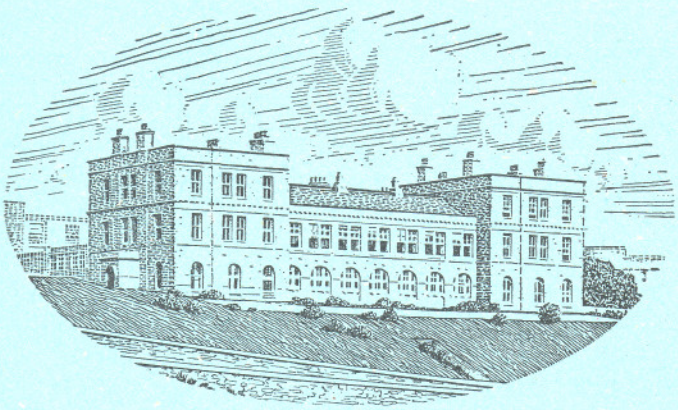
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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Walter Garstang

WALTER GARSTANG, 1868–1949

The death of Professor Walter Garstang, at the age of 81, on 23 February 1949, broke the last living link with the foundation of our Plymouth Laboratory. It is fitting that some record of his life should be found in the pages of our *Journal*; not only because he was one of the pioneers of marine biology in this country and one of the founders of fisheries research, but particularly by reason of his having taken such a prominent part in the early history of our Association. He was on the staff of our laboratory the day it opened, and in 1895 he initiated the first of the Easter Classes which ever since have made such an important contribution to the education of British zoologists. He continued to conduct these classes until 1901 when he became director of the fishery investigations undertaken by the M.B.A. on behalf of the government, as England's share in the then new International Investigations. Apart from his marine work, Garstang made fundamental contributions to biological theory, as in his paedomorphosis conception, and for more than half a century was one of the outstanding personalities of British Zoology.

In 1938, Garstang began to write an account of his experiences in fifty years of marine biology, but with other occupations in research and the coming of the war he abandoned it. Of what he wrote, however, he left some eighty pages of typescript describing the early days at Plymouth from 1888 to 1900; these have been deposited in the library of the Plymouth Laboratory for the benefit of those interested in our early history. I feel I cannot do better than begin this brief account of his life than by quoting the opening paragraphs of this fragment of his autobiography; here we have a vivid impression of the opening not only of his career but of that of our precious laboratory. It will serve, too, as some indication of what is in store for those who delve further into this very personal account of marine zoology in the nineties.

Fifty years ago, on June 21, 1888, having taken my degree at Oxford in the morning, I journeyed to Plymouth, picking up the old broad-gauge express at Swindon, to begin duty as Secretary and Assistant to the Director of the newly founded laboratory of the Marine Biological Association. It was to be only a temporary engagement,—to me a year or so for recuperation after a serious breakdown, to the Director some biological help at the outset, which otherwise he could not expect to get at the salary of clerk-assistant sanctioned by the Council (£80). The new Director was G. C. Bourne, then and long afterwards well known as a rowing Blue and coach, eventually (1906–1921) as Linacre Professor at Oxford, who, on returning from an expedition to the coral island of Diego Garcia, had been our demonstrator in the morphological laboratory. He had suggested this arrangement upon his appointment in April, and, after consultation with my people, I had gratefully accepted it. Bourne left Oxford early in June, and I was to follow immediately after my examinations and the taking of my degree. Our joint immediate task was to get the laboratory, which was still in the hands of contractors, ready for a ceremonial opening on June 30th. We took our coats off to it. My diary

records that on the 26th both of us were in shirt sleeves cleaning a heap of dirty collecting jars,—Bourne, the great 'Beejar' of the towing path! It's a man's valet who knows him best. Next day Bourne had to break off to attend a Council meeting in London. On his return he was delighted to find the laboratory washed down, in fair order, and with a red carpet on the stairs ready for the opening.

The ceremony went off without a hitch, or, as Lankester put it in a letter to Bourne, 'Everything went off splendidly on Saturday'. The weather was superb, the speeches were cheerful, the Fishmongers' Company gave a lunch in the Grand Hotel with wine from their own cellars, the Port Admiral lent his yacht for a trip, and everyone was in high spirits. All this, however, is on permanent record in the chronicles of the Association (*Journ. Mar. Biol. Soc.*, O.S., pp. 125–141). What is not recorded is that at Bourne's request I had put out an exhibit of living things under microscopes and otherwise in the main laboratory, and that after spending some minutes in expounding the life-history of *Obelia* to a portly and insistent visitor, whom I took to be a Fishmonger, the latter interrupted me to say, 'Very interesting! I suppose you don't know who I am?' 'I'm sorry, sir, No,' I said. 'I am Professor Lankester!' Thus I met the man who was largely to rule my destinies, and those of most other young zoologists, for the next 20 years.

He was born on 9 February 1868, the eldest son of Dr Walter Garstang of Blackburn, and was educated at Blackburn Grammar School and Jesus College, Oxford. He came up to the University with a scholarship in 1884, when only 16½, intending to read medicine. At heart he was a poet and a lover of nature. A new world opened before him as he came under the influence of that great Challenger naturalist, H. N. Moseley, who was then the Linacre Professor. He very soon decided to join the honours school of Zoology. He was only 20 when he took his degree and, as just recorded, joined Bourne at Plymouth a week before the laboratory opened in 1888. He had not then finally decided to give up a medical career, but the fascination of marine life at Plymouth was soon to cause him to do so. In 1891, he left the Plymouth staff for a year to go to Manchester as Berkley Research Fellow with Professor Milnes Marshall at Owens College, returning again as Assistant Naturalist. In 1893, he was elected a Fellow of Lincoln College and to a Lectureship in 1894; so for a time returned to Oxford and was there when Ray Lankester was in the Linacre Chair. But in vacations he continued to work at Plymouth, and in these early years he wrote many papers on the morphology, bionomics and distribution of marine invertebrates. He was particularly attracted to the nudibranch molluscs and did pioneer experiments to test and confirm the hypothesis of their warning coloration. He began his researches on the Tunicata, the group to which he was to return in later life; and it was in this period too that he published his delightful studies on the habits and respiratory mechanisms of the sand-burrowing crabs. It was from Oxford in 1895 that he brought a batch of undergraduates to Plymouth to inaugurate the first of the series of Easter classes. In the pages of reminiscences I have referred to he gives the names of some of the students in these classes who later distinguished themselves in zoology; it is an interesting list.

His life's work may be divided into three periods: the first occupied with these many and various researches in pure marine biology; the second devoted to fishery investigations; and the third, when a university professor and in retirement, occupied with more fundamental problems in zoology and his poetic interpretations of bird song.

The second period began in 1897 when he went back once more to the staff at Plymouth; this time as Naturalist in charge of Fishery Investigations. He became the moving spirit in the development of fishery science in England. He was clearly much impressed by Johan Hjort's pioneering research in Norway, and his first paper in this period was an extensive account of Hjort's methods. Like Hjort he planned his work on a wide front and soon he was publishing papers on such different aspects of fisheries work as 'The Surface Drift of the English Channel and Neighbouring Seas during 1897', 'On Variation, Races and Migration of the Mackerel' (1898), 'On the Plankton and Physical Conditions of the English Channel' (1899) and on 'The Impoverishment of the Sea' (1900). Great things were astir in oceanography at the turn of the century; in 1899 the King of Sweden invited all the countries interested in the fisheries of the North Sea and adjacent waters to send representatives to Stockholm to a conference to discuss the possibilities of collaboration in a programme of marine research. A second conference was held, this time in Christiania (Oslo), in 1901, and Garstang went as a delegate of His Majesty's Government; this was the conference which set up the International Council for the Exploration of the Sea. Each country participating undertook to investigate a particular region of sea and different problems in fishery research so that, as time went on and their results came in, the whole area would be covered and all the bits of research fit together as part of one great plan. The different nations equipped their separate research vessels and marine laboratories.

The English and Scottish fishery departments were then, as still they are to-day, separate institutions; and the Fishery Board for Scotland had already begun its investigations well before the beginning of the century. The English department, a small branch of the Board of Trade as it was then, commissioned the Marine Biological Association to start its research for it as part of the international scheme; so it was that Garstang became Director of these investigations and established a laboratory at Lowestoft. With his assistants, William Wallace, R. A. Todd and George Atkinson, and the famous old research trawler *Huxley*, he carried out from Lowestoft those classical investigations into the natural history of the North Sea plaice which have laid the foundations of English fishery research. By extensive age determinations and measurements, and particularly by liberating vast numbers of marked fish at different points (to be returned when recaught by fishermen), he studied the natural growth-rates and migrations of the fish in different areas. He realized how overcrowded the young plaice were on the nursery grounds off the Dutch

coast and how much more food there would be available for their growth on the Dogger Bank; so he tried the experiment of transplantation. He caught and marked large numbers of young fish on the coastal banks; half of these he returned to the sea where he caught them and the rest he carried in tanks of sea water to be released on the Dogger Bank. When in time the marked fish were recaught it was found that those taken to the richer feeding grounds had in two years grown twice as big as those left behind. Garstang had pointed the way to a farming of the sea, but he was before his time. In his Buckland Lectures in 1929 he returned to the subject and showed how such a transplantation on a large commercial scale could be made to pay, the increased yield of fish giving an ample margin of profit over the estimated cost of transport; but no nation was likely to undertake the cost of this, for all other nations would be free to reap the reward. While the nations work together in the science of the sea, the days of their co-operation in its exploitation are still far in the future; but one day surely the North Sea will be farmed in the way that Garstang showed—let us hope that his name will then be remembered.

In all these early years he played a prominent part in the development of the International Council; from 1902 to 1908 he was scientific adviser to the British Delegates and convenor of the International Committee on Trawling Investigations. In 1906 he was awarded his Oxford D.Sc.

Garstang was an individualist, a lover of freedom and independence, who resented what appeared to him to be interference in his scientific programme when official government policy did not coincide with his own plans. At the same time as the newly constituted government Fishery Department decided in 1907 to take over the investigations from the Marine Biological Association he received a letter inviting him to accept the Chair of Zoology at the University of Leeds. It was a difficult decision for him to make; on the one hand he loved his marine work, on the other he felt he would never be happy if he was not entirely free to shape his own policy. Very reluctantly he resigned from his Directorship at Lowestoft, and on becoming Professor Garstang the third phase of his life began. In passing, it may be said that he regained a connexion with this work in 1919 when he was appointed a member of the Development Commission Advisory Committee on Fishery Research, on which he served till the end of the recent war.

For a time his output of research was much reduced. He had all his lectures to prepare; he was building an honours school of zoology where none had existed before; and he was making himself a terrestrial naturalist instead of a marine one. Insects and birds became the objects of his field studies. It was at this time that his love of nature and his strong poetic feeling led him to delight in the study of bird song which he later interpreted in verse and musical notation in a little book *Songs of the Birds* which went through several editions.

After nearly twenty years of marine work he came back to more academic zoology, and took up again the study of those problems which had fascinated him when he was an undergraduate at Oxford in the heyday of speculation as to the evolutionary origin of the different groups of animals. The main trends of zoological interest had in the meantime flowed into the fields of more experimental and genetical work; by the time he came to publish his morphological and embryological speculations, now into the 1920's, they were considered by many as out of date. Nevertheless in this, for the time being unfashionable field, he made contributions to his science of outstanding and lasting value. In his essay on 'The Theory of Recapitulation' which he read before the Linnean Society in 1921 (published in the Society's *Journal* the following year) and in his presidential address to Section D of the British Association in 1928 he put forward his revolutionary views on the influence of modifications in ontogeny upon the course of evolution. With them he helped to overthrow the influence of Haeckel's so-called 'Biogenetic Law' which had dominated zoological thought for so long. Garstang coined the term *paedomorphosis* to apply to the evolutionary influence of larval characters upon adult organization. In two large papers, 'The Morphology of the Tunicata, and its bearings on the Phylogeny of the Chordata' (*Quart. Journ. Micr. Sci.*, Vol. LXXII, pp. 51–187, 1928) and 'The Morphology and Relations of the Siphonophora' (*Ibid.*, Vol. LXXXVII, pp. 103–93, 1946), he showed how paedomorphosis, by a process of neoteny, appeared to have played a leading role in the evolution of both chordates and the siphonophores. The theoretical importance of these ideas is more fully dealt with in an obituary written for the *Proceedings of the Linnean Society*.

He was a great teacher, who by his infectious enthusiasm, filled his pupils with a love of zoology; he was also their friend. I cannot do better than quote from the obituary notice written in *Nature* by Professor L. Eastham, one of his former pupils:

> Few who go from us will leave behind so much affection and such a sense of gratitude. It is inevitable that his students will remember Garstang for his perpetual youth and his genial kindness. They will think of their visits with him to the marine station which he established at Robin Hood's Bay; of teas in the laboratory at which he and Mrs Garstang were generous hosts and at which the week's problems were discussed; and of their open house at Meanwood where all students were welcome.

There was yet that other important side of his personality; his strong poetic feeling which partly found expression, as already stated, in his studies of bird song, but in addition provided a large number of poems of which only a few were published. Among the latter I may mention: 'The Song of the Tree Pipit' (*The Times*, 8 May 1919); 'The Return to Oxford: a Memorial Lay' (a long poem published by Blackwell of Oxford in 1919) describing his thoughts on visiting Oxford just after the war, seeing the young men returning, and mourning the death of his zoologist friends and former companions at Oxford:

Geoffrey Smith, Wilfred Jenkinson, Arthur Darbishire, Edward Minchin and George Grosvenor; 'To a Herring Gull' (*The Oxford Magazine*, 6 February 1920) and 'Friendship' (*Nature* 7 July 1921). Then there were his essays 'Wordsworth's Interpretation of Nature' which was published as a special supplement to *Nature* (16 January 1926) and 'Wordsworth's Green Linnet' (*Nineteenth Century*, September 1929).

After his retirement, Oxford became the home of the Garstang family, and here he continued his researches and writing up to the very end. On his 81st birthday, and less than a fortnight before he died, he went up to London to take part in the special symposium on Bird Song at the Linnean Society. His very happy life and biological interests were shared by Miss Lucy Ackroyd, of Newnham College, whom he met at the Plymouth Laboratory and married in 1895; she died in 1942 and they are survived by a son and five daughters.

A. C. HARDY

OBSERVATIONS ON THE LIFE HISTORY AND FUNCTIONAL MORPHOLOGY OF *CERITHIOPSIS TUBERCULARIS* (MONTAGU) AND *TRIPHORA PERVERSA* (L.)

By Vera Fretter

Department of Zoology, Birkbeck College, University of London

(Text-figs. 1–6)

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INTRODUCTION

Cerithiopsis tubercularis occurs along the west and south-west coasts of the British Isles. It may be collected from intertidal coralline pools, especially those in which ample sponge growth occurs, or from the sheltered sponge-covered slopes and crevices of rocks, and under boulders, in the lower third of the intertidal zone. It is also dredged in Plymouth Sound and outside where, again, it is associated with sponges. *Triphora perversa* is found in a somewhat similar habitat; inshore, however, *Triphora* is confined to rock crevices and slopes within, or immediately above, the laminarian zone. In their internal anatomy these two prosobranchs have many points of resemblance, and they are placed in consecutive families of the order Mesogastropoda (Thiele, 1929). Both are of approximately the same size, the pointed tuberculate shell attaining a height of 8 mm. in *Triphora*, and 7·5 mm. in *Cerithiopsis*. The former, however, is sinistrally coiled, the latter dextrally: the organs of the mantle cavity of *Triphora* and also the nervous system are, in their arrangement, mirror images of those of the dextrally coiled *Cerithiopsis*. Their anatomy is little known: Fischer (1887) gives a drawing of the radula of *Triphora*, though this is incomplete, and more recently Risbec (1943) gives a brief description of some points in the gross anatomy of the proboscis, oesophagus and nervous system of *Triforis* (= *Triphora*) *montrouzieri*. Pelseneer (1926) describes the eggs and newly hatched larvae of *T. perversa* from the coast of Brittany, and Lebour (1933) describes and figures the external features of these larvae as

well as those of two species of *Cerithiopsis*—*C. tubercularis* and *C. barleei*. She is also the first to describe the egg masses of *C. barleei* (1933) and *C. tubercularis* (1936), which are embedded in the tissues of the sponges *Ficulina ficus* and *Hymeniacidon sanguinea* respectively.

