrammatic view of the left half of the buccal mass. *b*, buccal cavity; *j.e*, biting edge of jaw; *m*, mouth; *o*, odontophore; *oes*, oesophagus; *r*, radula.

NEBALIOPSIS TYPICA

As already mentioned the feeding of *Nebaliopsis* cannot be observed, and thus its mechanism must necessarily be hypothetical. The accumulated evidence suggests that the process is as follows.

An egg is gripped by means of the long recurved setae on the mandibular palps (Cannon, 1931) and held close to the mouth. The dilator muscles on the walls of the oesophagus and the dorsal side of the foregut provide the suction necessary to draw part of the egg through the mouth. The action of these muscles also draws apart the heavily chitinized biting surfaces of the

'lateral thickenings' and the 'dorsal ridge'. The mandibles are soft and useless for biting, thus the egg is not punctured outside the mouth. The 'plated' walls of the oesophagus are then brought together by the circular muscles of this region and grip the slippery surface of the egg, while the

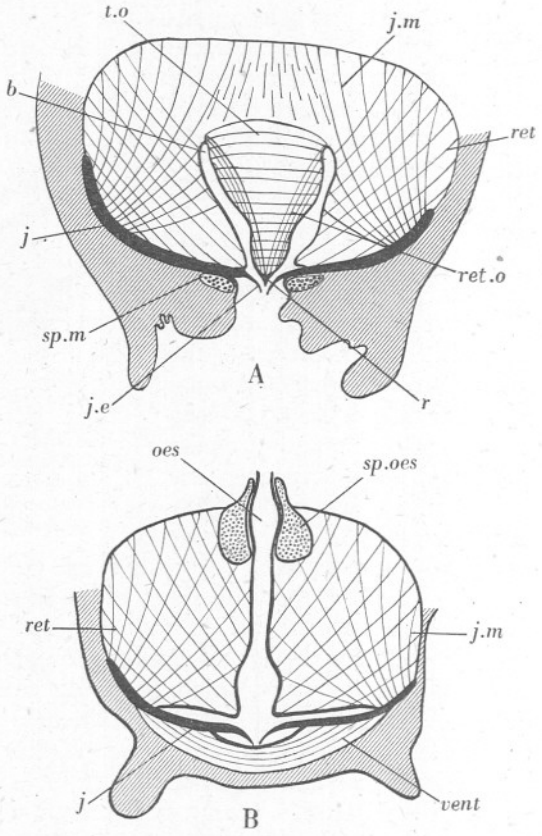

Fig. 2. *Calma*. A, semi-diagrammatic section of the buccal mass passing through the mouth and odontophore. B, semi-diagrammatic section of the buccal mass anterior to section A and passing through the oesophagus. *b*, buccal cavity; *j*, jaw; *j.e*, biting edge of jaw; *j.m*, muscles attached to the angle of the jaw; *oes*, oesophagus; *r*, radula; *ret*, retractor muscles of the buccal mass; *ret.o*, retractor muscles of the odontophore; *sp.m*, sphincter muscles of the mouth; *sp.oes*, sphincter muscles of the oesophagus; *t.o*, transverse muscles of the odontophore; *vent*, ventral transverse muscles.

circular muscles of the cardiac and pyloric regions of the foregut cause a biting action of the dorsal ridge against the lateral thickenings. Thus two slits are cut in the egg membranes through which the contents of the egg can be sucked. This then passes into the large digestive sac for storage, digestion and absorption. Digestive glands open into the anterior end of this sac by a number of small apertures. The intestine has an exceedingly narrow lumen

and leads from the anterior end of the digestive sac to the anus. It is very improbable that much waste matter will pass through it as, in addition to the narrowness mentioned, there are no suitable muscles to force evacuation of the blind digestive sac.

Comparison and Discussion

Method of attacking eggs

Fish eggs are very slippery objects and must be firmly gripped. *Calma* applies its 'face' tightly to the egg while *Nebaliopsis* probably uses its mandibular palps.

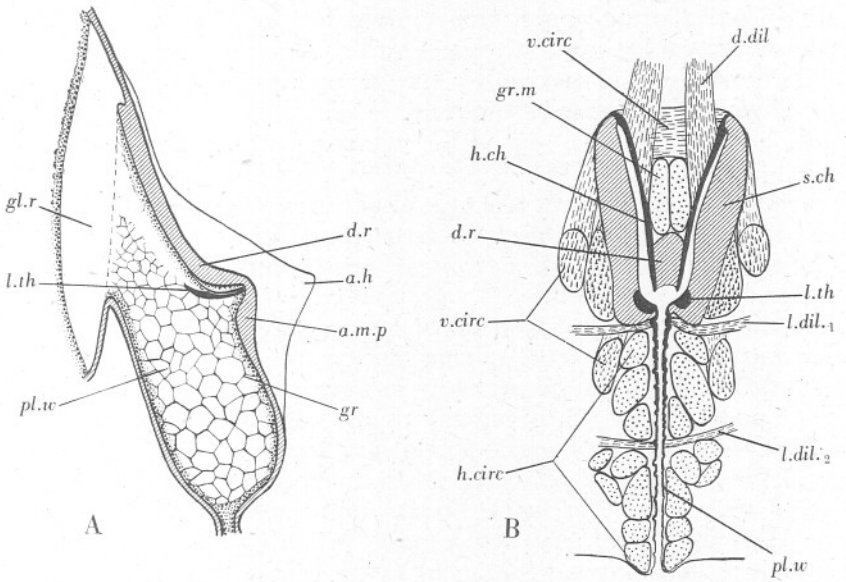

Fig. 3. *Nebaliopsis*. A, diagrammatic view of the left half of the fore-gut. B, semi-diagrammatic section of the oesophagus and foregut. *a.h*, anterior horn; *a.m.p*, anterior median projection; *d.dil*, dorsal dilator muscles; *d.r*, dorsal ridge; *gl.r*, glandular region; *gr*, grooves in chitin; *gr.m*, groove muscles; *h.ch*, hard chitin of dorsal ridge; *h.circ*, horizontal circular muscles; $l.dil._1$, $l.dil._2$, lateral dilator muscles of the oesophagus; *l.th*, lateral thickenings; *pl.w*, plated walls of the oesophagus; *s.ch*, soft chitin of lateral walls; *v.circ*, vertical circular muscles.

Piercing of the egg membranes

The egg once 'caught' is too large and slippery a sphere to be swallowed whole by either of the animals concerned, but it cannot be chewed in the usual way lest the liquid or semi-liquid contents be washed away and wasted. The membranes must therefore be pierced in such a position that there is little chance of loosing the contents of the egg. The structures concerned are extraordinarily similar in design and homologous in function.

In each case a part of the membranes is sucked in through the mouth and gripped by corrugated surfaces. In *Calma* these are formed by folds of the skin around the mouth and in *Nebaliopsis* by the curious 'crazy-paving' of

the chitin of the oesophagus which forms plates over each cell and grooves over each intercellular junction (Fig. 3 A, *gr*).

The similarity of outline of the cavities into which the membranes are drawn is obvious from a comparison of Figs. 2 A and 3 B. Both *Calma* and *Nebaliopsis* have one median and two lateral hard biting processes with deep channels between them in which folds of the egg membranes can lie. In *Calma* each of these processes has a sharp edge so that when the jaws come together and the radula meets them three slit-like incisions will probably be made. (*Note.* The sharp edges of the jaws appear to be equivalent to the 'strongly cuticularized ventral groove' described by Evans.) In *Nebaliopsis* the dorsal process has two sharp edges each of which bites against one of the lateral thickenings thus making two slits, or perhaps four if the double folds of membrane are perforated completely.

Removal of the contents of the eggs

Calma has been shown to take eggs at all stages of development. Without more material it is impossible to be certain on this point in *Nebaliopsis*, but the homogeneity of the food mass in the two specimens examined indicates that yolk only is swallowed.

The yolk or young embryos can be sucked through the slits in the egg membranes and passed to the storage chamber by the action of the musculature of the walls of the buccal cavity in *Calma* and of the oesophagus and stomach in *Nebaliopsis*. These muscles are the same as those used to produce the original suction on the membranes and to bring the biting parts together. In addition *Calma* has a sphincter muscle round the oesophagus which will prevent back suction from the gastric sac. In *Nebaliopsis* the circular muscles probably contract in turn, not simultaneously, thus causing a wave of motion such as is visible in living specimens of *Nebalia bipes*. This action would direct the flow of fluid in the correct direction.

Storage

Suitable eggs are only found at certain seasons of the year and therefore both *Calma* and *Nebaliopsis* must be prepared to take in large quantities of food while it is available and store it while it is slowly digested and utilized as required.

In *Calma* a definite cycle of feeding and reproduction has been demonstrated. The large gastric sac provides the storage chamber. This becomes enormously distended during the feeding period till it almost completely fills the body, while diverticula from it stretch into the cerata which also become swollen.

Nebaliopsis similarly has an enormous storage sac which like that of *Calma* almost completely fills the body. Owing to the chitinized body wall there is a limit to the distension possible and the size of the sac is probably maintained even when empty.

Digestion and absorption

In *Calma* salivary glands are present with ducts opening into the buccal cavity at the posterior ventral edges of the lateral pads, and the epithelium lining the cerata is also glandular. Secretion from these glands passes on to the food and causes partial digestion in the gastric sac. The thick fluid which results from this process passes into the cerata for final digestion and absorption.

In *Nebaliopsis* glands open into the anterior end of the digestive sac. Thus their secretion can be added to the food as it enters the sac and be mixed with it before storage so that continuous slow digestion of the whole food mass is possible. Absorption appears to take place over the entire surface of the sac.

Evacuation of waste

In correlation with the fact that fish eggs contain very little that is indigestible *Calma* has no anus and allows the small amount of residual matter to accumulate, while *Nebaliopsis* has such an extremely narrow intestinal lumen that it is doubtful whether waste matter could pass along it. In addition the attachment of the intestine to the anterior end of the large blind diverticulum and the absence of suitable musculature for the evacuation of the diverticulum make the use of the intestine most improbable.

Conclusion

The typical Eolid feeds by scratching particles of food from a solid surface by means of the radula. The conversion of this scratching action into a piercing one involves little structural change. The typical Nebaliacean, however, is a filter feeder and considerable adaptation is necessary to produce the piercing action. In both groups the typical forms feed almost continuously and prolonged storage of food is unnecessary, while in the specialized egg feeders storage is essential and cavities are provided for this purpose.

To the continuous feeders, whose food contains much indigestible material, evacuation of waste is essential, while in the egg feeders this is not so.

Thus the characters in which *Calma glaucoides* and *Nebaliopsis typica* differ from typical members of their groups may be associated with their specialized diet. Functional necessity has made the arrangements extraordinarily similar in plan in spite of the immense general difference between a mollusc and a crustacean.

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ON THE HABITS AND ADAPTATIONS OF *ALOIDIS (CORBULA) GIBBA*

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(Text-figs. 1–14)

CONTENTS

INTRODUCTION

Aloidis (*Corbula*) *gibba* (Olivi) is a small marine eulamellibranch belonging to the Myacea. It is an inhabitant of muddy gravel substrata from below the Laminaria zone to depths of some 80 fathoms, and ranges from Norway to the Mediterranean (Jeffreys, 1865). It is so typical a member of the bottom fauna that Forbes and Hanley (1853) remark that 'its extreme prevalence is a subject of almost petulant complaint from the habitual dredger'. The genus *Aloidis* has many species widely distributed on suitable substrata throughout the world, especially in the tropics, but there are a still greater number of fossil species ranging from the lower Oolite. Despite the abundance of *A. gibba* in British waters, little is known of its habits and nothing of the adaptations which have been responsible for its outstanding success over so wide a period of space and of time as a member of the mud fauna.

Specimens were obtained in adequate numbers by dredging in depths of between 9 and 12 fathoms in Balloch Bay, Isle of Cumbrae, and these were later examined in the Millport Laboratory. Acknowledgements are gladly made for assistance from the Director of the Station, Mr R. Elmhirst, and from members of the staff. The author is also indebted to his colleague, Dr H. F. Steedman, for histological assistance.

Shell Form

The specimens collected ranged in size from 0·5 cm. in length up to a maximum of 1·2 cm. long by 0·9 cm. deep. The shell is strikingly asymmetrical, the right valve being, in the words of Jeffreys (1865), 'much larger and more gibbous than the left which it overhangs to a considerable extent'. A variety of Lamellibranchia are inequivalve, e.g. the Anomiidae, many Pectinidae, *Spondylus*, *Ostrea* and the Chamidae. But these are all attached,

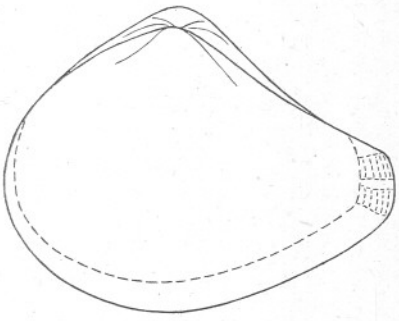

Fig. 1.

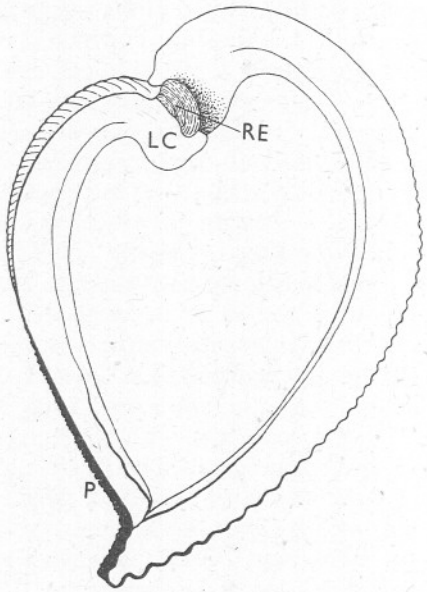

Fig. 2.

Fig. 1. *Aloidis gibba*, shell viewed from left side. ×4. Broken line indicates the extent of calcification in the left valve with the calcified marginal plates protecting the siphons shown.

Fig. 2. *A. gibba*, radial section through shell viewed from posterior showing resilium and hinge dorsally and intucking of uncalcified margin of the left valve ventrally. ×12. *LC*, left cardinal tooth; *P*, thick periostracum on left valve; *RE*, resilium.

by byssus or by cementation, with one valve underneath except for the free-living Pectinidae, such as *Pecten maximus*, which retain the horizontal disposition of the shell valves as a legacy from former byssal attachment (Yonge, 1936). Apparently *Pandora*, of the habits of which nothing is known, is the only lamellibranch apart from *Aloidis* in which an inequivalve shell is *not* associated with its horizontal disposition.

The relative size of the shell valves is shown in lateral view in Fig. 1 and in section in Fig. 2. It will be observed that, although the left valve fits into the right one, this is due not only to the smaller size of the former but also to a lack of calcification in the marginal zone. Approximately the outer ninth

of the valve consists exclusively of periostracum which, as shown in Fig. 2, fits tightly against the marginal region of the right valve when the shell is closed. This interesting point appears to have been overlooked by previous workers, none of whom, however, has undertaken a special study of this genus. Both Forbes & Hanley and later Jeffreys note the especially dense and somewhat fibrous periostracum ('epidermis') around the marginal area of the smaller valve (Figs. 2, 3, *P*) and to a less extent of the larger one. It is relatively soft and so rapidly worn away on the exposed, convex surfaces of both valves. In the posterior region of the marginal periostracum of the left valve there are two calcified areas (Fig. 1) which give added protection to the siphons when these are extruded. These areas consist of overlapping scales of calcareous matter. No previous reference to their presence in *A. gibba* has been found. They are not visible externally although easily seen from within, but they will be rubbed off with the periostracum in a dead shell. A very similar accessory area in the left shell valve, but apparently of a more solid character, has been described by Martin (1879–80) and Vincent (1890, 1909) in fossil species of *Corbula* and later by Martin (1918) in the recent *C. tunicata*. These authors also regarded this area of calcification as affording protection to the siphons.

Owing to the extent to which the margins of the shell valves are in contact when the adductors are contracted, the mantle edge is withdrawn some distance from the edge of the shell as shown in Fig. 3 A. The mantle edge has the typical tri-lobed character (see Yonge (1936) for details and references), the outer lobe (*OL*) being concerned with the secretion of the outer, calcareous layers of the shell and the periostracum (*P*) arising from the pit between it and the middle lobe (*ML*) the outer surface of which serves to guide the periostracum. This is thrown into folds on the outer surface of the shell and its secretion appears to be continuous because, as shown in Fig. 3 A, it lines the inner side of the marginal regions of the shell valves. This internal layer of periostracum is most developed at the two ends of the shell. Apart from the fact that the left mantle edge does not (after fixation) extend quite so far as the right one the two edges are essentially similar. But the absence of marginal calcification in the left shell valve indicates that the mantle edges must function somewhat differently when the valves are being enlarged. The right mantle edge will then secrete the outer calcareous layers of the shell (the nature of which has not been investigated; see Trueman (1942) for details and literature) and the periostracum at the margin together as in lamellibranchs generally. The probable positions of the outer and middle lobes of the mantle edge during this process are shown in Fig. 3 B, *r*. But the left mantle edge must be capable of laying down periostracum beyond the zone of calcified shell. A possible method whereby this could be brought about is indicated in Fig. 3 B, *l*. The outer lobe of the mantle edge is shown adding to the outer calcareous layers of the shell while the middle lobe, greatly extended (easily possible in lamellibranchs by distension with blood) guides the thick periostracal thread further out to extend the effective margin of the shell valve. The great variation in form and

function found in the marginal mantle lobes of the lamellibranchs makes this suggestion not improbable.

The shell is very thick as shown in Fig. 2, and the inner calcareous layer is especially dense. Jeffreys records numerous instances of shells bored by *Natica* in which the gastropod seems unable to penetrate beyond the somewhat chalky outer layers. These observations have been abundantly confirmed.

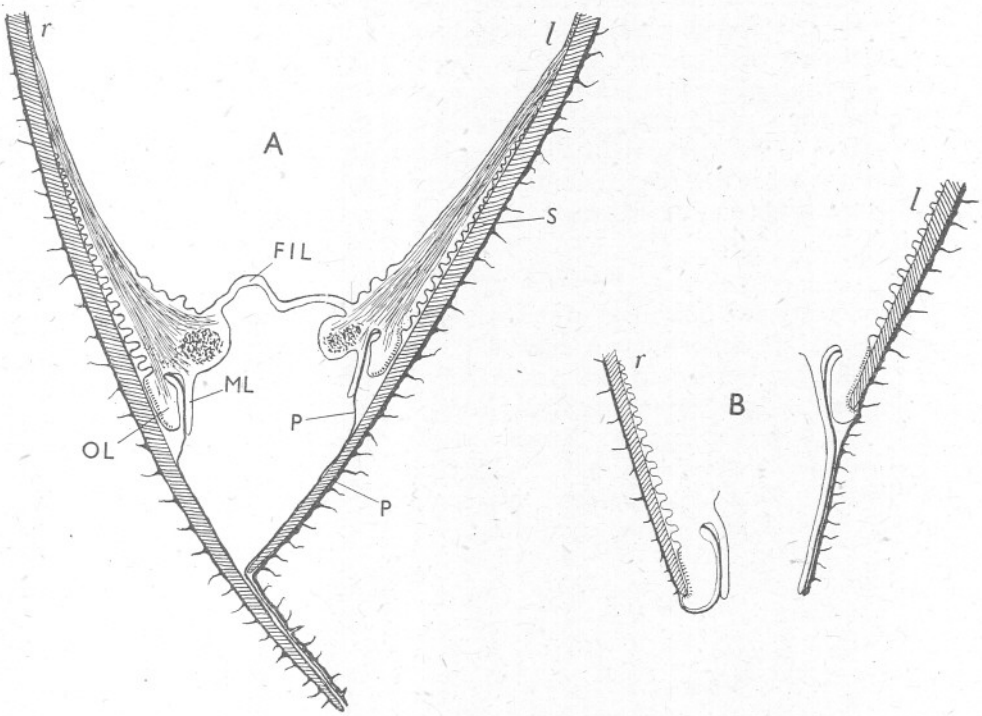

Fig. 3. *A. gibba*, transverse sections through margins of shell valves and mantle, viewed from anterior. A, semi-diagrammatical representation of conditions when shell closed and mantle edges withdrawn; B, indication of possible manner in which asymmetry of valves produced. × 100. *FIL*, fused inner lobe of mantle edge; *ML*, middle lobe, outer surface of which guides periostracum; *OL*, outer lobe which secretes outer calcareous layers of shell; *P*, periostracum; *S*, shell. *r*, *l*, right and left valves.

The hinge mechanism consists of a prominent recurved cardinal tooth in the right valve (Fig. 7, *RC*) and a more posterior, spoon-shaped cardinal in the left valve (Fig. 2, *LC*) with elongated lateral teeth on either side of each (Fig. 7). Into the cavity of the left cardinal tooth there fits the internal elastic ligament or resilium (Fig. 2, *RE*). This is roughly triangular in section (Fig. 7, *RE*) and is attached on the other valve within a cavity posterior to the right cardinal tooth as shown in Fig. 2. The partly external fibrous ligament (Fig. 7, *EL*) is a distinct structure lying dorsal to the resilium but is poorly

developed and hard to distinguish. If the ventral region of the shell valves are broken away, the tissues removed and the resilium then cut through from below, the valves drop apart because the external ligament unaided is too weak to hold them together. *Aloidis gibba* thus approaches the condition found in *Pholas* and other Adesmacea in which the external ligament has been lost and the shell valves are consequently enabled to rock in the antero-posterior axis, on the fulcrum of the condensed resilium (Anthony, 1905). This is an essential feature in the boring mechanism of these animals. In *Aloidis gibba* the reduction of the external ligament, although it also occurs to a less extent in allied members of the Myacea, is possibly associated with the asymmetry of the shell valves. A slight antero-posterior rocking action may be needed to enable the left valve to fit within the right one. The resilium is relatively long from one valve to the other and so permits the extensive hinge movements needed to enable the margins of the left shell valve to tuck into those of the right valve.

Habitat and Habits

A. gibba is a typical inhabitant of thick muddy sand with admixed gravel and small stones. In Balloch Bay it inhabits this type of substratum in company with such other burrowing mollusca as *Nucula nucleus* and *Nuculana* (*Leda*) *minuta* (herbivorous deposit feeders; Yonge, 1939); *Aporrhais pes-pelecani* (herbivorous deposit feeder; Yonge, 1937); *Turritella communis* (ciliary suspension feeder; Graham, 1938; Yonge, 1946); *Venus* spp. (ciliary suspension feeders); *Cuspidaria cuspidata* (carnivorous deposit feeder; Yonge, 1928) and species of *Natica* (boring carnivores).

Fig. 4. *A. gibba*, with foot extruded. ×4.

When placed on softer mud without gravel, *Aloidis gibba* appears to find difficulty in maintaining its siphons flush with the surface. The same difficulty has been noted in the case of *Aporrhais pes-pelecani* (Yonge, 1937) and *Turritella communis* (Yonge, 1946). On the other hand *Aporrhais serresiana*, specialized for life in soft mud, experiences difficulty in burrowing in a stiffer substratum (Yonge, 1937).

Placed on its normal substratum, *Aloidis gibba* extrudes the thin foot, rounded in cross-section, to a distance which may exceed the length of the shell (Fig. 4). A thin byssus groove extends along the under (posterior) surface (see Fig. 8). Cilia line the sides of this groove and beat towards the body. Their function is not obvious. In burrowing, the foot pushes almost vertically down and the

animal is drawn after it as a result of a series of intermittent but powerful contractions of the pedal muscles. At each of these the shell is erected almost vertically to fall back to an angle with the horizontal which gradually increases as burrowing progresses. When finally buried the long axis of the body is usually more or less vertical. The posterior end of the shell is then flush with, or slightly below, the surface of the mud. The last act of the foot is to plant a single byssus thread on a suitable piece of gravel or stone. Anchored in this way, the animal appears seldom to change position unless forcibly disturbed.

The process of burrowing is slow. For instance, an animal 1 cm. long took about 30 min. and, owing to the long intervals between successive contractions of the pedal muscles, the process is often slower. On the other hand specimens of *Abra abra* of about the same shell length disappeared below the surface in less than a minute. It is interesting to compare the two species, *A. gibba* a sedentary suspension feeder and *Abra abra* a deposit feeder which has frequently to change its feeding area (the inhalant siphon actively draws in the surface deposits). The former has a stout rounded shell and makes slow and difficult progress into the stiff substratum whereas the latter has a much flattened shell and foot and slides quickly into the softer mud it inhabits. The same contrast in habits is found in the gastropods *Turritella communis* and *Aporrhais pes-pelecani* which feed respectively in the same two ways (Yonge, 1946).

Siphons

As shown in Figs. 5 and 7, the siphons of *Aloidis gibba* are very short. The common sheath is fringed with some forty or more short tentacles which, when the animal is buried, extend outwards over the surface of the mud (Fig. 5) much as in the septibranch *Poromya* (Yonge, 1928). The inhalant siphon has a relatively large, rounded opening surrounded by a further ring of up to twenty tentacles which point upwards and inwards. The exhalant siphon is tubular, as noted by Forbes and Hanley and by Jeffreys, with a terminal opening smaller than that of the inhalant siphon. In an animal 1 cm. long this siphon was 1·75 mm. in length. The tentacles are colourless, but the siphons generally are flecked with reddish orange and opaque white areas, the edge of the mantle below being fringed with a dark brown band.

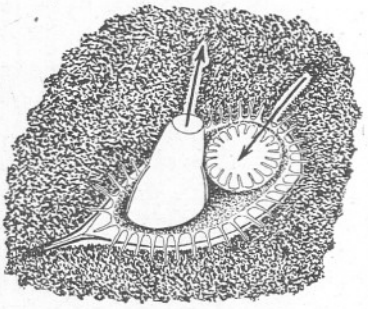

Fig. 5. *A. gibba*, siphons fully open after the animal has burrowed in the substratum. ×20. Arrows indicate the direction of the inhalant and exhalant currents.

The activities of the siphons are interesting and highly characteristic. When the shell valves separate and the siphons are extruded, the inhalant siphon opens first and water is drawn in owing to the increase in the volume of the

mantle cavity. The water passes through the ctenidia into the exhalant chamber and, apparently when a certain pressure of water is reached, the exhalant siphon, hitherto withdrawn, is extruded and opens. At the same time the inhalant siphon opens to its fullest extent (Fig. 5). An exceptionally powerful inhalant current is set up owing to the relatively large size of the ctenidia (see later section). Much sand and mud are frequently drawn in with this; the tentacles surrounding the inhalant opening are very insensitive, although they do appear to have some function as strainers by preventing the entrance of relatively very large particles. But a continuous stream of sediment may be introduced into the opening, by pushing it in from the surrounding substratum with a needle, without causing the siphon to close.

Eventually this continual inward passage of sediment does result in the contraction of the adductor muscles and the closure of both siphons. The exhalant siphon is very sensitive to contact stimuli closing immediately when

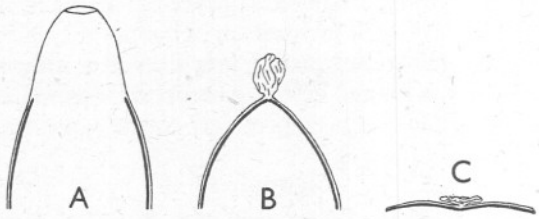

Fig. 6. *A. gibba*, diagrams to illustrate mode of closure of the exhalant siphon. A, open; B, partial contraction of the closing muscles; C, complete contraction.

touched with particles of mud or by the tip of a needle. By stopping the free passage of water through the mantle cavity, such closures cause a temporary stoppage of the inhalant current although the siphon remains open.

Closure of the exhalant siphon is produced by the contraction of two paired bands of muscles, one on the dorsal and the other on the ventral side. These muscles extend from the base along rather more than half the length of the siphon (Figs. 5, 6), a shallow encircling concavity marking their termination. The process of siphonal closure is indicated, semi-diagrammatically, in Fig. 6 A–C. In partial closure, which frequently follows mechanical stimulation, the muscles arch inwards until they meet while the distal regions of the siphon are gathered into a folded mass (B). This is usually followed, after a few seconds, by re-opening (as in A). More powerful external stimulation, and also stimulation from within the mantle cavity, causes the complete contraction indicated in C. The muscles then become horizontal, the proximal region of the siphon collapsing while the distal portion is gathered into a compact folded mass. Subsequent contraction of the siphonal retractors brings about a folding of the common siphonal sheath over both siphons and their complete withdrawal within the protection of the shell. On relaxation

of the muscles the siphons are again protruded, opening of the inhalant again preceding that of the exhalant siphon.

The form of the exhalant siphon and the restricted opening which concentrates the exhalant current combine to direct the powerful stream of water well clear of the inhalant opening, as indicated in Fig. 5, and also prevent stirring up of the soft surface deposits.

The relatively very large quantities of bottom material which must normally be carried in with the inhalant current lead to great accumulations of this within the inhalant chamber where, as in lamellibranchs generally, it is consolidated with mucus into pseudo-faeces and carried by ciliary currents along the ventral side of the mantle cavity to the posterior end where it collects (Fig. 7, *PS*). From time to time these masses are removed in the usual manner, namely by sudden contractions of the 'quick' portions of the two adductors which are well developed (Fig. 7, *AQ*, *PQ*). If the accumulations are small, partial contractions occur but on occasions the inhalant chamber must be almost filled with pseudo-faeces and then more powerful contractions are needed. Here the asymmetry of the shell probably plays its part by permitting a much greater reduction in the size of the cavity with a correspondingly greater outflow through the inhalant siphon than is possible in a bivalve with symmetrical shell valves. It may be that this process is assisted by a certain rocking action, the contraction of the anterior slightly preceding that of the posterior adductor, a process made possible, as already indicated, by the reduction of the external ligament and concentration of the resilium. The same need for extrusion of large masses of sediment carried into the mantle cavity appears to be the reason for the lack of marginal calcification in *both* valves of the protobranch, *Solenomya*, where both margins tuck in when the adductors contract (Yonge, 1939).

On one occasion, after much sediment had been taken into the mantle cavity of *Aloidis gibba*, the unique spectacle was seen of the tip of the *foot* being pushed out through the inhalant siphon. After groping round the surface of the surrounding substratum for about a minute or less the foot was withdrawn. To perform this operation the foot must have twisted round within the mantle cavity so that its tip pointed posteriorly. This extrusion was only observed once, but it may represent an extreme method of clearing the mantle cavity comparable to the action of the swab-like mantle gland of the Pinnidae (Grave, 1911) although this lies in the exhalant chamber. The habits of the animals are not dissimilar; both the Pinnidae and *A. gibba* live vertically embedded in the substratum with the exhalant opening in the one case and the inhalant opening in the other flush with the surface and liable to take in much bottom material. Both are sedentary and attached by byssus, although to a much greater extent and more permanently in the Pinnidae.