Cerithiopsis tubercularis (Montagu)

Cerithiopsis tubercularis rests on the surface of sponges, adhering by means of the copious supply of mucus from the foot, or buried in their superficial tissues so that only half the length of the shell, or even less, is visible. The animals are reluctant to feed in captivity, and it is probably for this reason that the feeding mechanism has not been observed, and the correlated structures described. Specimens collected inshore from the south coast of Cornwall show a preference for *Hymeniacidon sanguinea*, and during the late spring and summer months, which is the breeding season, a number of mature individuals may be found on a single cluster of the sponge; in early August as many as twenty have been collected from 12 sq. in. of *Hymeniacidon*. The molluscs feed on the tissues of this sponge as well as laying their eggs therein, and they suck up the tissues through a comparatively long proboscis. The feeding mechanism, however, may be difficult to see. On the few occasions when it has been observed the proboscis has been thrust out of sight through an osculum or into the irregularities of the broken surface of the sponge.

A number of young, immature specimens, averaging 1·25 mm. long, have been found on the shells of *Chlamys opercularis* in dredgings from the Rame-Eddystone Ground. These were collected in early January, presumably developed from summer spawn. In the same dredgings mature individuals 5·5 mm. long were obtained, though not on the bivalves, nor would they, like the younger ones, exploit these shells for their food when given the opportunity. The young will collect diatoms and detritus from the narrow crevices of the shells by means of the proboscis, and if separated from the bivalve will quickly return to it. Although the adult shows a special liking for sponges it will perhaps take other food, for Lebour (1933) states that 'adults were kept for a month in plunger jars and lived quite happily without the sponges, probably feeding on debris or small algae'.

The foot, by which the mollusc keeps a firm hold whilst feeding and when washed by the waves of the ebbing or flowing tide, is truncated in front and tapers to a blunt point posteriorly. It is capable of considerable and rapid distention, and frequently a temporary transverse groove demarcates the anterior half, which is rectangular in shape and contains the opaque white tissues of the anterior pedal mucous gland, from the triangular posterior half with the posterior pedal gland and the operculum. The anterior gland opens by a transverse slit along the anterior margin of the foot and comprises not only mucous glands, but a second type of cell with discrete spherules of a different

type of protein filling the cytoplasm. The sole of the foot is covered by a ciliated columnar epithelium with numerous mucous cells and between the ciliated cells run ducts from sub-epithelial mucous glands. The posterior pedal gland, as in other prosobranchs of small size (Fretter, 1948), is too big to be accommodated wholly in the tissues of the foot and spreads into the haemocoel of the head where it lies anterior to, and alongside, the nerve ring. Its opening is near the middle of the sole, just within the posterior half, appearing sometimes in the form of a longitudinal slit, sometimes as a deep pit, and from it a transient, median, longitudinal groove conveys the secretion, augmented by mucus from the surface of the sole, to the posterior tip of the foot. This fluid may be used as a viscid climbing rope which allows the animal to lower itself from its inverted swimming position on the surface film of water in a rock pool, or it may be used to secure the animal on a wave-swept rock. The opening of the posterior gland leads dorsally into a ciliated duct which resembles histologically the surface of the sole, and as the duct passes inwards it bifurcates, branching to each side of the head. Each lateral branch receives two diverticula lined by tall mucous cells; no sub-epithelial glands occur.

The head bears a pair of long, linear tentacles, beset, especially around the distal half, with bristle-like motionless cilia, and as the animal moves along the tentacles are waved as though sensing the pathway. In the base of each is embedded an eye, surrounded by connective tissue and separated from the columnar epithelium by a sparse layer of muscles. No snout is developed, nor a mentum: from the anterior pedal mucous gland the dorsal surface of the foot curves upwards and backwards to the head which is concave in the transverse plane between the eyes, and in the centre of the concavity lies a small inconspicuous opening. This is the opening of the introvert (Fig. 1A, O) at the base of which the mouth (M) is placed.

The introvert is lined by columnar epithelium, slightly cuticularized and rich in mucous cells. Immediately beneath the epithelium is an intrinsic musculature of circular fibres and beneath this lie muscles which form part of the mechanism for the retraction of the proboscis. The retractors run parallel to the length of the introvert and buccal cavity from which they arise, and posteriorly they converge to form a compact, closely knit sheet (Fig. 1 A–C, R), which lies ventral to the oesophagus, alongside the columellar muscle, and so passes up the spiral of the shell to be inserted on the columella itself. Other muscles run from the gut wall directly on to the body wall, passing through the nerve ring when the proboscis is retracted. Of these many from the anterior wall of the introvert to the wall of the head are short (Fig. 1 A, D) and act as dilators, and of the longer ones three bundles are particularly conspicuous (PR)—from the head they traverse the whole length of the introvert and buccal cavity to their insertion on the wall of the anterior oesophagus, and will help in the extension of the proboscis, though this is chiefly brought about by pressure on the blood in the haemocoel exerted by the musculature of the body wall.

When the proboscis is fully everted the mouth (M) is carried to its tip and just within the buccal cavity a pair of horn-coloured jaws (J) may be visible dorsally and the tip of the odontophore (OD) ventrally. The jaws are close together, one on either side of the mid-dorsal line, and each is composed of forty or so long spikes packed tightly to form a semicircular pad. Each spike is secreted by a single epithelial cell and has an irregularly blunted tip. When

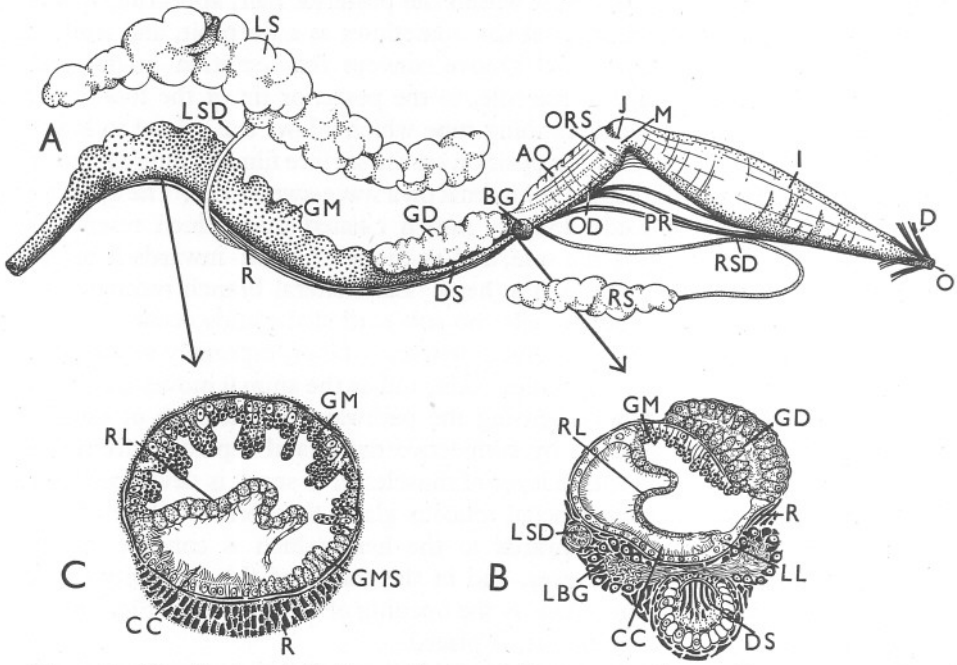

Fig. 1. *Cerithiopsis tubercularis*. A, anterior part of alimentary canal. × 40. B, transverse section at level indicated. × 240. C, transverse section at level indicated. × 170. AO, anterior limit of anterior oesophagus; BG, buccal ganglion; CC, ciliated channel; D, dilator muscles; DS, radular sac; GD, glandular diverticulum of oesophagus; GM, glandular wall of mid-oesophagus; GMS, second type of gland cell of mid-oesophagus; I, introvert; J, right jaw; LBG, left buccal ganglion; LL, left longitudinal fold; LS, left salivary gland; LSD, duct of left salivary gland; M, position of mouth; O, opening of introvert; OD, odontophore; ORS, opening of right salivary duct into buccal cavity; PR, protractor muscles of proboscis; R, retractor muscles of proboscis; RL, right longitudinal fold; RS, right salivary gland; RSD, duct of right salivary gland.

the mollusc is feeding, with the proboscis thrust through an osculum to get at the softer tissues of the sponge, the jaws loosen the tissues which are then raked up into the buccal cavity by the numerous fine radular teeth. The long median teeth of the radula (Fig. 2, M) are spoon-shaped with the free edge produced into a few long spike-like cusps; the teeth lateral to these bear more numerous and shorter cusps (L). The action of both jaws and radula is lubricated by the copious saliva from the salivary glands (Fig. 1 A, RS, LS) which open one behind each jaw (ORS).

The buccal cavity and the short anterior oesophagus (AO), which lies immediately behind the point where the radular sac separates from the rest of the gut (Graham, 1939), comprise a muscular tube, its posterior limit marked by the large, conspicuous buccal ganglia (BG), the size of which is correlated with the delicate manipulative power of the proboscis. Along the roof is a narrow dorsal food channel bordered by broad, muscular folds. In the buccal cavity the epithelium of the folds has no basement membrane and the intrinsic radial muscles which dilate the dorsal channel to suck in the food penetrate between the epithelial cells; interspersed with these muscles are occasional circular and longitudinal fibres. Posteriorly, in the region of the buccal ganglia, the bases of the longitudinal folds narrow, the left becoming inconspicuous, the right deep and glandular.

The two salivary glands (RS, LS), which appear as opaque white, lobular masses in the living state, are remarkably unequal in size, and their histology is also different. Each has a long, narrow, ciliated duct (RSD, LSD) which from its opening, posterior to the jaw (ORS), runs straight back through the wall of the buccal cavity and anterior oesophagus, and then, as a result of torsion, is twisted around the oesophagus. The right duct curves over the dorsal and then down the left wall of the anterior oesophagus immediately in front of the left buccal ganglion. It then lies freely in the haemocoel and describes, when the proboscis is retracted, a forwardly directed U-shaped bend, running forward as far as the nerve ring, bending ventralwards, and reversing its course to join the small salivary gland which lies ventral to the gut. When the proboscis is protruded the duct will be carried out into the introvert along the oesophagus. The right salivary gland is a simple tube and has only one type of secretory cell, which alternates with ciliated cells and produces mucus.

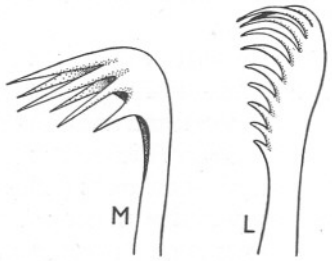

Fig. 2. *Cerithiopsis tubercularis*. Teeth of radula. ×3300. L, lateral tooth; M, median tooth.

The left salivary duct (Fig. 1 A, B, LSD) curves ventrally around the left wall of the oesophagus immediately behind the left buccal ganglion (Fig. 1 B, LBG), passes back through the thickness of the ventral retractor muscles (Fig. 1 A, R), and eventually, freed to the haemocoel, joins the central region of the relatively enormous left salivary gland (LS) which is displaced dorsally. The wall of this gland is deeply folded and, although ciliated cells alternate with gland cells in the main channels which open to the duct, it is difficult to trace ciliated cells in the finer ramifications of the gland. The secreting cells are of two types: some, the minority, produce mucus; the others are filled with small spherules which stain lightly with iron haematoxylin, whereas the surrounding cytoplasm is deep blue-black after this stain. Perhaps this second type of cell produces

an enzyme which is mixed with the tissues of the sponge as they are loosened.

The oesophagus is divisible into three regions: the anterior and posterior which are short, and the middle region (GM) which is long, glandular and has a continuation of the dorsal food channel (Fig. 1 B, C, CC). The right longitudinal fold from the buccal cavity and anterior oesophagus passes into the mid-oesophagus as a thin, deep sheet of tissue (RL) which stretches across the lumen to the opposite wall, and extends down the length of the mid-oesophagus separating the dorsal glandular section from the ventral ciliated area. The insignificant left fold is difficult to trace beyond the initial region of the mid-oesophagus (Fig. 1 B, LL). The first 90° of torsion occurs in the region of the buccal ganglia, and is an abrupt twist which brings the originally dorsal ciliated area on to the left side (CC), and the right longitudinal fold on to the dorsal wall (RL); to the right of this fold the wall of the oesophagus is glandular. The second 90° of torsion is more gradual and at its completion the glandular region comprises the dorsal and lateral walls; the smaller ciliated area is ventral.

If an animal be dissected the glandular area of the oesophagus is seen to be divisible into two regions: along the whole of its length the gland cells which form the dorsal and dorso-lateral epithelium of the mid-oesophagus are emerald green in colour (Fig. 1, GM) but, in contrast, there is anteriorly a mass of white glands against the right wall. This is a diverticulum (Fig. 1 A, B, GD) of mucous cells alternating with ciliated cells which opens at its anterior end to the anterior oesophagus beneath the small left longitudinal fold, and marks the posterior end of this part of the gut. The diverticulum is involved in the first 90° torsion of the gut so that its free end stretches back along the right wall of the oesophagus. A diverticulum in a corresponding position, though thin-walled and larger, is present in *Lamellaria perspicua* anterior to a large oesophageal pouch which has its secreting area increased by the development of deep septa. Behind it in *Cerithiopsis* there is no swollen pouch: the presence of such would be impracticable, for the mid-oesophagus must be narrow enough to pass through the confined space in the nerve ring when the proboscis is protruded. Thus, although an equivalent amount of secreting area is developed in *Cerithiopsis*, it is not concentrated, but spread along the elongated section of the oesophageal tube, covering three-quarters of the wall. In *Lamellaria* and in *Trivia arctica* and *T. monacha* the right longitudinal fold which borders the dorsal food channel and passes back from the buccal cavity to the oesophagus, is deeper than the left. This discrepancy is much more pronounced in *Cerithiopsis* (Fig. 1 B, C, RL), where the right fold partitions off the glandular area from the ciliated channel (CC), acting, perhaps, as a valve to prevent the suction of the secretion from the oesophageal glands into the proboscis when it is extended. The fold gradually tapers away towards the posterior end of the mid-oesophagus. It is formed of a fold of epithelium with very little connective

tissue between the two layers of cells. On one side, that facing the ciliated channel, the epithelium consists of large mucous cells and wedge-shaped ciliated cells between them; on the other side the cells are flattened and bear no cilia.

The common type of gland cell, which is filled with green spherules in the living tissue, is little affected by acid fixatives; with iron haematoxylin the spherules stain lightly and with azan they stain blue. Between these glands and the ciliated cells on the post-torsional right side of the mid-oesophagus, that is, facing the free edge of the longitudinal septum, is a longitudinal strip of another type of epithelial gland (Fig. 1 C, GMS) in which the cytoplasm is filled with globular secretion masses, colourless during life, dissolving readily in acid fixatives. The cytoplasm of these cells stains deeply with iron haematoxylin and red with azan.

The short posterior oesophagus is ciliated throughout; the tube is narrow, of capillary dimensions, and runs straight back immediately above the columellar muscle to open into the antero-ventral wall of the stomach which is a small bag receiving two ducts from the digestive gland—one ventral and not far behind the oesophageal opening, the other dorsal and not far behind the antero-dorsal intestinal opening. The stomach is lined by an epithelium on which the cilia are densely packed and in no part is there a cuticular covering; the musculature is rather poorly developed. After a meal the lumen may be filled with the tissues of *Hymeniacidon* including long monaxon spicules, and nothing but a sheet of mucus shields the gastric wall. This general simplification of structure, in which the stomach is little more than a crop in which the meal lies to undergo digestion and from which the products of digestion are passed to the digestive gland, is paralleled in dorids which have adopted a similar diet. Throughout the gastropods such simplification is mainly correlated with the development of a macrophagous carnivorous habit and extracellular digestive processes (Graham, 1949).