Pallial Organs

The appearance of the animal after the left shell valve and mantle fold have been removed is shown in Fig. 7. The mantle margins are fused except in the region of the siphons and of the long pedal gape, the margins of which are lined with tentacles (*T*) arising from the middle lobe of the mantle margin. The adductors are well developed and each approximately equally divided

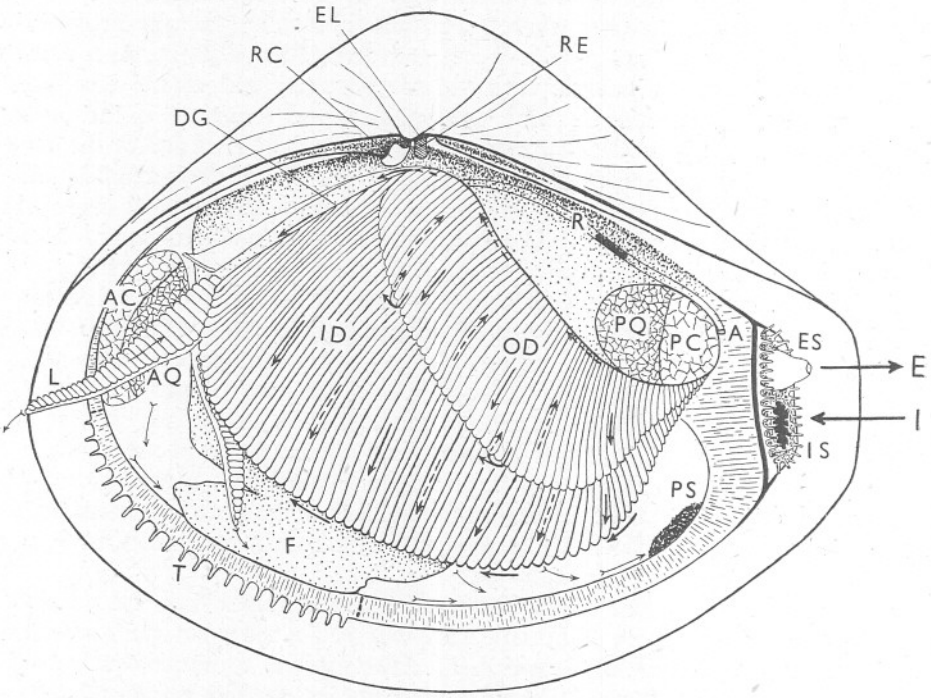

Fig. 7. *A. gibba*, body exposed after removal of the left shell valve and mantle lobe. × 10. *A*, anus; *AC*, *AQ*, 'catch' and 'quick' muscles of anterior adductor; *DG*, distal oral groove; *EL*, external ligament; *ES*, exhalant siphon; *F*, foot; *ID*, inner demibranch of left ctenidium; *IS*, inhalant siphon; *L*, labial palp; *OD*, outer demibranch; *PC*, *PQ*, 'catch' and 'quick' muscles of posterior adductor; *PS*, pseudo-faeces; *R*, rectum; *RC*, right cardinal tooth; *T*, tentacles on right mantle lobe lining pedal gape. Other lettering as before. Large arrows indicate inhalant (I) and exhalant (E) currents; small arrows ciliary currents on exposed surfaces, broken arrows currents on inner surfaces of demibranchs; feathered arrows rejection currents.

between outer 'catch' (*AC*, *PC*) and inner 'quick' muscle (*AQ*, *PQ*). The reason for the considerable development of the latter has already been noted. The ctenidia, details of which are given in the next section, consist of moderate sized outer (*OD*), and very larger inner (*ID*), demibranchs. The labial palps (*L*) are long with the usual ridges on their inner faces. They function in the customary manner, selecting smaller particles and masses and rejecting larger ones from their tips whence they pass on to the surface of the mantle. Here,

together with material rejected from the ctenidia (see next section), they are carried ventrally, as indicated by the feathered arrows in Fig. 7, and then posteriorly (i.e. upward) to accumulate as mucus-laden pseudo-faeces (*PS*) at the base of the inhalant siphon for later ejection. Paired masses of mucous glands, one on either side of the pedal gape, the other near the base of the siphon, provide the necessary mucus.

Ctenidia and Feeding

The arrangement of the ctenidia in semi-diagrammatic transverse section is shown in Fig. 8. There is a certain asymmetry between the two due to that of the shell valves and mantle, but this in no way affects their function. The inner lamellae of the inner demibranchs are not fused to the side of the visceral mass for some distance about the middle of their length as shown in Fig. 8[1]. Instead there is a ciliary connexion which separates on fixation and very readily in life so that direct connexion can here be temporarily established between the inhalant chamber below, and the exhalant chamber above, the ctenidia, and this may well be associated with the almost complete obliteration of the inhalant chamber when the shell is closed and the margin of the left valve tucks into that of the right valve. This will force water upward against the ctenidia and might impose an undue strain upon them were it not for this region of possible free passage into the exhalant chamber. It was noted in the intact animal that carmine added to the inhalant current was occasionally ejected by way of the exhalant siphon and so was other material, apart from the faecal pellets. This material may have passed into the exhalant chamber by way of these openings from the inhalant chamber.

As shown in Figs. 7 and 8, material is carried by the frontal cilia to the free margin on the outer side of the outer demibranchs and on both sides of the inner demibranchs, but to the axis on the inner side of the outer demibranchs. There is no food groove along the free margin of the outer demibranchs and material passes to the labial palps by way of the axis or by way of the food groove along the free margin of inner demibranchs. This agrees with the condition found in many other eulamellibranchs (Atkins, 1937*b*) although, as described below, there are a variety of interesting modifications in *A. gibba*. Material from the food grooves passes directly between the palps (see Fig. 7); material from the axis reaches the palps by way of the long distal oral groove (*DG*).

The detailed structure of the ctenidia is interesting and worthy of full description because *Aloidis* is one of the few British genera of Lamellibranchia the ctenidia of which have not been described by Atkins (1936, 1937*a*, 1937*b*, 1938, 1943) in her very beautifully detailed series of papers. The gill lamellae are flat and homorhabdic, i.e. all filaments are similar without enlarged principal filaments on which the frontal ciliation may differ from that of the ordinary filaments as in *Ostrea* (Yonge, 1926) and many other species (Atkins, 1936, 1937*b*). Interlamellar junctions (not indicated in Fig. 8) are numerous

[1] This limited freedom of the inner demibranch is found in other eulamellibranchia e.g. *Anodonta*.

although it is possible to separate the two lamellae of a demibranch by means of needles. The filaments are some 35μ broad and are relatively widely separated by distances of 20μ or more, this space being well guarded by the long latero-frontal cilia (*LFC*) as shown in Figs. 10 and 12. Adjacent filaments are united by interfilamentary junctions arranged in rows some 180μ apart. These run along the inner (suprabranchial) surface of the filaments and the skeletal supporting rods within the filaments are continued through them. Thus when

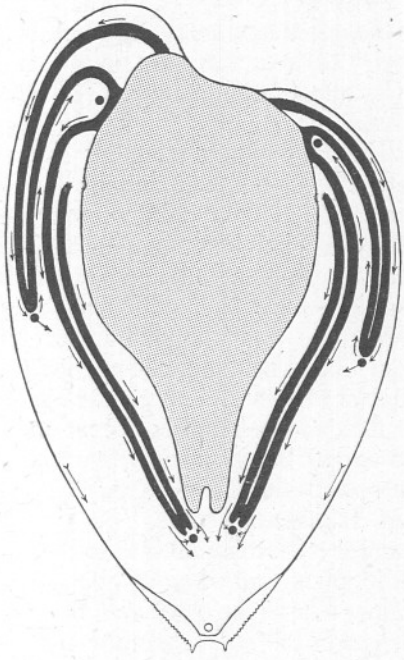

Fig. 8.

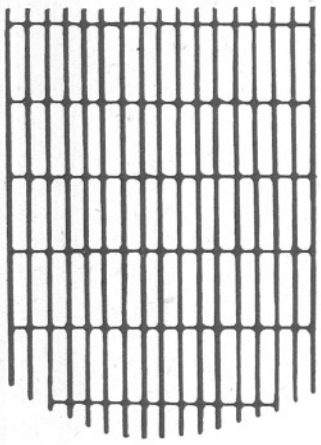

Fig. 9.

Fig. 8. *A. gibba*, semi-diagrammatical transverse section through middle of visceral mass, viewed from anterior. × 30. Arrows indicate direction of ciliary currents, filled circles position of currents directed towards mouth, hollow circle position of main rejection current for pseudo-faeces. The ciliary junctions between the inner lamellae of the inner demibranchs and the visceral mass are indicated.

Fig. 9. *A. gibba*, portion of edge of ctenidial lamella macerated to show the lattice-like skeletal framework. × 50.

the lamellae are macerated a lattice-like skeletal framework remains as shown in Fig. 9. These skeletal cross connexions, noted by Ridewood (1903) and described by Elsey (1935) in *Ostrea*, are very well developed in *Aloidis gibba* where the added support they supply permits the presence of the wide ostia (*O*) needed for the through passage of the powerful water currents.

Throughout the ctenidia lateral cilia (*LC*) are well developed and most active, producing the powerful respiratory and feeding current. Latero-frontal cilia (*LFC*) are large, some 30μ long, and agree with the description given by Atkins (1938) of eu-latero-frontal cilia having smaller subsidiary

pro-latero-frontal cilia (detectable only in sections) between them and the frontal cilia (*FC*) which are, as usual, small.

In the inner demibranch (Figs. 10, 11) the frontals give place, some 100μ from the free margin, to increasingly long terminal cilia (*TC*), which attain a length of 25μ. Near the margin these cilia deflect particles anteriorly. The food groove (*FG*) is protected on either side by a rampart of fine guarding

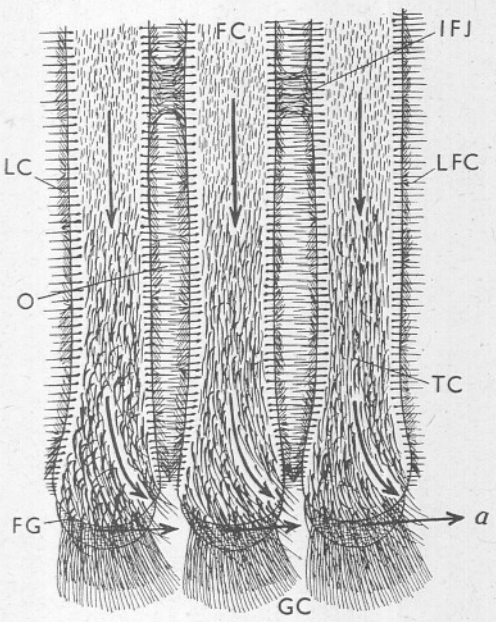

Fig. 10.

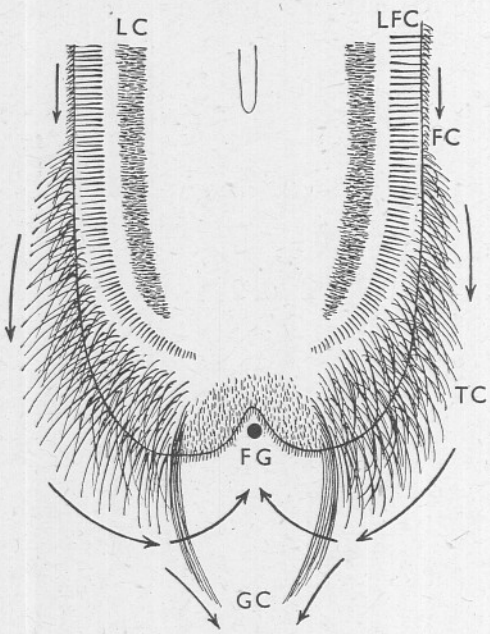

Fig. 11.

Fig. 10. *A. gibba*, portion of outer surface of inner lamella of right demibranch showing the food groove. ×290. *FC*, frontal cilia; *FG*, food groove; *GC*, guarding cilia; *IFJ*, inter-filamentary junction; *LC*, lateral cilia; *LFC*, latero-frontal cilia; *O*, ostium; *TC*, terminal cilia. Arrows indicate direction of ciliary currents, those in food groove being directed anteriorly (*a*).

Fig. 11. *A. gibba*, lateral view of free margin of a single filament from inner demibranch. ×450. Lettering as before.

cilia (*GC*) up to 45μ in length, which do not beat but act as a sieve preventing any but the finest particles from entering the food groove. Larger particles, as shown in Figs. 8 and 11, are largely deflected on to the mantle surface, whence they join the mass of pseudo-faeces. Atkins (1937*a*) has described guarding cilia in a variety of other lamellibranchs, and associated their presence with life in a substratum containing silt or mud. This correlation exists also in the case of *Aloidis*.

The outer demibranch (Figs. 12, 13) shows interesting differences from the inner one. As already noted there is no food groove, but a group of terminal cilia (*TC*) extending round from the free margin for some little distance along the inner face (see Fig. 13) deflect larger particles anteriorly, so that they

are carried for a short distance along the free margin but are soon transferred to the outer surface of the inner demibranch where they are carried towards the food groove. These terminal cilia on the outer demibranch thus act as a selective mechanism, preventing larger particles from passing along the inner surface of the demibranch and so into the food stream along the axis (see Fig. 8). It is interesting to note that the terminal cilia only extend over the posterior half of the tip of the filaments in the posterior region of the outer

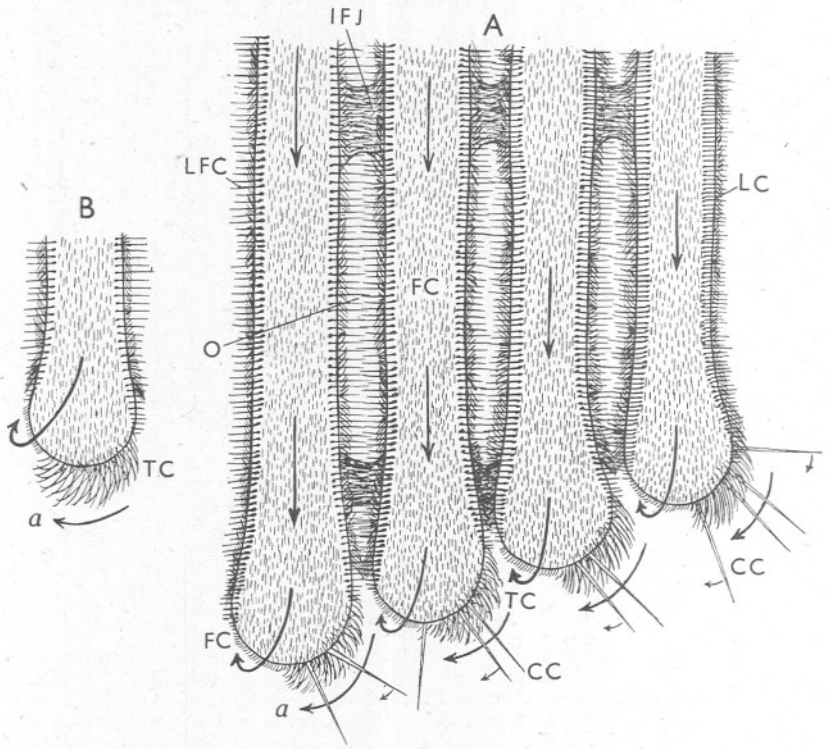

Fig. 12. *A. gibba*, portions of outer surface of outer lamella of left demibranch; A, filaments from posterior end of lamella; B, filament from anterior end. ×290. *CC*, coarse cirrus-like cilia. Other lettering as before.

demibranch (Fig. 12A) but gradually extend further forward until, in the anterior filaments, they cover the greater part of the free margin (Fig. 12B). The zone of unmodified frontal cilia is gradually displaced from the anterior half of the tip of the filaments round to the anterior surface (compare Fig. 12 A, B).

Coarse, cirrus-like cilia (Fig. 12, *CC*) some 50μ long, occur along the free margin of the inner demibranch. They are very numerous posteriorly, as many as four or five occurring on the tip of each filament, but they gradually diminish anteriorly and finally disappear (Fig. 12B). Similar cilia have been described in a variety of lamellibranchs (see Atkins, 1937*b*). They apparently

only beat on stimulation when they execute a relatively slow forward movement as indicated in Fig. 12. They are concerned with the movement of large particles and masses which tend to accumulate at the free margin, and they reinforce the action of the terminal cilia. Similar coarse cilia occur scattered at intervals of between 40 and 80μ over the inner surface of the outer demibranch (Fig. 13, *CC*) and, more sparsely, over the outer surface of the inner demibranch. They arise on the frontal surface near the posterior margin, extending over the breadth of the filament behind. Their beat is directed anteriorly, and so at right angles to the line of the filaments. Presumably in life they tend to move large particles forward between the opposed faces of the two demibranchs, but no appreciable activity was observed when the demibranchs were laid flat for inspection under the microscope.

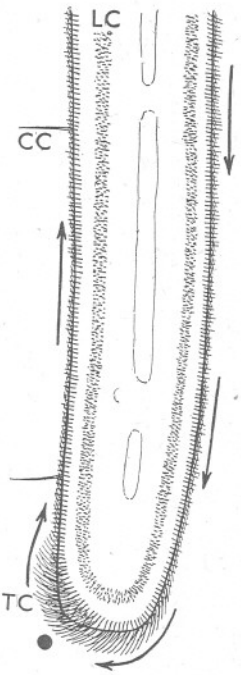

Fig. 13.

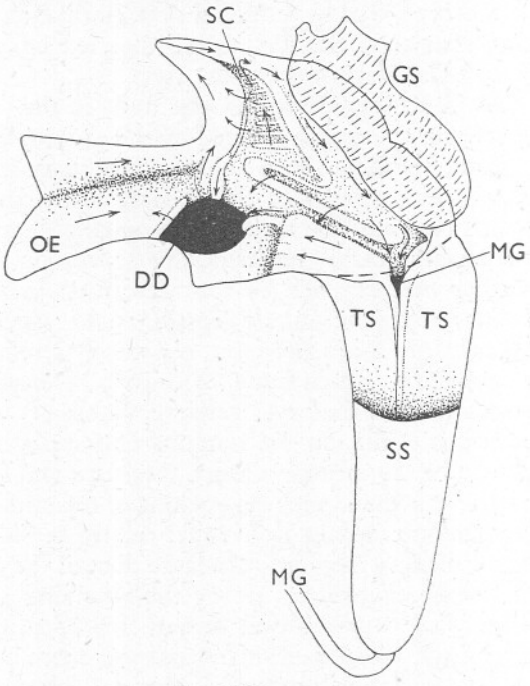

Fig. 14.

Fig. 13. *A. gibba*, lateral view of free margin of a single filament from outer demibranch. ×225. Lettering as before.

Fig. 14. *A. gibba*, stomach opened from right side. ×20. *DD*, single duct into digestive diverticula; *GS*, gastric shield; *MG*, mid-gut, opening from stomach and its separate course after end of style-sac; *OE*, oesophagus; *SC*, food-sorting caecum; *SS*, style-sac (cut away above, limit indicated by broken line); *TS*, typhlosoles separating cavities of style-sac and mid-gut. Arrows indicate direction of currents in stomach.

Alimentary Canal

The main feature of the alimentary canal is the relatively very large size of the stomach which lies somewhat to the left side of the visceral mass, the mid-gut coiling below and to the right of it. The appearance of the stomach when

opened from the left side is shown in Fig. 14. Material passed into the mouth from the labial palps is carried along the broad oesophagus (*OE*) into the elongated stomach. Into this opens a very broad style-sac (*SS*) which must normally contain a massive crystalline style. But the style-sac is in communication with the mid-gut, the two cavities being separated only by the two projecting typhlosoles (*TS*), and, as in all lamellibranchs without a separate style-sac, the style is dissolved when the normal activities of the animal are suspended (Yonge, 1926). It is interesting to note that, in the allied genus *Mya*, the style-sac is separated from the intestine (Yonge, 1923). The size of the style is indicated by the extensive gastric shield (*GS*), against which the head of the style bears normally, which covers the entire roof of the stomach. In life the style will rotate against this structure and the contents of the stomach be kept in continual slow circulation, any free starch from the plant constituents in the food being digested by the amylase liberated from the slowly dissolving mass of the style.

As in all lamellibranchs, the walls of the stomach are everywhere ciliated except for the region covered by the gastric shield. The effect of this ciliation, broadly speaking, is to separate the stomach contents into larger particles which are carried into the opening of the mid-gut (*MG*) and smaller ones which pass into the single, large opening into the digestive diverticula (*DD*). In lamellibranchs, generally, this separation is largely carried out by a food-sorting caecum such as that described in *Modiolus* (Nelson, 1918), *Mya* (Yonge, 1923) or *Ostrea* (Yonge, 1926). Such a caecum (*SC*) occurs in the stomach of *Aloidis gibba*, but is not well developed, and the details of its mode of operation (which must, of course, be considered in relation to the closed stomach with the style rotating within it) are difficult to determine with accuracy. Cilia, on the summits of a series of low ridges, carry particles to the tip of the caecum whence they turn and are carried along the side of the gastric shield and into the opening of the mid-gut. Smaller particles that pass into the intervening grooves are carried to the left (in the figure), and so pass either along a ridge into the large duct of the digestive diverticula or else into the zone occupied in life by the revolving head of the style. Cilia on the floor of the stomach beat towards the opening into the digestive diverticula. The single opening of this is unusual, there being, for instance, two openings in *Mya* and three in *Ostrea*. Material enters primarily by way of two ridges, one on the floor of the stomach and the other from the side of the food-sorting caecum; material rejected after intracellular digestion within the cells of the tubules of the diverticula is extruded along the side bordering the oesophagus as shown in Fig. 14.

The large size of the stomach, and possibly the single large opening into the digestive diverticula, is presumably correlated with the nature of the food, which is mixed with much inedible matter in the form of fine particles of mud and sand. In other words, a great deal of material has to enter the gut if the animal is to be able to obtain adequate nutrition from the relatively small proportion of organic matter contained in this. Selection on the gills and

palps is certainly effective in preventing large particles from entering the gut, but occasional sand grains up to 35 μ in diameter were found in the mid-gut.

The structure of the digestive diverticula, of the mid-gut and of the rectum (Fig. 7, *R*) calls for no special comment. The two latter regions are concerned exclusively with the consolidation of the material passed on from the stomach into compact, rounded faecal pellets, in which form they are expelled from the anus (Fig. 7, *A*) and ejected with force through the exhalant siphon.

Reproduction

In the course of this work certain general observations were made on reproduction. *Aloidis gibba* is not hermaphrodite and no evidence of change in sex was found. When the gonads are maturing it is easy to distinguish the males with white testes from the females with pink ovaries. When observations began in early August the gonads were filling but not ripe, the testes appearing better developed than the ovaries, but there were no active sperm. By the end of August the ovaries were filling, but ripe sperm were not found until the middle of September. Specimens examined on 25 September had ripe gonads, the relatively large, yolky eggs rounding off when liberated and the sperm being very active. Bad weather prevented further collecting until 10 October when all individuals, of both sexes, were spent.

It appears, therefore, that spawning occurs about the beginning of October. The only other mollusc from the same habitat which spawns at that time appears to be *Cuspidaria cuspidata*, the gonads of which were ripening with those of *Aloidis gibba* in late September, although no specimens were obtained later to prove the actual time of spawning. The other molluscs were all spent in August and had presumably spawned in spring or early summer. This autumnal spawning in *A. gibba* may indicate origin in deep water, already postulated for other reasons in *Cuspidaria* (Yonge, 1928), where the highest temperatures occur late in the season. Whether there is sufficient yolk in the eggs to permit of direct development or with a much shortened larval life, as in the great majority of arctic and arctic-boreal lamellibranchs examined by Thorson (1936) and also characteristic of deep-sea species, remains to be determined. Incubation in the mantle cavity does apparently not occur.

Discussion

Aloidis (*Corbula*) *gibba* is specialized for life in a substratum of muddy sand mixed with larger pieces of gravel and stone necessary for the planting of the single byssus thread. This habit of attachment, together with the rounded shell and the tapering foot which make movement cumbersome and slow, indicates a sedentary mode of life which observation has confirmed. The majority of mud- and sand-dwelling lamellibranchs are relatively mobile, apart from the filibranch Pinnidae, in which byssal attachment is highly developed, and *Panope* (the geoduck of the northern Pacific coasts of North America), in which the power of locomotion is lost and the animal relies for protection on

the exceptionally deep burrow made possible by the great length of the very extensile siphons.

In *Aloidis gibba* the inhalant siphon is flush with the surface of the substratum so that the feeding current is drawn in from the lowest water levels, and so contains much bottom material which will include bottom-living diatoms and bacteria as well as much organic debris. The animal is thus in a position to tap a valuable source of food. The necessary force to draw in this suspended material is supplied by the lateral cilia on the very extensive ctenidial surface. The wide ostia on the ctenidia aid in this, general support being given by the well developed lattice-work of skeletal rods. There is little evidence, either from observation of the living ctenidia or from sections, of a muscular control of the size of the ostia such as that demonstrated in life by Elsey (1935) and Nelson & Allison (1940) in species of *Ostrea*. Control of 'pumping' in *Aloidis gibba* appears to be largely, if not entirely, the function of the highly sensitive exhalant siphon with its two paired bands of closing muscles. There is the usual branchial musculature, details of which are given by Elsey (1935) and Atkins (1943), which will enable the ctenidia and the individual demibranchs to shorten when the shell closes, and possibly also the demibranchs of each side to draw together. But there is no such muscular aid to the selective activities of the gill as exist in genera such as *Ostrea* with plicated ctenidia (Yonge, 1926; Elsey, 1935).

An inevitable result of the collection of food from near the surface of the substratum is the accompanying entrance of much inorganic bottom material. It becomes necessary to dispose of the great mass of pseudo-faeces which consequently accumulates. This involves: (*a*) The asymmetry of the shell which enables the inhalant chamber to be largely obliterated when the adductors contract. In association with this are possibly the reduction in the external ligament and condensation of the resilium, and also probably the free communication between the inhalant and exhalant chambers in the region where the inner lamellae of the inner demibranchs are only attached by ciliary junctions to the visceral mass. (*b*) The large size of the 'quick' portions of the adductors which provide the force necessary for the periodical expulsions of pseudo-faeces. (*c*) The occasional action of the foot in clearing the inhalant chamber. (*d*) The great selective activity of the ctenidia with their highly developed terminal, guarding and cirrus-like cilia. Even after this necessarily quantitative rather than qualitative selection, much material must enter the gut if the animal is to obtain sufficient organic matter for adequate nutrition. The large size of the stomach makes this possible.

The asymmetry of the shell in *A. gibba*, while effectively reducing the inhalant chamber when the shell is closed, is an interesting feature in view of the fact that the same function is apparently performed by the absence of marginal calcification in *both* valves not only in the protobranch *Solenomya*, but also in the allied Pacific genus *Corbula luteola* in which, according to Johnson & Snook (1927), 'the margins turn inward, forming a submarginal ridge'.

Summary

1. *Aloidis* (*Corbula*) *gibba* is a eulamellibranch specialized for life in muddy gravel substrata to depths of up to about 80 fathoms.

2. The shell is asymmetrical, the margin of the smaller, left valve being uncalcified and so fitting within the marginal region of the right valve. A possible manner in which this asymmetry is produced by the differential secretory activities of the two mantle edges is discussed.

3. The marginal periostracum of the left valve has strengthening calcified regions posteriorly, probably to protect the siphons when extruded.

4. The external ligament is reduced and the resilium condensed, possibly permitting some antero-posterior rocking of the shell valves when the adductors contract.

5. The process of burrowing is described; on its completion the animal is anchored by a single byssus thread.

6. The siphons are very short, the tentacles of the siphonal sheath lying on the surface of the substratum. The inhalant siphon is wide and relatively insensitive; it draws in much bottom material. The exhalant siphon is tubular and very sensitive. It is controlled by two paired bands of muscle.

7. The great quantities of pseudo-faeces which accumulate are expelled by periodical contractions of the 'quick' portions of the adductor muscles, the asymmetry of the shell valves causing great reduction in the size of the inhalant chamber. The foot may also assist in clearing the chamber.

8. The large ctenidia create a very powerful current; they are adapted for dealing with large amounts of sediment by means of specialized terminal, guarding and cirrus-like cilia. Control of 'pumping' is primarily by means of the exhalant siphon.

9. The stomach is large in correlation with the great amounts of inorganic material carried in with the food.

10. Spawning occurs in early October.

11. *A. gibba* is regarded as having exploited the rich food supply of diatoms, bacteria and organic debris, on the surface of the substratum. It is specialized for dealing with the large quantities of inorganic matter inevitably taken in with this food.

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ON THE HABITS OF *TURRITELLA COMMUNIS* RISSO

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(Text-fig. 1)

Introduction

In his account of the food of the bottom fauna around Plymouth, Hunt (1925) separated *Turritella communis* and *Aporrhais pes-pelecani* from the other Gastropoda as deposit-feeders. He always found roughly sorted bottom material in their stomachs.

A. pes-pelecani was subsequently shown to be specialized for burrowing into muddy gravel (Yonge, 1937). The proboscis makes mucus-lined inhalant and exhalant passages to the surface and then proceeds to collect, from under the surface, detritus of vegetable origin by means of the small grasping radula.

T. communis, however, feeds in a very different manner. Graham (1938) has shown that it is a ciliary feeder. Owing to its mud-burrowing habit, it differs from the other ciliary feeding prosobranchs (for details of which see Yonge, 1938), most notably in the possession of a curtain of tentacles, the larger of them pinnate, which guard the entrance into the inhalant chamber. They effectively prevent the entrance of large particles into the mantle cavity. Graham gives a detailed account of the structure and function of the organs of feeding and digestion. He did not observe the animal in its natural habitat, and it was to fill this gap in knowledge that the present observations were made.

This work was carried out at the Marine Biological Station, Millport, and it is a pleasure to acknowledge the assistance received from the Director, Mr R. Elmhirst, and from the staff of the Station.

Observations

Specimens of *T. communis* were obtained from thick muddy gravel (which also contained *A. pes-pelecani*) in Balloch Bay, Isle of Cumbrae, at depths of from 9 to 12 fathoms. Samples of the bottom material were collected at the same time and the behaviour of the animals subsequently examined in the laboratory.

When placed on its normal substratum, *Turritella* soon protrudes the relatively small foot, rights itself and proceeds slowly to work its way diagonally down, at an angle of some 10° to the horizontal, into the mud. It moves in a series of slow and laborious jerks, turning from side to side as it works its way into the substratum. It thus comes to lie in a groove with a slight mound in front beneath which the larger whorls of the shell are buried.

Eventually the animal completely disappears under the surface, and then movement usually ceases. Unlike *Aporrhais* which, owing to exhaustion of the local supply of detritus, frequently changes its position, *Turritella* remains stationary for long periods (up to a week under observation in the laboratory), and possibly does so indefinitely under natural conditions unless disturbed. This stationary life is typical of a ciliary feeder.

An inhalant depression appears in the mud in front of the left side of the mantle cavity (see Fig. 1). This is made by the foot (*FT*) which bends over and pushes the mud to the right where it forms a low mound (*M*) in front of

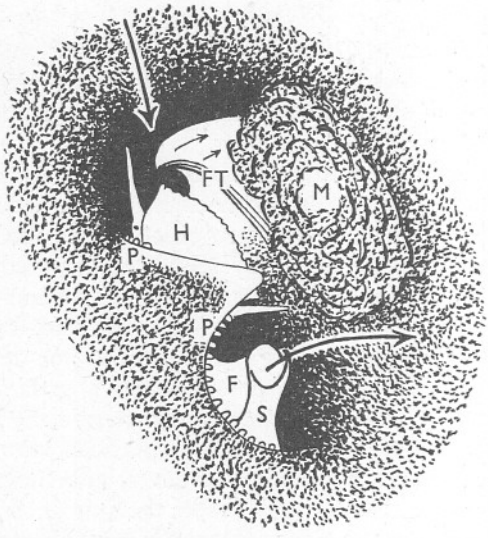

Fig. 1. *Turritella communis*, appearance when foot and head are extruded in connexion with clearance of the inhalant depression. ×5. *F*, flap at end of the right fold of the food groove; *FT*, foot; *H*, head; *M*, mound of mud consolidated with mucus from the pedal gland; *P*, pallial tentacles; *S*, siphonal process forming exhalant siphon with *F*. Large arrows indicate direction of inhalant and exhalant currents, small arrows of ciliary currents on the sole of the foot.

the head. Backwardly beating cilia on the sole of the foot aid in this and the mud is partly consolidated with mucus from the pedal gland which prevents it from falling back into the depression. After this process is completed, the foot and head are withdrawn and not again protruded unless mud falls into the inhalant depression and this has again to be cleared.

To the right of the mound is a smaller, shallower depression formed initially by expulsion of water from the right, exhalant side of the mantle cavity. Out of this depression there projects the upwardly directed tubular exhalant siphon. These depressions, the mound between them, and the tip of the siphon are the only indications of the presence of the animal when once it is completely buried.

The flow of water through the inhalant aperture into the mantle cavity is very gentle owing to the width of the opening, and the surrounding mud is not disturbed. The animal is very sensitive, closing the mantle cavity when even small amounts of fine mud or of carmine are introduced into the inhalant current. The guarding curtain of pinnate tentacles is normally hidden from view, but an outer row of simple pallial tentacles (*P*) which curl round the margin of the shell is visible. Similar tentacles fringe the exhalant opening.

Graham states that he does not, on the basis of his work, suggest that *Turritella* is an exclusively ciliary feeder. He considers it possible that the radula may also be capable of collecting food in the manner of a typical gastropod. But, during the present observations, no evidence was obtained that the mouth receives any material other than what comes to it from the ctenidium by way of the deep food groove on the right side of the head, as described by Graham. The reduction of the odontophore and of the salivary glands, noted by him, strongly supports the view that *Turritella* is an exclusively ciliary feeder.