From its origin the intestine passes dorsally over the kidney and forwards along the right side of the mantle cavity to the anus, which lies well within this cavity. It is ciliated throughout. The middle region is distinguished histologically by the large number of gland cells scattered amongst the ciliated cells. Each is filled with colourless spherules which respond readily to stains for protein, and when discharged the secretion droplet swells giving an irregular and indistinct outline, and presumably helps to elaborate the faecal rod around which the secretion can be traced. The rod contains not only sponge spicules but orange concretions pigmented like the sponge on which the mollusc feeds and similar to the concretions in the faeces of *Diodora apertura*, which also feeds on *Hymeniacidon*. Three types of cell occur in the tubules of the digestive gland: two are rather infrequent and confined to the crypts; elsewhere the digestive cell occurs. Fluid contents from the stomach and extremely minute particles of food can be traced to the vacuoles of the digestive cell, where

presumably digestion is completed. These vacuoles may occupy a half or two-thirds of the cytoplasm, whilst below them are tightly packed spherules. In a starved individual the spherules fill the entire cell, and sections of an individual which was interrupted at the commencement of a meal suggest that they are secretory: they can be traced into the tubules of the gland and into the ducts where they swell and their identity is ultimately lost. The cells in the crypts of the tubules are highly vacuolated throughout, and the vacuoles contain spherules. In one type of cell, the more numerous, the spherules, apparently colourless at first, may change in consistency and coalesce into brown masses which have the appearance of excretory matter. The second type of cell contains lime spherules.

In *Cerithiopsis* the sexes are separate and in both male and female the glandular pallial section of the genital duct is open along its length to the mantle cavity. As in other mesogastropods in which this duct is open—*Turritella communis* (Fretter, 1946), *Bittium reticulatum* and *Scala communis* (Johansson, 1947)—no penis is present. The transference of sperm to the female was once observed during August when ten individuals, together with the piece of *Hymeniacidon* on which they were found, were kept under observation. The molluscs were clustered together, and from the males sperm mixed with prostatic secretion left the mantle cavity in the exhalant stream and clouded the surrounding water. Little dispersal of the sperm occurred, however, for immediately the fluid was sucked through the short inhalant siphons of the adjacent females—the ultimate destination of the sperm was traced in sections.

In the testis both eupyrene and apyrene spermatozoa are developed and are stored in the large vesicula seminalis which constitutes the initial part of the vas deferens. The apyrene sperm have not been traced farther forwards in the duct, nor have they been seen in the female. From the vesicula seminalis a short vas deferens, closed by a sphincter except during copulation, passes forwards over the columellar muscle on the right side of the visceral mass and opens to the prostate, the pallial vas deferens, which lies along the junction of body wall with mantle skirt on the right side. The prostate has deep lateral walls joined by a narrow dorsal wall, and is open ventrally. Its epithelium consists of tall gland cells alternating with ciliated cells: proximally the glands respond to stains specific for mucus, whilst anteriorly, throughout the greater length of the duct, only an occasional cell secretes mucus, and there is a second type of gland in which the cytoplasm is uniformly vacuolated and the vacuoles contain spherules staining lightly with iron haematoxylin. The pallial duct extends along the mantle cavity as far as the level of the anus.

The disposition of the female genital duct is similar to that of the male. From the ovary a short ovarian duct, with an epithelium similar to that of the gonad, passes forwards along the right side of the visceral mass, just above the columellar muscle, to the renal oviduct. This is short and ciliated, leading to

the postero-ventral limit of the pallial duct. The pallial duct is better developed than the homologous region, the prostate, in the male, though, like it, it has deep lateral walls joined by a narrow dorsal wall, and, except at the extreme posterior end where there is a small cul-de-sac, it is open along its ventral edge. The cul-de-sac receives ventrally the renal oviduct and dorsally it accommodates spermatozoa received from the male by way of the inhalant water current. If a female be fixed immediately after taking up a supply of spermatozoa, sections

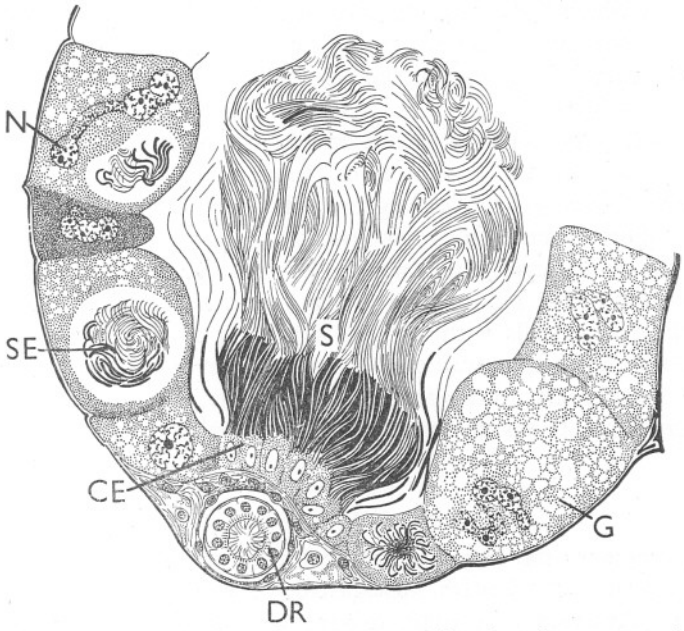

Fig. 3. *Cerithiopsis tubercularis*. Part of a transverse section through a receptaculum seminis. × 357. CE, columnar epithelium surrounding entrance to receptaculum; DR, duct leading to receptaculum; G, gland cells; N, nucleus; S, orientated spermatozoa; SE, spermatozoa in vacuoles of epithelial cells.

show that many of the sperm are concentrated in a limited region of the pallial duct, along the dorsal wall, at the entrance to the cul-de-sac. Here there is a small, shallow pouch, lined only by ciliated cells, where the sperm may be orientated. Still other spermatozoa have travelled up a muscular and ciliated duct which leads dorsally from this pouch and bifurcates at its distal end. Each bifurcation (Fig. 3, DR) opens to a receptaculum, the two receptacula lying one above the other on the right side of the rectum. They are approximately spherical sacs lined, except around the entrance, by relatively enormous cells (G) in which the long nuclei (N), each with a number of nucleoli, may be twisted into a variety of shapes. The cytoplasm of these cells is vacuolated and contains spherules which dissolve in acid fixatives. Around the entrance to the receptaculum is a circular patch of low, columnar epithelium (CE) and in its distal cytoplasm the heads of spermatozoa (S) are embedded. Not all the sperm

are thus accommodated: others lie in tangled balls in vacuoles of the giant epithelial cells (SE) and here they appear to undergo digestion.

The gland cells of the pallial duct alternate with ciliated cells and are especially tall in the lateral walls. The cul-de-sac has mucous cells only. Anteriorly, the spherules which fill the secreting cells are of uniform size and are colourless in living tissue: near the cul-de-sac they respond slightly to mucicarmine and celestine blue; elsewhere they stain lightly with iron haematoxylin and the cytoplasm in which they are embedded stains deeply. These anterior glands produce a colourless fibrillar secretion which forms the resistant coat of the egg capsule, the posterior part of the pallial duct giving the albumen in which the eggs are embedded.

At the level of the anus the gland cells of the pallial duct are replaced by ciliated cells, and the duct is reduced in diameter. It extends beyond the anus as a shallow, ciliated groove leading towards the mouth of the mantle cavity, and ends a short distance from this opening.

Within the mantle cavity alongside the posterior third of the pallial duct and extending back to the kidney aperture is a ventral gutter which is lined by mucous glands and cells with exceptionally long cilia. It runs between the body wall and the median wall of the oviduct, providing a pathway by which sperm are directed first to the proximal part of the pallial oviduct and then to the receptaculum. It has no homologue in the male.

TRIPHORA PERVERSA (L.)

Triphora perversa is the only British member of the family Triphoridae and consequently the only British mesogastropod which is typically sinistrally coiled. This direction of coiling, determined by a reversal of the normal cleavage pattern, brings about a reversal of the arrangement of the organs in the mantle cavity: the osphradium and ctenidium are on the right side, which receives the inhalant stream of water by way of a short siphon, and the rectum and genital duct are on the left. The visceral loop of the nervous system shows, moreover, that the direction of torsion is also reversed, for the left pleuro-visceral connective with its parietal ganglion is supra-oesophageal. The ganglion is thus close to the osphradium which it innervates, and the right connective runs ventral to the gut bringing the right parietal ganglion beneath the oesophagus. The pleuro-parietal connectives are short as in the Cerithiidae, concentrating the parietal ganglia in the head. The visceral ganglia, however, lie posteriorly, near the stomach, and their long fine connectives with the parietals, lengthened on account of the development of the introvert, are difficult to trace.

When the animal is crawling the exposed parts of the body, opaque white in colour, can be seen to resemble those of *Cerithiopsis*, and this resemblance extends to feeding habits as well.

Specimens of *Triphora perversa* collected from the laminarian zone of south Cornwall have frequently large numbers of monaxon, siliceous sponge spicules in their stomachs, and with these diatoms may occur. In captivity, the animals rarely feed though supplied with fresh *Hymeniacidon* and *Halichondria*—the sponges with which they are associated on the shore and in the substance of which the shell may be partly or completely hidden. On two occasions only has the protrusion of the proboscis been observed; on one of these tissues of *Halichondria panicea* were sucked into the gut. The proboscis was thrust out of sight through an osculum of the sponge, seeking presumably the softer tissues. The surface of the proboscis is covered by an epithelium containing two types of glands: the more numerous is a mucous cell; in the second the secretion appears as minute discrete granules which are colourless in the living tissue and

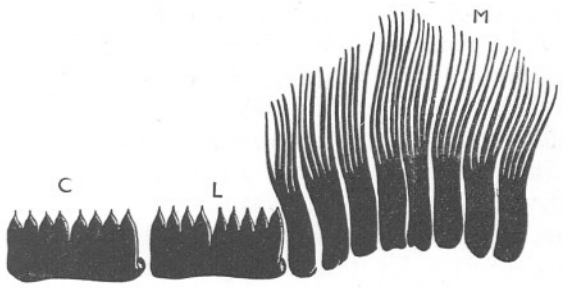

Fig. 4. *Triphora perversa*. Half row of radular teeth. × 1700. C, central tooth; L, lateral tooth; M, marginal tooth.

so numerous that they obscure the large basal nucleus. The epithelium is surrounded by its intrinsic layer of circular muscle fibres and external to these are the muscles of the proboscis which run back to their insertion on the columella.

When the proboscis is fully everted a pair of dorso-lateral jaws is brought to its tip, and ventral to them lie the teeth of the radula. The jaws form two large triangular plates which surround the buccal cavity anterior to the odontophore, the broad bases of the triangles meeting mid-dorsally. Their blunt spikes, each comprising the secretion from a single cell and providing a flattened plate slightly raised in the centre, are firmly sutured together, the sutures being slightly wavy. The superficial appearance of these jaws is reminiscent of the jaws of a skate. The radula consists of numerous rows of minute teeth. In each row the single central tooth (Fig. 4, C), attaining 10μ broad and 5μ high, has eight equal cusps, short and broad, and arranged in two groups which are separated from one another by a fissure. This tooth is bordered on each side by a single lateral (L) differing from it only in the number of cusps, nine, and these are again arranged in two groups separated by a fissure; the number of

lateral cusps varies from five to six, and in the median group there are either four or three. The numerous marginal teeth (M) are each about one-third the breadth of the central or lateral, and the longest may attain four times the height; the distal end is frayed out into fine pliable processes which sweep into the buccal cavity the tissues loosened by the jaws and by the biting teeth of the radula. Dorsal to the odontophore the buccal cavity is cuticularized.

Within the extended proboscis is the narrow, muscular oesophagus, which passes back from the buccal cavity, and the large salivary glands. The saliva is poured into the oesophagus, not far from its origin, by a single glandular duct which is divided histologically into two regions and is formed by the union of two short ducts from a pair of glands. These glands are enormous and unequal in size; when the proboscis is retracted the larger extends anteriorly as far as the nerve ring and posteriorly as far as the stomach; the smaller lies wholly behind the introvert, mainly ventral to the oesophageal tube and to the larger gland. It is a simple tubular gland, whereas the walls of the dorsal one are folded and its lumen insignificant. Three types of secreting cells occur in the salivary glands, and all of them are large with conspicuous nuclei. In both glands there are mucous cells, relatively more numerous in the ventral one, where they comprise more than half the epithelium. In the dorsal gland there is a second type of cell with spherules of irregular shape and size which stain with mucicarmine and also, deeply, with iron haematoxylin: the abundance of this kind of cell would appear to vary, for it may comprise about half the gland or only a small fraction; the frequency is inversely proportional to the third type of secreting cell which, although of constant occurrence and abundance in the ventral salivary gland, may be exceedingly infrequent in the dorsal. In this third type the cytoplasm is filled with spherules of uniform size which stain lightly with iron haematoxylin; the cytoplasm stains even lighter. A few of these cells may be found in the initial region of the duct from each gland, scattered amongst the mucous cells which comprise most of the epithelium. Along each duct, however, is a longitudinal strip of low cubical cells and after the ducts have united this non-glandular tract persists for a while together with the mucous epithelium. About half-way along its course the duct broadens and there is an abrupt histological change, and for the rest of its course—to its junction with the oesophagus—the most common type of cell is one filled with protein spherules which are not mucous and are unlike any in the gland. This cell makes up the whole of the secretory epithelium, except for a narrow longitudinal strip of mucous cells which continues to the oesophagus.

When the proboscis is withdrawn into the haemocoel, it passes through the confines of the nerve ring, which necessarily restricts its diameter, and comes to lie in the first two coils of the tightly spiralled shell: the mouth is now at its base; the long connectives between the cerebral and large buccal ganglia are directed posteriorly, the ganglia lying between the anterior end of the oesophagus and the ventral radular sac; the oesophagus is thrown into deep coils.

The oesophagus is a narrow muscular tube of uniform structure throughout the greater part of its length, surrounded by the retractor muscles of the proboscis. It is lined by a ciliated, columnar epithelium with only an occasional mucous cell; no dorsal folds can be traced along its length revealing the position of torsion. In *Triphora* the glandular areas are separated from the oesophageal tube. Not far from the stomach a pouch lies over the oesophagus and communicates with it dorsally at its posterior end (Fig. 5, GP). The dorsal and lateral epithelia of the pouch are thrown into numerous, deep, transverse folds (TF) which subdivide the lumen; radial muscles penetrate the folds and circular muscles form a thin outer coat. The epithelial cells are all secretory and they are of small size; the majority of the cells are filled with spherules which give

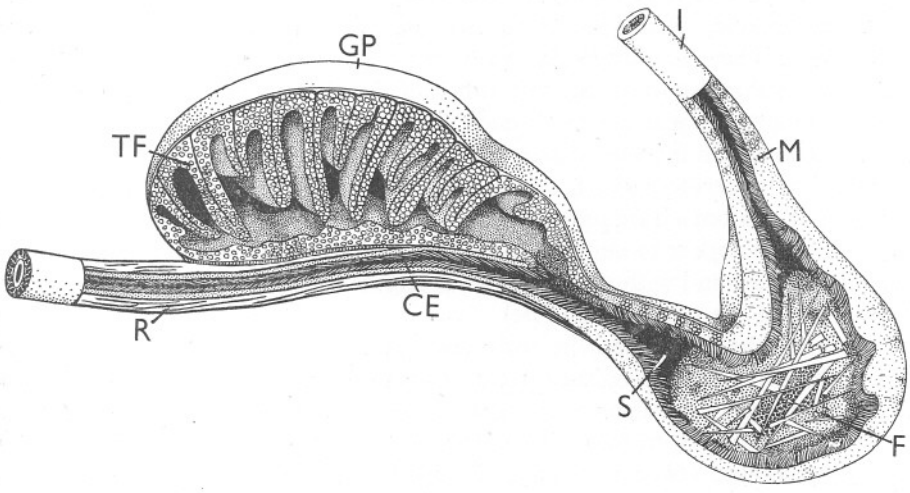

Fig. 5. *Triphora perversa*. Diagrammatic longitudinal section through the posterior oesophageal region, stomach and part of the intestine. × 140. CE, ciliated epithelium of oesophagus; F, food in stomach; GP, glandular pouch; I, intestine; M, mucous cells of mid-intestine; R, retractor muscle of proboscis; S, stomach; TF, transverse folds of epithelium.

the gland a yellowish appearance in the living state and are resistant to acid fixatives. With iron haematoxylin the spherules may all stain lightly, or some very deeply, and this difference in staining would appear to indicate stages in the elaboration of the final secretion—the lightly staining spherules being the precursors of the deeply staining ones. A considerable number of mucous cells also occurs in the epithelium; this is contrary to the typical condition in the lateral glandular pouches of the mid-oesophagus of gastropods for their function is to secrete enzymes, and only on rare occasions do they possess even a few cells secreting mucus or other lubricants (Graham, 1941).

At the posterior end of the oesophagus, between the opening of the gland and the stomach, the epithelium has exceptionally long cilia which direct a current posteriorly; along the dorsal wall are numerous mucous cells.