Graham describes two folds to the right of the head. The inner (*F*) represents the forward extension of the fold which bounds the right side of the deep food-groove, and it enlarges terminally 'to form a semi-elliptical flap of tissue set in a vertical position'. The outer one (*S*) arises more ventrally, is horseshoe-shaped and curved upwards. Graham writes of the apical portions as 'kept curled over each other so as to form an incomplete "siphon"'. As he notes, the presence of an exhalant siphon in the prosobranchs is unique. Reference to Fig. 1 will show that actually this siphon is formed by a combination of both of these folds, and not merely by the outer one. Their margins overlap so as to form an effectively complete tubular siphon through which water is expelled well above the surface of the mud, which is thus not disturbed. The presence of this siphon is clearly correlated with the mud-burrowing habit. The oval-shaped faecal pellets are also expelled for some little distance, usually to the other side of the exhalant depression, through the siphon. But this expulsion only follows partial withdrawal of the animal which, by reducing the size of the mantle cavity, causes a more powerful exhalant current.

The above observations confirm and extend those of Hunt and of Graham on the food and feeding of *T. communis*. The animal is a highly specialized burrower in stiff mud containing a fair admixture of shell gravel and small stones. When placed on a substratum of fine silty mud, such as that in which such species as *Abra abra* and, in more estuarine water, *Macoma baltica* occur, it finds difficulty in maintaining the inhalant depression while the foot becomes clogged in this medium. The same difficulty was previously noted in the case of *Aporrhais pes-pelecani* although *A. serresiana* is adapted for life in such a substratum (Yonge, 1937).

SUMMARY

Turritella communis is a highly specialized burrower in gravelly mud. Once buried, it moves little in correlation with its apparently exclusively ciliary feeding habit. An inhalant depression in the mud is made by lateral movements of the foot. There is a unique exhalant siphon constituted by two overlapping folds, and through this water and faecal pellets are expelled without disturbing the surrounding mud.

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THE SPECIES OF *TEREDO* FROM PLYMOUTH WATERS

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(Text-figs. 1–3)

In the many references to *Teredo* from Plymouth early workers assumed that the common form was *T. navalis* L. Orton (1913) refers to this species, but he has recently told me that he did not try to identify the species precisely. It is almost certain that he was dealing with *T. norvegica* Spengler, which, it is now known, is the common large species in these waters. Harington (1922) ascribes the species with which he worked at Plymouth to *T. norvegica*, with a query, and no doubt he identified the species correctly. Yonge (1926) states that the *Teredo* with which he worked from the experimental raft near Plymouth Breakwater were probably all *T. norvegica*. Later he identified them as that species. Unlike *T. navalis* it does not carry its young in a brood pouch, but sends its eggs directly into the sea.

Three species have been found in recent years from the Plymouth district, two from the experimental raft moored near the Breakwater and from other fixed wood, and one from driftwood. The two commonly occurring from the raft are (1) *T. norvegica* and (2) a much smaller species carrying its young in a brood pouch, closely related to, if not identical with, *T. navalis*. The third species, occurring occasionally in driftwood, is *T. megotara* Forbes & Hanley. Purchon (1941), who worked at the last species from specimens in a tank at the Plymouth Laboratory, saw no sign of a brood pouch; and in those collected later from Wembury and examined by myself it was found that the eggs, shed directly into the sea, were very numerous. It is then practically certain that the young are not carried by the parent.

Kofoid (1922) has identified specimens of a *Teredo* from Plymouth as *T. navalis*, but the small form noted above, although coming very close to that species, and possibly merely a variety, differs in many ways from the American species as described by him (1922) and recognized by Grave (1928). *T. navalis*, *T. norvegica* and *T. megotara* are the three common species usually recorded from British waters, and these are figured by Calman & Crawford (1936). *Xylophaga dorsalis* (Turton), a wood-boring mollusc recently studied by Purchon (1941) and placed by him in a separate family, although usually found in driftwood, was also found in the raft with *Teredo*. Nothing is so far known of its breeding, although Purchon regards it as possible, from the anatomy, that it possesses a brood pouch, and he shows that self-fertilization is possible. From the notes given below it seems, however, that it is unlikely that it carries its young.

T. navalis and *T. norvegica* are both recorded in the *Plymouth Marine Fauna* (1931), but the records of the former are based on notes made before the two species were discriminated and are unreliable. Mr R. Winckworth has kindly examined the small species for me and is of the opinion that it is *T. navalis*. Mr G. I. Crawford, of the British Museum, has also examined it and tells me that it seems to be the species normally regarded as *T. navalis*. It is therefore here placed in that species, as a variety, although it differs to a considerable extent in several particulars from available descriptions.

With the object of ascertaining the breeding seasons of the Plymouth species of *Teredo*, specimens from the raft were examined every month for over a year, and afterwards from time to time. Both species were almost constantly present and were breeding throughout the year. Although the breeding was heavier in both species in spring and summer, ripe ova were present in *T. norvegica* and active veligers in *T. navalis* (small form) in any month—a fact of interest since the breeding season of most or all the American species is much restricted.

It is the small species, here called *T. navalis* var., which has proved to be specially interesting. Compared with the American descriptions of *T. navalis* it differs in many ways. Apart from the old records from Plymouth, which, as is shown above, do not discriminate the species, and the fact that Kofoid (1922) has identified a species sent to him from Plymouth as *T. navalis*, this small species has not been specially noted here. Unfortunately there are no specimens available in the Plymouth collections, nor from any previous worker, except *T. norvegica*. It is probable, however, that this *T. navalis* var. has been present with *T. norvegica* for some time.

T. navalis var. differs considerably from *T. navalis* as described by the older workers. Forbes & Hanley (1853) and Jeffreys (1865) give long descriptions which may easily cover many forms; but by both it is described as capable of attaining a large size, and it may reach to over a foot in length, although it may breed at 4 in., whereas the present small form rarely exceeds 2 in. and is usually smaller, breeding at well below an inch. The figures of the pallets given by both authors agree with those of the American *T. navalis* and not with those of the small form from Plymouth. They also differ in certain points of their anatomy.

The form of the pallet is usually regarded as an important character, and in *T. navalis* it is always described as having a forked tip. Bartsch (1922) has, however, recognized several species with forked tips and separates *T. navalis* and its near relatives from certain other closely allied forms by the fact that the pallets end in a cup-shaped depression. The pallet is composed of a calcareous stalk and blade which is covered at its distal end with a dark periostracum. In *T. navalis* proper the calcareous portion ends in a cup-shaped depression, the contours being followed by the dark periostracum. In *T. townsendi* Bartsch and *T. diegensis* Bartsch the calcareous portion is rounded distally instead of being cup-shaped. In *T. townsendi* the periostracum rises up to form

a fork. In *T. diegensis* it projects a long way beyond the rounded calcareous end and bears a calcareous nodule distally, the distal margin being straight and not forked. In the small Plymouth form the pallets, unlike *T. navalis* proper, are rounded and not cup-shaped at the end of the calcareous portion, the dark periostracum projecting far beyond as in *T. diegensis*, but the ends may be either forked or straight, or may have an intermediate form. Usually there is no calcareous nodule, but in many cases there is a calcareous deposit at the end of the periostracal portion, thus approaching *T. diegensis*. It seems likely that the calcium is present to a greater extent in older specimens. Bartsch (1922) finds differences also in the shells of these species, but Miller (1922) has shown that the shells of *Teredo* vary enormously. As Bartsch's monograph deals with the hard parts only it is difficult to be sure that all his species are valid. It seems that *T. townsendi* and *T. diegensis* are very much alike, and the Plymouth *T. navalis* var. closely resembles the latter. All three are very small and stand apart in the matter of pallets from the typical *T. navalis*. Kofoid (1921) notes certain differences in his *T. navalis* and *T. diegensis* (the latter being the *T. townsendi* of Bartsch and not his *T. diegensis*), and his descriptions, together with those of Bartsch, seem to indicate two quite distinct forms, if not species. The three types of pallet are regarded by Bartsch as even of subgeneric value.

T. navalis proper and the small form from Plymouth, *T. navalis* var., have in common the following characters: the embryos are carried in a brood pouch; the pallets are forked or tend to be forked, are paddle-shaped and covered distally with a brown periostracum; the tube has a smooth calcareous lining without ridges or chambered partitions near the opening; the shell is very like that of *T. norvegica* but is smaller, and there are slight differences in the proportions of parts; the young are held in the brood pouch until they are strongly developed veligers which are released through the exhalant siphon; the anterior portion of the ctenidium is composed of five filaments, as described by Lazier (1924), who investigated the anatomy of *T. navalis* from America.

The following characters distinguish the two forms:

Teredo navalis L. (according to Kofoid) from America. The pallets have a cup-like indentation at the distal end, formed of both calcareous and periostracal portions; the siphons are very unequal and are coloured and spotted by a red pigment; the body is long and thin; the breeding season is between May and October, and no breeding females occur later than the middle of October nor earlier than May; the veligers, according to Grave, may swim about in the open sea for several days; they are of a dark grey colour and measure up to 0·090 mm. in length, being rather longer than broad; those fed on diatoms for a week measured 0·093 mm. in length (Grave). Nelson (1923) estimates the free-swimming life of a 'viviparous' *Teredo* (species not given) as from 3 to 4 weeks, the larvae increasing over one hundred times their original bulk. In 1924, he states that examples of *Teredo*, three-fifths of an inch in length, have been found to be breeding in less than 3 weeks from the

time that they attached themselves to the wood. When full grown they were 8 in. long. These last were from Barnegat Bay, New Jersey. Grave (1928) found that larvae of *T. navalis* were present in the sea at Woods Hole, Massachusetts, from early May to October and he estimated that in summer they matured in 6–8 weeks. The typical *T. navalis* as recognized by Kofoid, Grave and Miller from San Francisco, and as described by European workers, may breed at a length of 4 in., but usually the adult is from 6 to 8 in. in length, reaching in extreme cases to over a foot.

Teredo navalis var. from Plymouth (Figs. 1–3). The pallets have no cup-like depression of the calcareous blade, but the end is rounded and the dark periostracal sheath reaches to about one-quarter the length of the blade and is very dense, extending beyond the blade for a distance, sometimes as long as the blade itself, the distal portion being pale brown and either straight or forked. In some cases a calcareous deposit, hardly amounting to a nodule, occurs in this distal periostracal portion. The siphons are nearly equal and are perfectly colourless, the exhalant siphon ending simply, the inhalant with six tentacles with knobs in between. The shell is like *T. navalis*, the central portion being rather longer. It may breed at a length of less than an inch and is rarely more than 2 in. long. The body is stout and short; the brood sac contains veligers in every month of the year, some of them always in the free-swimming stage and ready to be extruded; the late veligers appear brownish owing to the edges being dark brown. These are briefly described in an earlier paper (Lebour, 1938). Since then they have been studied in more detail and reared after entering the wood until the beginning of the tube is formed. The latest veligers which are ready to emerge and are sometimes seen issuing from the exhalant siphon measure 0·32 mm. in length and are thus distinctly larger than those of *T. navalis* of the American workers. When the parent is removed from the tube there are generally some veligers emerging, and frequently the egg sac bursts and the veligers are freed. The veligers swim freely, and if placed in a bowl of water rise to the surface, swimming actively. If wood is near they usually swim to it and move about on it, creeping by the long retractile foot, feeling their way. If placed in a bowl of water or plunger jar with small pieces of wood, within 24 hr. they may be resting on these and sometimes, with difficulty, a small byssus thread at the base of the foot may be seen. Within 36 hr. the veliger may have begun to metamorphose. Mr D. P. Wilson has been making experiments on the settling of these larvae, the results of which he will publish later. After extrusion from the parent a pair of semicircular orange patches appear near the margin under the shell (the eyes?) which remain until burrowing begins. The velum is lost and the siphons are formed, whilst round the anterior margin a toothed ridge, followed quickly by a second, is formed. The ventral margin curves in where the knobs are forming and the blades appear. The foot is ciliated, long, and very flexible, but it soon dwindles when the animal settles down in the wood, anterior

margin downwards, siphons upwards. The toothed ridges are the burrowing organs and burrowing begins now the animal has settled down. In about four days or even less, a white cloudy mass may cover the shell, apparently the beginning of the limy tube, and a few days after there is a white chalky raised

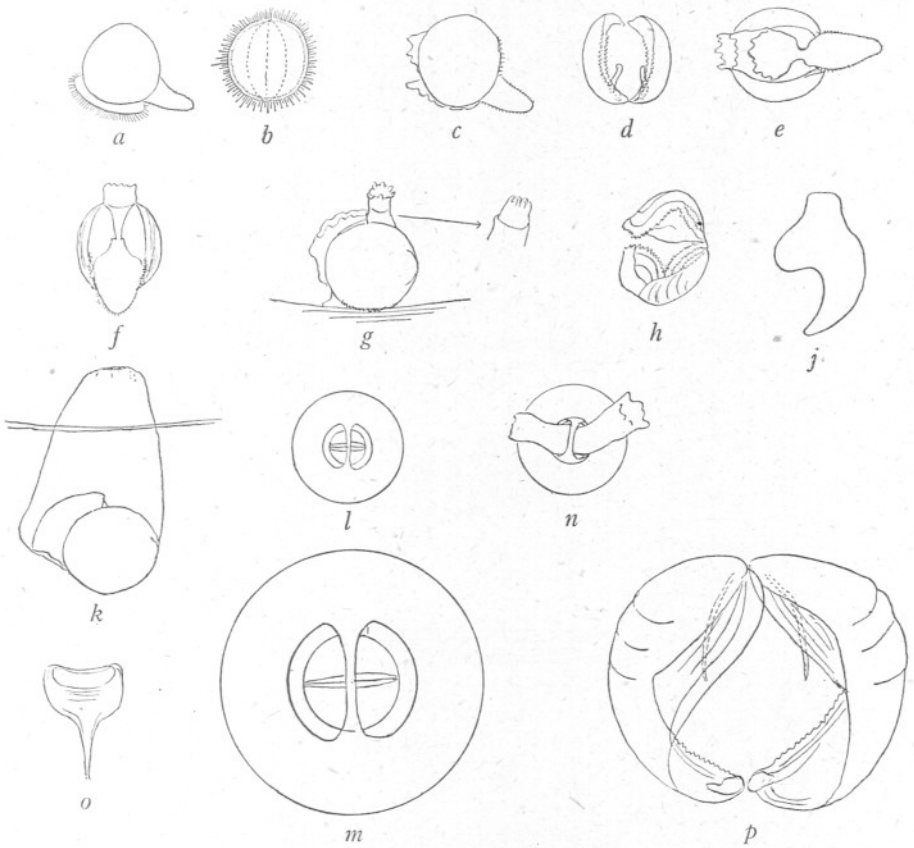

Fig. 1. *Teredo navalis* var. from Plymouth raft. *a*, *b*, veliger just emerged from parent, 0·32 mm. long; *c*, the same beginning to metamorphose; *d*, slightly older shell; *e*, seen from ventral aspect; *f*, shell 0·36 mm. long; *g*, larva settling on wood, 0·36 mm. long; *h*, older shell from wood, 0·40 mm. long and across; *j*, tube of shell 0·6 mm. long; *k*, slightly older animal showing portion of tube above and below the wood; *l*, top of tube of same looking down, showing double aperture with septum and pallets; *m*, the same enlarged; *n*, the same showing siphons extended; *o*, pallet, 0·16 mm. long, of animal with shell 0·6 mm. across; *p*, shell 0·6 mm. across.

covering, looking not unlike a very young sessile barnacle, rising up from the wood with an aperture divided into two by a partition. From the holes the siphons may hang out conspicuously. When the siphons are retracted the closed pallets can be seen within at right angles to the partition. The shell dissected out has the rudiments of the adult structure at about 0·4 mm. and there are

more toothed ridges which now extend on to the ventral margin. In a young animal with the shell 0·6 mm. across, the pallets are well formed and measure 0·16 mm. in length with the stalk about the same length as the blade, the latter being broader than long and hollowed distally. It is brown, but has not yet a

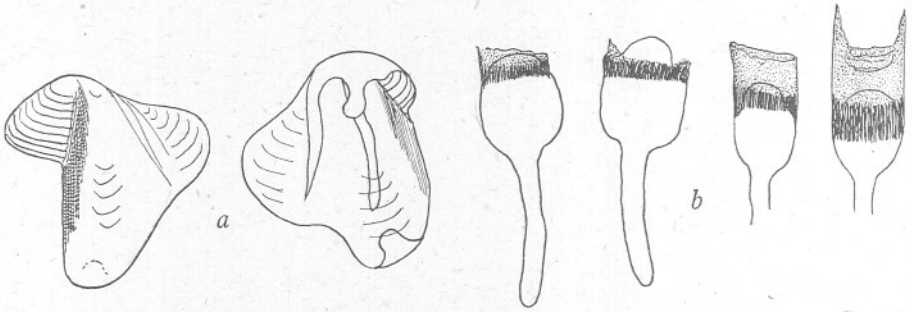

Fig. 2. *Teredo navalis* var. from Plymouth. *a*, shell of adult animal, 1·8 mm. long; *b*, pallets of various adults, *c*. 2 mm. long.

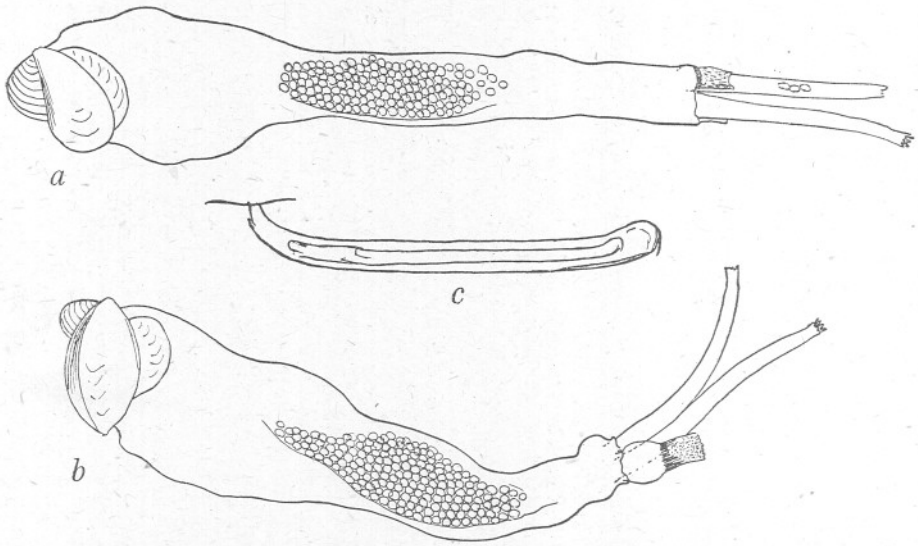

Fig. 3. *Teredo navalis* var. from Plymouth. Rough sketches of adult animals. *a*, *b*, dissected out of tube and *c*. 2·2 cm. and 2·0 cm. long respectively; *c*, typical adult in tube, natural size, 5·5 cm. long.

brown sheath projecting from its end. This young pallet is interesting as it is at this stage much more like that of the typical *T. navalis*. The tube now protrudes from the wood as a conical prominence, the tube itself inside the wood being rather longer than the shell itself and tightly attached to it. As the animal grows the division in the aperture of the tube disappears and there is only one hole, the limy top being hidden in the wood and the presence of the

Teredo only showing by a very small perforation, the siphons emerging when conditions are favourable.

Free-swimming veligers of this species have only rarely been seen in the plankton and these were isolated specimens. It is probable that any period of swimming in the sea is very short. The breeding season continuing throughout the year makes infection of the wood possible at any time, but the short period of free moving probably prevents long journeys in the water. On the other hand, they live for a long time in the wood which if broken off may be drifted far. The wood may be extensively infected but not very deeply, not so deeply as with *T. norvegica*, which nearly always occurs with it. The isopod *Limnoria* and the amphipod *Chelura* are nearly always associated with these two *Teredo* species in the raft.

Although the wood may be extensively infected it is probable that this small form would not do so much damage as the typical *T. navalis* nor as *T. norvegica*, but the fact that there is no cessation in breeding is an important point, as there would be no period when infection could not be carried out. This is contrary to the idea that in Holland few individuals survive the winter (Calman & Crawford, 1936, p. 14). The question whether the typical *T. navalis* and this small one are different species is left for future workers to decide. The nearest species so far described is *T. diegensis* Bartsch, but it also comes near *T. townsendi* Bartsch. These three small forms stand together in contrast to the typical *T. navalis*.

Teredo megotara Forbes & Hanley. This species is occasionally found in driftwood from the Plymouth district. On 1 September 1943 a large piece of a heavy wooden case which had drifted into Wembury Bay was brought to the laboratory by Mr F. G. C. Ryder. It was riddled with *T. megotara* and small specimens of *Lepas* (*anatifera*?) were hanging from it. The *Teredo* were of all sizes, the largest being females containing ova, but these were not quite mature. Pieces of the wood were taken to the raft by the Breakwater and fixed to it in order to see if ripe ova could be obtained. Examined a month later the ova were still immature. In January 1944 a curious formation of lime was seen round the mouths of the tubes, having the appearance of the tubes of *Serpula*. This closely resembled the calcareous tubes covering the siphons of *Teredo norvegica* in the Plymouth tank described by Yonge (1927) formed round faecal deposits. In *T. megotara*, however, the calcareous tubes were exposed in the water. It may well have been a response to uncongenial conditions when the life on free drifting wood ceased. The ova and sperm contained in different individuals were ripe at this time, or the animals were spent. The ova were running out of some of the females, which were much larger than the males. Fertilizations were attempted, but the eggs and sperm were not healthy and only a few fertilized ova were obtained which grew to a stage in which the embryo was active but soon died. It seems that the young are not held in a brood pouch but that the ova are shed directly into the sea.

Xylophaga dorsalis Turton. Pieces of wood bored by *Xylophaga* were brought in from a trawler by Mr A. Briggs. One of these was part of a branch dredged 5 or 6 miles south of Penlee (29 March 1943) which was riddled by *Xylophaga*. Nearly all contained ripe ova, some of which were extruded on touching with a needle. Any sperm present was non-motile and fertilizations were unsuccessful. There was no trace of live embryos, and the large clouds of ova coming from each individual when opened seem to be a clear indication that this species does not carry its young in a brood pouch, but is more like *T. norvegica* than *T. navalis*, sending its ova directly into the sea.

Pieces of driftwood were brought in from trawling 3 miles south of Rame (4 November 1943). One small piece contained both *T. norvegica* and *Xylophaga*. The *Teredo* contained ripe ova and sperm. The pieces were probably broken off from some fixed wood, and the *Xylophaga* may have entered afterwards. The other pieces all contained *Xylophaga* only, with ripe eggs and sperm, clouds of which issued when the animal was injured. There was no sign of contained embryos. Fertilizations were attempted and one was partially successful, the embryos living for a few days only. The ripe ovum measured *c.* 0·027 mm. across, the size scarcely altering after fertilization (the ova of *T. norvegica* measure *c.* 0·05 mm. across). It is shown by Purchon (1941) that self-fertilization is possible, but it seems from these observations that the embryos are not carried in a brood pouch. On one occasion specimens obtained from a piece of a branch of wood (2–3 miles south-east of Eddystone, 11 November 1943) were full of ripe ova, and in one it was seen that some of the loose ova were developing, showing almost certainly that self-fertilization had taken place, but there was no sign of embryos in the gills. Ripe ova also occurred in specimens from wood brought in from trawling outside the Sound (2 December 1943). The breeding season of *Xylophaga* thus extends at least from November to March.

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VERTEBRAL VARIATION IN TELEOSTEAN FISHES. III. ISOSPONDYLI

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Introduction

In coming now, after a number of years of delay due largely to the war, to discuss vertebral variation in fishes of a particular order, the Isospondyli, it must be assumed that Parts I and II have been read (Ford, 1937, 1941). In Part I a broad survey was made of the wide field of research presented by vertebral variation in teleostean fishes in general; Part II dealt expressly with vertebral statistics in the herring (*Clupea harengus*). In the present paper, observations mainly relate to the eight isospondylid species available for study at Plymouth, viz.:

Family	Genus	Species
Clupeidae	*Clupea*	*harengus, sprattus*
	Alosa	*alosa*
	Sardina	*pilchardus*
	Engraulis	*encrasicholus*
Salmonidae	*Salmo*	*salar, trutta*
Argentinidae	*Argentina*	*silus*

By way of introduction it may be said that recognition 'on sight' is as real a thing with fish backbones as it is with whole animals, or with things and persons in everyday life. Some one feature is recognized or a mental picture catches the eye, which in our past experience we have learned to associate with a particular individual or class of individuals. Mayr (1942) very rightly points out that such discriminating characters may be, and very often are, of no particular importance to the species. But in so far as they serve as 'markers' they are of both interest and significance. The degree of their significance depends, of course, on what we wish to know, since the value of a vertebral character varies considerably as a diagnostic criterion.

In an isospondylid fish the variable characters of the backbone are numerous and the incidence of variation is often high. Consequently it is in practice little more than a matter of statistical routine to resolve a very large sample of backbones of the same species into individual specimens, each visibly different from all the rest. Yet, as has been suggested above, each specimen thus segregated nevertheless bears the unmistakable 'markers' of a particular species, both in the backbone as a composite whole and in every one of its components. I would even go as far as to suggest that 'markers' (or 'hall-marks', as I called them in Part II) of different biological groups of the same species are within practical possibility. On the other hand, it is equally

straightforward to show that many of the vertebral characters are common to a number of species; and some of them are also to be seen in species at present outside the Isospondyli altogether.

This leads naturally to an enquiry into the composition and validity of the order Isospondyli itself. All that need be said here is that it must still be regarded as a somewhat tentative, if not entirely, artificial assemblage of diverse families, as distinct from a proven phylogenetic series (cf. Goodrich, 1909, p. 386). Fishes which differ greatly in form and habit are brought together within its compass because they are believed to be among the most primitive of the teleosts; but comparatively little is known of the phylogenetic relationship between them or their ancestors (cf. Gregory, 1933, p. 136). In such circumstances, it is not surprising to find much variation among the species within the order, as well as considerable agreement with others not included in it.

Lastly, some words of Gregory (1933, p. 149) are not without interest in the present work:

> Thus the skulls of the Clupeidae afford numerous examples of what might be called a general principle of the morphology of the vertebral skeleton, namely that 'the holes are more important than the bones'; that is, the form and position of the bony tracts are largely determined by the form and position of the sensory vesicles, blood vessels, nerves, muscles, etc.; the strengthening ridges and eminences appear between and around the openings caused by the presence of the various parts mentioned above.

A similar statement might well be made concerning the vertebrae and their appendages which, according to the precise position they occupy along the length of the backbone, conform to the general lay-out of the body as a whole. Vertebral variation, therefore, may be studied as a reflection of variation in other bodily organs and parts.

Primitive Vertebral Features in the Isospondyli

Two vertebral characters are of wide occurrence among fishes of the order Isospondyli, namely, autogenous neural or haemal (or both) arches on a number of the vertebrae, and the bifid condition of some of the anterior neural spines. Garstang (1931, p. 243) distinguishes between the 'archispondylous' condition of vertebral arches and the 'neospondylous' in which arches and centra are co-ossified, and we may agree with him in regarding the former as the more primitive. The archispondylous condition is very generally accompanied by bifid neural spines; that is to say, the spines arising from the left and right neural arches retain their separate identity above the neural canal, instead of becoming fused to form a single one.

These two characters are to be seen in fishes referred to orders other than the Isospondyli. For example, in the pike (*Esox lucius*), of the order Haplomi, the first 40 or so of the total of about 60 vertebrae (both numbers being subject to individual variation) have autogenous neural arches and bifid neural spines; in the pre-caudal vertebrae the haemal arches are also autogenous; while at the

hinder end of the backbone, where vertebrae enter into the composition of the tail-root, both epural and hypural elements are likewise autogenous. In the order Apodes, the conger (*Conger conger*) has autogenous neural arches on the first 16 or 17 vertebrae, while in the freshwater eel (*Anguilla anguilla*) they occur on the first 5 vertebrae. In species of the order Ostariophysi autogenous haemal arches are of very general if not universal occurrence.

Within the order Isospondyli itself, there is variation between two extremes. There are thus many species in which archispondylous vertebrae and bifid neural spines are comparatively numerous, but there are others in which all the vertebrae are neospondylous and all the neural spines single; the remaining species exhibit intermediate conditions between these two extremes.

During several short visits to the British Museum (Natural History) at South Kensington, I have by the courtesy of the Trustees and of the Director made a rapid survey of isospondylid skeletons with respect to these characters. The observations made, though very incomplete and subject to minor correction in light of more detailed study, may be briefly summarized as follows:

CLUPEOIDEA

ELOPIDAE: In *Elops machnata* and *Megalops cyprinoides* the cylindrical vertebrae throughout the length of the backbone have autogenous haemal and neural arches. In *Elops*, vertebrae 1–32, and in *Megalops*, vertebrae 1–36, also have bifid neural spines.

ALBULIDAE: In *Albula vulpes*, as in *Elops* and *Megalops*, all the vertebrae have autogenous haemal and neural arches; the neural spines of vertebrae 1–30 are bifid.

ALEPOCEPHALIDAE: In *A. rostratus* autogenous neural arches are present only on vertebrae 1–30, the remainder being co-ossified with the centra; autogenous haemal arches occur only on vertebrae 1–25, except for hypural elements in the tail-root; bifid neural spines are present on vertebrae 1–31.

CLUPEIDAE: Species of the genera *Clupea*, *Alosa*, *Sardina*, *Sardinella*, *Opisthonema*, *Harengula*, *Brevoortia* and *Nematalosa* agree in having a specific number of autogenous haemal and neural arches, as well as of bifid neural spines. A common feature, perhaps a significant one, is that the number of vertebrae with autogenous haemal arches is less than that of vertebrae with autogenous arches which, in turn, is less than the number of vertebrae with bifid neural spines. In *Clupea*, *Alosa* and *Sardina*, of which many backbones are available for statistical study, it has been shown that there is marked specificity in these characters.

Engraulis encrasicholus agrees with the above species in having autogenous neural arches and bifid neural spines, but unlike them, the abdominal vertebrae show haemal arches co-ossified with the centra.

CHANIDAE: *Chanos chanos* has autogenous haemals on the first 12 or 13 vertebrae, and autogenous neurals on the first 16; but only the 1st (possibly also the 2nd) has bifid neural spines.

SALMONOIDEA: The condition in the salmonoid fishes is similar to that in many clupeoids. Autogenous haemal and neural arches, as well as bifid neural spines are thus to be seen in *Salmo*, *Coregonus*, *Thymallus*, *Mallotus*, *Microstoma* and *Argentina*. In *Salmo salar* and *S. trutta*, the number of vertebrae with autogenous neural arches is not substantially different from that of the vertebrae with auto-

genous neurals; but in *Argentina silus* the number with autogenous haemals is much in excess. Autogenous epurals and hypurals are a feature of the primitive salmonid tail-root.

OSTEOGLOSSOIDEA: In *Osteoglossum bicirrosum* all the haemal arches seem to be co-ossified with the centra; and except for the first two neural arches, which may be autogenous, co-ossification appears to be the rule for the neural arches as well. Bifid neural spines occur only on the 1st vertebra.

NOTOPTEROIDEA: In *Hyodon alosoides*, although all the haemal arches seem to be co-ossified with the centra, the neural arches of vertebrae 1 to about 28 are autogenous; the neural spines of vertebrae 1–26 are also bifid. By contrast, in *Notopterus afer* all haemal and all neural arches are co-ossified with the centra and all neural spines are single.

MORMYROIDEA: In *Gymnarchus nilotus* some 76 of the anterior neural arches and about 70 of the haemal arches appear to be autogenous; of the neural spines, the first 7 may be bifid. In *Mormyrops anguilloides*, *Gnathonemius cyprinoides* and *Mormyrus kannume*, the ribs are sessile on the abdominal vertebrae, but the neural arches are all co-ossified with the centra and the neural spines are single.

STOMATIOIDEA and GONORHYNCHOIDEA: No observations made.

Used as numerical variates the number of autogenous arches and bifid neural spines have an undoubted value in diagnosing species. To what degree they are also indicative of phylogenetic relationship between species, and hence may be used in the classification of fishes, is another question. While they are ancestral characters, they are not diagnostic of the orders, families and genera as at present constituted; but to reclassify the species in accordance with the condition of the arches and spines would produce merely another arbitrary series for which proof of natural affinity might still be lacking. Even so, they are characters which can be determined with precision and are constant enough to merit full consideration with other characters of like constancy in the work of classification.

It should be noted that, when making counts of vertebrae with autogenous arches, it is necessary to distinguish between counts along the left side of the backbone and those along the right, because these may differ (Ford, 1937, p. 17; Ford, 1941, p. 158). Homoeotic variation of this kind is pronounced, both with the neural and the haemal arches. Thus in *Clupea harengus*, *C. sprattus*, *Sardina pilchardus*, *Alosa alosa*, *Engraulis encrasicholus* and *Argentina silus*, for which sufficient data for statistical study have been available, it can be taken as a general guide that in every 100 backbones, not more than 60 and not less than 50 will give the same count of autogenous haemal arches on left and right sides; the corresponding estimates for autogenous neural arches are 70 and 60. The matter has been pursued by drawing up correlation tables between left and right counts. It will suffice here to reproduce such a table (p. 394) giving the figures for this correlation in respect of autogenous haemal arches in a sample of 100 pilchards (*Sardina pilchardus*).

It is seen that the arithmetic mean for the left-side counts differs little from that for the right, despite the fact that the counts along the two sides differ in

(y) = No. of autogenous haemals counted along left side		(x) = No. of autogenous haemal arches counted along right side					Total of (y) arrays	Mean value of (x) (x_m)	Diff. $(x_m - y)$
		18	19	20	21	22			
	18	1	—	—	—	—	1	(18·00)	(0·0)
	19	1	2	8	1	—	12	19·75	+0·75
	20	—	3	35	17	1	56	20·29	+0·29
	21	—	—	15	15	—	30	20·50	−0·50
	22	—	—	—	1	—	1	(21·00)	(−1·00)
		2	5	58	34	1	100	20·27	+0·09

Arithmetic mean for (y) arrays = 20·18.

47 backbones. In only two specimens is the difference greater than 1, the right-side count in both cases exceeding the left by 2. In the remaining 45, where the difference is 1, the left-side count is the greater in 20 and the lesser in 25. A comparison between the values of $(x_m - y)$ given in the right-hand column of the table shows, however, that the average right-side count is in excess when the value of (y) is low, but falls short when (y) is high. This is a curious result. I do not think it can be regarded as entirely fortuitous, for it is typical, not only for the pilchard, but for the herring and sprat. It has also been obtained in counts of autogenous neural arches as well. Maybe more study should be made of the significance of side-to-side variation in the teleostean backbone, particularly in isospondylids where it is so evident.

Diagnostic Value of Vertebral Counts

In Part II a statistical study was made of twelve counts which can be made along the length of a herring backbone. Each of these can be precisely defined and then determined by straight counting. With odd exceptions according to the species examined, these same counts can be made along the backbones of a great many other isospondylid fishes. Probably not one of them is, by itself, diagnostic of a particular species; but taken in conjunction, they not only diagnose the species but a single individual of that species. These counts are:

1. Pre-caudal vertebrae with autogenous haemal arch, as counted along left side of backbone.
2. As in (1) but counted along right side.
3. Pre-caudal vertebrae with 'open' haemal arch.
4. Vertebrae with autogenous neural arch, as counted along left side of backbone.
5. As in (4) but counted along right side.
6. Vertebrae with bifid neural spines.
7. Position in the vertebral series of a caudal vertebra with a characteristically enlarged haemal canal.
8. The number of vertebrae in the 'trunk' as counted along the left side.
9. As in (8) but counted along right side.
10. The number of vertebrae in the 'tail-root' (i.e. vertebrae in which the haemal spines are cross-tied to the centra), as counted along the left side.
11. As in (10) but counted along right side.
12. Total count of vertebrae between the skull and the terminal urostylar segment.

There is little point, I feel, in going into detail concerning the absolute values and degree of variation for each of these counts in the particular eight species examined at Plymouth. The points to be emphasized are (*a*) that they are precise measurements of variation, and (*b*) they could be used in statistical analyses intended to distinguish between species and species, or between biological groups of the same species, over a wide range of fishes. The conclusions which can rightly be drawn from their use in this way must clearly depend upon the particular circumstances of the enquiry. In other words, the counts are instruments—effective instruments if correctly used—to be employed in diagnosis.

But, as was said in the introduction, there is another kind of vertebral character which is more direct in its diagnostic indication than any of the counts described above. Such characters or 'markers' may be more difficult to define, because their diagnostic value rests less upon their absolute value as a statistic than upon the actual visual impression they create in the observer's eye. The form-picture presented by a piscine backbone is really a composite one, spread over a graded series of separate elements, the vertebrae, each of which normally differs only a little from its neighbours. Every species presents a different picture depicting the sum-total of variation from one vertebra to the next throughout the backbone. It is not to be expected that such a picture can be easily defined, but it is none the less real, both as a whole or in its separate parts.

In the eight isospondylid species available for study at Plymouth, three families and six genera are represented. The briefest inspection of the tail-root suffices to distinguish between the clupeoids and the salmonoids. Of the latter the two species of *Salmo* are readily separable from *Argentina* by the characteristic sculpturing of the centra and the form of the neural and haemal arches. Of the clupeoids, *Engraulis* can at once be placed apart from the rest because of the long series of unbridged haemal processes co-ossified with the centra of the pre-caudal vertebrae. There remain two species of *Clupea*, one of *Sardina* and one of *Alosa*. *Sardina pilchardus* and *Alosa alosa* agree in showing a strong development and elaboration of both neural and haemal apophyses, with a very pronounced interlocking of vertebrae in the tail-base, and are readily distinguished from *Clupea harengus* and *C. sprattus*. The backbone of *Alosa alosa* will not be mistaken for that of *Sardina pilchardus* because it reflects in its over-all form the much greater depth of body in *Alosa*, and is more clear-cut in its vertebral elaboration. It is less easy to describe the difference between the backbone of a sprat and that of a herring comparable in size, since both are more generalized in form. Possibly in this particular instance it would be safer to fall back on one or two of the statistical counts, which would certainly establish identity. This, however, is not necessary for an observer who has had occasion to handle herring and sprat backbones frequently.

These observations, of course, relate to a very small number of well-known

species, but they are quite sufficient to illustrate the nature and usefulness of vertebral 'markers': by their use, species have been both identified and classified. Their limitations have been exemplified in a comparison between the herring and sprat, where more precise diagnostic criteria might with advantage be employed.

The Backbone as a Bodily Component

Generally speaking, the morphological 'lay-out' of any fish is largely reflected in the form of the backbone. This is rather to be expected in a metamerically segmented animal, organized about a long axis, the backbone itself. Seeing that the number of segments is large, while basic metamerism is in great measure persistent, counts of successive vertebrae are often counts of other repetitive organs also. In Part II (Ford, 1941, p. 167) it was shown that in the herring there exists this kind of correlation between vertebral counts and the number of 'keeled scales' situated along the mid-ventral line of the body between the head and the anus. This is true also for the pilchard, sprat and shad, each species, however, presenting some variation in the immediate region of the pelvic fin.

Another correlation of this kind exists between the anterior neural spines and a median series of bony elements between the head and the insertion of the dorsal fin.[1] The first of the series lies immediately anterior to the neural spines of the first vertebra, and the succeeding ones in front of the neural spines of the second, third, etc., vertebrae, to the end of the series. The last one is thus immediately anterior to the first radial element of the dorsal fin (*vide* Ford, 1941, fig. 3). In the herring the total number in the series is about 17 or 18; it is of a similar order in the sprat, but is much reduced to the order of 10 or 11 in the pilchard. From casual observations made at the British Museum it is believed that this count would prove of great taxonomic use over a wide range of species.

The study of alizarin-stained dissections and radiographs makes it possible to express other bodily features, both external and internal, in vertebral terms. For example, the siting of the fins and anus, the boundaries and contour of the body cavity, can be correlated with the vertebrae by tracing the path of the ribs, false ribs, and other vertebral processes, from the feature in question back to the vertebrae themselves. The accumulated knowledge thus obtained affords the means of interpreting differences to be observed in the isolated backbone, and of actually visualizing in the latter the form of the whole fish. It does not take long in such studies to realize that pronounced differences in external bodily form are often concomitant with comparatively small differences in the form of associated vertebral structures. In point of fact, both

[1] There still appears to be some difference of opinion as to the homology of these bony elements (*vide* Eaton, 1945). Whether they are to be considered as distal, separately ossified, elements of the neural processes, or as vestigial elements of a pre-existent median fin, need not concern us here.

are concomitants of differences in the configuration of the complexly folded and W-shaped myomeres, which are fundamental in nature. It is easily appreciated that a comparatively small difference in the relative lengths of the arms of the W, and of the angles subtended by the arms, must result in change of position of all structures associated with the myomeres; and the farther removed from the centre of the myomere a structure is, the more pronounced will be the change in its position. The only alternative to this is the actual breaking down of the meristic agreement—which does occur during ontogeny, when the fins move in relation to myomeres and vertebrae, in the act of metamorphosis from the post-larval to adolescent stage.

Summary

This paper does not give a detailed description of the backbone of any one of the eight isospondylid species examined. Instead, selected data have been used in a discussion of the broad principles of vertebral variation, as seen in fishes of the order Isospondyli. This was considered to be of greater value than a catalogue of vertebral details for each of a small number of already well-known species. Even so, sufficient has been said to enable any worker to identify the backbone of any one of the eight species, as well as to obtain a most discriminative description of the backbone of any other species of Isospondyli he may examine. A distinction is drawn between the countable vertebral characters, which are statistics for the precise measurement of vertebral variation, and the 'marker' characters, which provide the means for recognition 'on sight'. It is believed that vertebral characters of both kinds might be profitably employed in the study of different biological populations of the same species. The correlation between vertebral characters and other bodily features, such as keeled scales, position of fins and anus, and contour of body cavity, receives attention, and is related to metamerism. Finally, the occurrence of autogenus vertebral arches and the bifid condition of the neural spines in the isospondylid backbone is shown to be primitive and not restricted to the order.

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HADDOCK ON THE PORCUPINE BANK, SEPTEMBER 1944

By C. F. Hickling, M.A.

Colonial Office

(Text-figs. 1–6)

In September 1944 I wished to see at first hand the state of the fishing grounds after five years of much reduced fishing due to the war-time requisitioning of the fishing fleet. I sailed from Cardiff on 18 September on the steam-trawler *Iwate*, by courtesy of Messrs Neale and West of Cardiff, and of the skipper, Mr Walter Rymer. I would here express my thanks to Messrs Neale and West, and to Skipper Rymer and Mr W. Payne, mate of the *Iwate*, for their kindness and hospitality, and for all they did to help me.

The *Iwate* steamed to the Porcupine Bank, and put in some 140 hr. of fishing time between 20 and 28 September. The depths worked were between 120 and 180 fathoms, but chiefly between 140 and 160 fathoms. The ship landed some 1125 cwt. of fish on 2 October, including 524 cwt. of hake and 355 cwt. of haddock.

I measured samples of the hake and haddock caught, and made a collection of haddock scale samples. The present paper deals with the haddock. The scales were read for age estimation by Mr W. Main, of the Scottish Home Department's technical staff, and I will here thank Dr R. S. Clark, Director of the Fisheries Laboratory at Aberdeen, and Mr Main, for their help. The counting of the sclerites in the scales, and the calculation of the growth rates, however, were my work, and I am responsible for the results here described. My secretary, Mrs F. R. Kellen, gave me valuable help in the preparation and examination of the scales.

The Porcupine Bank

This Bank lies in the Atlantic, about 120 miles west of Ireland. The shallowest water on the Bank is 80 fathoms, but the extent of the Bank, as demarcated by the 100-fathom line, is some 45 miles long by 15 miles wide. Unlike Rockall Bank, which is entirely separated from the Continental Shelf, the Porcupine is a knoll on the westerly edge of the Continental Shelf itself. Between the Bank and the Irish coast the water deepens to about 185 fathoms.

Most of the fishing is done on the northern slopes of the Bank; the top of the Bank is too rough for much fishing except in fine weather. Though the species chiefly fished for is the hake, there are always haddock on the upper slopes of the bank, which are valued as giving variety to the catches made.

These haddock form an outpost of a northerly species of fish in the midst of an area dominated by a southerly species, hake. It is probable that, as on the Rockall Bank (Hickling, 1928*a*), colder water on the Porcupine favours the local establishment of a haddock population. The only hydrographical section across the Porcupine which I have found, made in May 1905 (Conseil International, 1905), confirms the existence of this slightly colder water. This section is reproduced in Fig. 1.

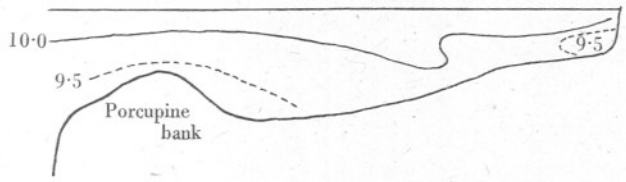

Fig. 1. Hydrographical section across the Porcupine Bank, May 1905. Isotherms in °C.

The results of my cruise show clearly that haddock were most plentiful in the shallower water, whereas hake were most abundant in the deeper water. Table I summarizes the average number of baskets of hake and haddock respectively taken per haul of $4\frac{1}{2}$ hr. at each of four depths.

TABLE I

Depth fathoms	Baskets of hake	Baskets of haddock
125	21	23
145	42	14
150	40	12
185	33	6

As a result of a survey of the fishing grounds to the west of Scotland (Hickling, 1928*b*) I showed that haddock were not caught in water deeper than 220 fathoms, whereas hake were caught as deep as 400 fathoms. Since the sea bed, connecting the Porcupine Bank with the Irish coast, is not deeper than 185 fathoms, it is debatable whether the stock of haddock on the Porcupine is continuous with the stock caught close in to the Irish coast and in the bays there. Raitt (1939) says the haddock 'is not of general occurrence, but is confined to certain definite locations'. 'There is no continuity of occurrence between these different regions. Beyond the limit of, approximately, the 200 metre depth contour, in each separate area, the species is not found.' 'There exists a number of independent stocks of haddock, isolated from each other geographically and bathymetrically, each self-contained, and each self-supporting.' In terms of Raitt's definition, the Porcupine haddock possibly form a distinct stock, and some confirmation of this may be got from an inspection of the abundance of haddock in each statistical rectangle in the area to the west of Ireland. I have taken 1938 as a sample year, and have

extracted from the note-books of the collectors of statistics at Milford Haven for that year all voyages made by the Milford trawlers to the west of Ireland (including the Porcupine Bank). Thence I have calculated the average weight of haddock caught per 100 hr. fishing in each statistical rectangle.

In Fig. 2 the figures represent in each rectangle (the boundaries of which are not shown) the average weight of haddock per 100 hr. fishing. The approximate area worked by the *Iwate* is shown by an arrowed line.

Haddock were most abundant close in to the west and south-west coasts of Ireland, but there was a decided secondary increase of abundance at the Porcupine. The apparent capture of haddock in the deep water to the south

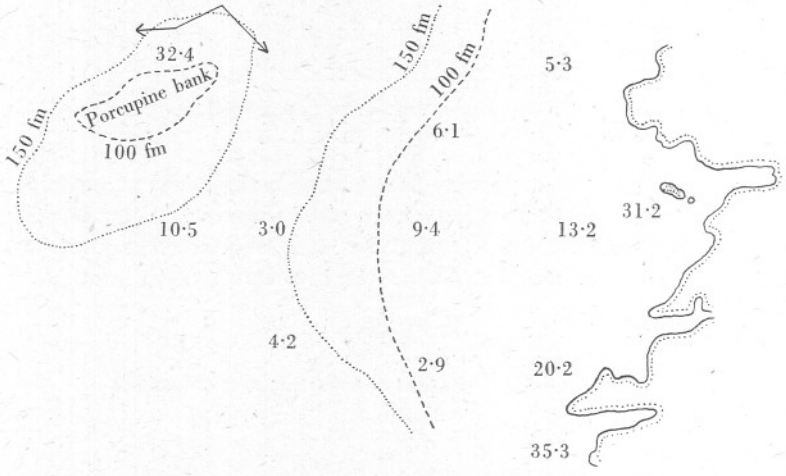

Fig. 2. Catch of haddock per 100 hr. fishing in each statistical rectangle to the west of Ireland, 1938.

and south-east of the Porcupine may be misleading, for the collectors' note-books necessarily allot the whole of a catch of a ship to that area where most of the fishing took place. A trawler which fishes most of her voyage in the deep water, but which has a day's work in shallower water on the way out or on the way home (a very common practice) will have the whole of her catch allotted to the deep-water ground, and this probably accounts for most of the haddock apparently caught in the deep water. Bearing this in mind, the data in Fig. 2 give some reason for believing that the haddock on the Porcupine form to a large degree a self-contained stock, though doubtless with much exchange with the haddock of the Irish coast.

Statistics

The Porcupine Bank was worked to a considerable extent by Milford trawlers in the pre-war years, though not to as great an extent as by ships from Cardiff. The amount of fishing done on the Porcupine varied, of course, with the yield

of other grounds. The trawlers would not visit this distant ground when better results were to be got nearer home. Table II gives the number of hours' fishing, and the average weight of haddock per 100 hr. fishing, by Milford steam-trawlers in August, September and October 1935–1940, and 1944. For the years 1938 to 1940 the catches are distinguished into large, medium and small haddock. The data are extracted from the note-books of the collectors of statistics at Milford Haven.

TABLE II

Year	Hours of fishing	Catch per 100 hr.			
Aug., Sept., Oct. 1935	1,130	24·6			
1936	10,655	31·4			
1937	5,087	12·8	Large	Medium	Small
1938	7,213	11·0	2·7	5·4	2·9
1939	3,780	40·3	3·8	3·0	33·6
1940	1,016	31·1	0·3	0·8	29·9
1944	818	200·5	50*	130*	20*

* Estimated.

The amount of fishing by Milford trawlers varied widely in the four years 1935–8; in 1939, 1940 and 1944 the war reduced the amount of fishing. In spite of the danger of attack by enemy aircraft, trawlers continued to work the Porcupine throughout 1940 until, in December 1940, a Cardiff trawler was bombed and sunk with loss of life. From that date until September 1944, no fishing took place on the Porcupine. My voyage on the *Iwate* was therefore among the first to this ground after a rest of four years.

The abundance of haddock also varied widely. The years 1935 and 1936 showed a comparative abundance of haddock, whereas the years 1937 and 1938 showed a great scarcity. The years 1939 and 1940 were again years of comparative abundance, and the table shows that this was wholly due to an influx into the catches of 'small' haddock.

In 1944, after a four years' respite from trawling, haddock were five times as abundant as in 1939, the best pre-war year in this series. From the measurements given later, it is estimated that these heavy catches were largely in the pre-war categories of large and medium, and in the proportion of roughly 3 to 1 medium to large haddock. Few 'small' haddock were caught.

THE HADDOCK CAUGHT IN SEPTEMBER 1944

Length and age

All the haddock examined during my voyage were in excellent condition, their livers creamy with fat. The gonads were in the spent-recovering condition, few showing any advanced recovery. Feeding was heavy, chiefly on echinoderms and shell-fish, though some crustacea, including euphausiids, were noted.

In Fig. 3 are given the measurements, grouped by 5-cm., of the male and female haddock caught. The frequency curves for both sexes are strongly

bimodal; in both males and females the first mode is at about 43 cm., but the second mode is at about 56 cm. in males and 58 cm. in females. Females are more numerous among the largest fish; in fact, the largest male was 63·3 cm. long, the largest female 67·0 cm. Females were also more abundant than males among the smaller fish. Measurements of Porcupine haddock, made on the Milford Market in January 1945, confirm these measurements made at sea in September. In Fig. 4 the measurements are grouped according

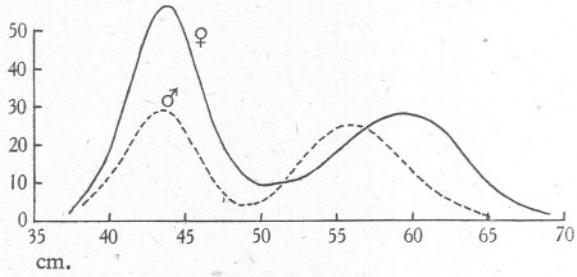

Fig. 3. Frequency distribution of measurements of male and female haddock on the Porcupine Bank, September 1944.

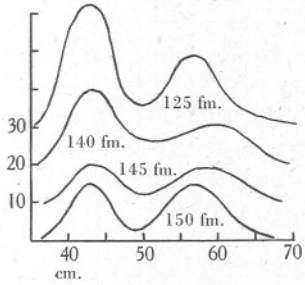

Fig. 4.

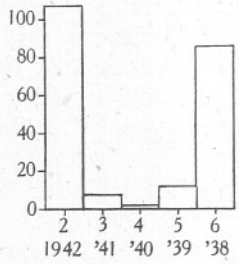

Fig. 5.

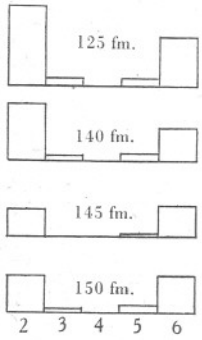

Fig. 6.

Fig. 4. The effect of increasing depth on the length-distribution of haddock on the Porcupine Bank, September 1944.

Fig. 5. The age distribution of the haddock on the Porcupine Bank, September 1944.

Fig. 6. The effect of increasing depth on the age distribution of haddock on the Porcupine Bank, September 1944.

to depth, both sexes being combined. Again the curve takes a bimodal shape, but it will be noted that, whereas in 125 and 140 fathoms the mode at 43 cm. is dominant, in 145 and 150 fathoms the two modes are about equal. There is therefore a decided tendency for the larger fish to be found in the deeper water.

The sex ratio shows no definite tendency with increase of depth. Females always predominated. Some 130 females, but only 80 males, were found among the fish measured.

In Fig. 5 is shown the frequency distribution of the year classes. It will be seen that two year classes, the 2+ and the 6+, spawned respectively in 1942 and 1938, dominate all others. In fact, the broods of 1939, 1940 and 1941 are almost unrepresented.

These findings also were confirmed in January 1945, on a sample of haddock from the Porcupine, examined on the Fish Market at Milford Haven. Below are given the age distribution of the haddock samples examined on the Porcupine Bank in September 1944, and on Milford Fish Market in January 1945:

	2+	3+	4+	5+	6+
September 1944	107	8	2	12	85
January 1945	188	7	7	28	78

In the January samples the narrow winter sclerites are clearly visible at the margin of the scales, and in one or two female fish, in which slovenly gutting had allowed the ovary to remain, the latter was seen to be ripening, even in fish as small as 43 cm.

In Fig. 6 the samples are grouped in order of depth, and it appears that the younger fish are found more in the shallower water, thus confirming the evidence of Fig. 5. The larger and older fish obviously tended to occupy the deeper water, the younger and smaller fish the shallower.

The Sclerite Number

On a large number of the scales of both sexes in the two dominant age-groups the number of sclerites in each annual scale zone were counted. The average numbers are given in Table III.

TABLE III

	Average number of sclerites in brood					
	1	2	3	4	5	6
1938	32	21	15	12	9	7
1942	32	24				

I tested these means statistically, and found that except in the first year's growth among the 1942 brood, there was nowhere any significant difference between the numbers of sclerites in males and females. In the exception, the males had an average of 34 sclerites in the first zone, the females 30, and the difference was significant.

There is no significant difference between the number of sclerites in the first and second scale zones of 2-year-old and 6-year-old fish (the 1942 and 1938 classes).

These sclerite numbers may be compared (Table IV) with those found in the scales of haddock from other regions, as given by Thompson (1928).

In the first scale zone the Porcupine haddock had more sclerites than in any of the regions listed, the Irish coast coming nearest. In the second zone

TABLE IV

Region	Year 1	2	3	4	5	6
North Sea	22	15½	12	9	8½	8
Norway	20	14	13½	13	9	8
Faroe	22	19	16½	14	11½	10
Iceland	20½	20½	16	14½	14	14
Nantucket, U.S.A.	23	24	18	15	—	—
Irish coast	26	19	16	13½	12	10½
Porcupine	32	22½	15	12	9	7

the Porcupine haddock were only exceeded by those from Nantucket, U.S.A. But in the third zone they had a sclerite number less than in all regions except the North Sea and Norway, and in the later zones had almost the fewest sclerites in any region.

A false ring appeared fairly regularly between the 9th and 19th sclerites, with the average at the 14th sclerite. Thompson (1922) states that in North Sea haddock this false winter ring appears at the 7th to the 12th sclerites. Thompson says that this false winter ring appears in many haddock, 'presumably those which...have taken to the bottom in fairly deep water and encountered a sharp change of temperature'. 'The young haddock must be accommodating itself to the new conditions it may meet on seeking the bottom.'

The Growth Rate

Below are given the average lengths, in cm., of the successive year classes in my Porcupine samples. There were, however, very few specimens of 3+, 4+ and 5+ fish on which to base an average (see Fig. 6). They are compared with the average lengths of fish in each class in other regions, as listed by Thompson (1928). But since my samples were collected in September, when wide sclerites were still being laid down at the margin of the scale and when therefore the year's growth had not finished, in Table V my 2+ fish are compared with the 3-year fish in the other regions.

TABLE V

Region	Year 1	2	3	4	5	6	
South-east North Sea	18·5	29·8	35·6	40·8	46·3	49·2	
Deep central North Sea	16·4	23·4	27·1	29·0	31·6	33·3	
Iceland	16·5	30·6	39·7	47·9	55·1	60·4	64·0
Faroe	16·5	31·7	41·6	48·3	54·8	60·6	65·8
Porcupine, observed length	—	—	43·3	50·9	54·5	55·2	58·6
Do. calculated:							
(*a*) from 1942 year-class	21·6	35·9					
(*b*) from 1941 year-class	20·8	37·9	45·6				
(*c*) from 1940 year-class	20·8	33·3	41·9	48·5			
(*d*) from 1939 year-class	19·7	31·8	40·6	47·6	52·8		
(*e*) from 1938 year-class	19·2	31·9	39·1	45·5	51·5	55·4	

The table shows that the average length of the 2+ haddock on the Porcupine was already greater than that even of the Faroe haddock, and the same is true of the 3+ haddock. But from the 4+ fish onwards, the Porcupine haddock were smaller than both the Faroe and the Iceland haddock. But they were much larger than the fastest-growing North Sea haddock. The figures suggest, in conjunction with the sclerite numbers, that the Porcupine haddock grow more rapidly, during the first four years of life, than any other stock of haddock, but that growth then slows down, so that it is overtaken by the steadier rapid growth of the Iceland and Faroe fish.

These findings are confirmed by the calculated rates of growth, also given in the above table. The calculated length attained at the end of each winter apparently increases from the older fish (the 1938 class) to the younger (the 1942 year class). This is almost certainly due to Lee's phenomenon, and the youngest year-class will give the best estimate. The table shows that the Porcupine haddock reach an average length of about 22 cm. at the end of their first complete year; and about 36 cm. at the end of their second complete year.

The false winter ring, which appears on a large number of these scales, is formed when the fish has a calculated average length of 11·5 cm. in the 2+ fish, of 10·0 cm. in the 5+ fish, and of 9·4 cm. in the 6+ fish. Again allowing for Lee's phenomenon, these figures suggest that the Porcupine haddock take up a bottom-living habit at a length of about 12–13 cm., thus at a somewhat larger size than those in the North Sea, which according to Thompson (1922) take up this habit at a length of about 11 cm.

Haddock become legally marketable at a length of $9\frac{1}{2}$ in., or about 24 cm. The Porcupine haddock therefore become marketable in their second year of life, and the sudden big increase in the abundance of small haddock in 1939 and 1940 (Table II) was clearly due to the growth to marketable size of the 1938 year class, which is still so strongly represented in my samples. Maturity sets in, in the haddock, in the third year of life, and this rich year-class would therefore spawn in full strength in 1942. The extraordinary abundance of haddock on the Porcupine in 1944 is therefore due to a good year class, that of 1938, growing up, after its second year, free from fishing-mortality, and in turn spawning, in 1942, a year-class which had also suffered no mortality due to fishing.

Discussion

Bückmann (1939) shows that, in the German Bight, in the years from 1924 to 1938, the growth rate of the plaice was inversely proportional to the density of the stock of fish on the grounds. Fischer (1939) found that the thinning of the stock of plaice and flounder in the Baltic, due to intensive fishing, resulted in a more rapid rate of growth of the survivors. Still more relevantly, Raitt (1939) shows that, in the North Sea haddock, 'there is close agreement between these variations in growth rate and the degree of brood density, the poorer the brood the less the competition for available food and the faster

the rate of growth. It follows that increased depletion will itself have had a similar tendency, the poorer the brood the faster its growth, the faster the growth the quicker its depletion, and the quicker the depletion the less competition for the upcoming stock and the greater its growth'.

But it is clear that the converse of these findings do not apply to the haddock of the Porcupine Bank. The complete cessation of fishing there at the end of 1940 saw the Bank populated with abundant small haddock (Table II). This brood, spawned in 1938, continued to grow for 4 years without depletion due to fishing, and it was joined, in 1942, by another good brood, the broods of 1939–41 having failed. Consequently, by the time fishing on the Porcupine was resumed in September 1944, the Bank carried a haddock population five times as dense as in the best of the years immediately before the war, and indeed was the best fishing for haddock ever known there. Yet when the calculated growth-rate of the 1938 brood in its first 2 years of life is compared with that of the 1942 brood, as in Table V, it is plain that, even allowing for the effect of Lee's phenomenon, the 1942 brood, growing up under comparatively crowded conditions, grew no less rapidly than that of 1938, and this is confirmed by the sclerite numbers (Table IV). Moreover, all the haddock were in excellent condition: these facts do not suggest that competition for the available food had stunted the growth of this much denser population of haddock.

It may be that the 4 years' cessation of trawling allowed the bottom fauna on which these haddock feed to increase in abundance, yet this fauna would throughout have been cropped by an increasing stock of fish.

Summary

1. It is suggested that the population of haddock (*Gadus aeglefinus* L.) on the Porcupine Bank is largely a self-contained stock.

2. This stock had complete immunity from trawling from December 1940, to September 1944.

3. In 1939 and 1940 there was an abundance of small haddock in this stock, due to the good brood of 1938. In 1944, this brood was still very abundant, and was then joined by the good brood of 1942.

4. These two good broods, growing up immune from fishing mortality, caused the Porcupine Bank to carry, in 1944, the densest stock of haddock ever experienced there.

5. The average number of sclerites in the first zone of the scales of these fish is the highest recorded in any region. It is still high in the second zone, but in the later zones falls below that found in the scales of haddock from other regions.

6. The growth rate was faster, in the first four years of life, than even that of Iceland and Faroe haddock, but in the later years it fell behind these, though still superior to the growth rate of the North Sea haddock.

7. The expectation that this greatly increased stock of haddock, due to the war-time cessation of fishing, would show a slowing in its rate of growth, due to intensified competition for the available food, is not supported by the facts.

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THE HERRING FISHERIES AT MILFORD HAVEN

By C. F. Hickling, M.A.

Colonial Office

(Text-figs. 1–6)

CONTENTS

INTRODUCTION

Milford Haven is primarily a trawling port, with hake as its chief product, but it also has herring fisheries which are of interest because they last almost the whole year round. Though Milford ranks fourth or fifth among the herring ports of England and Wales, landing only some 2–4 % by weight of all the herrings landed, its herring fisheries have considerable local importance, and Watkin, whose two papers (1933*a*, 1933*b*) are the only ones dealing with these fisheries, shows that the summer trawl-caught herrings sold at a price twice as great as the contemporary average for the whole of England and Wales. Farran (1944) has very recently published the statistics of the herring fisheries in Eire, and his results are of interest in connexion with the present paper because at least one of the Irish herring fisheries may be based on shoals which contribute, at least in part, to the Milford herring fisheries.

Each year there are three herring fisheries. The spring fishery is a drift-net fishery, and, as Watkin shows, lasts from March to July and even August. The fishery in the summer and autumn is a trawl fishery, and lasts from June and July until November. Finally, the winter drift-net fishery lasts from December to February or March. It will be seen in Fig. 5 that, except for a gap in March and again in late November and early December, herrings are landed at Milford Haven in every month of the year.

Watkin states that the spring drift-net fishery began in 1925, but I am told that it was flourishing as early as 1900. The winter drift-net fishery is genuinely of recent date: it was started in 1933, when some drifters, disappointed by the

failure of the Plymouth winter season, broke their voyage north to Buncrana and Stornaway to have a shot off Dunmore. They got good results, and the fishery has been an annual event since. The trawl fishery for herrings in the summer and autumn is of long standing.

Watkin shows that, during the spring drift-net fishery, the herrings are mainly spent fish. They are feeding heavily on krill (euphausiids) and red feed (copepods). Towards the end of the season, however, in June, the roes show a considerable degree of recovery. Farran (1944) writes that, in the Irish fisheries of Waterford and East Cork 'the fish taken in April are at first in poor condition after spawning, but, owing to the rich feeding on the south coast, they rapidly improve and by the middle or end of May almost all are matties in first-class condition'. 'Fish taken in April, May and June have usually food in their stomachs, sometimes in large quantities. The main food is the copepod *Calanus*, but larval Crustacea and fish are also eaten at this time; in April, euphausians, small shrimp-like Crustacea, sometimes occur in large numbers.'