The plan of the rest of the digestive system is similar to that of *Cerithiopsis*: the stomach (S), a simple ciliated sac receiving anteriorly the opening of the oesophagus and above that the opening of the intestine; the intestine (I), a practically straight tube which leads over the kidney to the mantle cavity where, however, it runs along the *left* side to open towards the anterior end. The main duct from the digestive gland opens to the posterior wall of the stomach and anteriorly there is a small lobe of the gland which opens behind the opening of the intestine. The epithelium of the gland consists of tall club-shaped digestive cells, and excretory cells confined to the crypts of the tubules. The cytoplasm of the digestive cell is always vacuolated, although the details of its appearance depend upon the exact physiological state in which it is examined. In a starved individual the vacuoles appear to contain a uniform type of spherule, homogeneous in consistency and presumably containing a zymogen. There is only slight evidence that these are secretory for I have seen a few spherules freed into the lumen of the gland only on rare occasions. Sometime after a meal the distal ends of many of the digestive cells contain food vacuoles with ingested matter, fluid and minutely particulate; and much later yellow spherules, which can be traced to the faeces, occur in the same position. The stomach frequently contains numerous siliceous sponge spicules (F), and these appear to constitute the greater bulk of the faecal pellets; they are wrapped around with mucus which is secreted in large quantities from the epithelium of the mid-intestine (M).

The reproductive system in both sexes of *Triphora perversa* has an open pallial duct without sub-epithelial glands, and in the male there is no penis. It may be assumed from their close similarity in structure that the functioning of these ducts is similar to that of *Cerithiopsis*. There is, however, a difference in the receptaculum seminis which in *Triphora*, although lined by gland cells, shows no evidence of sperm absorption.

Discussion

Amongst the carnivorous gastropods there are several which browse on the tissues of sponges: *Diodora apertura* and some dorids may live exclusively on siliceous forms, rasping the surface tissues and taking relatively large mouthfuls into the gut. *Cerithiopsis tubercularis* and *Triphora perversa* are also sponge feeders, but they have adopted a different feeding habit. The acrembolic proboscis characteristic of many families of the mesogastropods has been lengthened in these two small animals so that it is long enough to pass through an osculum and reach the inner tissues of the sponge. In this way the spicular cortex which protects the sponge externally is avoided, and the softer parts sucked into the oesophagus; nevertheless, some spicules are taken up. The development of a long proboscis demands some modifications of the anterior part of the gut since this must move forwards through the narrow gap in the

nerve ring when the animal is about to feed and be withdrawn later. This involves an increase in length and a removal of projections which might obstruct its movement.

The oesophagus of the primitive gastropod is divisible into three regions: the anterior oesophagus which begins at the point where the radular sac separates from the gut; the mid-oesophagus with the dorsal food channel along its roof, and on each side a glandular region from which digestive enzymes are secreted; and behind this the posterior oesophagus. In this original condition the mid-oesophagus is swollen. The oesophageal glands are lost in some mesogastropods and the diameter of the tube then becomes uniform. This, however, occurs mainly in herbivorous forms, especially those with a constant stream of food into the gut, and the pouches are then replaced by a crystalline style in the stomach producing an amylase. In carnivores (Graham, 1939) where the next meal is unpredictable, the extracellular enzymes are better supplied by a gland under nervous control than by an automatic crystalline style; moreover, the demand is much more likely to be for a free proteolytic enzyme. In *Cerithiopsis tubercularis* the modifications of this region are met by the modification of the mid-oesophagus which is lengthened, with a consequent narrowing of its total diameter, and the glands are no longer concentrated in lateral areas as in the primitive prosobranch, but spread along the morphologically ventral and lateral walls; all trace of their paired origin is lost. The ciliated food channel covers the remaining wall and is separated from the glands by a longitudinal septum: this is the right dorsal fold which originates in the buccal cavity, bordering the dorsal channel, and remains normal in size until it reaches the posterior end of the anterior oesophagus when it rapidly enlarges and extends across the lumen to reach the opposite wall, even when the oesophagus is dilated. It not only provides mucus to lubricate the ciliated food channel where mucous cells are lacking, but also acts as a valve to prevent the sucking forwards of secretion from the oesophageal glands when the proboscis is extended during feeding.

The mid-oesophagus is, in all prosobranchs, involved in torsion; in *Cerithiopsis* this twisting of the gut includes also the posterior end of the anterior oesophagus. Into this posterior end opens a mucous pouch, attached ventrolaterally, but rotated on to the right side. There is no evidence that food is taken into the pouch: its epithelium is tall and glandular and the lumen relatively small; its opening beneath the small left dorsal fold may be covered by the free edge of the right fold. A ventral diverticulum from the oesophagus, immediately anterior to the oesophageal gland, is described by Amaudrut (1898) in *Cypraea arabica* and occurs in *Lamellaria perspicua*; in these molluscs, however, the diverticulum is larger, thin-walled and not differentiated histologically from the surrounding tissue: it may merely provide extra space in the oesophagus. The diverticulum in *Cerithiopsis* secretes a lubricant to augment the secretion from the right dorsal fold; the left fold has no mucous cells and cannot be traced beyond the anterior oesophagus.

The modifications in the oesophagus in *Triphora perversa* are more difficult to interpret. This region of the gut shows several anomalies: it consists of a muscular and ciliated tube which is elongated so that it must be looped within the haemocoel when the proboscis is withdrawn; it receives anteriorly the secretion from the salivary glands by a median glandular duct which is divided histologically into a proximal and distal part; the gland which opens into its dorsal wall posteriorly has a secreting epithelium which differs from that of the typical oesophageal glands in that it includes an appreciable number of mucous cells. From the structure of the oesophagus it is impossible to deduce the site of torsion. The fusion of the two ducts of the salivary glands to a single broad channel where, in the distal part, the common type of secreting cell is unlike any in the glands, and the fact that they discharge into the oesophagus,

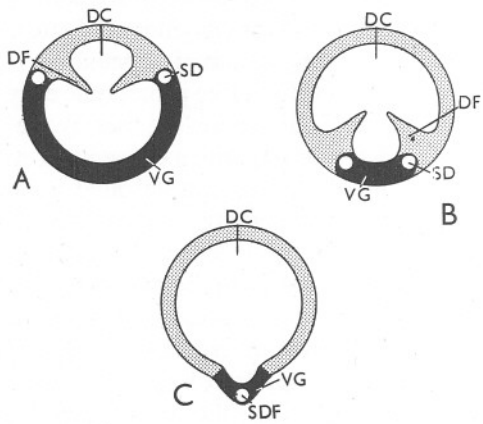

Fig. 6. A–C. Diagrams to illustrate the suggested relations of the dorsal food channel, ventral glandular region of the oesophagus and salivary ducts described on p. 578. DC, dorsal channel; DF, dorsal fold; SD, salivary duct; SDF, fused salivary ducts; VG, ventral glandular part of mid-oesophagus.

are, it would seem, conditions unparalleled in the gastropods. Typically, as in *Cerithiopsis*, the salivary ducts open into the buccal cavity, one on the outer side of each dorsal fold, and they (Fig. 6A, SD) may run back through the connective tissue of the anterior oesophagus along the base of the folds (DF) before passing to the haemocoel. Now the dorsal channel (DC) may be expanded and the ventral glandular part (VG) of the mid-oesophagus correspondingly reduced by the dorsal folds migrating ventrally (Fig. 6B), as has happened for example in the Stenoglossa (Graham, 1941), and when this takes place the salivary ducts (SD) migrate with them so that they come to lie side by side under the reduced ventral part of the oesophagus (VG). They may eventually fuse with one another and by losing their anterior sections open into the oesophagus here instead of into the buccal cavity (Fig. 6C). Now suppose that the ventral glandular part of the oesophagus, into which the single median salivary duct

now opens, is stripped off the remainder of the oesophagus from the anterior end backwards, then the conditions which obtain in *Triphora perversa* have been accurately reproduced—the oesophageal tube representing the dorsal food channel, the median glandular duct the oesophageal gland which has fused along its length with the proximal end of the salivary duct so that this opens into its posterior part, the line of fusion being represented by a longitudinal strip of mucous cells.

This interpretation of the oesophagus of *Triphora* does not account for the presence of a posterior dorsal gland which is constricted from the oesophagus not far from its junction with the stomach. The gland may represent a novel structure. That the oesophagus of the gastropod does give rise to such new parts is evident in the Buccinacea, the only family of the Stenoglossa with a dorsal caecum on the posterior oesophagus. The gland in *Triphora* agrees with this caecum in position, in the deep folding of its walls, and in possessing a number of goblet cells; but it differs from it in having an epithelium which, except for mucous cells, is histologically distinct from any other in the oesophagus. Brock (1936) suggests that the caecum in *Buccinum undatum* is merely an enlargement of the oesophagus to provide extra accommodation, and food with digestive enzymes enter it from the oesophagus; in *Triphora* there is no evidence that food is taken into the gland.

An open pallial genital duct in both sexes is known to occur in a number of families of the mesogastropods (Johansson, 1947) and is associated with the absence of a penis. It was described in *Turritella communis* (Fretter, 1946), a ciliary feeder living in a muddy situation, and was thought to be associated with the precautions which prevent excessive sediment entering the mantle cavity. To account for the open duct in such forms as *Bittium reticulatum*, *Scala communis* (= *Clathrus clathrus*) (Johansson, 1947), *Cerithiopsis tubercularis* and *Triphora perversa* seems perhaps at first sight more difficult; it is undoubtedly secondary and presumably advantageous.

It is well known that the mantle cavity of gastropods has to subserve a variety of functions mainly effected by a stream of water through it. In gastropods with a helicoid spiral shell the shape of this cavity varies considerably and is reflected in the form of the shell. This may be a close spiral with a small apical angle (e.g. *Cerithiopsis* and *Triphora*) or a rapidly expanding spiral with a large apical angle (e.g. *Lamellaria*); in the former case the mantle cavity is narrow and deep, in the latter broad and comparatively shallow. In the second group of gastropods the swelling of the pallial oviduct in the female, which occurs during the breeding season, and the presence of the penis in the male with its insertion into the pallial oviduct during copulation, would not interfere with the efficient functioning of the mantle cavity—in fact in viviparous forms like *Littorina saxatilis* there is sufficient space for the pallial oviduct to form a brood pouch accommodating a large number of embryos. The deep mantle cavity of *Turritella*, *Bittium*, *Cerithiopsis*, *Triphora* and *Clathrus*, which contains

a large gill following the course of the tight spiral of the shell, may have reached the minimal breadth for maintaining a proper ventilation of the whole cavity, and should it be still further restricted by the presence of a penis or a swelling genital duct its breadth might be brought below the limit for efficiency. Perhaps it is for this reason that the penis is lost and the sperm transferred to the female by a method involving an open pallial duct; moreover, in these molluscs the duct is long and thin without sub-epithelial gland cells. To test this hypothesis the examination of the shells of a series of mesogastropods was made.

The general appearance of a helicoid spiral shell depends upon (i) the angle of the equiangular spiral α, and (ii) the angle β which a tangent to the whorls makes with the axis of the shell—the half apical angle (Thompson, 1942).

TABLE I

Species with an open pallial genital duct in both sexes	No. examined	Average value for β
Turritella communis	10	8·5°
Bittium reticulatum	5	5·25°
Cerithiopsis tubercularis	6	3·25°
Triphora perversa	5	5·5°
Clathrus clathrus	8	7·5°
Species with a closed pallial genital duct in both sexes		
Littorina littorea	12	40·6°
Littorina saxatilis	12	39·0°
Rissoa parva	8	16·0°
Natica poliana	6	47·3°

These two values may change with age. A mean low value for the half apical angle β indicates a tall spire which, with tightly packed whorls, would have a high value for the spiral angle α, as in *Tenebra triseriata* where the spiral angle is 89·2° (Moore, 1936); on a flattened shell it would be impossible to pack the whorls so tightly. A flattened spire has a high value of β, e.g. *Velutina*, *Lamellaria* and *Planorbis*, the extreme case being in the pulmonate with a half apical angle of 90°; the two members of the Lamellariidae have a lower value of α, for their shells are rapidly expanding spirals. The difference in the magnitude of the spiral angle of such diverse shells as *Turritella* and *Natica* may only be 2° (Thompson, 1942), and since such a very small change in α may be associated with such disparity in shape it is clear that it is upon the angle β that the difference in their form mainly depends. Consequently, β is taken as the value of importance in the present consideration, and has been measured as the angle between the tangent to the last two whorls of the shell of mature individuals and the axis of the shell. The last two whorls were selected as they enclose the mantle cavity (Table I).

In all the British mesogastropods in which an open genital duct has been described in both sexes and there is no penis, β does not on the average exceed

8·5°, and in these species the mouth of the shell is small, about one-fifth of the height or less; the ctenidium is well developed and occupies a large part of the mantle cavity. In such tightly coiled spirals there will be a greater degree of shortening of the right side of the body and so less space for the right half of the pallial complex, which is, in the mesogastropod, the genital duct and rectum.

In some other mesogastropods the penis is lost and the pallial genital duct is open at least in one sex. From the description of a female *Cerithium telescopium* by Berkeley & Hoffman (1835) one may conclude that the pallial duct is open; the shell of this species is tightly coiled, with a small value for β (11·5°) and a very restricted opening. The pallial duct is also open in *Fagotia esperi* (Soós, 1936), in the male of *Cerithium vulgatum* (Johansson, 1947) and in the female of *Melanopsis dufourei* (Sunderbrink, 1929), but in these the body whorl of the shell is deep, though compressed, and its opening long, suggesting the presence of a more spacious mantle cavity. It may be that the specialized condition in these three molluscs is to be related to some unknown factor in their mode of life rather than to the shape of the shell. An alteration in shell shape may be recent and the structure of the genital duct not yet changed from the ancestral condition to conform to the new type of shell.

Summary

Cerithiopsis tubercularis and *Triphora perversa* feed on siliceous sponges: a long proboscis is thrust through an osculum of the sponge, or into breaks in the surface, to reach the softer parts. These are loosened by jaws, entangled in saliva and swept into the buccal cavity by the radula.

The formation of a long introvert, which must be withdrawn through the narrow space in the nerve ring and narrow enough to go through an osculum, has brought about (i) a lengthening of the mid-oesophagus in *Cerithiopsis*, with a narrowing of its diameter, and a spreading of the oesophageal glands along its length, (ii) in *Triphora*, a reduction of the ventral glandular part of the mid-oesophagus, its stripping from the food channel and a displacement of the salivary ducts so that they open into the glandular part of the oesophagus. In *Triphora* there is a dorsal gland of unknown function on the posterior oesophagus.

The stomach in both species is a simple ciliated sac: the oesophagus opens anteriorly and ventrally, and the intestine originates above this opening; there are two ducts from the digestive gland.

The pallial region of the male and female genital duct is open; and there is no penis. It is suggested that the open condition of the duct and the absence of a penis in the mesogastropods is correlated with a long, narrow mantle cavity which contains a relatively large ctenidium.

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STUDIES OF WATER MOVEMENTS AND WINDS AT VARIOUS LIGHTVESSELS

II. AT THE SEVEN STONES LIGHTVESSEL NEAR THE SCILLY ISLES

By J. N. Carruthers, D.Sc., F.Inst.P,[1]
Commander A. L. Lawford, R.N. (rtd.)[1]
and Instructor-Lieutenant V. F. C. Veley, B.A., R.N.[2]
with the assistance of
Lieutenant-Commander J. F. Gruning, D.S.C., R.N.[2]

(Plates I–IV and Text-figs. 1–9)

[This paper is published with the approval of the Lords Commissioners of the Admiralty, but the responsibility for any statements of fact or opinions expressed rests solely with the authors.]