During the summer and autumn trawl fishery, the roes are in an advanced stage of development, but never 'mazy', or running with eggs. Watkin does not mention whether these fish are feeding or not, but Mr Hewett, one of the most consistent of trawl herring skippers at Milford, has told me that, at least off Kinsale, the herrings may have 'black-gut', that is, contain some food.

Finally, in the winter drift-net fishery, the beginning of the season in December and January, finds the fish 'full', and in good condition, but in February and March the fish become spent. Farran (1944) shows that in January 41 % of the fish are full and 40 % actually spawning. The stomachs are empty.

The herrings taken in these three fisheries, therefore, show a continuous change, with spawning in the winter, and recovery in the spring and summer; and until the contrary is proved, it is reasonable to believe that they are all of the same stock of herrings. Evidence will be given later in this paper in support of this. The fact that Watkin found differences between the spring drift-caught herrings and the summer trawl-caught herrings, in respect of the size of the fish, the age of the fish and the rate of growth, does not necessarily indicate different stocks, for the trawl takes all herrings without selection, whereas the drift-net, as Farran (1936) has shown, is very selective in its effect, picking out from the shoals of herring fish of the size and bodily condition appropriate to the size of mesh used. I have shown, in connexion with the pilchard (Hickling, 1939) that this net selection can change the apparent rate of growth.

Ships and Gear

The drift-net fisheries are carried on by steam drifters from the east coast, which make seasonal visits to the port. The trawl fisheries are carried on by local steam trawlers, usually of the largest type fishing from the port, namely,

'Castles', of 125 ft. length and about 270 gross tons. A special herring trawl is used; Davis (1936) gives a description of this trawl. It has ordinary wings, but the 'straight piece' is many feet longer than in the ordinary trawl and is braided of fine mesh throughout. The herring trawl must be towed as fast as possible, and so only the largest and most powerful trawlers usually take up this fishery. But in the autumn of 1939, owing to the uncertainty as to the course which the war might take, all trawlers were working on the herring grounds off Kinsale and the Smalls, and a comparison of the catches of herrings made by ships using the ordinary trawl and the herring trawl shows that the herring trawl catches about $2\frac{1}{2}$ times as much herring in unit fishing time as the ordinary trawl.

In 1940, the trawl fishery for herrings off the Old Head of Kinsale was the heaviest ever known. One trawler, the *Rudilais*, Skipper A. Riby, landed 1019 cwt. of herrings in a single voyage, an all-time record. Trawlers of all types took part, using the herring trawl, and this allows of a comparison between the performances of the different classes of trawler. The average weight of herrings caught, per 100 hr. of fishing time, was as follows:

Type	Average length	Average gross tonnage	Average catch per 100 hr.
Small trawlers	110 ft.	180	210 cwt.
Medium trawlers	115	220	254
Large trawlers	125	270	307

It is seen that the large 'Castle' type trawlers, which normally carry on the fishery, have a performance 50% greater than the small trawlers, and 20% greater than the trawlers of medium size. The performance, in fact, increases in direct proportion with the gross tonnage.

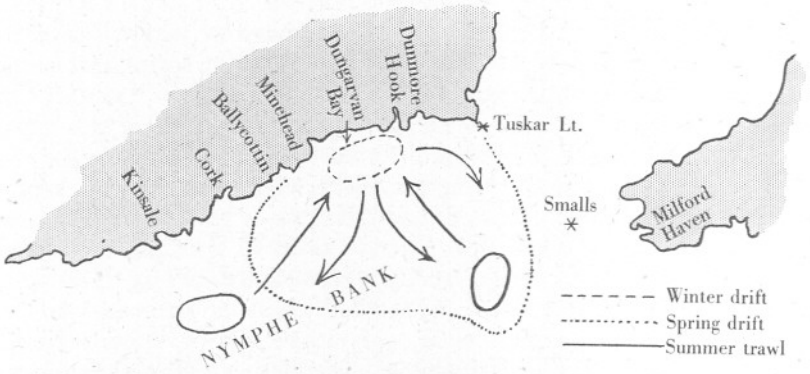


Fig. 1. The location of the herring fisheries; the arrows mark the suggested migrations.

The Location of the Fisheries

The localities in which the herring fisheries are carried on are shown in Fig. 1. The winter drift-net fishery takes place in a comparatively small area off the

south-east corner of Ireland, in Dungarvan Bay between Hook Point and Minehead, and occasionally as far west as Ballycottin.

The spring drift-net fishery covers a much wider area. Apart from small outlying catches, it extends from off Cork along the south coast of Ireland to the Tuskar, and to a considerable distance southwards into the St George's Channel and on to the Nymphe Bank.

Finally, the trawl herring fishery occurs in two well-defined and quite separate localities, namely, off the Smalls, and, again, some 90 miles farther west, off the Old Head of Kinsale.

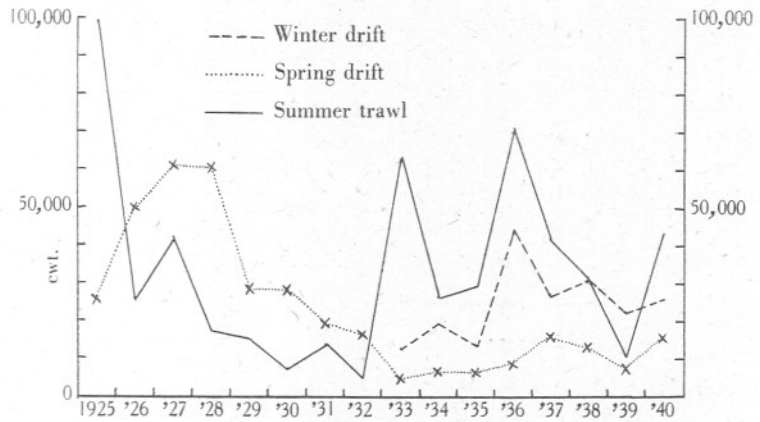


Fig. 2. The total catch of herrings in each year at Milford Haven.

The Yield of the Fisheries

In Fig. 2 are shown the total annual weights of herrings caught in each of the three fisheries from 1925 to 1940. There were no herring fisheries in the years 1941–4 because war conditions so hampered the operations of the drifters that they did not work from Milford, while the trawlers found herring trawling less profitable than trawling for hake.

Referring to Fig. 2, both the summer trawl fishery and the spring drift fishery showed a downward trend in the years 1927–32, after years of high yield in 1925 in the trawl fishery and 1926–8 in the drift fishery. From 1933 to 1937 the drift fishery showed some recovery, though not to the previous best levels; but the trawl fishery recovered very substantially, and the years 1933 and 1936 were good years. In 1936 the quality of the herrings was particularly good. The winter drift fishery showed an upward tendency throughout.

Fig. 2 shows the total yield, and this is affected quite as much by the fishing effort expended as by the abundance of herrings. A truer picture of the yearly variations in the fortunes of the fisheries is to be got by calculating the weight of herrings caught per voyage. Even this, however, leaves something to be desired, for the amount of fishing time may vary in each voyage. But, generally

speaking, the effect of this variation will be to exaggerate the goodness or poorness of the apparent catches per voyage, for when fishing is poor, a longer time is necessary on the fishing grounds to make a trip, whereas, when fishing is good, a satisfactory trip is made in a short time. But, in the case of herrings, which do not keep well, there is a limit to the length of any voyage, which may be put at about five days.

In Fig. 3 the average weight of herrings caught per voyage in each year is shown. The abundance of herrings, as measured by the catch per unit of fishing effort, declined from 1925 to 1932, but from 1933 to 1938 all three fisheries showed an increasingly high yield per unit of fishing effort. The trawl herring season of 1939 was apparently poor, but the outbreak of war occurred during

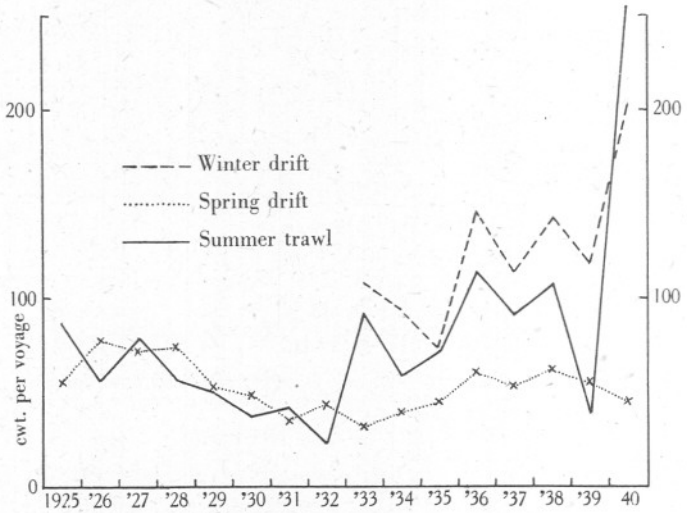
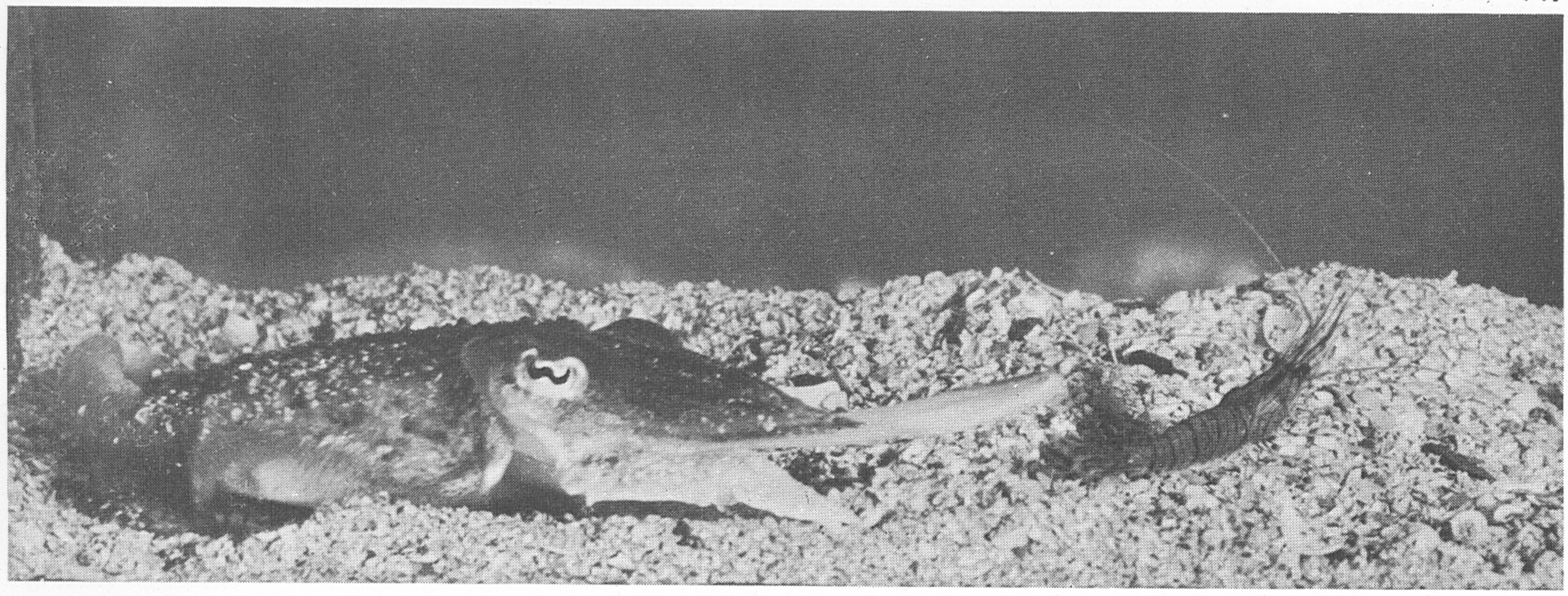


Fig. 3. The average weight of herrings per voyage in each year at Milford Haven.

the period which is normally most productive, and the large-scale requisitioning of trawlers, together with the general uncertainty as to the effect of the war at sea, so handicapped the fishing fleet that the apparent catch per unit of fishing effort is much lower than it would normally have been. The season would undoubtedly have been poorer than that of 1938, and I have estimated that it would have given an average weight of about 80 cwt. per voyage.

The Relations between the Fisheries

There is a considerable correspondence between the annual changes in the abundance of the herrings caught in the spring drift-net fishery, and those in the summer trawl fishery, especially from 1925 to 1932. But from 1933 to 1940 the herrings taken in the spring drift-net fishery, while increasing in abundance as did those in the trawl fishery, did not do so in the same relation



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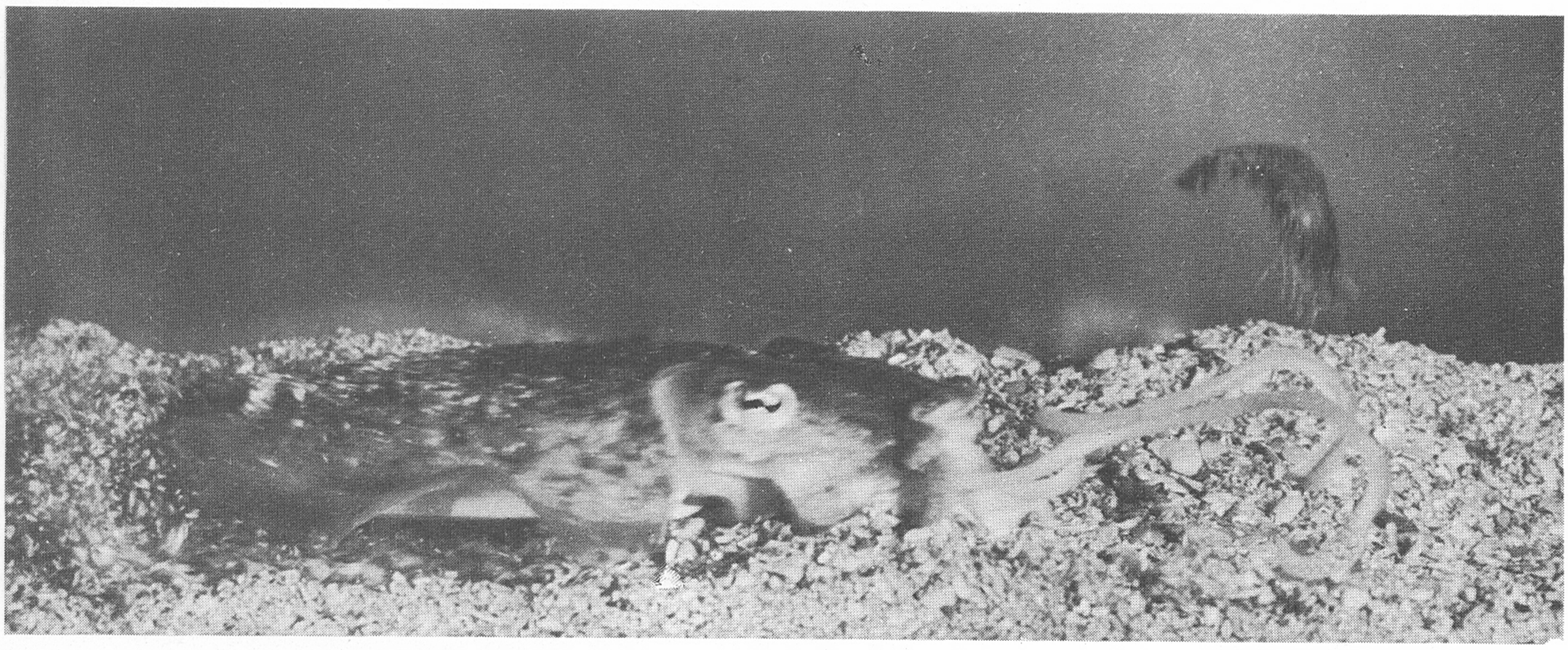

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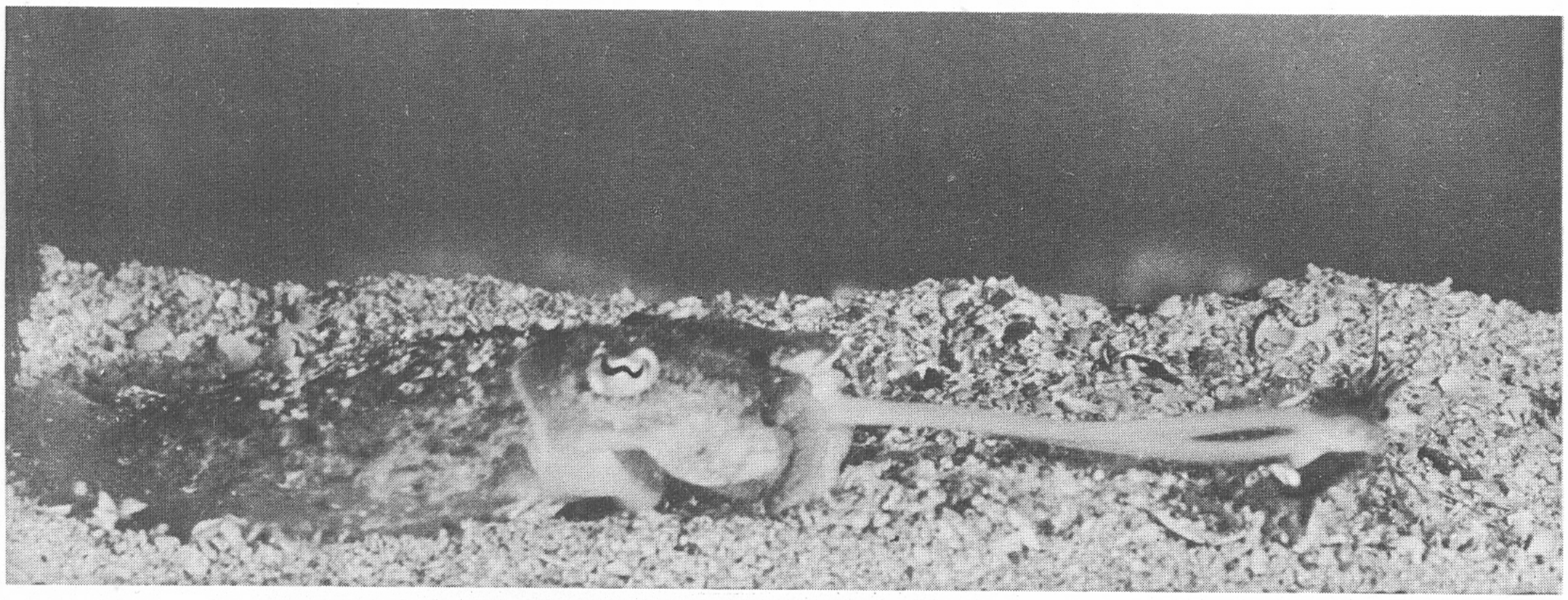
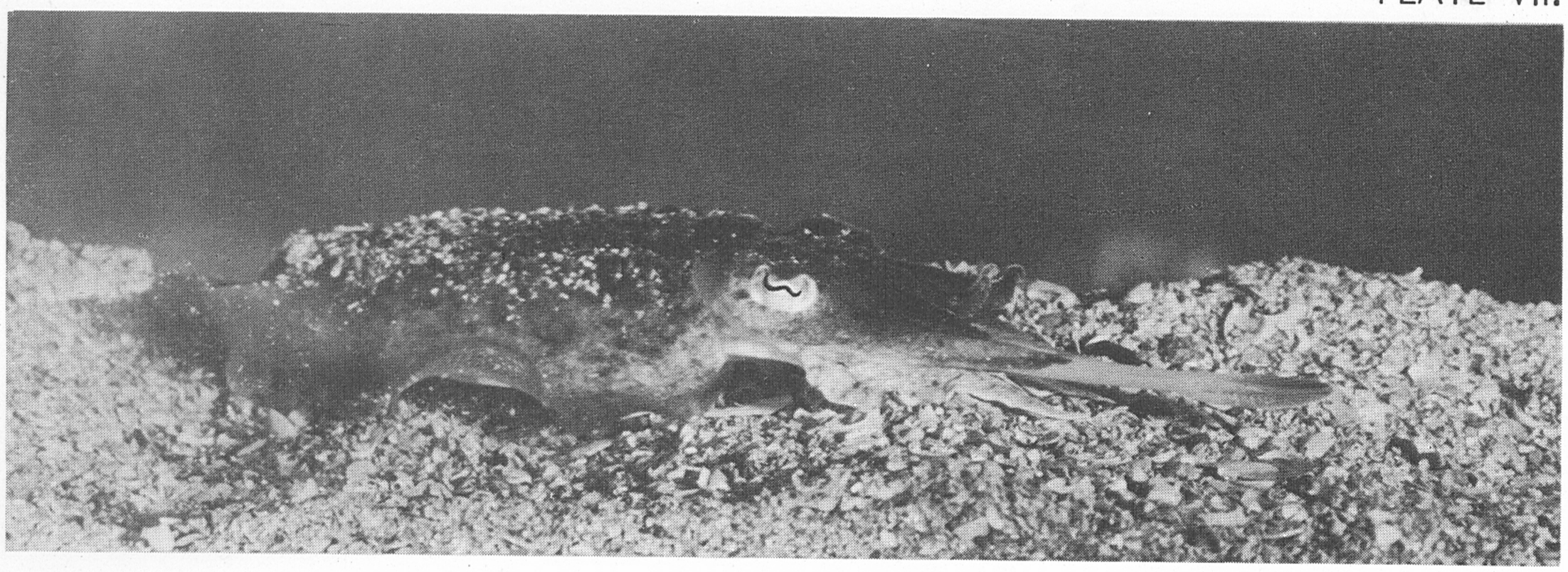


Fig. 3.

Sepia officinalis. Catching a prawn.



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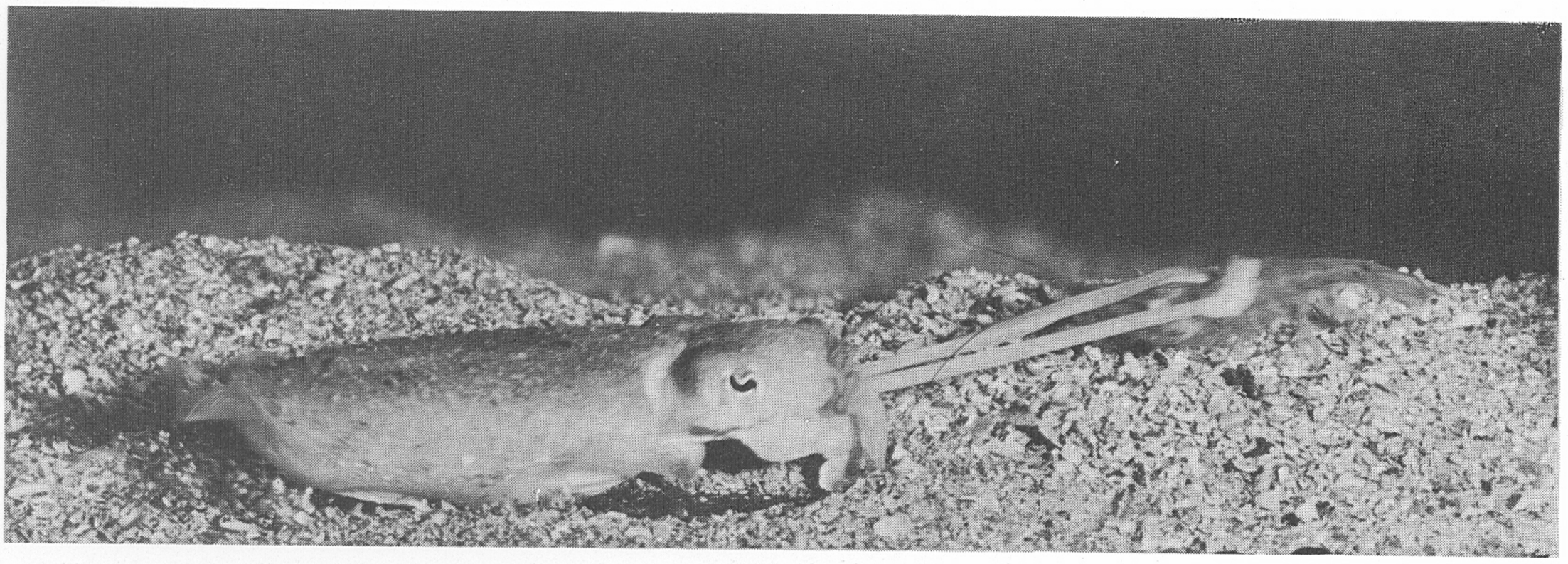

Fig. 2.

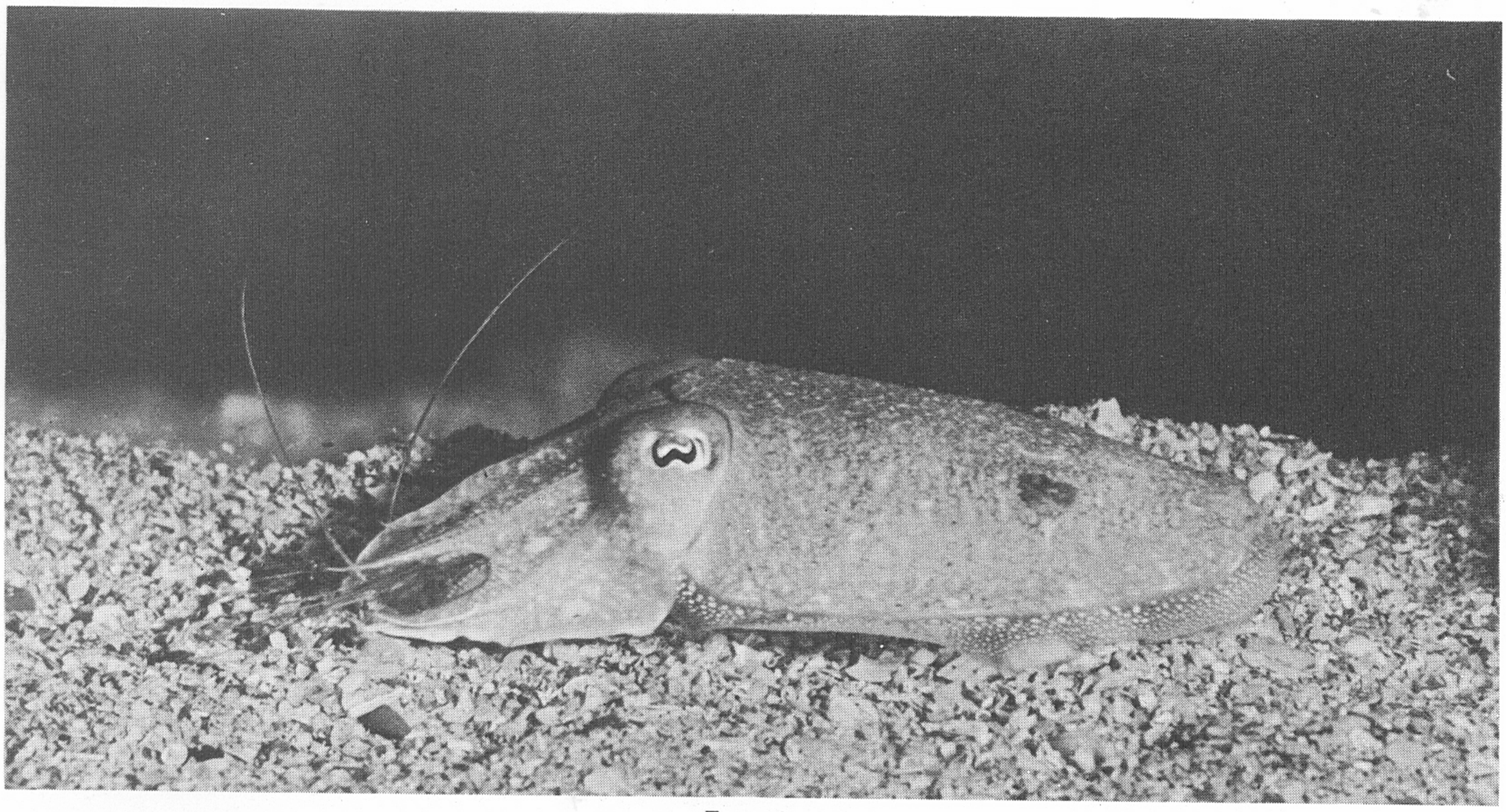

Fig. 3.

Sepia officinalis. Catching and eating a prawn.

to the latter as in the years 1925–32. The two average yields per voyage were, by a coincidence, of the same order of weight in the years 1925–42, but, from 1933 to 1940, the recovery in the drift-net fishery fell much below that of the trawl fishery. In 1933 the winter drift-net fishery began, and I think it very probable that the new fishery, by taking large quantities of herrings, has lowered the yield of the spring fishery. If this is so, it is a desirable development, for the winter-caught fish are in a good condition, at least during the earlier part of that season, while the spring-caught fish are spent and in poor condition until towards the end of the spring season.

There is a very close correlation, as Fig. 3 shows, between the catch per trip in the winter drift-net season and the subsequent trawl herring season. Using the estimated figure for 1939, the correlation between the eight pairs of average catches from 1933 to 1940 gives a coefficient of +0·908, a very significant figure which would be obtained by chance in uncorrelated material less than once in a hundred trials.

It follows that, by the end of the winter drift-net fishery, in March, an estimate may be made of the prospects in the trawl fishery which begins in June or July and ends in November. A good winter drift-net season is very likely to be followed by a good trawl season, while if the winter season is below the average, or a poor season, the prospects for the summer trawl season are likely to be poor. Where, as at present, no estimate whatever may be made as to the prospects of a herring season, which means a lot to the port's prosperity, the guide given by the correlation described above may be of help.

The correlation holds equally well whether the bulk of the trawl-caught herrings are taken off the Smalls or off Kinsale. In the table below are given the weights of herrings caught by the trawl at each of these grounds in each year:

Year	Kinsale	Smalls
1933	14,886	48,557
1934	8,457	19,861
1935	2,718	26,704
1936	13,986	50,077
1937	27,290	13,595
1938	25,638	5,892
1939	5,679	3,021
1940	43,059	Closed by minefield

The correlation shown in Fig. 3 holds as well for the years 1933 to 1936, when most of the herrings were caught off the Smalls, as for the years 1937–40, when the Kinsale fish provided most of the catches.

Evidence of Herring Migrations

It has already been shown that the changes in the roes of the herrings caught by the three fisheries show a continuous series, suggesting that the three fisheries are based on the same stock of herrings. Now it has been shown that the annual fluctuations in the abundance of the winter spawning herrings

off Dunmore are linked with those of the summer trawl-caught herrings, and that there also is a considerable amount of agreement between those of the widely scattered spring-spent herrings, and those of the trawl fisheries. The suggestion that all three fisheries are based on the same stock is reinforced.

As to the trawl-caught herring, it has been shown that both the Smalls and the Kinsale herrings are related to the same winter fishery at Dunmore, and further light on the connexion between the two trawl fisheries may be got by comparing the course of the seasons on each ground.

In Fig. 4 the weight of trawled herrings caught in each month from June to November is shown for each year from 1933 to 1940. The figure shows that,

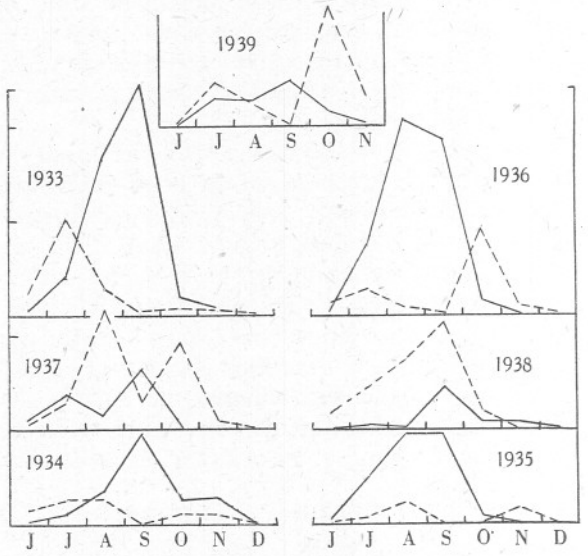

Fig. 4. The weight of trawl-caught herrings landed monthly at Milford Haven from the Smalls and the Kinsale grounds, 1933–40. Broken line—Kinsale, continuous line—Smalls.

in each year except 1938, the two fisheries tend to show an alternation. The fishery at Kinsale shows two peaks, in July or August, and again in October or November; between the peaks, in September, the weight of herrings caught at Kinsale falls, in some cases to zero. This is not because fishing ceases off Kinsale at that time: such data as I have show that fishing is still carried on there. So the decline in the abundance of herrings there is genuine. On the other hand, the fishery off the Smalls tends to rise to a single peak, usually in September, and falls at the time of the secondary peak at Kinsale. In 1938, however, both fisheries reached their maximum in September.