Introduction

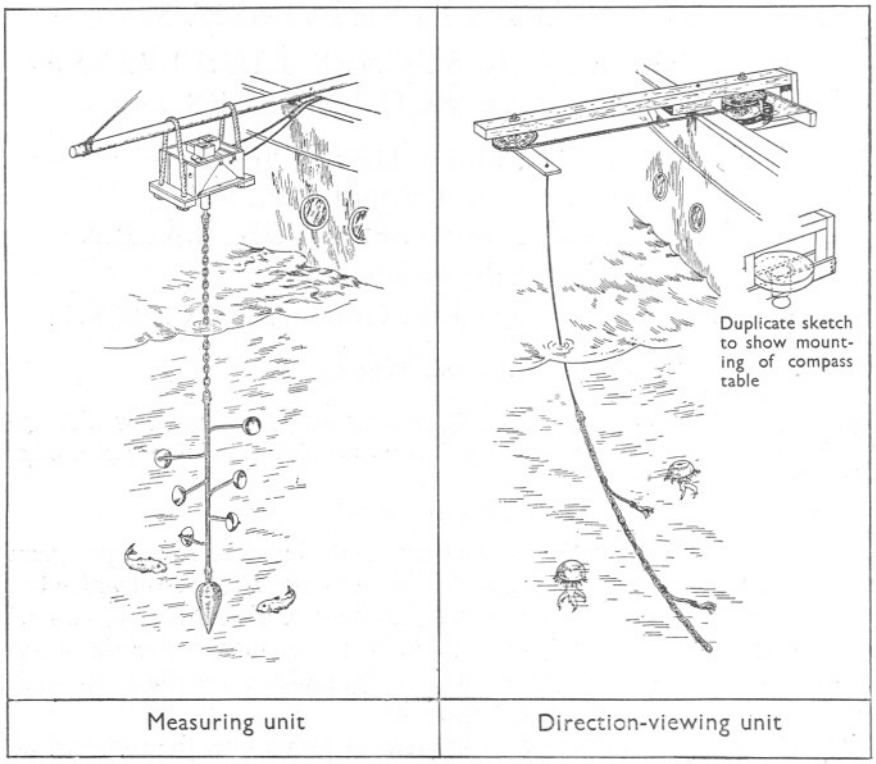
The purpose of this paper is to review the results obtained from a programme of continuous current measuring at the Seven Stones Lightvessel which lasted for upwards of 600 days. It is expected that the actual records amassed during that considerable period will be published in due course. For the present, reviews such as this are being prepared and published *seriatim* in advance of any major presentation of the detailed data.

This present paper follows shortly upon an earlier one, the subject matter of which was information entirely comparable in nature but very much less in extent. The briefer paper (Carruthers & Lawford, 1950) dealt with the water movements past the Mouse Lightvessel in the Thames Estuary, and is no. 1 in the series.

Marine biologists in general, and fishery research scientists in particular, attach importance to schemes of investigation which produce solid information on water movements adequate in time span to serve studies of the dispersal of passively drifting marine organisms. Because of this, there had come into being, by the time World War II broke out, a wide scheme of observations which aimed at amassing simple data on water flow past an ever-increasing number of lightvessels. The aim was to learn for all days of whole years (without intermissions imposed by bad weather) how a thick surface layer of water had moved at a sufficient number of places in the southern North Sea and the English Channel to produce a synoptic picture of value to workers

[1] Royal Naval Scientific Service.
[2] Serving with the authors in the Hydrographic Department of the Admiralty.

concerned with the life histories of fish and other organisms. The information gathered had real interest for others besides, such as engineers concerned with coast erosion, and seamen.



Text-fig. 1. The vertical log current meter as used aboard lightvessels. With this extremely robust (but not in this form automatic) instrument, a very large body of data on water-flow past lightvessels has been amassed. The observations have been carried on without any intermissions imposed by wild weather, and, throughout the entire winter of 1938–39, 'non-stop' observations were made with this instrument from ten lightships (English, French, Dutch and Danish) in the southern North Sea and English Channel... and also from the Seven Stones lightship near Land's End. A modified form of the instrument can provide for automatic observations from anchored ships, and a special version of it now exists for use from an unattended buoy so that the immobilization of an observing vessel is avoided. The resulting data on water movements are directly applicable to navigational needs because a thick layer of water is investigated; it has been customary to submerge the 5 ft. long cup system about 1 fathom below the sea surface. No considerations of magnetic disturbance arise to prohibit the use of this instrument from steel vessels other than at 'safe' depths, and there is a virtual absence of registration of spurious current from revolutions put on in response to ship movements.

Text-fig. 1 shows the instrument (the original 'Vertical Log') with which the information was gathered, and its legend tells something about the employed apparatus.

Before the War, it was customary to publish a yearly presentation of the results obtained from the various lightships aboard which the work was in

train. Such annual publication was made in the pages of the *Rapports et Procès-Verbaux* of the International Council for the Exploration of the Sea.

When War came, a considerable body of data perforce went unpublished, and to this was added information from such lightships in which it was possible to continue the work. That such continuance into the period of hostilities was sometimes possible was due jointly to the good offices of the Hydrographic Department of the Admiralty, and to the kindness of the English Department of Fisheries, in allowing the senior author not only to continue in possession of the apparatus which he had been using, but also to have the services of his assistant (the late Mr R. S. Minchin) to run the programme whilst he himself was engaged upon other duties.

Amongst the bodies of unpublished data held when the War ended was that for the Seven Stones Lightvessel. The position in question is perhaps second in interest only to that of the Varne Lightship anchored in the Straits of Dover. The amount of information is by itself noteworthy, and the position concerned has its own particular interest.

Various authors (quoted later) have put forward views on the possible scheme of water circulation in the area off the western entrance of the English Channel and the adjacent region lying off the southern entrance to the Irish Sea. It seemed that the data from the Seven Stones might serve to throw light upon this matter, or at least might provide help to anyone trying to decide whether or not the Rennell Current is a real entity.

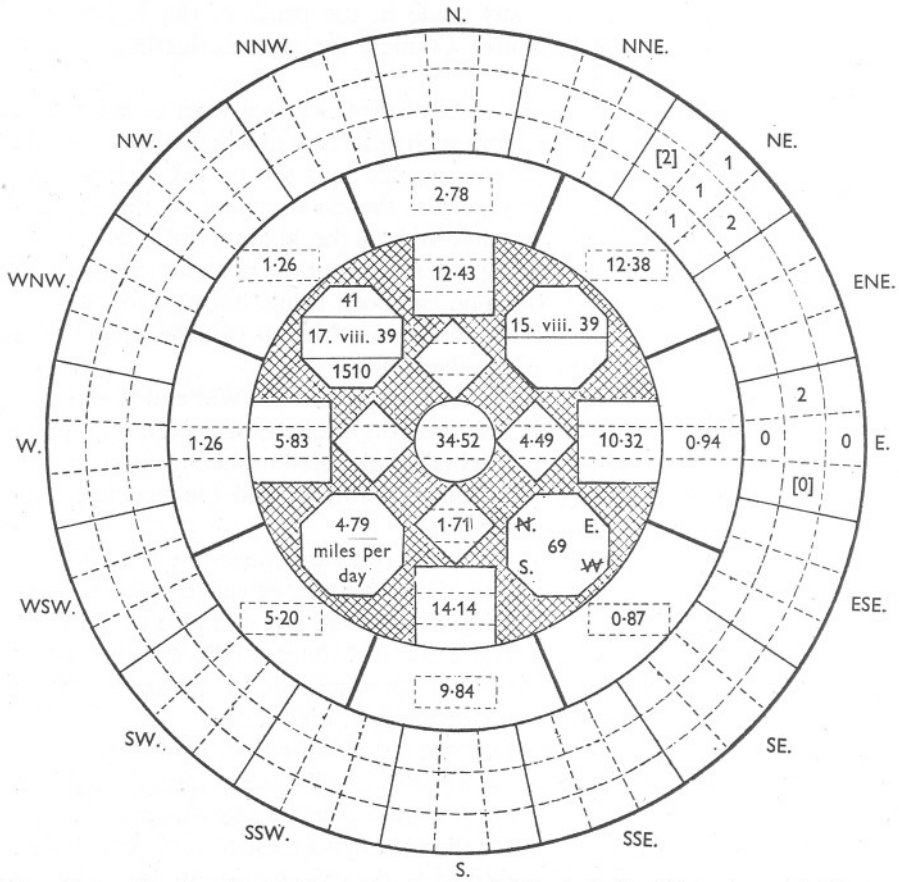
In an earlier paper (Carruthers, 1934) the Rennell Current topic was touched upon. At that time it was possible to discuss the results obtained in the course of only 28 days observing from the Seven Stones Lightship.

The instrument then used was not the same, and the depth of observation was greater, but the 1934 results testified to the existence of an overall water movement towards the south-east quadrant of the compass. This direction of residual flow, we shall see, was evidenced by the very much larger body of data to be discussed below.

It was considered that the mass of continuous data available amply merited a measure of detailed study, and it has been deemed worth while to investigate it rather thoroughly in respect of wind influence on water movement.

When the time comes to publish the collection of daily records *in extenso*, they will probably be presented in a form which lets the associated wind conditions be seen at a glance. It is intended to publish them entered in 'clockface' form, of which a specimen is included here (Text-fig. 2.)

The authors desire to express their thanks to the crew of the lightvessel, by whom the observations were made.



Text-fig. 2. Circular diagram for presenting data (with winds data) from the vertical log.

Explanation of circular diagram

OUTER RING. (Pecked squares.) The nine wind strengths (Beaufort scale) recorded for the 24 hr. upon which the observation is approximately centred.
INNER RING. The water movement in sea miles recorded against each octant during the day.
SQUARES. The gross cardinal components of the latter.
DIAMONDS. The net values of the cardinal components.
CIRCLE. The total water movement.
OCTAGONS. *Top left*—from top to bottom the *serial number*, *date* and *mid-time* of the particular observation.
Top right—the date of the nearest *new* moon in the *upper* half or of the nearest *full* moon in the *lower* half
Bottom left—the *magnitude* of the residual water movement.
Bottom right—the *direction* of the residual water movement.

THE OBSERVATIONS

Observations were commenced aboard the Seven Stones Lightvessel on 4 July 1939, when she was in a position 50° 03·3′ N., 6° 05·1′ W. After some 4 months (20 November) the vessel was moved to a position 50° 03·5′ N.,

6° 05·1′ W.; observations were, of course, interrupted during the move, but otherwise the change of position, which only amounted to 2 cables, does not seem to have disturbed the sequence of the recorded data. Work was resumed at the new position on 21 November 1939, and continued until 1 May 1941, when the vessel was withdrawn owing to the war situation.

For various reasons breaks in the observations occurred on nineteen occasions, including the one referred to above. In all, 624 observations, each lasting one lunar day, were made (although 625 observations are listed, serial numbers 132 and 133 only produced sufficient data for one observation owing to an error in the timing of the observations).

The Seven Stones Lightvessel lay in a mean depth of 40 fathoms about 2 miles to the north-eastward of the Pollard Rock, one of the Seven Stones. This position is some 14 miles due west of Land's End and 12 miles north-east of St Mary's (Scilly Isles). The passage between land and land is 22 miles wide, the mean depth being about 36 fathoms (see Text-fig. 3).

Water movements at this position were recorded on all eight octants, but the overall or residual movement was principally east-south-easterly.

During the period under review the centre of the cup system of the measuring unit was 21 ft. below the sea surface. The water-layer in which observations were taken was from 3 to 4 fathoms below the surface.

The wind was estimated every 3 hr., the strength being recorded in Beaufort scale numbers. When the local tractive effect of the wind is considered in this paper, sight is not lost of the fact that the observations relate to a water-layer well below the surface.

The total revolutions, and the revolutions of the eight individual octant counters, per lunar day, were simply obtained by subtracting the readings of the day before. The total daily revolutions and the sum of the revolutions on the octants agreed to within twenty-two revolutions, on the average, though very much larger discrepancies occasionally occurred. This average disagreement represents $\frac{1}{2}\%$ of the total revolutions, and was presumably due to the time lost in changing over the octant counters.

The water movement in sea miles per lunar day was obtained by applying the 'calibration constant' of the instrument to the revolutions. In this case, 300 revolutions were the equivalent of 1 mile (6080 ft.) of passing water.

The mean wind for the day was calculated by geometrically averaging the winds recorded between the initial and final readings of the counters each day.

A plot of the total water movement showed a strong resemblance to a tidal cycle, with maxima occurring from 1 to 3 days after full and new moon (see Pls. I and II). A smooth and regular curve could be drawn through a large percentage of the points.

Superficially, a plot of the magnitude of the residual water movement showed much less tendency towards regularity, but comparison with the total

Text-fig. 3. Position of Seven Stones Lightvessel.

water-movement plot revealed that it was periodic, with marked minima and with double maxima spaced on either side of the total water-movement maxima. A regular curve was also superimposed upon this plot.

(For details of the method of construction of these regular curves, see below, p. 601).

A plot was also constructed of the magnetic direction of the residual water movement, centred approximately on the mean for the whole period.

As a first step in analysis, the monthly averages of water and wind movements (shown at the tops of Pls. I and II) were investigated, as these gave reasonably smoothed values for comparison over approximately equal periods of time. It was found that the following conditions of water movement obtained in association with the mean residual wind:

(*a*) Larger *total* water movements than usual were associated with winds from east, through south, to west-north-west, while smaller movements than usual were associated with winds from other directions. 'Doubtful' sectors existed on the boundaries between the two areas. Also, lower total water movements occurred when the residual wind velocities were medium (4–8 m.p.h.), and higher when the wind velocities were both low (0–4 m.p.h.) and high (8–12 m.p.h.).

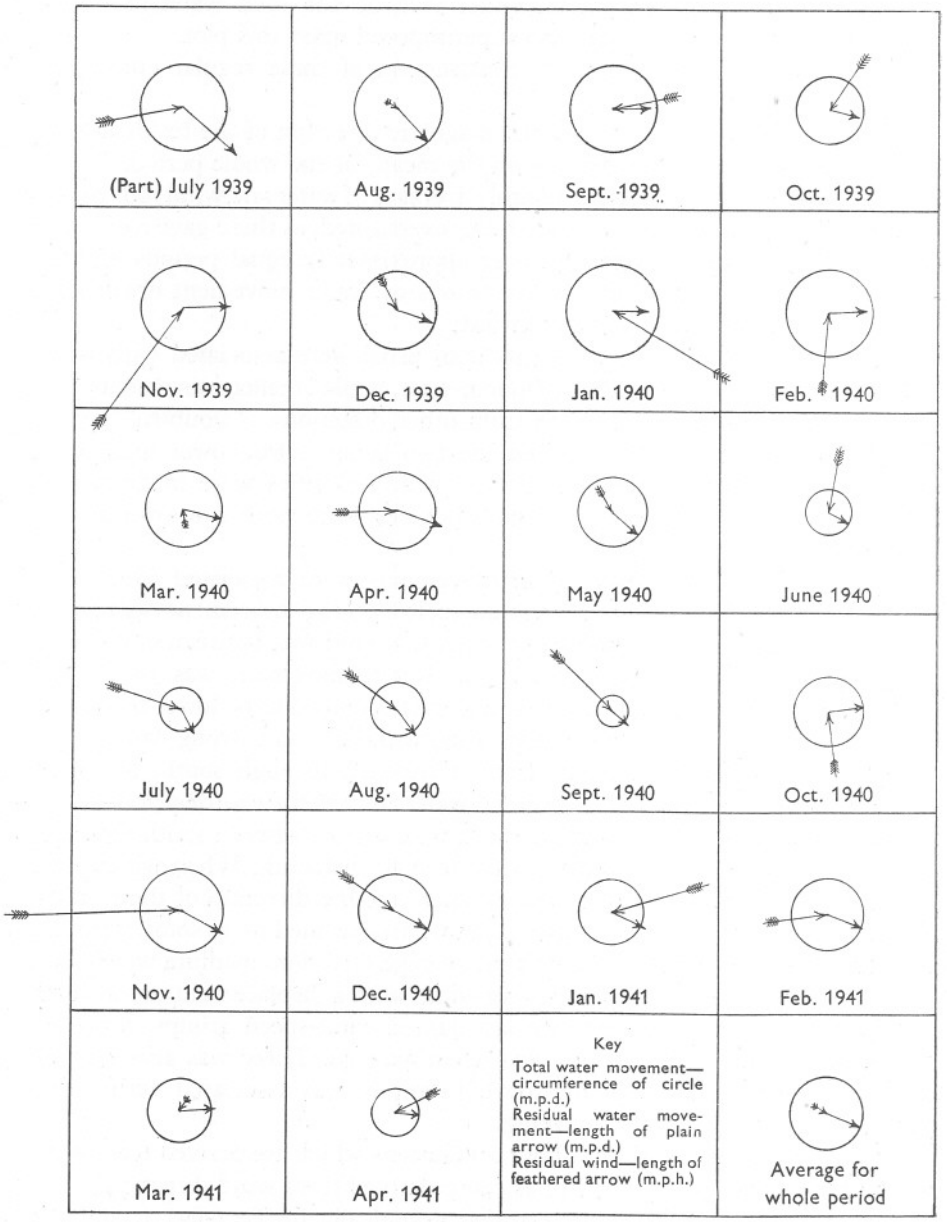
(*b*) Above average *residual* water movements were associated with winds from south-south-west to north-west, and below average movements with winds from north-west to east-south-east; when the wind was between east-south-east and south-south-west the residual water movement was of average magnitude. Also, the residual water movements tended to be lower than usual with medium winds and higher than usual with light and strong winds.

(*c*) In association with winds from north-east, through south, to south-south-west the *direction* of the residual water movement was displaced to the north of the mean for the whole period; with winds between south-west and north-north-east the direction was displaced to the south. When winds were from the small sectors between these major arcs the direction of the residual water movement remained average. Also, there seemed to be some tendency for light winds to be associated with the average direction, medium winds with a displacement to the south and strong winds with a displacement to the north of the average. Between the two last-named wind-speed groups, however, was a band where the direction was again average. There was also a single indication that a residual wind above 12 m.p.h. was associated with a displacement to the south of the average.

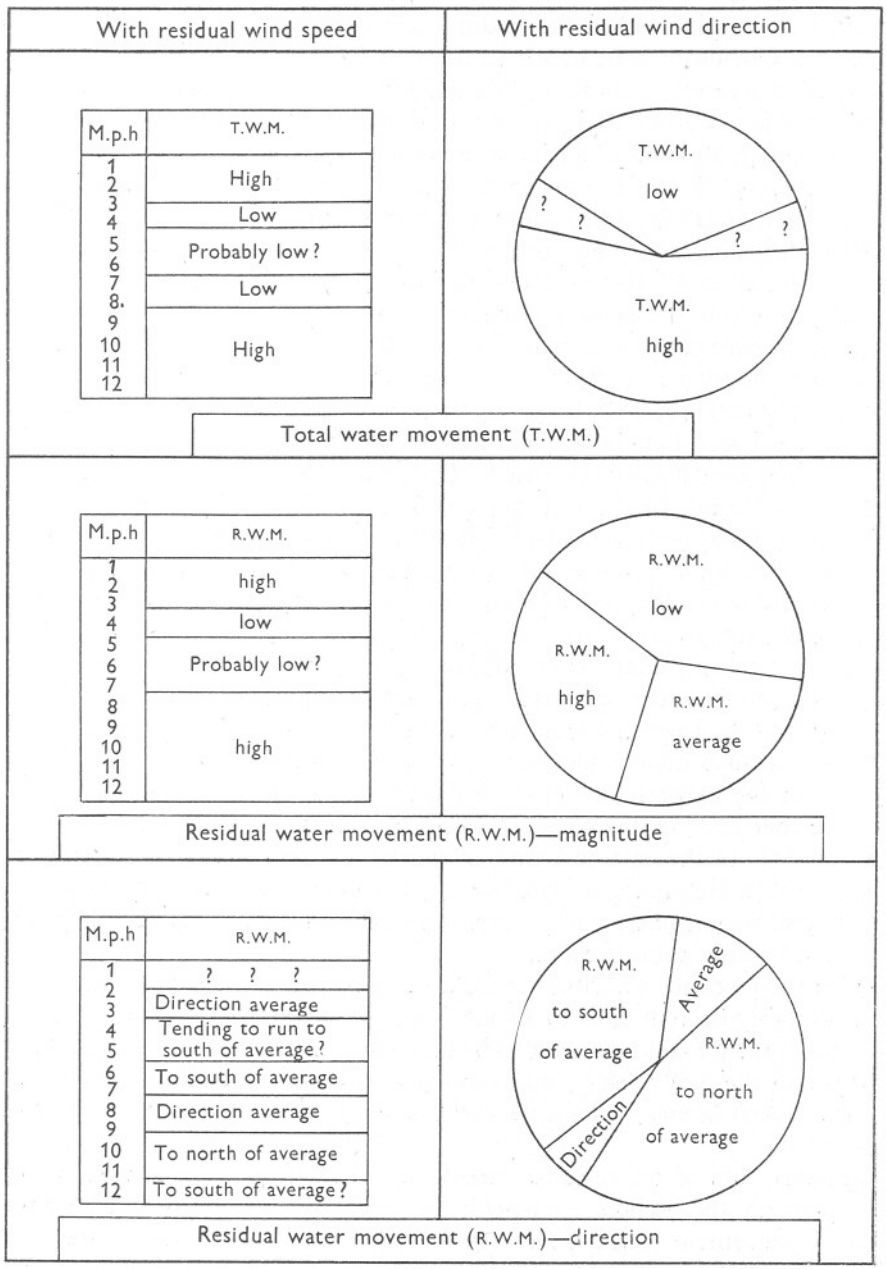
(It must be emphasized that those conclusions which are derived from wind strength are by no means as firm as those derived from wind direction.)

The monthly averages are illustrated graphically in Text-fig. 4, and the findings in Text-fig. 5.

The above findings were checked by inspection of the plotted observations of wind and water movements for individual days or groups of days, and were



Text-fig. 4. Monthly averages of total and residual water movement and residual wind. (All directions are true—variation 13½° W.)



Text-fig. 5. Association of water movements with wind. (All directions are true—variation 13½° W.)

found to agree reasonably closely, although it is not denied that there are a number of occasions when the findings appear to be in direct opposition to the facts. Obviously some unknown factor, such as the wind at some distance from the lightvessel, must have made its influence felt, and on these occasions, it is assumed, its effect was greater than that of the local wind.

The average residual water movement *over the whole period* was 2·5 m.p.h. in a direction S. $56\frac{1}{2}°$ E. (magnetic) = S. 70° E. (true). In an earlier paper (Carruthers, 1934) the senior author calculated, from twenty-eight observations made in August and September of 1933, that the residual water movement was 1·9 m.p.d. in a direction S. 20° E. (true). Obviously these earlier figures differ widely from the average of the observations here discussed; nevertheless, they agree reasonably well with the monthly averages for the August and September of 1939 and 1940.

Harvey (1924) indicated, however, that there was a northward movement of the water between Land's End and the Scilly Isles, and in a diagram showed a north-north-west movement close to Land's End forming part of a cyclonic flow round Scilly. In a later paper (1929) he stated that there was a north-north-west movement at a daily speed of $1\frac{1}{2}$ knots at a depth of 60 m., and that a cyclonic flow existed in the upper layers as a component of the currents at 60 m. Matthews (1913), who was quoted by Harvey, remarked that the northerly current passed only a few miles to the westward of Land's End. A noteworthy reference by Matthews, however, was to a paper published by Dr Bassett in which the latter stated that water from the Bristol Channel escaped into the English Channel between Scilly and Land's End.

It is of course undeniable that 13% of the observations show a residual current in the magnetic octants north-west, north and north-east, and that on a further 12% of the days it pursues courses between the limits of these octants ($67\frac{1}{2}°$ to the east and west of north) and east and west (magnetic). The monthly averages (see Text-fig. 4), however, show that during only 5 months, all winter ones, was the residual current to the north of east (true), and then by only a few degrees.

With the evidence available it would be impolitic to dispute the existence of a northerly current *close* to Land's End (some 12 miles distant) and at a greater depth. What does appear to be somewhat more doubtful is the cyclonic flow round the Scilly Isles, and in this connexion information obtained from Tizard (1909) seems to indicate the existence of an *anti-cyclonic* residual movement.

The direction of the residual current at the Seven Stones is more across than through the Land's End-Scilly passage. If the existence of an anti-cyclonic movement round Scilly can be accepted, it is suggested that the east-south-easterly residual current is perhaps an offshoot of this system which turns further to the north as it crosses the passage and finally joins the north-going flow north of the Longships. It is only fair to state, however,

that Tizard's logship observations also indicate a south-easterly residual current at three positions to the south-east of the Seven Stones. On these grounds the inference is that the residual current at the Seven Stones Lightvessel is, in fact, part of a general south-easterly flow through the passage.

Text-fig. 6 illustrates the possible circulation referred to above. The water movements are the resultants of the figures given in the tables by Tizard, assuming that the hourly observations represent the average movement for an hour.

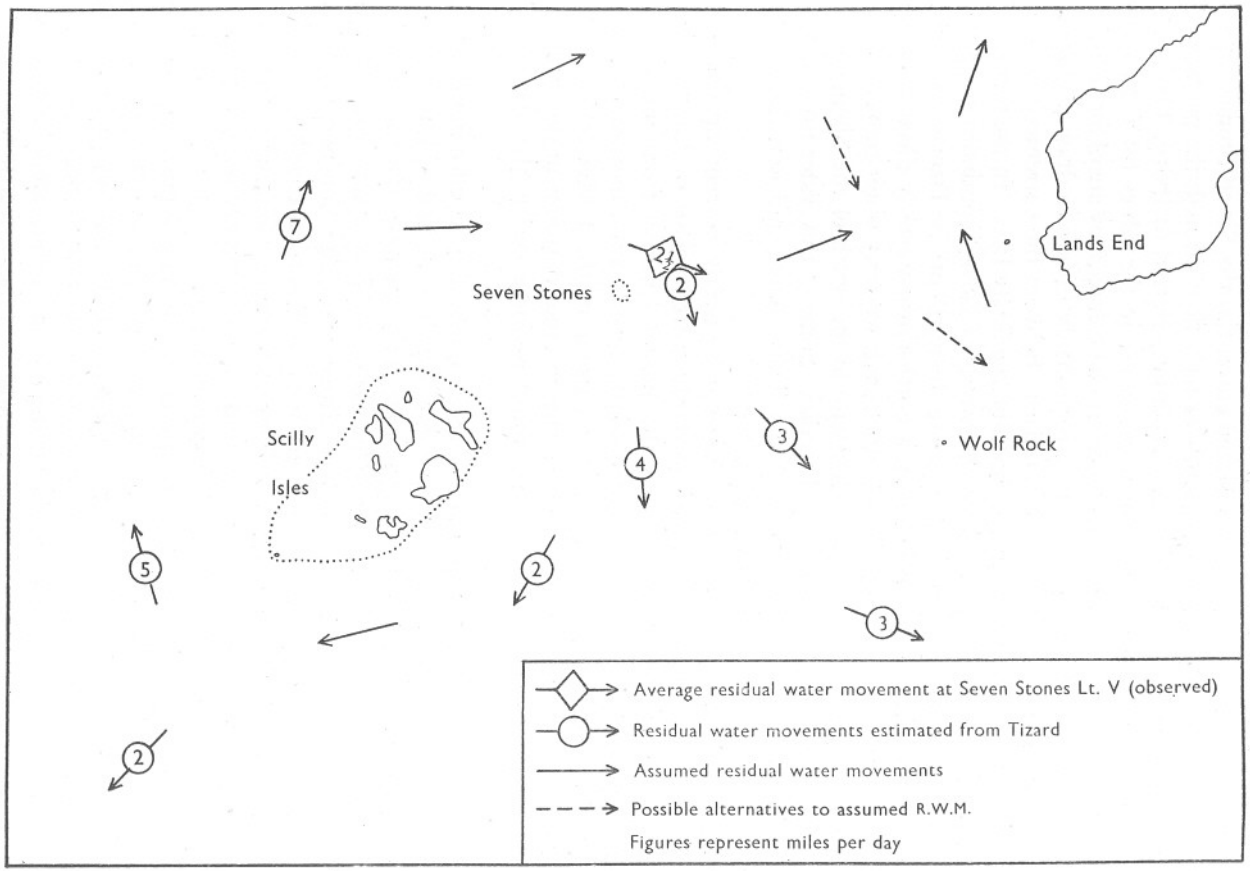
In the study of water movements it is probably unsafe to draw analogies, but there does seem to be a certain similarity between the current systems in the North Sea and in the neighbourhood of the Scilly Isles. In the former, a north-easterly current emerges from the Straits of Dover, continues along the coasts of the Low Countries, turns more to the north off the Danish coast and finally escapes from the North Sea in a north-north-westerly direction after skirting the coast of Norway. Part of the north-westerly water movement to the west of the British Isles turns clockwise to the north of the Shetlands to enter the North Sea in a southerly direction. Some of this water turns to the eastwards to flow past the vicinity of the Fisher Banks and join the north-going movement along the Norwegian coast.

In the Scilly area, there are the east-north-easterly current up-Channel to the south of the area and the northerly current close to Land's End, while to the northward water enters the Bristol Channel from the south-west. If the analogy has force, the east-south-easterly water movement at the Seven Stones is the counterpart of the current in the Fisher Banks area. Until data are available of water movements in other positions in the vicinity, however, suggestions such as these must perforce be in the nature of speculation.

Turning to the plotted information, there are notably small minimal total water movements (less than 1 mile per day) between the end of July and the end of September 1940. Minimal total water movements of less than 4 miles a day also occur in October 1939, and January, March and April 1941. These minima are not associated with any particular wind direction nor, with the exception of the one occurring in January 1941, with particularly strong winds.

This was considered sufficiently striking to warrant calling upon the local knowledge of the lightvessel personnel, and a letter of inquiry was accordingly addressed to the competent Trinity House authority.

In his reply to the Chief Superintendent of Trinity House, one of the masters of the lightvessel (Mr D. Appleby) remarks that on some days a 2 lb. lead can be kept on the bottom during the whole of the tidal cycle, flood and ebb. Bearing in mind how very little water movement is necessary, in 40 fathoms, to take such a light weight off the bottom, it can safely be assumed that the tidal stasis on such occasions extends from the surface to the sea-bed. Mr Appleby adds that these periods occur during neap tides, especially when the succeeding spring tides are not 'very hot', providing weather conditions



Text-fig. 6. Possible circulation in Scilly-Land's End area.

are normal. A glance at the plotted observations for the dates referred to will show that Mr Appleby's statements are in good agreement.

Scrutiny of the plotted record of total water movement will also reveal that, if a smoothed curve were drawn through it, the resultant curve would exhibit sinusoidal characteristics. It is suggested that the minimal total water movements coincide with the minima of such a smoothed curve, which occasionally approaches very close to the zero line, and that they are therefore regular and would be predictable occurrences. Indeed Mr Appleby predicts in his letter, which was written in 1947, that minimal movements would occur on about 24 or 25 September of that year; unfortunately there are no records to confirm this. It appears possible that the period of these minima is about twice yearly, and that they have alternate higher and lower values.

A further point of interest arises in connexion with the plotted observations of residual current direction. Nearly always the direction changes, usually in a marked manner, from one side of the mean to the other at, or shortly after, the minima of the total water movement (i.e. neaps). This shift is mostly from south to north of the mean direction. At about the time of springs there is a shift to the south of the mean, but this movement is very much less marked and may take some days to accomplish. The shifts may sometimes be of degree and not of 'sign'. Viewed in this light, the otherwise irregular plot of residual current direction exhibits 'saw-tooth' characteristics with reasonably well-marked periodicity.

Again, if a smoothed curve were drawn through the residual current-direction plot, the resultant curve would oscillate from side to side of the mean direction. From Pl. I, which covers 1 year, it is tempting to assume that the oscillation is annual, with maximum northerly deflexion in winter and maximum southerly in summer, but Pl. II, for the succeeding 10 months, does not confirm this, and the point must await the collection of more data.

Summarized Results

A survey of the water and wind movements recorded during the 624 days of observing at the Seven Stones Lightvessel brings the following facts of chief interest to light:

(i) Water moved towards all octants of the compass.

(ii) The maximum/average/minimum values of the total water movement (the summed daily mileage of the travel in all eight octants) were 39·7/15·0/0·2 miles/day.

(iii) The daily water movements in the individual octants are given in miles per day in Table I.

Table I.

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	5·1	13·7	5·8	5·4	14·7	7·3	5·5	3·7
Average	1·3	3·8	1·2	1·2	4·0	1·5	1·0	0·9
Minimum	0·0	0·0	0·0	0·0	0·1	0·0	0·0	0·0

(iv) The maximum/average/minimum residual current (the net travel or 'overall make' of the water) and its direction of flow (magnetic) were:

11·0 m.p.d. towards S. 15° W.,
2·5 m.p.d. towards S. 56½° E. (vector resultant),
0·1 m.p.d. towards N. 47° E.

(v) The residual water movements in the individual octants are given in miles per day in Table II, together with the percentage frequency with which they occurred.