Therefore, though the two trawl fisheries are separated by some 90 miles of sea, they are related to one another by their common relation to the winter drift-net fishery, and by this alternation in the seasonal course of the fisheries.

But it is also well known that, during the trawl herring season, shoals of herring may be seen at the surface between the two trawl herring grounds: I have myself seen them. I think it probable that the herrings which are shoaling in preparation for spawning may be more or less continuously distributed between the Smalls and Kinsale, but that hydrographic or other conditions drive them to the sea-bed within reach of the trawl only at the two ends of their zone of distribution. An oscillation of these shoals from west to east and back again, would cause the seasonal variation in the abundance of herrings at the two ends of the zone.

Therefore in Fig. 1, I have sketched arrows to indicate what appear to be the movements of these herrings on which the three fisheries at Milford Haven are based. After spawning in winter off Dungarvan Bay, they scatter southwards on a feeding movement and are then caught in the spring drift-net fishery. Still later, in summer and autumn, they gather again in a zone, in two areas of which they are caught by the herring trawl, and finally they move back, in late autumn and winter, to Dungarvan Bay to spawn.

One notable feature about the shoaling of these herrings is the fact that, although the trawl fishery ends in October or November, and the winter drift-net fishery begins a few weeks later in December, during these few weeks there must be a reshuffling of the shoals. For, as Fig. 3 shows, the yield of the winter drift-net fishery is not in any way correlated with the yield of the summer trawl season which so recently ended, but with the trawl season still some seven months ahead.

Watkin (1933*a*) suggested that the herrings trawled off the Smalls later move south to the coast of Cornwall to spawn, but when he studied the subject the winter fishery off Dungarvan was unknown. I realize that these suggestions lack proof and that only further research, using biometrical methods, can establish whether the three Milford herring fisheries are in fact based on the same shoals. For example, the continuous cycle in the developing roes might be shown by distinct races of herrings which happen to spawn in the same season, and the observed correlation between abundance of the winter drift herrings and the summer trawled herrings may be due to some environmental factor common to both.

There is a fruitful field of work on the three herring fisheries for a study in the seasonal cycle of the herring, the relation between drift-caught and trawl-caught herring, and even in the behaviour of the herring shoals. In no other port, to my knowledge, are herrings available almost all the year round and possibly from the same stocks of fish.

The Influence of the Moon

Savage & Hodgson (1934) have shown that, in the great East Anglian autumn drift-net season for herrings, there is a relation between the phases of the moon and the catches of herrings, such that the best landings tended to occur at full moon. Further, the success of the herring season as a whole depends

to a large extent on the date of full moon. These authors say 'the best condition for a productive fishery appears to be when the October full moon occurs during the second week, for in this case it is found that the peak in the landings which accompanies this moon is approximately equal to the peak which appears at the time of the November full moon. Under these circumstances a period of about five weeks of good fishing can be expected'. This factor overrides the change in the age-composition of the herring shoals in its effect on the success of the season.

Fig. 2 and 3 show that the yield of the Milford drift-net and trawl seasons show great fluctuations from year to year. These can hardly be due to changes in the age composition of the shoals, for Watkin shows that, in the whole series of years 1923–8 (which included such good years as 1924, when the average weight of herrings per voyage was some 120 cwt., and such poor seasons as 1928 when the average per voyage was only some 56 cwt., or less than one-half) the mean length of the herrings varied only as between 29·2 and 28·4 cm., and the average age as between 6·3 and 6·8 years. These changes, as I have shown elsewhere for the herrings of the southern North Sea (Hickling, 1940), would represent only slight seasonal variations in the mean weight of the fish, of nothing like the order of magnitude of the variations in the yield per voyage. Some other factor, associated with shoaling, must thus account for the greater part of the observed variations from year to year in the abundance of herrings as judged by the catch per unit of fishing effort, as in the southern North Sea.

It is to be noted that Savage & Hodgson could find no regular relation between the moon's phases and the seasonal course of the drift-net fisheries for herring at North Shields and Grimsby.

In Fig. 5 the yield of the Milford drift-net and trawl fisheries, per unit of fishing effort, in each lunar week of each year from 1933 to 1940 is shown. The lunar weeks are the days centred about each phase of the moon, and may consist of 6, 7 or 8 days, according to the adjustment necessary to keep the moon's phase central.

Fig. 5 shows no sign of lunar periodicity in the winter drift-net fishery, and there appears to be no connexion between the date of full moon in January, at the height of the fishery, and the season's yield. Below are given the dates of full moon, and the average weight of herrings per landing in the appropriate full season:

Date in January	5	8	11	16	19	24	26	30
Year	1939	1936	1933	1938	1935	1940	1937	1934
Cwt. per landing	119	146	118	141	73	203	114	95

In the spring drift-net fishery there is a slightly better relation between the catches and the date of full moon. Thus, peaks in this fishery occurred at full moon twice in 1933, once in 1934, twice in 1935, and twice in 1936, once in 1938, and twice in 1940. But there are also many peaks not at full moon, and no definite relation can be stressed.

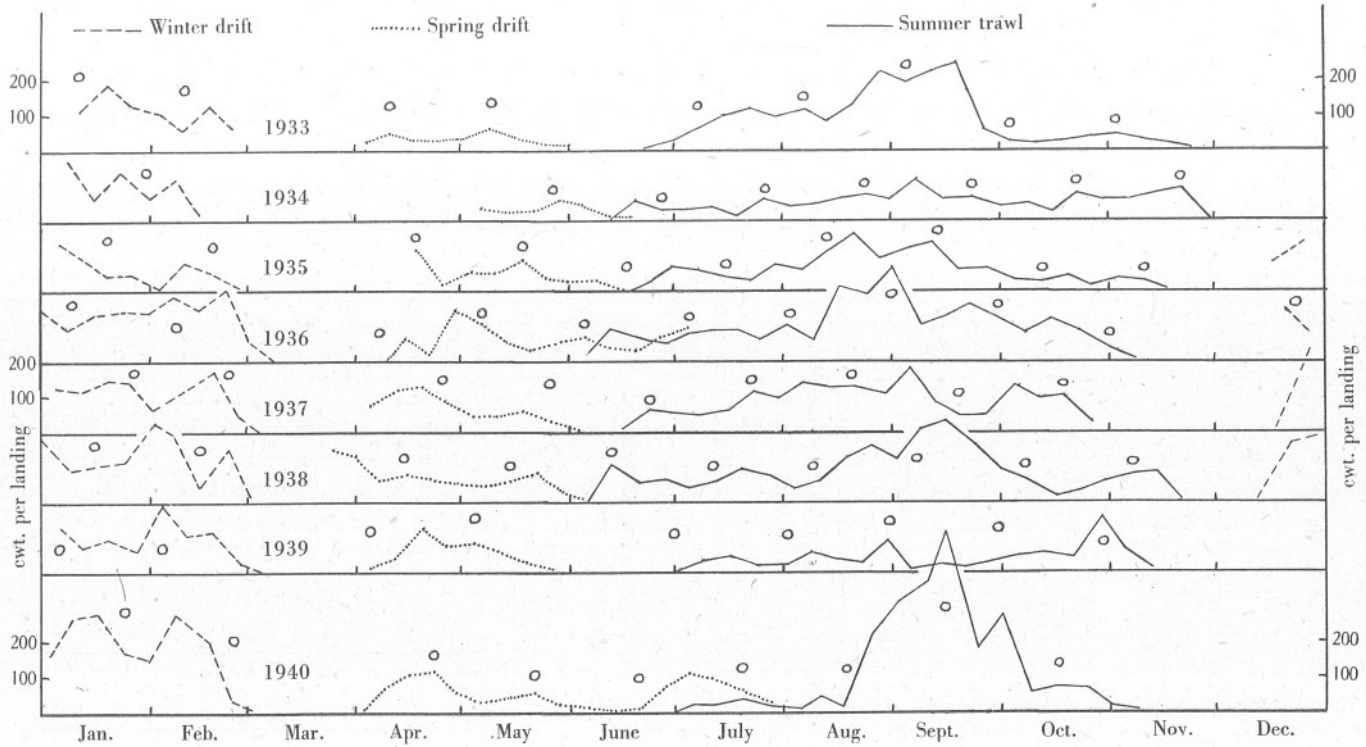

Fig. 5. The average weight of herrings per voyage in each year from 1933 to 1940, calculated by lunar weeks. Full moons inserted.

When the date of the full moon in May is compared with the average yield of the season per unit fishing effort, again, as in the winter drift-net fishery, there appears to be no relation between the two. I have divided this series into two, one series including the years 1925–32, and the second including the years 1933–40, when as I have shown earlier the advent of the winter drift-net fishery may have lowered the yield of the subsequent spring drift-net fishery:

Date in May	4	7	12	16	19	23	26	31
Year	1928	1925	1930	1927	1932	1929	1926	1931
Cwt. per landing	75	56	49	72	44	54	78	34
Date in May	3	6	9	14	18	21	25	28
Year	1939	1936	1933	1938	1935	1940	1937	1934
Cwt. per landing	57	60	31	61	44	46	53	39

Again there is no tendency apparent in these figures to suggest that the season may be a better one when the full moon occurs at any particular time in May.

Finally, in the summer trawl herring fishery there has been no regular and constant tendency for the fishery to improve at full moon. In two of the best seasons, namely, 1936 and 1940, the heaviest fishing did occur at full moon, but in the next best seasons, those of 1933 and 1938, the peaks occurred between full moons, and in all the other years an improvement in the catch was just as likely to occur at any other phase of the moon as at full moon.

If, in the whole series of years, the average weight of herrings per landing at each phase of the moon is calculated, it appears that full moon did produce the largest average catch, as may be seen below:

Full	Last	New	First
94·1	72·0	89·0	84·8

But when these means are tested, it is found that a difference as great as that observed between the lowest mean catch, at last quarter, and the highest mean catch, at full moon, would be found by chance twice in ten trials, and no significance can be attributed to them.

Finally, to compare the yield of the trawl herring seasons with the date of full moon in September, use can be made of the Sea-Fisheries Statistical Tables of the Ministry of Agriculture and Fisheries. From these can be extracted the average weight of herrings landed by steam-trawlers, per days absence from port, in Region VIIG–K, which includes both the Smalls and the Kinsale fishing grounds, in each year since 1907. Years in which fewer than 10,000 cwt. of herrings were landed have been omitted, as being so small a total that the fishery was not adequately sampled. The years omitted are 1909, 1915–19, and 1930.

In Fig. 6 the average weight of herrings per day's absence has been plotted, for each year, against the date of September full moon. The figure shows that all but one of the best seasons occurred when the moon was full in the first 16 days of September, and that all seasons in which full moon fell in

the last fourteen days of September, with that one exception, were poor seasons. The average weight of herrings per day's absence from port, when full moon fell in the first 16 days of September, was 25, whereas when full moon fell in the last fourteen days of September the average was 10. When these averages are tested statistically, they are found to be significant, since a difference in the averages as great as this would be found by chance less than once in a hundred trials.

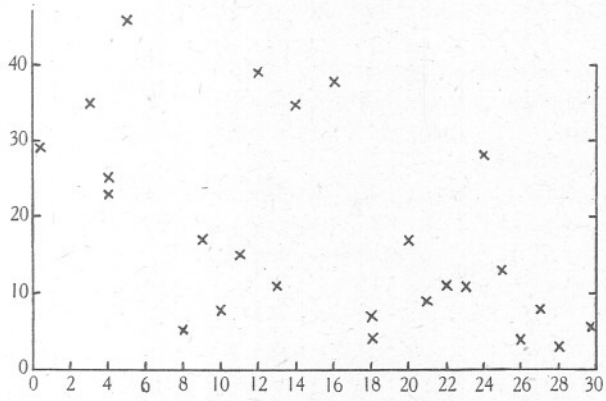

Fig. 6. The average weight of herrings (cwt. per day's absence) plotted against the date of full moon in September 1907–39.

The data may be further considered as a fourfold table. The average weight of herrings per day's absence from port over the whole 25 years was 18 cwt.:

	Season above average	Season below average
Full moon in the first 16 days	8	5
Full moon in the last 14 days	1	11

A statistical test again shows that these figures are significant. It appears, therefore, that when full moon falls in the first sixteen days of September, the trawl herring season may be either good or bad, with the odds slightly on the good; but when the moon is full in the last fourteen days of September the season is likely to be below the average.

The Daily Variation in the Catches

Lucas (1936) showed that, in the North Sea trawl herring fishery, the average catches increased from midnight to a maximum at midday, falling again to a minimum at midnight. I have no data as to the diurnal variations of the trawl fisheries in the Milford Haven area, but skippers are agreed that herring catches are best at night off the Smalls, and by day off Kinsale. On both occasions when I have been at sea on herring trawlers off the Smalls, the night gave the best catches, and the ship would steam away a few miles, when daylight came, to fish for mackerel.

Summary

1. There are three herring fisheries carried on from Milford Haven, namely, a winter drift-net fishery, a spring drift-net fishery, and a trawl fishery in the summer and autumn. These fisheries provide herrings nearly all the year round.

2. There is evidence that the three fisheries are based on the same stock of herrings, and the annual migrations of these herrings are deduced from statistical data.

3. There is a correlation between the results of the winter drift-net fishery and the following summer and autumn trawl fishery, so that it is possible to make an estimate of the prospects of the important trawled herring fishery some months in advance.

4. There is no evidence that the catches in any one season fluctuate with the moon's phases, but it is found that, in seasons when the moon was full in the last fourteen days of September, the result of the trawl herring fishery has almost always been poor.

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A NOTE ON THE CAPTURE OF PREY BY *SEPIA OFFICINALIS* L.

By Douglas P. Wilson

Naturalist at the Plymouth Laboratory

(Plates VI and VII)

There are various short and incomplete accounts of the capture of prey by *Sepia* scattered throughout the literature (Grimpe, 1928; Hertling, 1929; Holmes, 1940, are all typical and fairly recent), but I have not found any really satisfactory figures. Those I have seen are little better than rough sketches (Grimpe, 1928, p. 372; Naef, 1923, text-fig. 304*b*; Tompsett, 1939, plate i, fig. 2) and there do not appear to be any photographs at all. A few observations, and some photographs I have taken recently should therefore be of interest, especially as the photographs reveal some points that do not appear to have attracted attention previously. The final stages of the capture take place so rapidly that the eye fails to observe the details, whereas photographs can be studied at leisure afterwards.

The specimen of *Sepia* that forms the subject of these pictures was of medium size with a shell about 12 cm. long. It had been living in a tank, with others of about the same size, for several months, during which time it had been fed on living prawns. It was photographed in mid-November when the water temperature was 12·5° C. (in a later paper I shall show that below about 11° C. *Sepia* often ceases to feed). The photographs were taken by flashlight on two evenings between 7 and 8.30 p.m., the tank being lit, for viewing purposes, by a 100 W. bulb in a reflector above one end (the left side in the pictures). Each photograph was taken at $\frac{1}{100}$ sec. with one Baby Sashalite bulb and a synchronizer of my own design, the shutter being released electrically. In Pl. VII, figs. 2 and 3, two photoflood lamps were added to give better illumination on the shadow side, and these were also synchronized with the shutter so that they were switched on to reach maximum intensity just as the latter was released. Thus the cuttlefish was not influenced by the brilliance of their light before the exposure was made. At the flash, and the simultaneous switching on of the photofloods, the *Sepia* would momentarily hesitate, giving time for the prawn to be rescued so that the apparatus might be set for another exposure. Once, however, the cuttlefish had actually seized its prey it would not let go and would not show interest in another prawn placed in the tank. In the aquarium, before the war, I have often seen large *Sepia* catch two or three prawns in quick succession and eat them all, and Dr Anna M. Bidder tells me she has recorded an even larger number of crabs and prawns taken one after another during an hour or so.

When a prawn or a crab (*Portunus depurator* was often used to feed *Sepia* at Plymouth) is first introduced, the cuttlefish, which is probably resting quietly on the bottom partially covered with sand, immediately takes notice. The eyes open a little, and colour changes begin to shimmer rapidly over arms and back. Often a deep flush spreads over the arms and around the eye region, extending sometimes on to the back, as the *Sepia* rises slightly and turns to face its prey. Colour reactions vary a little between individuals and in the same individual from time to time, but broadly are always the same. They have been well described by Holmes (1940, p. 28), who gives a good brief account of the hunting. The *Sepia* swims stealthily towards its victim, manoeuvring, if it be a crab, to approach from behind, for very rarely will it seize a crab from in front; prawns are taken from any angle. With undulations of the lateral fins and gentle backwardly directed jets from the siphon (Russell & Steven, 1930) it endeavours to approach within range. At the same time the eight arms are stretched out towards the victim, the upper pair frequently being raised vertically, or curled upwards in the form of an S, and depressed again, the lower pair directed slightly downwards and often parted to each side. Colour changes pass rapidly over them. The pale tentacles are partially extended in advance of the arms (Pl. VI, fig. 1). Whilst Holmes may be partly right in suggesting that 'the colour movements...serve to distract the attention of the prey from the tentacles which spring out towards it', I have no doubt that many crabs and prawns do watch these tentacles and stand ready to dodge at the moment they are shot forward. Until that moment they may not shift their position, though a crab will circle, if it can, to keep its face and claws towards its enemy. I have watched a prawn in a small tank successfully dodge five times in succession, only to be caught at the sixth attempt. That last time it was not in such a favourable position for escaping, having got itself into a top corner of the tank close up against the water surface, the *Sepia*, meanwhile, approaching from the middle of the tank and shooting obliquely upwards. In a large tank crabs and prawns often get away, and this must be a regular occurrence in the sea once the enemy has been sighted; surprise must play a big part in aiding *Sepia* to catch its food. As it lies on the bottom, partially covered in sand, prey must often approach closely, unaware of its presence until too late. However, there is little doubt that *Sepia* does at times chase its prey, especially when really hungry, as can be seen in a large tank when crabs are dropped in many feet away and the *Sepia* rush towards them. When well fed, cuttlefish may be content to wait until the prey approaches closely.

Pl. VI, fig. 2, is an example of a prawn successfully escaping. It had stood still as the cuttlefish approached with outstretched tentacles and then, as they were suddenly shot forward, it jumped violently upwards with a sharp flexing of the abdomen. The switch operating the photographic mechanism had been thrust down into contact the instant the tentacles were shot forwards and as the prawn jumped. The whole process had taken place too quickly for the eye to

follow, but the photograph suggests that the cuttlefish was rushing forwards when the ends of the tentacles struck the ground after missing the prawn and, overrunning them, had thrown them into loops. The siphon is directed backwards and there is a scurry of gravel particles under the *Sepia*, appearing in a cloud behind. Evidently a powerful backward jet of water had brought about a sudden forward movement of the cuttlefish which was sufficiently rapid to blur at $\frac{1}{100}$ sec. The arms are bent around to each side ready to receive the prey, which has, however, escaped, and, in the sea, might reach a safe distance before the *Sepia* has recovered itself. A moment later the tentacles were retracted and the cuttlefish retreated in the opposite direction, but this direction may have been influenced by the sudden bright flash in front of it.

Pl. VI, fig. 3, and Pl. VII, fig. 2, are photographs of the successful capture of a prawn. They were taken on succeeding evenings, and in both the shutter has exposed the plate at about the very instant of contact of the tentacles with the prey. The sucker-bearing heads are blurred, indicating the rapidity of the movement and, whilst it is difficult to be quite certain, it does appear as though the distal ends of the tentacles were travelling more rapidly than the proximal. At any rate this is a point worth future investigation. The extended tentacles are relatively straight from their sockets to the prawn, which in one picture is well blurred, probably indicating an escape movement, although there is the possibility that it is the beginning of the sudden pull back to the mouth of the *Sepia*. In the other picture the head of the prawn is sharp and the tail blurred in a way that suggests violent flexure in an attempt to escape. In both instances the prawn is held by the middle region of the body; this seems to be usual. The pictures show the siphon to be curled back, and in Pl. VII, fig. 2, there is a slight disturbance of particles in the tail region, which may, however have been due to currents induced by the lateral fins; the scurry in Pl. VI, fig. 2, seems to have been too violent to be accounted for solely by the action of the fins. At the same time as the tentacles are shot out the head is craned forward on the neck (compare with Pl. VII, fig. 3). The arms are suddenly curled back ready to receive the prey.

It would be interesting to know how protraction of the head is brought about. Tompsett (1939) mentions only retractor muscles to the head in the neck region. The drawing in his pl. i, fig. 2, shows something of the outstretched neck, but nothing is said about it in the text. The swift protraction of the tentacles is almost certainly brought about by their internal musculature which includes numerous circular and radiating fibres in addition to longitudinal muscles (Tompsett, 1939). A large nerve runs down the centre of each tentacle to the tip.

A prawn is held across the mouth with the head to one side and the tail to the other and with the back towards the beak. A prawn that is caught in such a way that the ventral side is towards the mouth is turned round in the arms. It is then bent head to tail and bitten into about the region of the main dorsal

arch of the body. A crab is held with the back of the carapace to the beak in such a way that the claws are unable to nip the cuttlefish anywhere. I have occasionally seen crabs, which had been badly secured, manage to nip the arms; they were immediately released and made good their escape. The prey is soon dead and is almost wholly consumed, very few fragments being left. This is in contrast to *Eledone* and *Octopus* which discard most of the shells of the crabs they eat.

Sepia relies on its eyes when hunting and probably receives little or no help from its other sense organs. The olfactory pits, situated behind the eyes, function in all likelihood as osphradia (Tompsett, 1939) and have nothing to do with the capture of prey. The reliance on sight is emphasized by the fact that on two occasions when taking these photographs the cuttlefish directed its tentacles to one side of the prawn, hitting the glass some distance away from the intended victim. This it appears to be about to do in Pl. VI, fig. 1, but it was startled into retreat by the flash which exposed the plate before the tentacles had been shot out. It will be remembered that the photographs were taken after dark with a strong viewing light above and directed into the tank, the laboratory outside being dimly lit. Under these conditions the *Sepia* would see a good reflected image of the prawn in the glass and evidently was unable to distinguish it from the real thing.

Whilst in captivity the food of *Sepia* consists largely of living prawns, shrimps and small crabs, particularly *Portunus depurator*, which has a relatively thin shell. I have also seen small fishes taken whilst they were swimming (Hertling (1929) records the capture of *Ammodytes* though Grimpe (1928) says he has never seen free-swimming prey caught). When very hungry after a period of starvation *Sepia* will resort to cannibalism, the larger individuals eating the smaller. This is especially liable to happen in warm summer weather when their metabolism is at a high level and their feeding requirements correspondingly great.

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EXPLANATION OF PLATES VI AND VII

PLATE VI

Fig. 1. *Sepia officinalis* approaching a prawn with outstretched arms and protruded tentacles. A deep flush extends over the upper surface of the arms and face.

Fig. 2. Prawn escaping by a quick upward jump, the tentacles of the *Sepia* missing and hitting the ground. The *Sepia* is rushing forward with outstretched neck and arms parted to each side.

Fig. 3. Prawn successfully seized. The head of the *Sepia* is craned forwards on the neck and the arms are parted to each side ready to receive the prey when it is drawn back on to them.

All exposures by synchronized flashlight at $\frac{1}{100}$ sec.

PLATE VII

Fig. 1. *Sepia officinalis* moving after a prawn which is out of sight on the right. In this picture the two upper arms are partially raised in the form of an S. A deep flush spreads over the upper surface of the arms and face and on to the back which is sprinkled over with sand.

Fig. 2. The prawn is seized as it is about to move away (for an alternative interpretation see text). The head is craned forwards on the neck and the arms are parted to each side ready to receive the prey.

Fig. 3. The prawn was caught a few minutes before and the *Sepia* is settling itself down to eat it.

All exposures by synchronized flashlight at $\frac{1}{100}$ sec.

SABELLA PAVONINA SAVIGNY VAR. *BICORONATA* HORNELL AND THE GENUS *SPIROGRAPHIS* VIVIANI (POLYCHAETA, SABELLIDAE)

By D. W. Ewer

(Text-figs. 1–4)

Hornell (1891) described a variety of *Sabella pavonina* Sav., which he called *bicoronata*, from Hilbre Island at the mouth of the river Dee near Liverpool. This variety has recently been found at Plymouth where it may be trawled at Laira and in the Tamar estuary near Saltash Bridge. The variety is characterized by the inequality of the number of filaments of the two sides of the branchial crown.

The Sabellid genera *Sabella* Linnaeus, 1758 and *Spirographis* Viviani, 1805 as recently defined (Fauvel, 1927; Johansson, 1927) differ only in the inequality of the number of filaments of the two sides of the branchial crown. Hornell remarks that at first he was inclined to assign his variety to the genus *Spirographis*, but further examination showed that, apart from the number of branchial filaments, the worm differed in no way from *Sabella pavonina*. The specific descriptions of *Sabella pavonina* Sav. and *Spirographis spallanzanii* Viv. are also almost identical. Since the variety *bicoronata* shares with *Spirographis spallanzanii* one of the few characters which have heretofore been used to separate the two species, I have made a fresh examination of the three organisms to find further distinguishing characters. The descriptions of the species which are given below aim only at pointing out these differences and are not complete in themselves. Full descriptions may be found in such works as Fauvel (1927).

SABELLA PAVONINA SAVIGNY[1]

The two sides of the crown have an almost equal number of filaments. The total number of filaments is variable, there being usually between 25 and 50 on each side. Typical filament counts are 27–24, 29–30, 23–23 and 29–31. The rachis of the crown from which the filaments arise is rolled through one complete revolution on each side (Fig. 1 A). When the crown is retracted the dorsal edges of the two sides of the crown at the level of the basal membrane are usually well separated. Viewed from the ventral surface the two sides of the branchial crown do not overlap, both turning inwards medially (Fig. 2 A). The palps are straight, long and end in a fine tip (Fig. 3 A). They are joined proximally by a fine membrane and are at least five times the length of this membrane.

[1] Johannson (1927) considers that this species should correctly be called *S. penicillus* L. I have here followed Fauvel.

The dorsal collar fold arises immediately dorsal to the first chaetal bundle (Fig. 1 A). When reflected anteriorly the fold covers at least half the length of the peristomium. The ciliated faecal track runs along the dorsal mid-line of the thorax; where this track crosses the peristomium there is a shallow depression whose sides are never raised to form thin, clearly marked lips.

The ventral edge of the uncinal ridge of the second thoracic chaetigerous segment is separated from the dorsal edge of the ventral gland shield by at least half the length of the ridge.

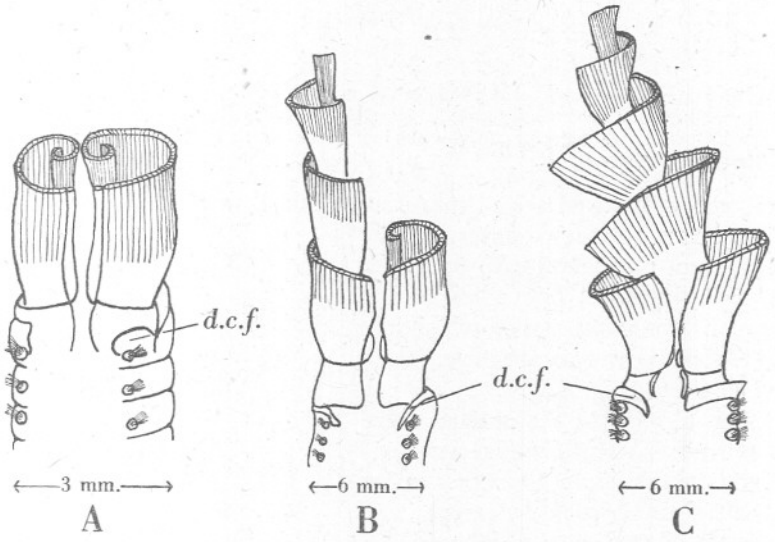

Fig. 1. Diagrams showing the shape of the rachis of the branchial crowns of A, *Sabella pavonina*; B, its variety *bicoronata*; and C, *Spirographis spallanzanii*. All three specimens are viewed from the dorsal side. *d.c.f.* dorsal collar fold.

S. PAVONINA VAR. *BICORONATA* HORNELL

The two sides of the crown do not carry the same number of filaments. The proportions are variable. Typical counts on adult specimens are 41–83, 45–84, 36–45 and 43–52. Hornell gives values of 30–61 and 37–55. The rachis of the crown on the greater side is spirally rolled and may make up to three complete revolutions. On the lesser side the rachis makes one complete revolution. In the retracted condition the diameter of the lowest turn of the larger side of the crown is slightly greater than half the breadth of the thorax. As a result the radius of curvature of the whorls of the crown diminishes slowly (Fig. 1 B). When the crown is retracted the dorsal edges of the two sides of the crown nearly touch at the level of the basal membrane. Viewed from the ventral surface the two sides of the branchial crown do not overlap, both turning inwards medially (Fig. 2 B). The palps are variable in form,

commonly short and ending bluntly, but they may be long, with fine tips as in *S. pavonina*. They are usually bent (Fig. 3 B, C).

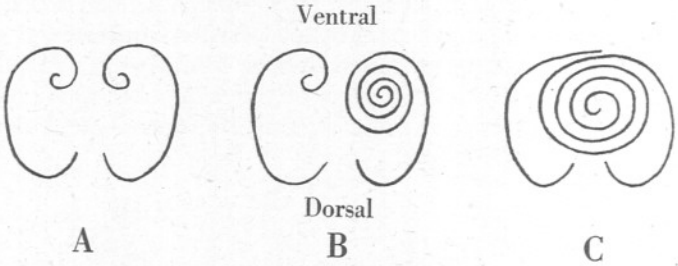

Fig. 2. Projection, in the transverse plane, of the rachis of the crowns of A, *Sabella pavonina*; B, *S. pavonina* var. *bicoronata*; and C, *Spirographis spallanzanii*. Note that the lesser side of the crown of *Spirographis* makes only half a revolution and overlaps the greater half of the crown ventrally.

The dorsal collar fold arises immediately dorsal to the first chaetal bundle (Fig. 1 B). When reflected anteriorly the folds cover not more than half the length of the peristomium. The sides of the peristomial depression across which the ciliated faecal groove runs are never raised to form thin lips (Fig. 4A).

The ventral edge of the uncinal ridge of the second thoracic chaetigerous segment is separated from the dorsal edge of the ventral gland shield by at least half the length of the ridge (Fig. 4A, *u.r.*).

The blood vascular systems of *Sabella pavonina* and *Spirographis spallanzanii* have lately been described (Ewer, 1941). In the abdomen of the variety *bicoronata* the arrangement of the blood vessels differs only slightly from that of *S. pavonina*. There is no sign of the septal plexus or of capillaries in the ventral muscle blocks which are characteristic of *S. spallanzanii*. Fox (1946) has examined the spectra of the chlorocruorins of *S. pavonina*, the *bicoronata* variety and *S. spallanzanii*. His results may be summarized as follows. The wave length of the α-band of oxychlorocruorin in *S. pavonina* is 6061 A.; in var. *bicoronata* it is 8 A. shorter and in *S. spallanzanii* 11 A. shorter. The span (difference between the α-band wave lengths in the oxy- and carboxy-compounds) is the same in *S. pavonina* and var. *bicoronata*, but differs in *S. spallanzanii*.

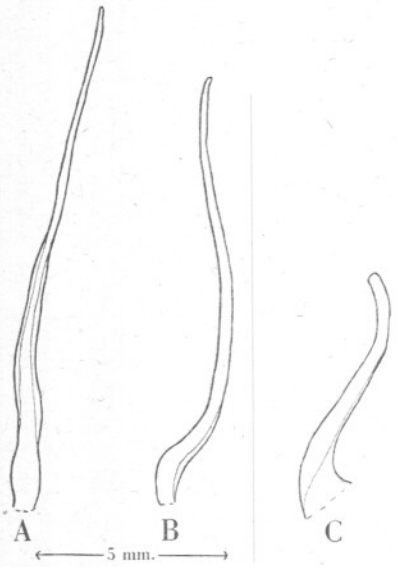

Fig. 3. Palps of A, *Sabella pavonina*; B and C, its variety *bicoronata*.

SPIROGRAPHIS SPALLANZANII VIVIANI

The number of branchial filaments is very unequal on the two sides of the crown. Typical counts on adult specimens are 36–138, 28–162 and 43–109. The rachis of the crown on the greater side is spirally rolled and may make more than four complete revolutions. On the lesser side the rachis makes only half a revolution. In the retracted condition the diameter of the lowest complete turn of the greater side of the crown is slightly less than the breadth of the thorax. The radius of curvature of the whorls of the crown diminishes rapidly. When the crown is retracted the dorsal edges of the two sides of the crown almost touch at the level of the basal membrane (Fig. 1 C). Viewed

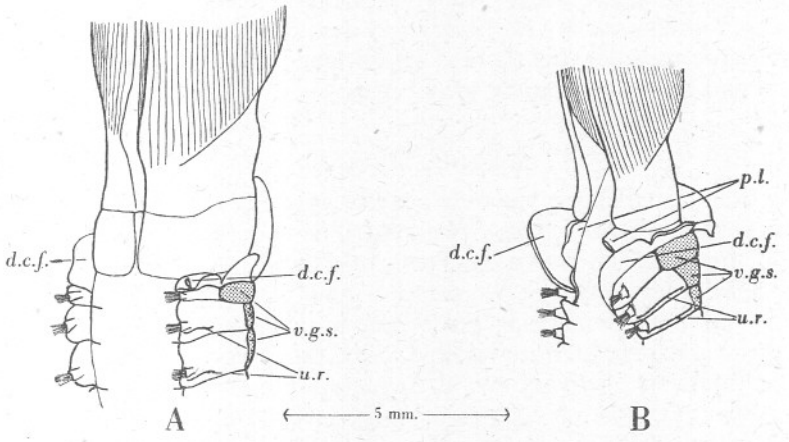

Fig. 4. Sketch of the peristomial region of A, *Sabella pavonina* var. *bicoronata*; and B, *Spirographis spallanzanii*. *d.c.f.* dorsal collar fold; *p.l.* peristomial lip; *u.r.* uncinal ridge; *v.g.s.* ventral gland shield.

from the ventral surface the lesser side of the branchial crown overlaps the greater. The free edge of the lesser side does not turn inwards medially (Fig. 2 C). The palps are short, end in a fine tip and are never more than three times the length of the membrane which joins them proximally.

The dorsal collar fold arises more dorsally than the first chaetal bundle (Fig. 1 C), the two halves of the collar fold often almost touch. When reflected anteriorly the dorsal folds cover the whole length of the peristomium. The sides of the peristomial depression across which the ciliated faecal track runs are nearly always raised to form thin lips, which run along the edges of the groove (Fig. 4 B, *p.l.*).

The ventral edge of the uncinal ridge of the second thoracic chaetigerous segment usually touches the dorsal edge of the ventral gland shield, but may be separated from it by less than half the length of the ridge (Fig. 4 B, *u.r.*).

The Systematic Position of *Sabella pavonina* var. *bicoronata*

Hornell (1891) considered that the specimens from Hilbre Island were a variety of *Sabella pavonina* for they only differed from the normal form in the development of the crown. As shown above the palps may also be different.

In *S. pavonina* and the variety *bicoronata* the ventral edge of the uncinal ridge of the second thoracic chaetiger is well separated from the dorsal edge of the ventral gland shield. In *Spirographis spallanzanii* the two structures almost touch. The condition in this latter species is also found in all other species of *Sabella* which I was able to study at the British Museum. These were *S. crassicornis* Sars, *S. oatesiana* Benham, *S. bipuntulata* Baird, *S. nigromaculata* Baird and *S. fusca* Grube. This fact emphasizes the close relation between Hornell's variety *bicoronata* and the normal *pavonina* type.

I therefore consider that there is insufficient reason for reversing Hornell's opinion and raising his variety to a species.

The Genus *Spirographis*

As has been stated above, the only positive generic character which has been used to separate *Sabella* from *Spirographis*, namely the inequality of the two sides of the branchial crown, is shown by Hornell's variety of *Sabella*. The other differences between *S. pavonina* and *Spirographis spallanzanii* are certainly not worthy of being made generic in value, especially as many of them are characters which are variable within the two genera. For example, the form of the rachis of the crown in *Spirographis braziliensis* Treadwell is the same as that in the variety *bicoronata*; palps as short as those in *S. spallanzanii* are also found in the *bicoronata* variety of *Sabella pavonina*; the dorsal origin of the collar folds is variable in position—in *Sabella nudicollis* Pruvot they arise at the level of the third chaetigerous segment. There are, moreover, no noteworthy differences between the chaetae of *S. pavonina*, its variety *bicoronata* and *Spirographis spallanzanii*.

For these reasons it is considered that the genus *Spirographis* is not valid and that species previously assigned to this genus should be referred to *Sabella*.

The genus *Sabella* would then be defined as follows:

Body cylindrical or subcylindrical. Two branchial lobes of which at least one is not rolled spirally. Branchial filaments lack dorsal appendages and subterminal eyes, but paired eye spots may occur. Ventral gland shields rectangular and divided into two portions in the abdomen by the faecal groove. Two palps. One dorsal and two ventral lips. Collar bi- or quadrilobed. In the thorax the neuropodium has avicular uncini and pennoned chaetae, the notopodium chaetae with narrow wings. No uncini or pennoned chaetae in the first chaetigerous segment. In the abdomen avicular uncini occur dorsally, chaetae with narrow wings ventrally.

My thanks are due to Mr D. P. Wilson, of the Marine Biological Association, who drew my attention to this variety of *Sabella*, to the Director of the Laboratoire Lacaze-Duthiers, Roscoff, who kindly gave me many specimens of *Spirographis* and to both the Director of the Marine Biological Laboratory at Plymouth and Professor H. Munro Fox, F.R.S., in whose laboratories this work was undertaken.

Summary

A variety of *Sabella pavonina* Sav. described by Hornell as *bicoronata* has been found at Plymouth. It is characterized by the unequal development of the two sides of the branchial crown. The characters by which *Sabella pavonina*, its variety *bicoronata* and *Spirographis spallanzanii* may be distinguished are described. It is concluded that the genus *Spirographis* is not valid and that its species should be referred to the genus *Sabella* which is redefined.

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PERMEABILITY AND PROPERTIES OF THE MEMBRANES SURROUNDING THE DEVELOPING EGG OF *HOMARUS VULGARIS*

By C. M. Yonge, F.R.S.

University of Glasgow

(Text-fig. 1)

CONTENTS

Introduction

The non-protoplasmic membranes surrounding the developing eggs of *Homarus vulgaris* M.-Edw. and other decapod Crustacea have been shown (Yonge, 1937) to consist of an inner chitinous membrane secreted by the oviducal epithelium and an outer one of cuticle (protein, probably with adsorbed lipin) formed by the cement (tegumental) glands in the pleopods of the female. They thus correspond in nature and origin to the two constituents of the integument (Yonge, 1932). In the present paper an account is given of experiments on the permeability of these membranes. The results provide further evidence of the presence and distinct properties of the two membranes, and also show that they have similar properties of permeability to those demonstrated for the cuticular and chitinous layers of the integument (Yonge, 1936).

The Recently Attached Egg

The experiments were carried out on eggs taken from the abdomen of a berried female which had recently spawned. The eggs were therefore still spherical and development had barely begun, so that the contents consisted almost exclusively of yolk. This possesses a dark green pigment, and the change in colour of this to red which occurs when certain substances penetrate the surrounding membranes is a useful initial indication of their entry. The inner, chitinous membrane is closely applied to the protoplasmic membrane, formed

in the ovary, which surrounds the egg. The outer, cuticular membrane does not lie so close to the inner membrane. This is due to its different mode of formation. The secretion of the cement glands flows round the eggs when they pass back from the genital openings to the under side of the abdomen during the process of egg laying. This flowing round is possible owing to the low surface tension of the cuticle (Yonge, 1932). A 'funiculus' of twisted strands of the cement attaches the eggs to the egg-carrying setae on the pleopods. The appearance of such a recently attached egg is indicated in Fig. 1*a*.

In the experiments described below detached eggs were placed in small glass dishes and the effect upon them of various fluids was followed, with the aid of a low-power binocular microscope, for appropriate periods. Controls left in sea water for the same periods showed no change.

Effect of Distilled Water and of Urea

In distilled water the eggs remained green but quickly swelled, increasing in diameter by up to 30 % at the end of 4 hr. (Fig. 1*b*). After 24 hr. the swelling had decreased, to not more than 10 % above the initial diameter. These changes are due to changes in size of the egg contents as shown in Fig. 1 *b*, the inner and outer membranes stretching and the space between them being obliterated. The outer membrane, it will be noted, stretched initially and then shrank, i.e. it must possess considerable elasticity. The inner membrane ruptured although this was difficult to see owing to the tightness with which it was forced against the intact outer membrane, but occasionally, as shown in Fig. 1 *b*, a distinct irregularity of the surface was noted which can only have been the result of rupture. When the stretched outer membrane was punctured with a fine needle the whole burst with some force indicating considerable internal pressure.

The effect of exposure to molar solutions of urea was very similar. Swelling was slower, the diameter increasing by 10 % at the end of 24 hr. Subsequently this sometimes increased further. The inner membrane was observed to rupture in several cases.

The results of these experiments are explicable on the assumption that the outer and inner membranes have the same properties of permeability as those demonstrated for the cuticle and chitin respectively (Yonge, 1936), namely restricted, almost semi-permeability for the former and free diffusion for the latter. With the destruction of the egg and its protoplasmic membrane, high internal osmotic pressure would cause inward passage of water through the largely semi-permeable outer membrane. Consequent swelling of the egg mass would explain the rupture of the inner membrane but the elasticity of the outer membrane prevented this from bursting. The later shrinkage may have been due to some outward passage of solutes through this membrane, or possibly to coagulation of the egg mass and so reduction in osmotic pressure.

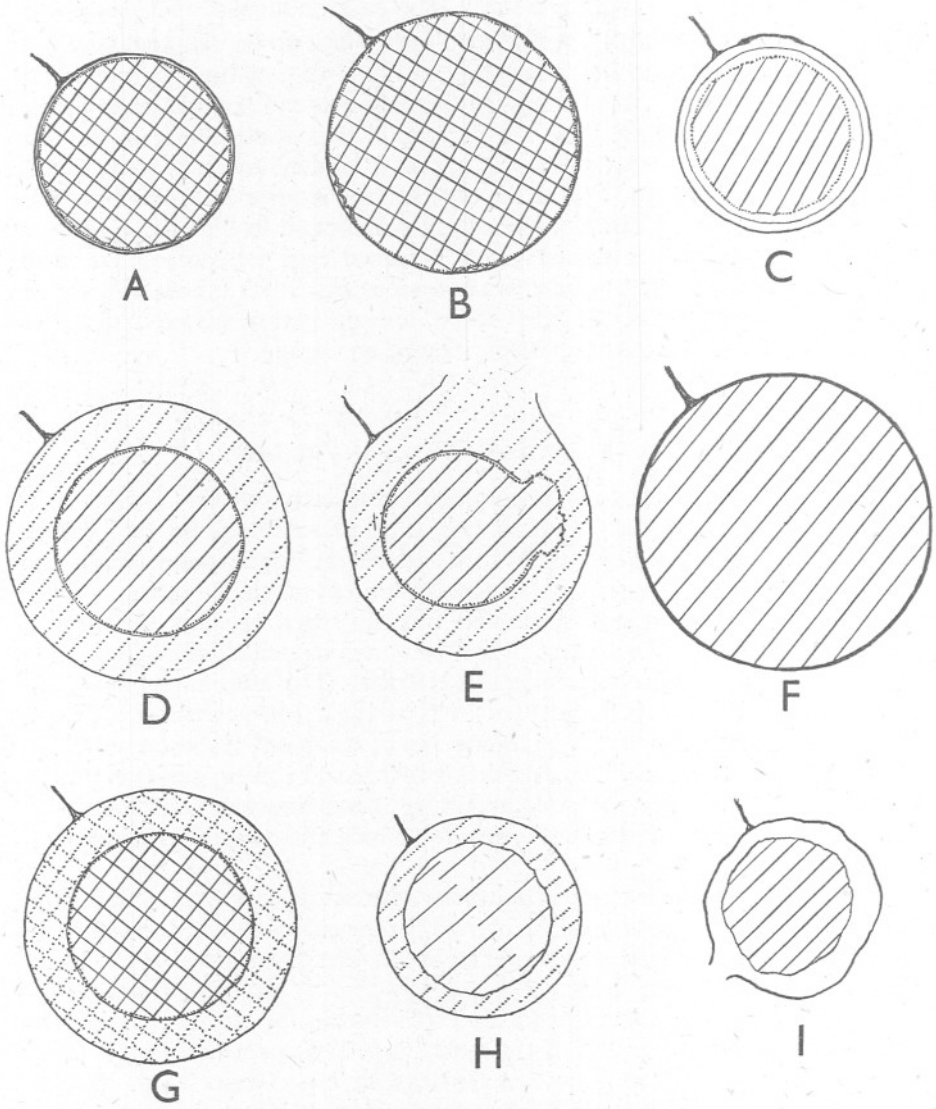

Fig. 1. Egg of *Homarus vulgaris* after varying treatment. × 12. Crossed lines indicate green colour in egg mass, oblique lines red, incomplete oblique lines yellow. Similar dotted lines indicate dissolved pigment between membranes. Outer membrane (with attached "funiculus") shown somewhat thicker than inner membrane: limit of egg mass indicated where necessary by dotted line. *a*, normal (and control) egg; *b*, after 4 hr. in distilled water; *c*, after 24 hr. in *N* hydrochloric acid; *d*, after 4 hr. in *N* formic acid; *e*, final appearance after exposure to *N* formic acid, both membranes ruptured; *f*, after 4 hr. in *N* potassium hydroxide, prior to disintegration of outer membrane; *g*, after 6 hr. in *N* ammonia with inner membrane intact; *h*, after 24 hr. in absolute ethyl alcohol; *i*, after 24 hr. in acetone.

Effect of Acids

The eggs were immersed in normal solutions of two strong mineral acids, hydrochloric and nitric, and the two low fatty acids, formic and acetic. Both mineral acids penetrated rapidly. The eggs began to turn red after 12–15 min. and were red throughout within 30 min. The contents were at the same time coagulated and shrank away from the inner membrane which in turn receded somewhat from the outer membrane (Fig. 1 *c*). The absence of internal pressure was revealed when the two membranes, well separated from one another, were successively punctured. The eggs remained indefinitely in the condition described.

Judging from the speed with which the eggs changed colour, the fatty acids penetrated somewhat more slowly. But since these acids certainly penetrate cuticle quicker than do mineral acids (Yonge, 1936) and the outer membrane has in all other respects identical properties with the cuticle, the slower change in colour is probably due to the weaker and less toxic nature of the acids, not to their slower penetration. Swelling occurred more rapidly with formic acid (known to penetrate the cuticle quicker than acetic (Yonge, 1936)). An increase in diameter of about 50 % was observed within 4 hr. This swelling, as shown in Fig. 1 *d*, was due to an increase in the space between the two membranes which filled with a reddish fluid revealing diffusion of dissolved material through the inner membrane. The dissolved pigment never passed through the outer membrane. The high internal pressure was again demonstrated by puncturing the outer membrane. The inner membrane usually burst, sometimes after about 3 hr. with formic acid (Fig 1 *e*). It always retained its original diameter, as indicated in Fig. 1 *d*, until it burst, revealing its rigid character. The outer membrane subsequently frequently also burst (Fig. 1 *e*) and the egg mass finally disintegrated.

Dissolution of the fatty constituents of the yolk in the fatty acids and consequent swelling will explain the bursting of the inner membrane and the high osmotic pressure the stretching and eventual bursting of the outer membrane. The passage of red pigment into the space between the two membranes, but not through the outer membrane, reveals the different properties of the two membranes.

Effect of Alkalies

Eggs were exposed to normal solutions of potassium and sodium hydroxides and of ammonia. It had previously been found (Yonge, 1936) that the special properties of permeability possessed by the cuticle are destroyed by exposure to normal potassium or sodium hydroxide. Uncalcified integument so treated possesses the free permeability of chitin. Both strong alkalies penetrated rapidly through the egg membranes causing a change in colour in 5 min. with potassium, and 10 min. with sodium hydroxide. Swelling followed almost immediately, the diameter increasing by about 50 % after 4 hr. The inner

membrane soon burst and permitted the egg mass to fill the entire space within the outer membrane (Fig. 1 *f*), i.e. as with fatty acids. But the substance of this membrane was attacked, it became swollen and soft and finally disintegrated, unlike that of the inner membrane which persisted. When punctured while still intact (but *after* distension had occurred) there was *no* evidence of internal pressure and no change in shape. The egg mass finally disintegrated.

The explanation of these results would appear to be that the egg contents were dissolved by the strong alkalies, their swelling caused rupture of the inner membrane and the high osmotic pressure distension of the outer membrane. The substance of this membrane was affected, *after* initial distension had occurred, by these alkalies and its special properties of permeability lost, exactly as had previously been demonstrated for the cuticle (Yonge, 1936). The dissolution of the outer and persistence of the inner membrane indicates that only the latter is chitinous.

Ammonia had much the same effect as fatty acids but there was no change in colour, a greenish fluid diffusing outward through the inner, but never the outer, membrane. Stretching of the outer membrane began after about 1 hr., the diameter increasing up to 40 % (Fig. 1 *g*). Puncturing revealed high internal pressure. The inner membrane frequently ruptured (not shown in Fig. 1 *g*) but the outer membrane never did so. Elasticity of this was revealed by a decrease, usually within 24 hr., to about 20 % above the initial diameter. This weak alkali had no effect on the substance of the outer membrane and its effects are those of a fat solvent, like those of the fatty acids, precisely as found in experiments on the cuticle (Yonge, 1936).

Effect of Ethyl Alcohol and Acetone

Alcohol penetrates rapidly and eggs began to turn red within 5 min. but later turned yellow and this colour extended into the area between the membranes. An initial reduction in diameter of up to 17 % at the end of 4 hr. was followed by expansion to slightly over the original diameter. The substance of the egg mass coagulated and shrank with the inner membrane adhering to it so that the two membranes became widely separated (Fig. 1 *h*). Acetone, judging by the rate of colour change, penetrated more slowly; complete change in colour took about 4 hr. There was a marked irregular shrinkage of the outer membrane leading to rupture although it remained *in situ* (Fig. 1 *i*). The inner membrane was similarly shrivelled and both became very hard. There was no outward flow of pigment through the inner membrane.

Uncalcified integument, with or without cuticle, when treated in air with alcohol or acetone becomes impermeable owing to dehydration (Yonge, 1936). There is apparently sufficient water within the outer membrane to prevent this effect with alcohol but not with acetone. In the former pigment diffuses out through the inner (but, as always, not through the outer) membrane, while the outer membrane stretches when the internal osmotic pressure is raised

owing to the dissolution of some constituents of the egg mass. With acetone both membranes are apparently dehydrated, and so become shrunken and impermeable.

Discussion

The presence of two non-living membranes around the developing eggs is clearly demonstrated. They frequently separate widely from one another while the egg mass may also separate from the inner one, as after treatment with mineral acids (Fig. 1 *c*). The absence of any appreciable development in the egg disposes of the suggestion that the inner one may be a larval integument while this has already been shown to be present when the egg leaves the oviduct where it is formed (Yonge, 1937). The different behaviour of the two membranes is explicable on the assumption that the outer has the restricted permeability already demonstrated for cuticle while the inner has the free diffusion of chitin. The former distends when high osmotic pressure is generated within it, the latter allows pigment and other dissolved material to diffuse through it. It frequently bursts owing to swelling of the egg mass but in ammonia, for instance, it never bursts although the outer membrane may distend to 40 % above its initial diameter owing to the passage of dissolved material through the inner membrane and consequent rise in osmotic pressure. The irreversible action of strong alkalies on the outer membrane is identical with their action on the cuticle of the integument.

The cuticle is known to be harder than chitin (Yonge, 1936), but a new point which emerges from these experiments is the extent to which the outer membrane can stretch and also its elasticity. Shrinkage frequently followed initial distension. This elasticity is therefore probably a property of the cuticular constituent of the integument also. In the case of the eggs this has biological significance. The outer membrane attaches the eggs to the pleopods in the decapod Crustacea, but it also protects them and has to withstand the pressure of adjacent eggs and the effect of the constant beating of the pleopods needed to produce the respiratory current around the developing mass of eggs. In this connection its elasticity as well as its firm consistency will be of real value. Moreover during development the egg increases in size, becoming oval with the long axis 50 % greater than the original diameter. The inner membrane appears to be ruptured and absorbed, its place being effectively taken by a series of larval integuments. But the outer membrane remains intact until hatching which, as already suggested for other Crustacea (see Yonge (1937) for references), may possibly involve its rupture by osmotic pressure. Certainly the outer membrane could not remain around the developing egg, securing it to the pleopods and protecting it, were it not capable of stretching greatly.

With Crustacea which liberate their eggs freely into the sea, such as the Penaeidea and the Euphausiacea, the problem of pressure has not to be overcome but expansion during development remains. We have no exact knowledge about the membranes surrounding the eggs in these animals, but Bargmann

(1937) has shown that in *Euphausia superba* Dana the oviduct is surrounded by a mass of glands which in all probability do secrete an outer membrane similar to that in the higher Decapoda. The presence of an inner, chitinous membrane secreted by the oviduct remains to be determined in these animals. But in view of the fact that two secreted membranes exist in Branchiopoda, e.g. *Chirocephalus* (Mawson & Yonge, 1938) and in Copepoda (Häcker, 1901; Ziegelmayer, 1926) as well as in Decapoda it is not improbable that the characteristic properties of this cuticular (i.e. protein) substance are widely employed to protect the expanding developing egg throughout the Crustacea. Chitin would certainly seem to be useless for this purpose. Indeed the difference between the two membranes is similar to the difference between the cuticular integument of the Annelida, which stretches as the animal grows, and the chitinous integument of the Arthropoda which has to be moulted to permit increase in size.

Summary

Subjection to a variety of fluids confirms the presence of two non-living membranes round the developing eggs of *Homarus*. It also reveals that the outer membrane has the restricted permeability of cuticle and the inner membrane the free permeability of chitin.

The inner, chitinous membrane bursts when the egg contents swell; the outer membrane stretches, up to 50 % above its initial diameter, when the internal osmotic pressure rises. It also has considerable elasticity.

These properties of the outer membrane enable it to withstand the pressure to which the developing eggs are subjected and also to stretch during the development of the embryo, hence they have considerable biological significance. The inner, chitinous membrane, which does not stretch, is probably ruptured and absorbed during development.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Structure and Conduction Velocity of the Medullated Nerve Fibres of Prawns

By W. Holmes, R. J. Pumphrey and J. Z. Young

Journ. Exp. Biol., Vol. 18, 1941, pp. 50–4

A preliminary account is given of the structure of the nerve fibres of the prawn *Leander serratus*. These fibres resemble those of vertebrates and differ from those of most invertebrates in possessing a thick myelin sheath. Most of the larger fibres are provided with nodes similar to the nodes of Ranvier in vertebrate nerve: this fact suggests that nodes play an essential part in the process of impulse conduction in fibres which possess a thick lipide sheath. The relative thickness of the myelin sheath in prawn fibres of various sizes increases with decrease in the total diameter of the fibres along a curve similar to that found in vertebrates.

The conduction velocity of certain large nerve fibres in the ventral nerve cord was measured: these fibres have a mean axon diameter of 26μ and a total diameter of 35μ, and they conduct impulses at a mean rate of 20 m. per sec. They thus conduct at a rate much greater than that of the largest fibres in other crustacea, but less than that of the myelinated fibres of vertebrates.

W.H.

The Structure and Function of the Alimentary Canal of *Aplysia punctata*

By H. H. Howells

Quart. Journ. Micr. Sci., Vol. 83, 1942, pp. 357–97

The feeding process of *Aplysia* is adapted to the rapid intake of vegetable food. While the stomach is reduced the anterior gut consists of large dilatations freely movable in the body cavity. It is here the food is subjected to the action of a strong amylase, together with sucrase, lactase, maltase, pectinase, lipase and proteases secreted by the digestive diverticula and salivary glands. No successive action of enzymes from different sources is possible. A cellulase is present but of extremely weak action. The gizzard, however, is efficient and almost entirely responsible for the exposure of the contents of the plant cells. The caecum is concerned solely with the elaboration of a faecal mass of material excreted from the digestive diverticula. The structure is also found in closely allied genera and the Thecosomatous Pteropods which share a

similar need for a means of avoiding the fouling of ciliary mechanisms in the neighbourhood of the anus in the absence of a spiral caecum which supplies a highly efficient cleansing organ in the mantle cavity of other tectibranchs.

H.H.H.

The Life Activities of Foraminifera in Relation to Marine Ecology

By Earl H. Myers

Proc. Am. Phil. Soc., Vol. 86, 1943, pp. 428–58

Statistical and cytological data on the seasonal variations in the life activities of *Elphidium crispum* in Plymouth Sound are correlated with the varying food supply, temperature, salinity, nutrient salt content of the water, hydrogen ion concentration, oxygen tension, illumination, turbidity, turbulence and currents together with the influence of tidal variations upon these factors. Animal associates, parasites, and natural enemies are discussed. Additional data from the Mediterranean, Pacific and Java Sea are also presented.

E.H.M.

The Reproductive System and Associated Organs of the Brittle-star *Ophiothrix fragilis*

By J. E. Smith

Quart. Journ. Micr. Sci., Vol. 82, 1940, pp. 267–309

A description is given of the morphology and histology of the gonads, gonoducts (here described for the first time as occurring in brittle-stars), genital bursae and axial organ complex of *Ophiothrix fragilis*.

The axial organ, within the substance of which the germ cells have their origin, is made up of two closely apposed parts; one part is believed to be derived as a proliferation of the wall of the left and the other of the right anterior coelom of the larva. These coelomic cavities persist to form a bipartite axial sinus; in the adult each cavity surrounds its own moiety of the axial organ.

The germ cells migrate along the genital rachis to the gonads, there to mature. In the female the ova are discharged periodically, probably at monthly intervals, from about March to October. Males may contain ripe sperm at all times of the year. The eggs are not discharged into the genital bursae nor do they develop there. Young animals which are found in the bursae of adults have attained that position only after a period of free-swimming larval life.

J.E.S.

The Genus *Kuhnia* n.g. (Trematoda: Monogenea). An Examination of the Value of some Specific Characters, Including Factors of Relative Growth

By Nora G. Sproston

Parasitology, Vol. 36, 1945, pp. 176–90

Kuhnia n.g. is created for the gill trematodes of mackerel, with *K. scombri* (Kuhn) as the type; *K. minor* (Goto) is re-described from some large forms from British waters. The clamps on the posterior end are newly interpreted as being formed of a continuous double cuticular loop with a middle, opposable piece (as in *Mazocraës* also, but differing from that genus in the disposition of the genital armature and in the absence of a vagina). An alternation of sex phases in Monogenea is proved by the study of a large series of *K. scombri*, and other developmental changes indicate that neither the absolute size, nor the ratios of parts, alone, are of any diagnostic value. Comparison of differential growth characters shows that they may be utilized in forming a polytypic species concept, and may contribute to a synoptic picture of a genus.

N.G.S.

A Note on the Comparative Anatomy of the Clamps in the Superfamily Diclidophoroidea (Trematoda: Monogenea).

By Nora G. Sproston

Parasitology, Vol. 36, 1945, pp. 191–4

The homology of the clamp sclerites is traced throughout the Diclidophoroidea, and it is shown that the type of clamp is a useful basis for the classification of families. A probable phylogenetic sequence is traced from the most generalized mazocraeid clamp, with its unbroken double loop and middle, opposable piece and incompletely cuticularized median tendon; through the discocotylid, in which the dorsal loop is reduced, and the cuticularized tendon forms the spring tending to open the clamp, the parts of which are jointed; to, on the one hand, the most complex diclidophorid type, where the sclerites are further jointed and separated, and made asymmetrical by the tendency to develop a lateral sucker; and on the other hand, to the hexostomatid, extremely reduced type, where three sclerites are imbedded in a cuticular sucker.

N.G.S.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1944–45

The Council and Officers

By the death of Lord Moyne, assassinated in Cairo on 6 November 1944, the Association has lost a very distinguished member who had contributed generously to improvements at the Plymouth laboratory and had himself made important contributions to Marine Biology. Lord Moyne had been a Governor since 1929; he was President of the Association from 1930 to 1939 and was a Vice-President at the time of his death. During the past year the Association has also suffered by the loss of Mr J. R. Norman of the staff of the British Museum, who had served on a number of occasions as a member of Council.

Four ordinary meetings of Council were held during the year, two in the rooms of the Royal Society in London, one in the Zoological Laboratory at Cambridge and one at Plymouth. At these the average attendance was 11. The Association is indebted to the President and Council of the Royal Society and to Prof. Gray for their kindness in providing accommodation for three of the meetings.

The Plymouth Laboratory

During the year considerable progress has been made in the restoration of the laboratory buildings. When it became evident that enemy raids on Plymouth had ended repairs to the asphalt roofing of the buildings were carried out and the lantern light in the library was renovated, while extensive work was undertaken by the laboratory staff. Included in the latter was the replacement of numerous panes of glass in the main laboratory, the reglazing and complete internal redecoration of the library, and repairs to the constant temperature rooms.

Plans for the full restoration of the premises, including extensive alterations in the aquarium, a new Easter class and conference room, an additional east wing linking the main laboratory with the north building and a library extension, prepared by Mr Easton, have now been approved; but much more work is needed on the details of the internal accommodation. An estimate for the permanent restoration of a series of rooms in the north building has been accepted and it is hoped that this work will be undertaken in the near future.

The Ship and Motor Boat

The laboratory is still without the use of the *Salpa*, which remains under requisition by the Admiralty. The motor-boat *Gammarus* has continued her

work, but the areas in which she can be used are greatly restricted. The arrangements, mentioned in last year's report, for the collection of specimens from one of the trawlers working from Plymouth have continued.

The Staff

Dr A. Sand has been elected to the Fellowship of the Royal Society. Mr D. P. Wilson has been awarded the medal of the Royal Photographic Society for his studies of the development of *Aurelia*.

Dr L. H. N. Cooper relinquished his temporary appointment in the Chemical Inspection Department of the Ministry of Supply and returned to the laboratory in December. It is hoped that during the coming year several other members of the staff who now hold National Service appointments will be able to resume duty at Plymouth.

On the recommendation of the Development Commissioners a grant has been made to Miss N. G. Sproston to enable her to continue her parasitological work at the Plymouth laboratory.

The Director has attended meetings of the Colonial Fisheries Advisory Committee and of a Committee, with Sir John Graham Kerr as Chairman, convened by the Development Commissioners to draw up programmes for post-war marine biological research in this country. He has also been asked for advice on proposals for fishery development in India. Dr W. R. G. Atkins and Dr H. W. Harvey have continued their work on the Marine Corrosion Committee of the Iron and Steel Institute.

During the year improved scales of pay for the laboratory assistants have come into force.

Occupation of Tables

The following have occupied tables at the Plymouth laboratory during the year:

Miss M. E. Bennett, Tetbury (Algae).
Dr S. P. Chu (Nutritional requirements of phytoplankton).
Dr V. Fretter, London (Prosobranchs).
Dr T. J. Hart, Discovery Committee (Falkland Islands' fisheries).
Dr R. S. Hawes, Exeter (Gregarine parasites of Polychaetes and Tunicates).
N. A. Holme, Exmouth (Classification of Crustacea).
G. R. Howat, Accra (Plankton).
A. G. Lowndes (Density of aquatic organisms).
Dr M. Parke and Miss E. Clay (Algae).
R. B. Pike, Reading (*Galathea*).
Hon. M. Rothschild (Colour responses under reduced temperatures).
Miss H. Rowett, Plymouth (Plankton).
A. N. Scott, Bristol (General zoology).
Dr J. E. Smith, Cambridge (General zoology).
Miss N. G. Sproston (Parasites of marine animals).

Prof. J. B. S. Haldane, Dr C. F. A. Pantin, Prof. C. M. Yonge, Miss Bidder, Mr Sidney Smith and several of the staff who are away on National Service,

have visited the laboratory during the year. Dr Narayana Murti of the Indian Forest Department, and Mr L. Littlejohn, who is concerned with fishery development in Cyprus, also came to Plymouth for discussions with the laboratory staff.