TABLE II

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	4·6	10·1	10·0	8·7	11·0	5·8	4·0	1·2
Average	2·7	3·6	3·6	3·4	3·7	1·7	2·0	0·8
Minimum	1·4	0·1	0·3	0·1	0·6	0·1	0·4	0·4
Frequency %	1·0	11·4	27·4	29·6	26·3	3·2	0·5	0·6

(vi) The maximum/average/minimum residual wind, expressed as a vector resultant for a whole day, and its direction, were:

38·5 m.p.h. from north-west by north (magnetic),
1·1 m.p.h. from west-north-west (magnetic).
Nil

(vii) The residual winds on the individual octants, expressed as a mean for a whole day, are given in miles per hour in Table III, together with the percentage frequency with which they occurred.

TABLE III

Octant (magnetic)	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.
Maximum	31·3	29·6	35·8	31·3	36·2	33·6	30·8	38·5
Average	9·0	13·3	13·3	12·8	13·1	11·9	12·4	11·1
Frequency %	11·1	10·1	13·9	8·8	8·0	14·6	14·9	18·1

In addition, there was no wind on 1 day, and on 2 days the vector resultant of the winds was nil (0·5% frequency).

CORRELATION BETWEEN WIND AND WATER MOVEMENT

In order to study graphically the effect of an outside influence (the wind) on daily water movement it is first essential to construct some form of ideal curve. The latter is defined as that curve which will pass through all the readings of water movement/time (graphically plotted) should external factors be neglected and only the effect of spring and neap tides be considered. A number of such ideal curves were constructed during the analysis of the Seven Stones data. The final object was to produce an ideal residual water-movement curve which would enable large deviations of the actual readings from this curve to be studied in conjunction with a graphical representation of wind strength and direction. Results in one form or another would then be obtainable, but the

accuracy of the deductions drawn from these results would naturally be dependent upon the accuracy of the ideal curve.

The residual water movement in general showed a definite tendency towards periodicity, and therefore Fourier analysis would show it to be composed of an infinite number of harmonics of a fundamental curve. Very few of these harmonics can be introduced into an ideal curve because of the difficulty of their construction, and indeed most of the harmonics are spurious, being explicable in terms of wind and other effects.

From the water-movement data the following components were obtainable:

(i) Total water movement for the whole day over the octantal headings.

(ii) Residual water movement in strength and direction.

(iii) $N+S$ and $E+W$ components of the total water movement.

(iv) $N \sim S$ and $E \sim W$ components of the residual water movement.

(*Note.* All the above water movements were measured in sea miles per lunar day.)

The $N+S$ and $E+W$ components of the total water movement were first plotted (see Pls. III and IV) and the two resultant shapes studied (plots K and L). It was found that the springs and neaps were readily discernible and that their total periods were equal to 28 ± 1 lunar days. In accordance with tidal analysis it was assumed that the two ideal wave forms required were each composed of two waves, one of period 28 days and the other of half-yearly period. On this assumption two smooth curves were drawn for the $N+S$ and $E+W$ components (curves K and L) and were found to pass through approximately one-third of the points.

Since the readings of the vertical log current meter were taken on the octantal headings the following relationships hold:

($N+S$ component) of the total water movement $= N+S+0{\cdot}7\ (NE+SE+NW+SW)$ readings.

($E+W$ component) of the total water movement $= E+W+0{\cdot}7\ (NE+SE+NW+SW)$ readings.

Therefore: ($N+S$ component) together with ($E+W$ component),

$$= N+S+E+W+1{\cdot}4\ (NE+SE+NW+SW)$$

$$= \text{total water movement (plot E)} + 0{\cdot}4\ (NE+SE+NW+SW).$$

With the negative correction term $0{\cdot}4\ (NE+SE+NW+SW)$ applied, the ideal curve for the total water movement (curve E) was obtained from the $N+S$ and $E+W$ component curves. This curve was later studied in conjunction with the wind.

In the same manner the readings for the $N \sim S$ and $E \sim W$ components of the residual water movement (R.W.M.) were plotted for magnitude *and direction*. On studying the two shapes obtained (plots M and N) it was found that the movements were periodic as before. However, in most cases where there was a maximum in the $(N+S)$ or $(E+W)$ curves there was a minimum in the

$N \sim S$ and $E \sim W$ plots. It was therefore deduced that a maximum component of total movement did not mean a maximum component of residual movement, but rather a maximum change in magnitude (a change in direction being regarded as a further change in magnitude). Thus for every maximum in a total component curve there would be two maxima and one minimum in the corresponding residual component curve. Assuming this, and that the waves comprising the ideal curves were again of periods 28 days and half yearly, curves M and N were drawn for the $N \sim S$ and $E \sim W$ residual components. The wind appeared to have a greater effect on the component water movements and the ideal curves passed through only one quarter of the points.

Resolving vectorially, the resultant residual water movement is equal in magnitude to

$$\sqrt{[(N \sim S \text{ comp.})^2 + (E \sim W \text{ comp.})^2]},$$

and therefore its ideal curve (curve G) could then be constructed from the two component curves. The actual residual readings were then plotted with respect to magnitude only (plot G) and the ideal curve was found to be in fair agreement.

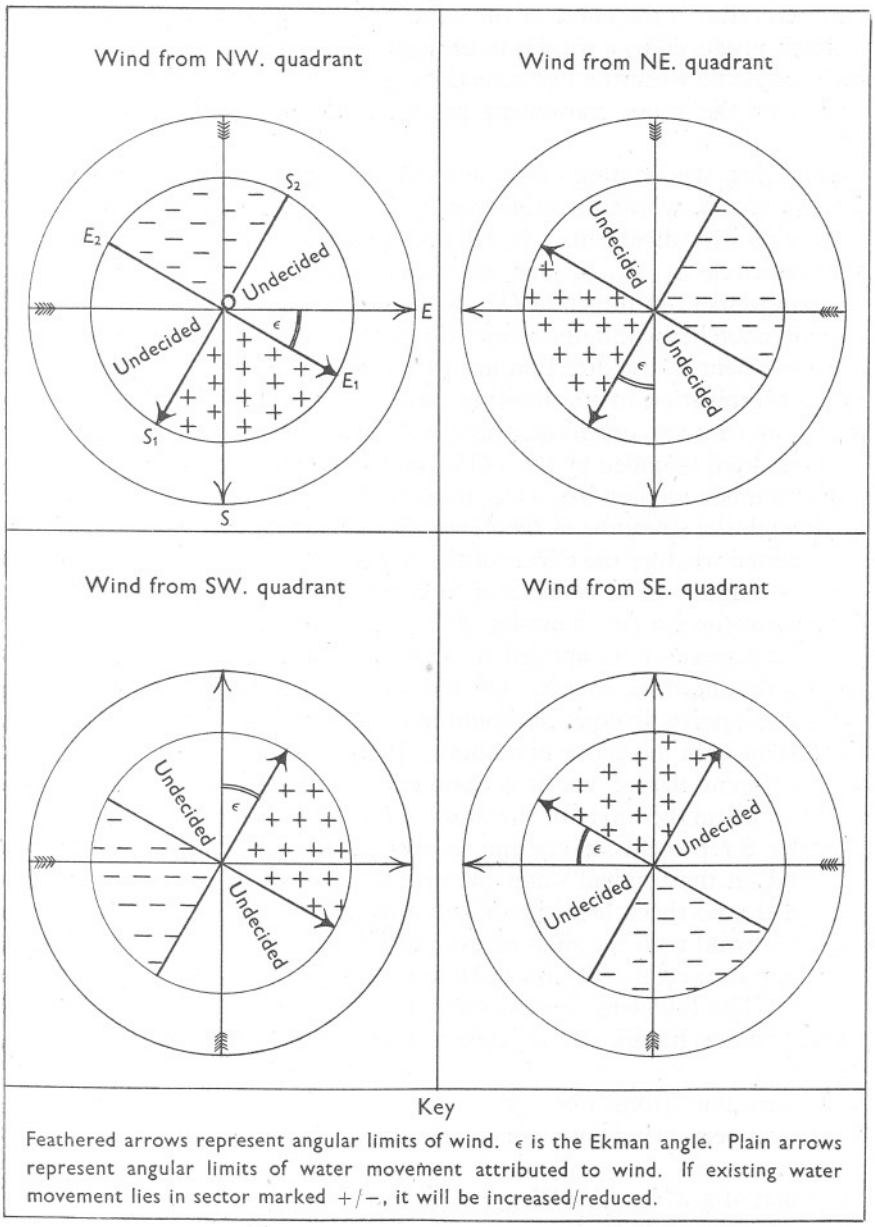
Finally, the wind was analysed into $N \sim S$ and $E \sim W$ components and its force reverted to Beaufort scale. The two components were plotted in magnitude and direction and the plots (H) studied in relation to large deviations from the ideal curves. The following deductions were made assuming that the non-factual curves were authentic.

On comparing the ideal residual water movement (R.W.M.) curve (G) with the observed plot, it was found that although on the whole there was a definite agreement between the two, for a number of observations there was a marked divergence in magnitude. Considering the ideal curve as a datum, a positive divergence was said to exist if the factual plot was above the curve and a negative divergence if below. Noting the wind components where the divergences occurred, a table of the following form was prepared:

No. of observation	Residual water movement		Wind (Beaufort scale)			
	Direction	+ve or −ve divergence	N.	S.	E.	W.
27	S. 20° E.	+6·5 m.p.d.	2	—	—	3

The table was studied with the object of relating the divergences to wind effect. Considering in each case the wind and the direction of the R.W.M. as belonging to one of the quadrants, the frequency of positive and negative divergences was found for each of the quadrants. From this frequency distribution it was discovered that the effect of the wind on the R.W.M. followed a logical hypothesis.

Text-fig. 7 is a diagrammatic representation of wind effect for each quadrant. Considering the north-west quadrant alone, the limits of the wind



Text-fig. 7. Theoretical effect on residual water movement of winds from various quadrants.

direction lie along OE, OS. Ekman's theory states that for the northern hemisphere, due to the effect of the earth's rotation, the direction of a water movement produced by a wind is to the right of the wind direction. Assuming that the angle between the two directions is of magnitude ϵ, the limits of the direction of the water movement produced by the wind lie along OE_1, OS_1.

Considering the limiting cases, a water movement in direction OE_1 will assist any R.W.M. whose direction lies in the semicircle S_1, E_1, S_2, thereby causing a positive divergence. It will oppose any R.W.M. whose direction lies in the semicircle S_1, E_2, S_2, and will create a negative divergence. Likewise a water movement in direction OS_1 will assist any residual water movement whose direction lies within the semicircle E_1, S_1, E_2, and will oppose a residual water movement whose direction lies within the semicircle E_1, S_2, E_2.

For a combination of the limiting cases, i.e. the effect of a general wind from the north-west quadrant, there will be a definite positive divergence for the quadrant bounded by OE_1, OS_1, and a definite negative divergence for the quadrant bounded by OE_2, OS_2; the other two quadrants will be undecided, for, although the strengths of the N and W components are known, it cannot be ascertained whether the effects of the components are directly proportional to their strengths, i.e. a N wind of force 2 might have a greater effect than a W wind of force 3 (see Text-fig. 5).

These arguments were applied to all four of the wind quadrants and the diagrams produced as shown. Of 180 cases considered, where a definite positive or negative divergence should have occurred, 80% were found to be in agreement with the above hypothesis. It should be noted that the latter is of a very general nature, and it is again emphasized that its validity depends entirely on the authenticity of the ideal residual water-movement curve.

Text-fig. 8 represents an attempt to explain vectorially the effect of a constant wind on the residual water movement. The only assumption required is that in the northern hemisphere the direction of a water movement produced by a wind is to the right of the wind direction (Ekman's theory). The results from the vector analysis can be used with the ideal R.W.M. curve shown in Pl. III. The following demonstrates that a deduction can then be made regarding the magnitude of the angle between the directions of the wind and the water.

Wind direction (from) = N. ϕ E.

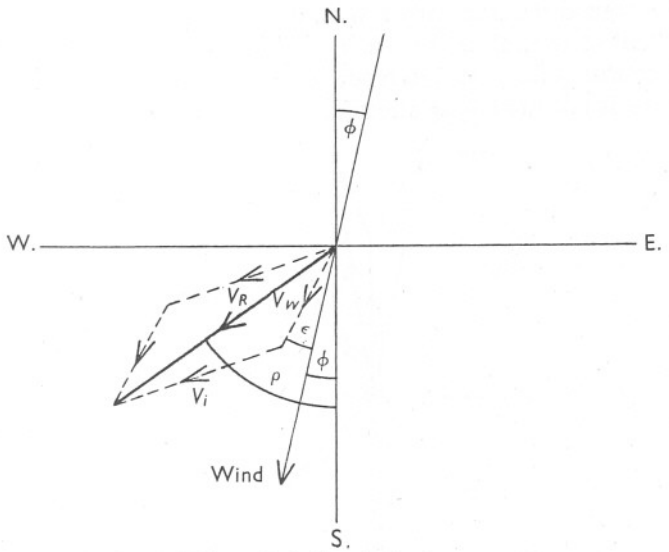
Angle between wind and water movement produced by wind (Ekman angle) = ϵ.

Direction of R.W.M. = S. ρ W.

V_R = velocity of R.W.M.

V_i = velocity of intrinsic water movement, i.e. the water movement if wind had not been present (given by the ideal R.W.M. curve).

V_w = velocity of water movement due to wind.



Text-fig. 8. Effect of wind on intrinsic water movement.

Then
$$V_R = V_i + V_w. \tag{A}$$

In the triangle of sides V_R, V_i, V_w, the angle between V_R and $V_w = \rho - (\phi + \epsilon)$.
Then
$$V_i^2 = V_R^2 + V_w^2 - 2V_R.V_w.\cos(\rho - (\phi + \epsilon)). \tag{B}$$

But from Thorade (1914)

$$V_w = \frac{1{\cdot}26V}{\sqrt{(\sin\lambda)}} \text{ for winds above Beaufort strength 3,} \tag{C}$$

where V = wind velocity and λ = latitude.

Since V_R, ϕ and ρ are known and V_i is obtainable, ϵ may be determined.

In (C), V_w is in cm./sec. and V in m./sec. Converting to other units and substituting 50° for λ:

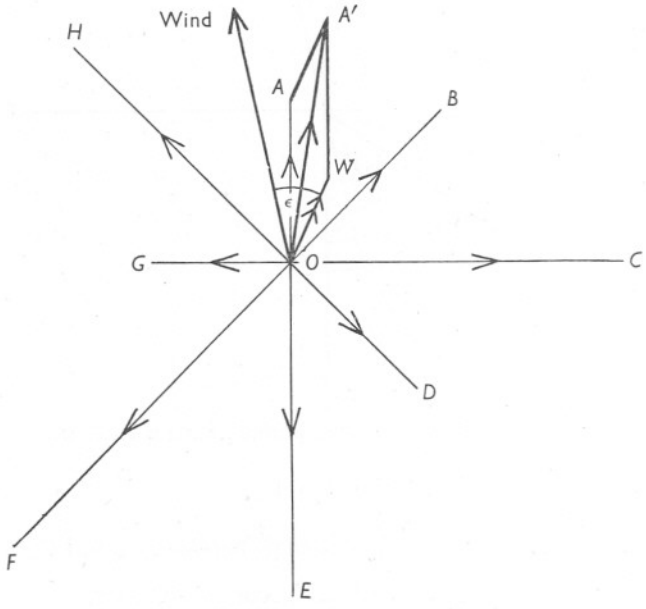
$$V_w \text{ (m.p.d.)} = 0{\cdot}35\ V \text{ (m.p.h.)}, \tag{D}$$

or, water movement = $1\frac{1}{2}\%$ of wind movement.

Rearranging (B):
$$\epsilon = \rho - \phi - \cos^{-1}\frac{(V_R^2 + V_w^2 - V_i^2)}{2V_R.V_w}. \tag{E}$$

For a number of observations, the mean ϵ was found to be 12° to the right of the wind. This is in accordance with Ekman's theory and supports, to some degree, the validity of the ideal R.W.M. curve.

It may be argued that the daily R.W.M. does not exist as a single vector, but is the resultant of several vectors each of which are acted upon by the wind. This is, of course, a fact, but reference to Text-fig. 9 will show that the foregoing analysis is not materially affected.



Text-fig. 9. Effect of wind on residual water movement components.