Scientific Work of the Laboratory Staff

Dr H. W. Harvey has continued work on antifouling by paint films composed of cuprous oxide and other poisons held in a matrix of copper soaps. Some of these have remained as tough, strongly adherent films for periods exceeding two years under water, and the most efficient have remained free from marine growths for periods of twelve to eighteen months when applied as a single but thick paint coat. The investigation has been made in collaboration with the group working on antifouling for a committee of the Iron and Steel Institute, who are repeating and extending trials on the more promising of these copper soap paints. Meanwhile a body of observations is being built up concerning the antifouling life of such films, with the object of ascertaining the effects of changes in composition and film thickness which cannot at present be foreseen. The aim of the experiments is rather to find out what is happening at the paint surface after several months under water than to devise an efficient and economic antifouling composition; since these copper soap paints behave in some respects differently to the more usual types it is thought worth while to continue. Dr Harvey has also made some preliminary experiments on the hydrolysis and bacterial breakdown of organic phosphorus compounds in sea water; if the 'winter phosphate maximum' could be linked with estimates of the total phosphorus or phosphate plus hydrolysable phosphorus in the water at any time of year, it might open up a new method of investigating the different fertility of different water masses. Publication of a book on the chemistry and biology of sea water, held up owing to paper shortage, is expected early in the new year.

Dr M. V. Lebour has published a paper in the current number of the Association's *Journal* on the larval stages of *Portumnus* and related forms. The Zoological Society has accepted for publication a paper on larval Prosobranchs from Bermuda. She has continued a regular examination of the inshore plankton, but the large amount of oil in the Sound has materially affected the catches.

Continuing her work on the Pycnogonida of Plymouth she has found the Phoxichilidiidae specially interesting. This family, the larvae of which parasitize hydroids, is in great confusion, but there are more species belonging to it in the Plymouth area than was formerly supposed. *Anoplodactylus angulatus* Dohrn is common high up between tide-marks and this species is added to the British fauna for the first time. *A. virescens* Hodge occurs commonly with *A. angulatus*, and although they look much alike and are frequently regarded as being closely related, it is now found that *A. virescens* belongs to the genus *Phoxichilidium* and is probably identical with or very closely related to Dohrn's

P. robustum, which is also a true *Phoxichilidium*. The vexed question of the identity of *Anoplodactylus petiolatus* and *A. pygmaeus* has been investigated thoroughly, with the result that the latter must almost certainly be regarded as a distinct species, identical with Dohrn's *Phoxichilidium exiguum*.

A paper is almost ready for publication in which fifteen species are recognized from Plymouth, twelve of which have been collected during the last two years in shallow water between tide-marks. It is hoped to study their life histories in more detail, especially those of the Phoxichilidiidae. In this family, so far as is known, each species behaves differently in its larval state and further work on the subject is much needed.

Mr D. P. Wilson has added to and so far as possible completed his observations on *Nitzschia closterium*, observing new details and confirming previous results. Some progress has been made in preparing a paper for the *Journal* and this will be published in due course.

A suggestion that the laboratory should supply photographic prints and lantern slides of marine animals through its sales department was considered and approved by the Council at their July meeting. Owing to shortage of photographic materials the proposal cannot be introduced until the end of the war, but Mr Wilson has prepared a set of duplicate negatives, and a first series of prints has been mounted in an album for circulation to zoological departments and institutions.

Mr Wilson has again devoted much of his time to the plans for the post-war reconstruction of the laboratory, paying attention to detail and incorporating improvements which have from time to time been suggested. He has also reported on the biological condition of materials immersed in the sea for test purposes on behalf of industrial firms.

Mrs E. W. Sexton has continued her work on the multiform Amphipod species, *Jassa falcata* (Montagu). The variation in the species is shown principally in two characters, the second antenna and the second gnathopod, and an attempt is therefore being made to figure and classify the whole range of variants. So far the gnathopods of about thirty-five specimens with their correlated antennae have been drawn, but the line of inheritance is not yet evident. A further problem has arisen in that one of the variants, of the 'short-thumb' type, appears to be intersexual. The Antarctic *Jassa ingens* (Pfeffer) has also been figured in detail to show its relationship to *J. falcata*.

Algal Research

During the year the Development Commissioners have taken over financial responsibility for the continuation of the special research on brown algae which began in October 1942. The work is being undertaken by Dr M. Parke, assisted by Miss E. Clay, and in collaboration with Dr M. Knight who is conducting similar investigations in the Isle of Man. Field work on the West coast of Scotland has now been concluded and that near Plymouth is drawing to a close; but it will be some time before the analysis of the large accumulation of data can be completed and prepared for publication. Though some

deficiencies remain in our knowledge of *Laminaria Cloustoni*, the main features in the life histories of the other common species have been traced by growth on cleared patches up to an age of 2 or 3 years.

The Library

The library, which had been stored for safety near Tavistock since 1941, was brought back to Plymouth in November and December and was re-arranged in its proper order by the end of the year. The books were found to be in excellent condition, but the bindings of an extremely small number showed some evidence of attack by mice and insects. The thanks of the Association are due to those institutions and authors who have presented books or papers.

Published Memoirs

Vol. XXVI, No. 1, of the *Journal* of the Association was published in September 1944.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ATKINS, W. R. G., 1944. Measurement of potential difference as a method for studying the action of water on lead pipes. *Nature*, Vol. 154, pp. 211–12.

ATKINS, W. R. G., 1945. Presentation of scientific data. *Nature*, Vol. 155, p. 361.

LEBOUR, M. V., 1944. Larval crabs from Bermuda. *Zoologica*, Vol. XXIX, pp. 113–28.

LEBOUR, M. V., 1945. The lobster and its relatives. *School Sci. Rev.*, No. 99, pp. 208–14.

LOWNDES, A. G., 1944. Densities of the embryonic stages of sea-urchins. *Nature*, Vol. 154, pp. 55–6.

LOWNDES, A. G., 1944. Shape of sea-urchins. *Nature*, Vol. 154, pp. 675–6.

LOWNDES, A. G., 1944. The swimming of *Monas stigmatica* Pringsheim and *Peranema tricophorum* (Ehrbg.) Stein and *Volvox* sp. Additional experiments on the working of a flagellum. *Proc. Zool. Soc.*, Vol. CXIV, pp. 325–38.

Membership of the Association

By the death of Lord Moyne the Association has lost a Vice-President. One Associate member has died during the year, the total number now being four. There were 314 annual members on 31 March 1945, being two more than at the corresponding date in 1944. The number of life members at the end of the year was 52.

Finance

Grant from the Development Fund. The Council has again to express its thanks to the Development Commissioners for their continued support of the Plymouth Laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the

Laboratory: The Universities of Cambridge (£105), London (£105), Oxford (£52. 10s.), Bristol (£25), Birmingham (£15. 15s.), Manchester (£10. 10s.), Sheffield (£5); the British Association (£50), the Physiological Society (£30), the Ray Lankester Fund (£20) and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1945–46:

President

G. P. BIDDER, Sc.D.

Vice-Presidents

The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS WATERHOUSE, K.B.E.
Sir SIDNEY HARMER, K.B.E., Sc.D., F.R.S.
Sir P. CHALMERS MITCHELL, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. PEEL, D.S.O., M.C.
Lord MILDMAY OF FLETE, P.C.
Col. Right Hon. Sir REGINALD DORMAN-SMITH, M.P.
Sir JOSEPH BARCROFT, Kt., C.B.E., F.R.S.
Prof. J. STANLEY GARDINER, F.R.S.
Prof. WALTER GARSTANG, D.Sc.
Prof. E. S. GOODRICH, D.Sc., LL.D., F.R.S.

COUNCIL

To retire in 1946

Prof. F. E. FRITSCH, D.Sc., F.R.S.
MORLEY H. NEALE
Miss MARGERY KNIGHT, D.Sc.
MICHAEL GRAHAM
J. E. SMITH, Ph.D.

To retire in 1947

Prof. F. W. ROGERS BRAMBELL, D.Sc.
Prof. H. MUNRO FOX, F.R.S.
O. D. HUNT
L. HARRISON MATTHEWS, M.A., Sc.D.
Prof. JAMES RITCHIE, M.A., D.Sc.
J. F. DANIELLI, D.Sc.

To retire in 1948

C. F. A. PANTIN, Sc.D., F.R.S.
Prof. C. M. YONGE, D.Sc.
Admiral Sir JOHN EDGELL, K.B.E., C.B.
Prof. J. H. ORTON, D.Sc.

Chairman of Council

Prof. JAMES GRAY, M.C., Sc.D., F.R.S.

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

STANLEY KEMP, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
A. T. A. DOBSON, C.B., C.V.O., C.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
Major E. G. CHRISTIE-MILLER
J. Z. YOUNG, M.A., F.R.S. (Oxford University)
Prof. J. GRAY, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. CHALMERS MITCHELL, Kt., C.B.E., D.Sc., F.R.S. (British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, O.B.E., Sc.D., F.R.S., M.P. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1945

	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:						
Accrued Expenses	103	6	9			
Subscriptions received in advance	25	4	0			
Grant received in advance	125	0	0			
				253	10	9
Biological Investigations in Algae				0	0	0
AQUARIUM GUIDE PRINTING FUND:						
As at 31st March 1944				22	1	6
SPECIAL APPARATUS FUND:						
As at 31st March 1944	10	4	11			
Add: Donation received during the year	100	0	0			
				110	4	11
E. T. BROWNE BEQUESTS FUNDS:	£	s.	d.			
Building Fund, as at 31st March 1944	1156	8	9			
Interest on Investment	35	3	7			
				1191	12	4
Library Fund, as at 31st March 1944	1021	13	9			
Interest on Investment	31	4	5			
				1052	18	2
Special Apparatus Fund, as at 31st March 1944	2322	16	4			
Interest on Investment	70	11	11			
				2393	8	3
Scientific Publications Fund, as at 31st March 1944	1742	1	10			
Interest on Investment	52	19	1			
				1795	0	11
				6432	19	8
"SALPA" DEPRECIATION FUND:						
As at 31st March 1944	4800	4	2			
Add: Amount receivable from Ministry of War Transport on account of Hire	396	8	4			
Interest on Investments	142	4	10			
				5338	17	4

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director as at 31st March 1941:						
S/S "Salpa"	2000	0	0			
Motor Boat "Gammarus"	100	0	0			
Nets, Gear and General Equipment	30	0	0			
				2130	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director as at 31st March 1941 plus additions at cost:						
As at 31st March 1944	4050	0	0			
Additions during the year	100	0	0			
				4150	0	0
LIBRARY, at valuation of Mr Ridgill Trout in January 1941 plus additions at cost:						
As at 31st March 1944	16000	0	0			
Additions during the year	70	0	0			
				16070	0	0
STOCKS ON HAND, as valued by the Director:						
Specimens	600	0	0			
Chemicals	150	0	0			
Journals	400	0	0			
				1150	0	0
SUNDRY DEBTORS:						
Sales of Specimens, etc.	226	6	7			
Ministry of War Transport—Hire of S/S "Salpa"	33	10	0			
Expenditure on reinstatement of War Damage recoverable under War Damage Act	290	16	7			
				550	13	2
PREPAYMENT				14	5	6
GENERAL FUND INVESTMENT, at market value as at 31st March 1931:						
£352. 2s. 3d. Local Loans 3% (Market value at date £337. 2s. 11d.)				232	7	10
E. T. BROWNE BEQUESTS FUNDS INVESTMENT, at cost:						
£6516. 1s. 1d. Conversion Loan 3% (Market value at date £6695. 4s. 11d.)				6432	19	8

REPAIRS AND RENOVATIONS FUND:						
As at 31st March 1944	377	17	5			
Add: Transfer from Income and Expenditure Account	50	0	0			
Interest on Investments	11	2	3			
				438	19	8
COMPOSITION FEES FUND:						
As at 31st March 1944	252	0	0			
Add: Fees received	47	5	0			
				299	5	0
CAPITAL RESERVE ACCOUNT:						
As at 31st March 1944				21688	8	2
SURPLUS ACCOUNT:						
As at 31st March 1944	3845	16	8			
Add: Surplus for the year, as per Income and Expenditure Account	355	3	11			
				4201	0	7
				£38,785	7	7

"SALPA" DEPRECIATION FUND INVESTMENTS, at cost:						
£590. 6*s.* 0*d.* Local Loans 3%	506	10	9			
£4707. 5*s.* 0*d.* Conversion Loan 3%	4798	16	7			
(Market value at date £5401. 18*s.* 3*d.*)				5305	7	4
REPAIRS AND RENOVATIONS FUND INVESTMENT, at cost:						
£429. 17*s.* 11*d.* Conversion Loan 3%				438	19	8
(Market value at date £441. 14*s.* 4*d.*)						
COMPOSITION FEES FUND INVESTMENTS, at cost:						
£18. 8*s.* 6*d.* Local Loans 3%	15	15	0			
£277. 8*s.* 4*d.* Conversion Loan 3%	283	10	0			
(Market value at date £302. 13*s.* 7*d.*)				299	5	0
CASH AT BANK AND IN HAND:						
Coutts & Company	1090	1	11			
Lloyds Bank Limited	836	1	8			
Cash in Hand	51	17	4			
				1978	0	11
RECOVERABLE EXPENDITURE:						
Biological Investigations in Algae:	£	s.	d.			
Expenditure				1307	12	11
Less: Balance as at 31st March 1944	7	17	3			
Grant Received	1267	10	0			
				1275	7	3
				32	5	8
Cellon Account:						
As at 31st March 1944	4	13	3			
Expenditure	1	2	10			
	5	16	1			
Less: Amount recovered ...	4	13	3			
				1	2	10
				33	8	6
				£38,785	7	7

J. GRAY
O. D. HUNT } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1945 according to the best of our information and explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & Co.

5 *St Lawrence Road, Plymouth.*
11*th May*, 1945.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1945

	£	s.	d.	£	s.	d.
To Salaries, including Association's Contributions to Superannuation and War Bonuses ...				6126	14	10
,, Laboratory and Boats' Crews' Wages, including National Insurance, Contributions to Superannuation Scheme, War Bonuses and Employers' Liability Insurance ...				4004	0	6
,, Upkeep of Library				181	11	7
,, Scientific Publications, less Sales				225	17	8
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	30	6	3			
Electricity, Oil, Gas, Coal and Water ...	386	13	2			
Chemicals and Apparatus	218	3	5			
Fire Insurance, Tithe, Ground Rent and Rent of Store	77	4	5			
Travelling Expenses	67	1	11			
Stationery, Postages, Telephone, Carriage and Sundries	294	16	6			
Specimens	381	10	10			
				1455	16	6
,, Maintenance and Hire of Boats:						
Petrol, Oil, Paraffin, etc.	21	11	1			
Maintenance and Repairs with Nets, Gear and Apparatus	17	15	1			
Purchase of Materials for Nets, etc. for Sale	7	3	9			
Boat Hire and Collecting Expenses		9	9			
Third Party Insurance	5	0	0			
				51	19	8
,, Bank Charges				7	7	0
,, Transfer to Repairs and Renovations Fund				50	0	0
,, War Time Expenditure:						
War Damage Premiums	46	13	3			
War Risk Insurance	11	19	2			
Storage and Return of Library	45	16	2			
Payment of Firewatchers	9	0	0			
				113	8	7
,, Balance, Being Surplus for the Year ...				355	3	11
				£12,572	0	3

	£	s.	d.	£	s.	d.
By Grants:						
Ministry of Agriculture and Fisheries Grant from Development Fund	10081	0	0			
Fishmongers' Company	500	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				10721	0	0
,, Subscriptions (excluding Subscriptions received in advance)				279	6	0
,, Donations				27	2	0
,, Fees for Tests of Materials				93	3	0
,, Sales:						
Specimens	926	17	2			
Nets, Gear and Hydrographical Apparatus ...	15	16	6			
				942	13	8
,, Table Rents (including University of Cambridge £105; Oxford £52. 10*s.* 0*d.*; London £105; Bristol £25; Birmingham £15.15*s.* 0*d.*; Manchester £10. 10*s.* 0*d.*; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20 and Ministry of Works £104)				487	17	6
,, Interest on Investments				18	1	1
,, Sale of Dr M. V. Lebour's Book				1	17	6
,, Sale of "Plymouth Marine Fauna" ...					19	6
				£12,572	0	3

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1946

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 26 *Great Tower Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
The Prime Warden. (**Council**, 1886→)
Smith, Admiral Sir Aubrey C. H., K.B.E., C.B., M.V.O., *Hay's Wharf and Dock, Southwark, S.E.* 1. (**Council**, 1938→)
Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Hon. Treasurer**, 1941→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, *St Stephen's House, Victoria Embankment, S.W.* 1
Bayly, Robert (the late). (**Council**, 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council**, 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council**, 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Cambridge*. (**Council**, 1899→; **President**, 1939–45)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President**, 1929; 1939–45; **President**, 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late). (Honorary.) (**Council**, 1895–1942; **Secretary**, 1895–1936; **Hon. Governor**, 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall*, 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council**, 1884–92; **Hon. Treasurer**, 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary**, 1884–90; **President**, 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road, Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall, Princes Street, E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., 32 *Thornhill Road, Plymouth*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square, S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc., *Bayworth Corner, Boars Hill, Oxford*. (**Council**, 1932–35)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens, W.* 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R., *The Court, St Fagan's, Glamorgan*
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., *Ocean House, Pudding Lane, E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1
1925 Discovery Committee, *Colonial Office, Downing Street, S.W.* 1
1927 Bidder, Miss Anna, Ph.D., *Cavendish Corner, Cambridge*
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd., P.O. Box* 331, *Alexandria, Egypt*. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*

MEMBERS

* Life Members

1939 Abercrombie, M., *Department of Anatomy, Medical School, The University, Birmingham* 15
1945 Aberdeen University Library, *The University, Aberdeen*
1941 Aberystwyth (*see* Wales)

1934 Adam, Mrs K. M. G., *c/o Vallis, Porton, Wiltshire*
1940 Adrian, Prof. Sir E. D., O.M., M.D., D.Sc., LL.D., F.R.S., *Trinity College, Cambridge*
*1927 Amirthalingam, C., Ph.D., *Director of Fisheries, Colombo, Ceylon*
1932 Aquario Vasco da Gama, *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1944 Ashby, D. G., *The Outlook, Haddenham, Ely*
*1911 Viscount Astor, 4 *St James's Square, London, S.W.* 1. (**Vice-President**, 1911→)
1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *Derry House, Downderry, Cornwall*
*1910 Atkinson, G. T., *Apsley House, Esplanade, Lowestoft, Suffolk*

1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, E., Ph.D., *Biochemical Laboratory, Tennis Court Road, Cambridge*
1939 Barnes, H., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, E. J. W., *Department of Zoology, University College, Nottingham*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth*
1939 Bassindale, R., *Zoology Department, The University, Bristol*
1932 Bateman, J. B., Ph.D., *Mayo Aero Medical Unit, Mayo Clinic, Rochester, Minnesota, U.S.A.*
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne* 1
1928 Beer, G. R. de, D.Sc., F.R.S., *University College, Gower Street, London, W.C.* 1
1926 Bělehrádek, Prof. J., M.D., *Albertov* 4, *Prague II, Czechoslovakia*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames*
*1945 Bingley, F. J., *Holywell Row Farm, Nr Bury St Edmunds, Suffolk*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., 90 *Stephen's Road, Tunbridge Wells, Kent*
1945 Black, J. A., *Ash House, Caton, Nr Lancaster*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1930 Bogorov, Dr B. G., *State Oceanographical Institute,* 17 *Werchnia Krasnoselskaja, Moscow, U.S.S.R.*
1936 Bogue, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., *Ivydene, Grosvenor Road, Crownhill, Plymouth*
1928 Borowik, Dr J., *San Marino,* 71 *Kosciuszki Torun, Poland*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1944 Boyd, Lt. David, R.N.V.R., 261 *Woodstock Road, Oxford*
1940 Brambell, Prof. F. W. Rogers, D.Sc., *University College of North Wales, Bangor, Caernarvonshire.* (**Council**, 1944→)

1926 Branfoot, J. M., *Oundle School, Oundle, Peterborough, Northants*
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1933 Bristol University, *Department of Zoology, Bristol*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1939 British Ropes Ltd., *Western Avenue, Cardiff*
1946 Brough, Prof. James, D.Sc., *University College, Newport Road, Cardiff*
*1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*
1928 Brown, Miss E. M., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames*
1936 Brown, Herbert H., Ph.D., *Fisheries Investigation, c/o Colonial Secretary, Barbados, B.W.I.*
1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., *Monkschester, Blue House Lane, Limpsfield, Surrey*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)

1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester*. (**Council**, 1927–30, 1932–34, 1937–41, 1942–45)
1927 Carruthers, J. N., D.Sc., *Hydrographic Department, Admiralty, Cricklewood, London, N.W.* 2
1923 Carter, G. S., Ph.D., *Zoological Laboratory, Downing Street, Cambridge*
1945 Carter, Lt. P., *Littlewood, Beadon Road, Salcombe*
*1931 Cattell, Dr McKeen, *Cornell University Medical College, 477 First Avenue, New York City, U.S.A.*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1946 Chipperfield, Philip N. J., 46 *Broadoak Road, Northenden, Manchester*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W.* 2. (**Hon. Treasurer**, 1941→)
1934 Church, R. G., *Northridge, 97 Heene Road, Worthing*
1924 Clark, R. S., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen*. (**Council**, 1938–41)
1944 Clarke, Lt. Robert, R.N.V.R., 19 *Malvern Road, Southsea*
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., '*Discovery*' *Staff, British Museum (Natural History), Cromwell Road, London, S.W.* 7
*1886 Coates and Co., *Southside Street, Plymouth*
*1945 Cobham, Lt.-Cdr. A. J., R.N., 44 *Strand-on-the-Green, London, W.* 4
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *The Royal South Hants and Southampton Hospital, Centenary Appeal Office, 105 Graham Road, Southampton*
1933 Cole, H. A., *Fisheries Experimental Station, Castle Bank, Conway, Caernarvonshire*
*1885 Collier Bros., *Plymouth*
1930 Colman, J. S., *Department of Zoology, The University, Sheffield* 10
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter*
*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth*
1937 Corbin, P. G., *Hunstrete Cottage, Nr Pensford, Somerset*
1937 Corbin, Mrs P. G., *Hunstrete Cottage, Nr Pensford, Somerset*
1946 Corlett, John, 74 *Belvidere Road, Liverpool* 8
1937 Cosway, C. A., 20 *Maurice Road, King's Heath, Birmingham* 14
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1936 Crawford, G. I., 1 *Dryburgh Road, Putney, London, S.W.* 15

*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
1929 Crofts, Miss D. R., D.Sc., *King's College for Household and Social Science, Campden Hill, London, W.* 8

1922 Dale, Sir Henry H., G.C.M.G., C.B.E., M.D., F.R.S., *The Royal Institution, 21 Albemarle Street, London, W.* 1. (**Council**, 1922–28)
*1919 Damant, Capt. G. C. C., C.B.E., R.N., *Slade House, Bideford, North Devon.* (**Council**, 1928–31, 1937–40)
1939 Danielli, J. F., D.Sc., *The Laboratory, Citadel Hill, Plymouth.* (**Council**, 1944–45)
1929 Darby, Dr H. H., 155 *Lockwood Avenue, New Rochelle, New York, U.S.A*
1946 Das, S. M., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay*
1943 Davies, D. J., 1 *Mayfield Terrace, Cwmburla, Swansea*
1931 Dawes, B., D.Sc., *University of London, South Kensington, London, S.W.* 7
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey*
1939 Dennell, Ralph, *Department of Zoology, Imperial College of Science and Technology, South Kensington, London, S.W.* 7
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, South Africa*
1944 Digby, P. S. B., 199 *Coleridge Road, Cambridge*
1910 Dobell, C. C., D.Sc., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3
1939 Dobson, A. T. A., C.B., C.V.O., C.B.E., *Ministry of Agriculture and Fisheries, St Stephen's House, Victoria Embankment, London, S.W.* 1. (**Council**, representing Ministry of Fisheries, 1938→)
1942 Dollner, H., 32 *Grange Hill, Edgware, Middlesex*
1939 Dorman-Smith, Col. the Rt Hon. Reginald H., M.P., *Stodham Park, Liss, Hants.* (**Vice-President**, 1939→)
1940 Dowson, Capt. W. B., *Agricultural Service, Nigeria, c/o Crown Agents for the Colonies, 4 Millbank, London, S.W.* 1
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1939 Dundee University College Library, *Dundee*
1937 Dyke, Frederick Montague, *Branksome, Boreham Wood, Elstree, Herts*

1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield* 10
1945 Edgell, Admiral Sir John, K.B.E., C.B., F.R.S., 1 *Glenalmond House, Manor Fields, Putney, London, S.W.* 15. (**Council**, 1945→)
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, Devon*
*1944 Elmhirst, Richard, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, South Africa*

1929 Faouzi, Dr Hussein, *Dean of Faculty of Science, Farouk I University, Alexandria, Egypt*
1922 Farran, G. P., *Department of Fisheries*, 3 *Kildare Place, Dublin.* (**Council**, 1922–26)

1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth*
1935 Ford, E. B., F.R.S., *University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
*1942 Forster-Cooper, Sir Clive, Kt., Sc.D., F.R.S., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1942–45)
1939 Fowell, R. R., *Municipal Technical College, Mount Pleasant, Swansea*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944→)
1942 Foxon, G. E. H., *Zoology Department, University College of Wales, Cardiff*
1934 France: Office Scientifique et Technique des Pêches Maritimes, *Laboratoire de Lorient, Port de Lorient-Keroman, France*
1934 France: Office Scientifique et Technique des Pêches Maritimes, *Laboratoire de la Rochelle, France*
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1935 Fraser, F. C., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
*1935 Fraser, James H., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, Ph.D., *Zoology Department, Birkbeck College, Fetter Lane, London, E.C.* 4
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., *Botanical Laboratory, Queen Mary College, Mile End Road, London, E.* 1. (**Council**, 1931–34, 1937–40, 1943–46)

1941 Gardiner, Mrs A. C., *c/o Mrs Walter Gardiner*, 4 *Grange Road, Cambridge*
1935 Gardner, Adrian, *Roach River Fishery Co., Ltd., Burnham-on-Crouch, Essex*
1936 Gardner, Major Austin, M.C., *Seasalter and Ham Oyster Fishery Co., Ltd., Whitstable, Kent*
*1907 Garstang, Prof. W., D.Sc., *Five Elms, Apsley Road, Oxford.* (**Council**, 1907–10, 1923–28; **Vice-President**, 1940→)
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Department of Botany, King's College, Strand, London, W.C.* 2
1932 Ghardaqa Marine Laboratory of the Egyptian University, *Ghardaqa, Red Sea District, Egypt*
1935 Gilson, H. Cary, *Trinity College, Cambridge.* (**Council**, 1940–43)
1945 Glasgow University, *Zoology Department*
1946 Glover, R. S., *Department of Oceanography, University College, Hull*
1945 Goodland, W. S. L., 2 *Northfields, Woodborough Road, Radstock, near Bath*
1939 Goodrich, Dr Helen, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow*
1931 Graham, Alastair, *Zoology Department, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Graham, Michael, *Fisheries Laboratory, Lowestoft.* (**Council**, 1931–32, 1933–36, 1943–46)
1930 Grant, R., *c/o International House, Chicago University, Illinois, U.S.A.*
1930 Gray, Dr A. M. H., 69 *Harley Street, London, W.* 1

1912 Gray, Prof. J., C.B.E., M.C., Sc.D., F.R.S., *Zoological Laboratory, Downing Street, Cambridge*. (**Council**, 1920–24; representing Cambridge University, 1928–45; **President**, 1945→)
1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby*
1944 Grieg-Smith, P., *Botany Department, The University, Manchester* 13

1932 Hamilton, Ian I., *Dauntsey's School, West Lavington, near Devizes, Wilts*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*. (**Council**, 1938–41, 1942–45)
1929 Harington, Prof. C. R., Ph.D., F.R.S., *National Institute of Medical Research, Mount Vernon House, London, N.W.* 3
1946 Harling, Miss K. E., *The Arches, Looe, Cornwall*
*1885 Harmer, Sir Sidney F., K.B.E., D.Sc., F.R.S., *The Old Manor House, Melbourn, near Royston, Herts*. (**Council**, 1895–1912, 1918–23; representing Royal Society, 1925–44; **Vice-President**, 1934→)
1932 Harris, Prof. J. E., Ph.D., *Zoology Department, The University, Bristol*
1946 Harris, T. R., 21 *All Saints Road, Wyke Regis, Weymouth*
1939 Harrison, R. J., M.R.C.S., L.R.C.P., *Pateley, Chelsfield, Kent*
1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth*
1934 Hartley, P. H. T., *Freshwater Biological Association, Wray Castle, Ambleside, Westmorland*
1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth*
1933 Harvey, L. A., *Department of Zoology, University College of the South West, Exeter*. (**Council**, 1940–43)
1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S.*
1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S.*
1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory*, 23 *Sandport Street, Leith, Edinburgh* 6
1939 Henry, Dr Herbert G. M., *City Bacteriological Laboratories*, 150 *Great Charles Street, Birmingham*
1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1
1939 Herklots, G. A. C., Ph.D., *Secretary for Development, Civil Affairs Staff, Hong-Kong*
1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W.* 7
1926 Hickling, C. F., *Room* 140, *Colonial Office, Palace Chambers, Bridge Street, London, S.W.* 1
1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N.* 6. (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942–43; representing Royal Society, 1944→)
1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*
1919 Hillier, W. T., M.R.C.S., 73 *Francis Road, Edgbaston, Birmingham*
*1921 Hindle, Prof. E., Sc.D., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8
1937 Hinton, M. A. C., F.R.S., 23 *Polworth Road, Streatham, London, S.W.* 16
1926 Hirasaka, Prof. K., *Zoology Department, Imperial University, Formosa, Japan*
1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne* 2
1939 Hodgkin, A. L., *Trinity College, Cambridge*
1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*
1925 Hogben, Prof. Lancelot T., D.Sc., F.R.S., *Department of Zoology, The University, Edgbaston, Birmingham*. (**Council**, 1924–25)

1946 Holmes, E. J., *Education Offices, Cobourg Street, Plymouth*
1939 Holmes, W., *Department of Zoology, University Museum, Oxford*
1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1928 Hunt, O. D., *Corrofell, Newton Ferrers, South Devon.* (**Council**, 1944→)
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., 31 *Pond Street, London, N.W.* 3. (**Council**, 1920–25)

1945 Imperial Chemical Industries Ltd., *Nobel House*, 2 *Buckingham Gate, London, S.W.* 1

1945 Jefferies, H. S., 10*a Newtown, Bradford-on-Avon, Wilts*
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
*1921 Jenkins, Mrs W., *Westhide, Hereford*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
1934 John, D. Dilwyn, *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box* 630, *Accra, Gold Coast Colony*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*
1946 Jones, Prof, R. V., C B., C.B.E., D.Phil., F.Inst.P., 14 *Richmond Hill Court, Richmond, Surrey*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth*

1945 Katz, Max, 1915E, *Spruce Street, Seattle* 22, *Washington, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940–43)
1946 Kelley, Major D. F., *Gulmarg, Elmsleigh Park, Paignton*
1946 Kenya: The Game Warden, *Game Department, Nairobi*
1928 King, Mrs A. Redman, *Weetwood Hall, Leeds, Yorks*
1927 Kirtisinghe, P., *Zoology Department, University College, Colombo*
1930 Kitching, J. A., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., *Marlborough College, Wilts*
1938 Kollmann, Prof. M., *Bibliothèque de la Faculté des Sciences*, 40 *Allées Léon Gambetta, Marseille, France*

*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth*
1935 Le Mare, D. W., *c/o Fisheries Department, Malaya*
1946 Lloyd, Capt. R. W. M., R.N., *c/o National Provincial Bank, Plymouth*
1926 Lowndes, A. G., *c/o The Laboratory, Citadel Hill, Plymouth*
1931 Lucas, C. E., D.Sc., *Department of Oceanography, University College, Hull*
1930 Lumley, Adrian, *Sunnyside, Castle Gardens, Torquay*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
*1929 McEwen, Mrs Lawrence, 15 *Blackett Place, Edinburgh*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2. (**Council**, 1938–42)
1937 Mackintosh, N. A., D.Sc., 7 *Hinde House, Hinde Street, London, W.* 1
*1925 Magdalen College, *Oxford*
1945 Maitland-Adams, C. W., *The Old Rectory, Hawkwell, Sussex*
*1902 Major, H. G. T., 24 *Beech House Road, Croydon, Surrey*
1925 Mann, G. I., *Trencrom, Briar Road, Hartley, Plymouth*
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THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, 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 £23,000.

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 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 marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by a research vessel and by a motor boat and these also collect the specimens required in the Laboratory.

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

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