Consider a number of water movements acting at a point O. If the R.W.M. be **OR**, then

$$\mathbf{OR} = \mathbf{OA} + \mathbf{OB} + \mathbf{OC} + \ldots + \mathbf{OH}.$$

Now consider another water movement, **OW**, produced by the wind, acting in conjunction with each. Then

$$\begin{aligned} \mathbf{OA} + \mathbf{OW} &= \mathbf{OA}' \\ \mathbf{OB} + \mathbf{OW} &= \mathbf{OB}' \\ &\cdots \\ \mathbf{OH} + \mathbf{OW} &= \mathbf{OH}' \end{aligned}$$

If the new R.W.M. be represented by **OR′**, then

$$\begin{aligned} \mathbf{OR}' &= \mathbf{OA}' + \mathbf{OB}' + \ldots + \mathbf{OH}' \\ &= (\mathbf{OA} + \mathbf{OW}) + (\mathbf{OB} + \mathbf{OW}) + \ldots + (\mathbf{OH} + \mathbf{OW}) \\ &= \mathbf{OR} + n.\mathbf{OW}. \end{aligned}$$

Thus the new R.W.M. is equivalent to the old resultant acted upon by a vector of magnitude n.**OW**.

However, since **OA**, **OB**, etc. do not act for the whole time, but only for times (say) t_a, t_b, etc.

$$n = \frac{t_a + t_b + \text{etc.}}{\text{Total time}} = 1.$$

Therefore, $\mathbf{OR}' = \mathbf{OR} + \mathbf{OW}$.

Directly related to the matter of considering the wind as producing a water movement within an area of sea already possessing its own intrinsic movement is the finding of Carruthers (1941). In the experiments cited, the area concerned was one having tidal streams of continually varying magnitude and direction. It was established beyond any doubt that the winds affected the water movements to a marked degree, not only on the surface but to a depth of several feet. The effect was such that, given a persistent wind from any quarter, the tidal streams were found to produce an overall movement roughly downwind.

Summary

A review is given of the results obtained from upwards of 600 days of current measuring at the Seven Stones lightvessel during 1939–41. From the plotted observations, an attempt is made to deduce the association between the total daily water movement, irrespective of direction, the residual daily water movement or current, and the mean local residual wind.

The average residual water movement over the whole period was $2\frac{1}{2}$ m.p.d. towards east-south-east. Statements made by earlier authors regarding the water circulation in adjacent areas are examined, and reconciliations are suggested where they seem to conflict with this finding.

An endeavour is made to correlate the wind and water movement mathematically.

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EXPLANATION OF PLATES

PLATE I

Water movement and wind at the Seven Stones Lightvessel, July 1939 to July 1940.

PLATE II

Water movement and wind at the Seven Stones Lightvessel, July 1940 to April 1941.

Key to Plates I and II

A: Average total daily water movement during the month, in miles per day.
B: Average residual daily water movement and direction (vector resultant) during the month, in miles per day.
C: Average of mean residual daily wind and direction (vector resultant) during the month, in miles per hour.
D: Full and new moon.
E: Total daily water movement, in miles per day, i.e. the sum of the water movements in all octants, regardless of direction. The thick line represents the recorded observations; the thin line is the 'ideal' curve.
F: Direction of residual daily water movement, i.e. the vector resultant in all octants.
G: Residual daily water movement, in miles per day, i.e. the resultant of the water movements in all octants. The thick line represents the movement calculated from the recorded observations; the thin line is the 'ideal' curve.
H: Mean daily residual wind force and direction, in Beaufort scale. The full line represents northerly and southerly winds; the pecked line easterly and westerly winds.
J: Calendar; the alternate black and white bars represent weeks of seven solar days.

Notes. (i) All miles are '*sea* miles' of 6080 ft. (ii) All days are *lunar* days of 24 hr. 50 min., unless otherwise stated. (iii) All directions are *magnetic*.

PLATE III

Components of water movements at the Seven Stones Lightvessel, July 1939 to July 1940.

PLATE IV

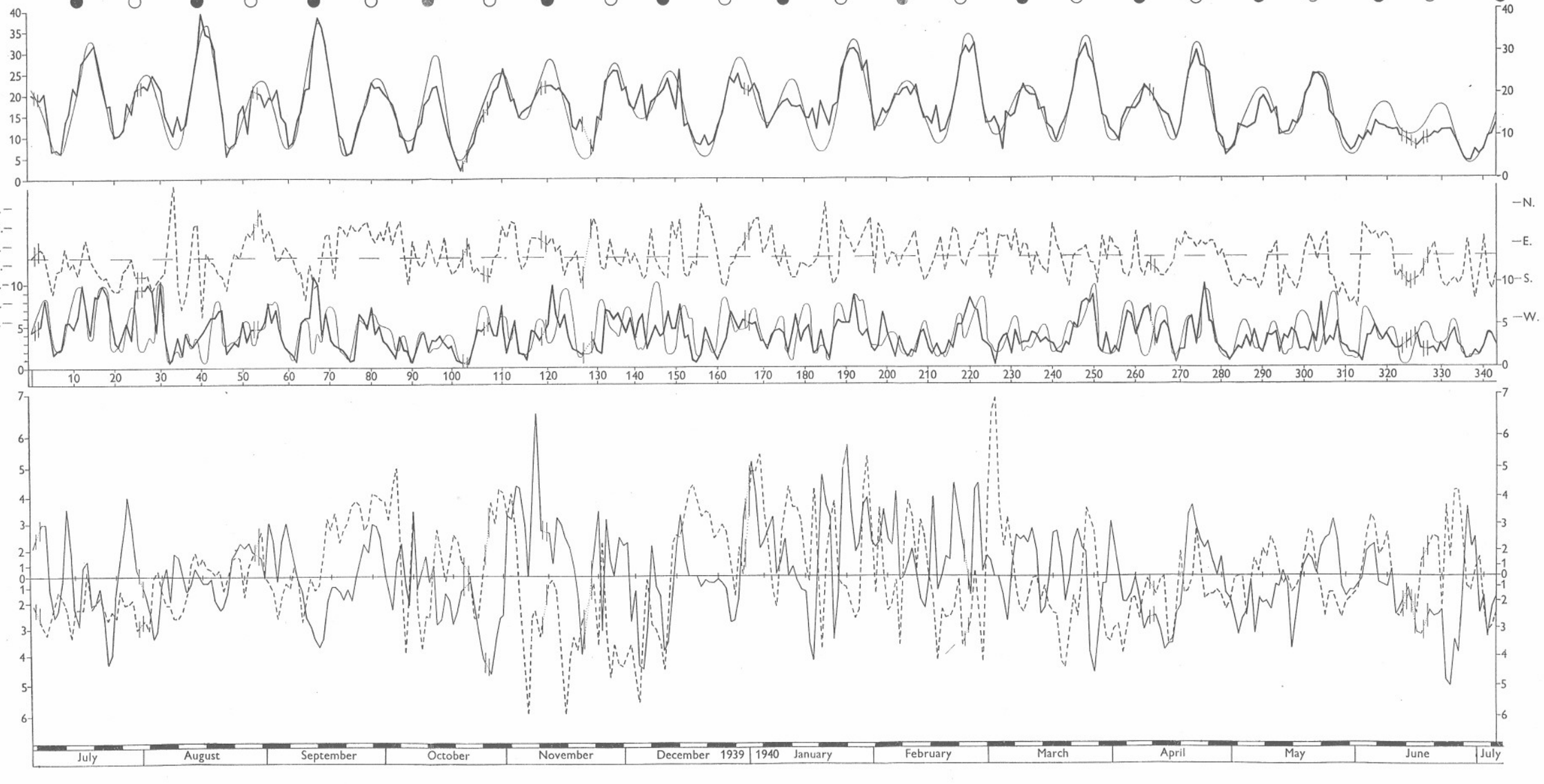
Components of water movements at the Seven Stones Lightvessel, July 1940 to April 1941.

Key to Plates III and IV

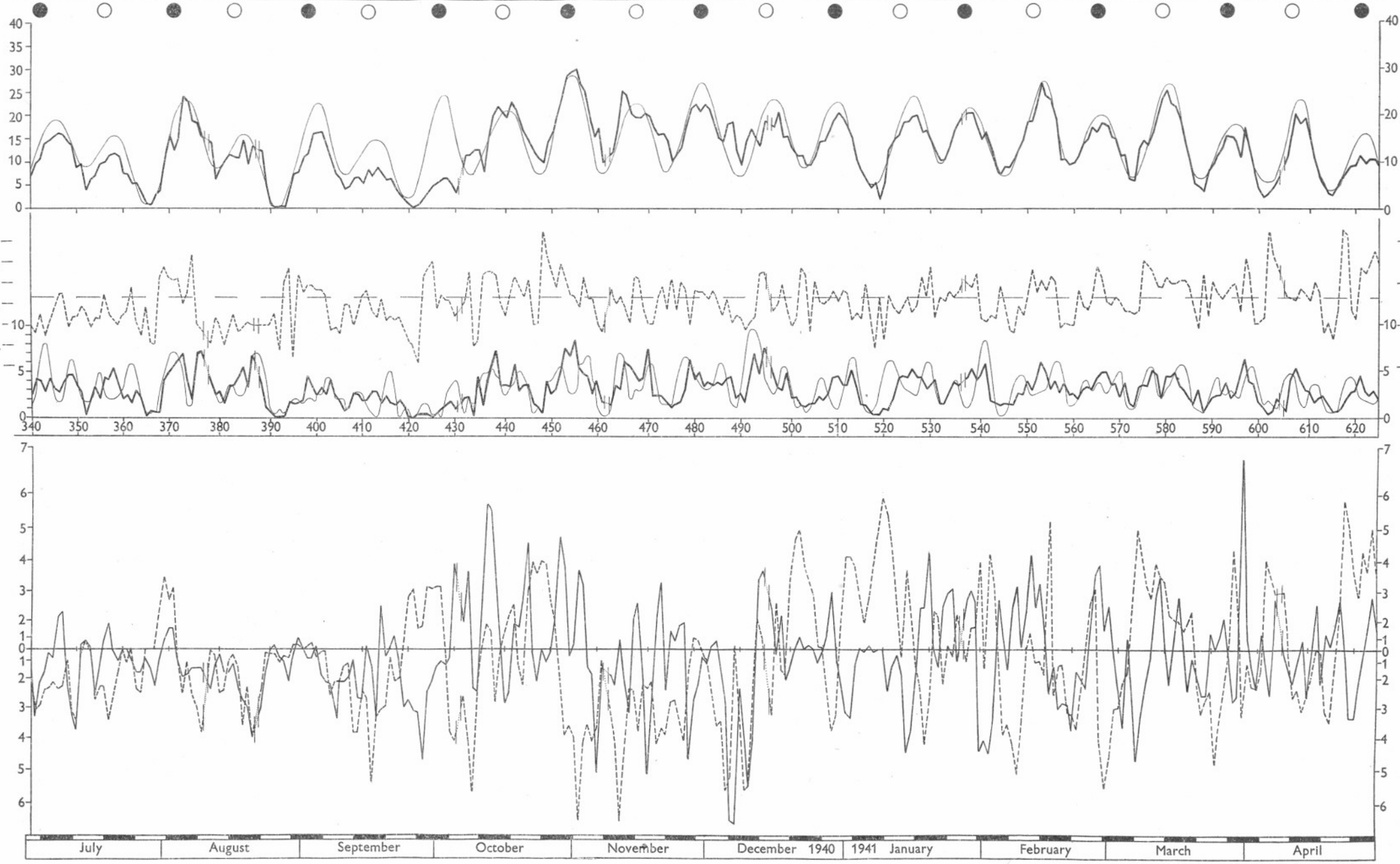
K: North + south component of total daily water movement, in miles per day.
L: East + west component of total daily water movement, in miles per day.
M: North-south component of residual daily water movement, in miles per day.
N: East-west component of residual daily water movement, in miles per day.

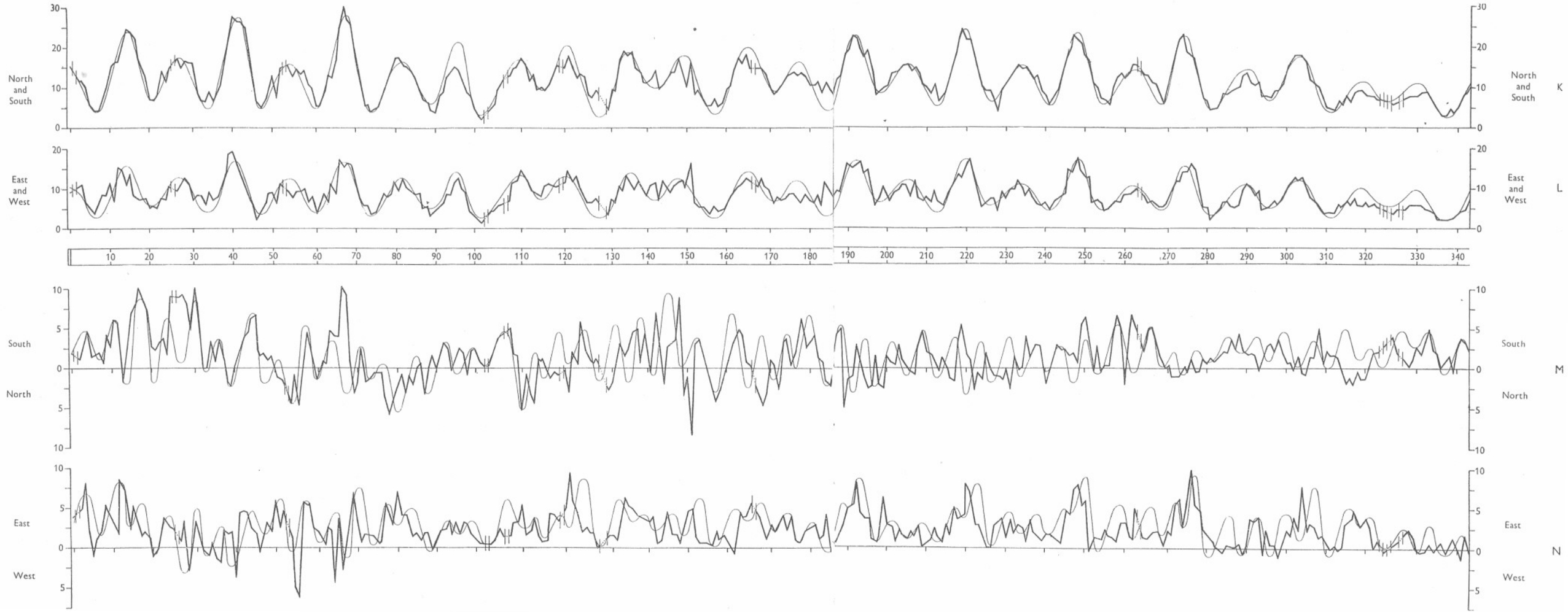
Notes. (i) All miles are '*sea* miles' of 6080 ft. (ii) All days are *lunar* days of 24 hr. 50 min. (iii) All directions are *magnetic*. (iv) The thick lines represent the movements calculated from the recorded observations; the thin lines are the 'ideal' curves.

		18·02		19·54		18·39		14·17		18·49		16·97		19·35		18·83		17·47		16·76		14·48		9·47	
A	Water movement — *Total*	4·86	S. 37° E.	2·99	S. 31° E.	2·67	S. 81° E.	2·09	S. 63° E.	3·21	S. 79° E.	2·55	S. 60° E.	2·57	S. 79° E.	2·73	S. 73° E.	2·82	S. 63° E.	3·32	S. 58° E.	2·30	S. 37° E.	1·56	S. 50° E.
B	Water movement — *Residual*	6·20	N. 88° W.	1·04	N. 48° W.	4·98	S. 89° E.	5·01	N. 45° E.	11·50	S. 49° W.	2·84	N. 12° W.	9·70	S. 47° E.	5·63	S. 17° W.	1·08	South	4·66	N. 69° W.	1·96	N. 8° W.	4·82	N. 22° E.
C	Wind	●	○	●	○	●	○	◐	○	●	○	●	○	●	○	◐	○	●	○	●	○	●	○	●	○



A	Water movement	*Total*	8·72		11·70		7·02		15·15		18·80		15·41		13·75		15·18		13·39		9·34	
B		*Residual*	1·97	S. 18° E.	2·13	S. 25° E.	1·50	S. 38° E.	2·30	S. 85° E.	3·12	S. 48° E.	2·74	S. 50° E.	2·62	S. 54° E.	2·48	S. 55° E.	2·50	S. 79° E.	1·46	S. 75° E.
C	Wind		5·50	N. 60° W.	4·62	N. 39° W.	6·00	N. 32° W.	4·70	S. 6° W.	12·30	N. 79° W.	4·83	N. 42° W.	7·40	N. 86° E.	4·44	N. 85° W.	1·15	N. 54° E.	3·79	N. 75° E.




North and South
East and West
South North
East West
K
L
M
N
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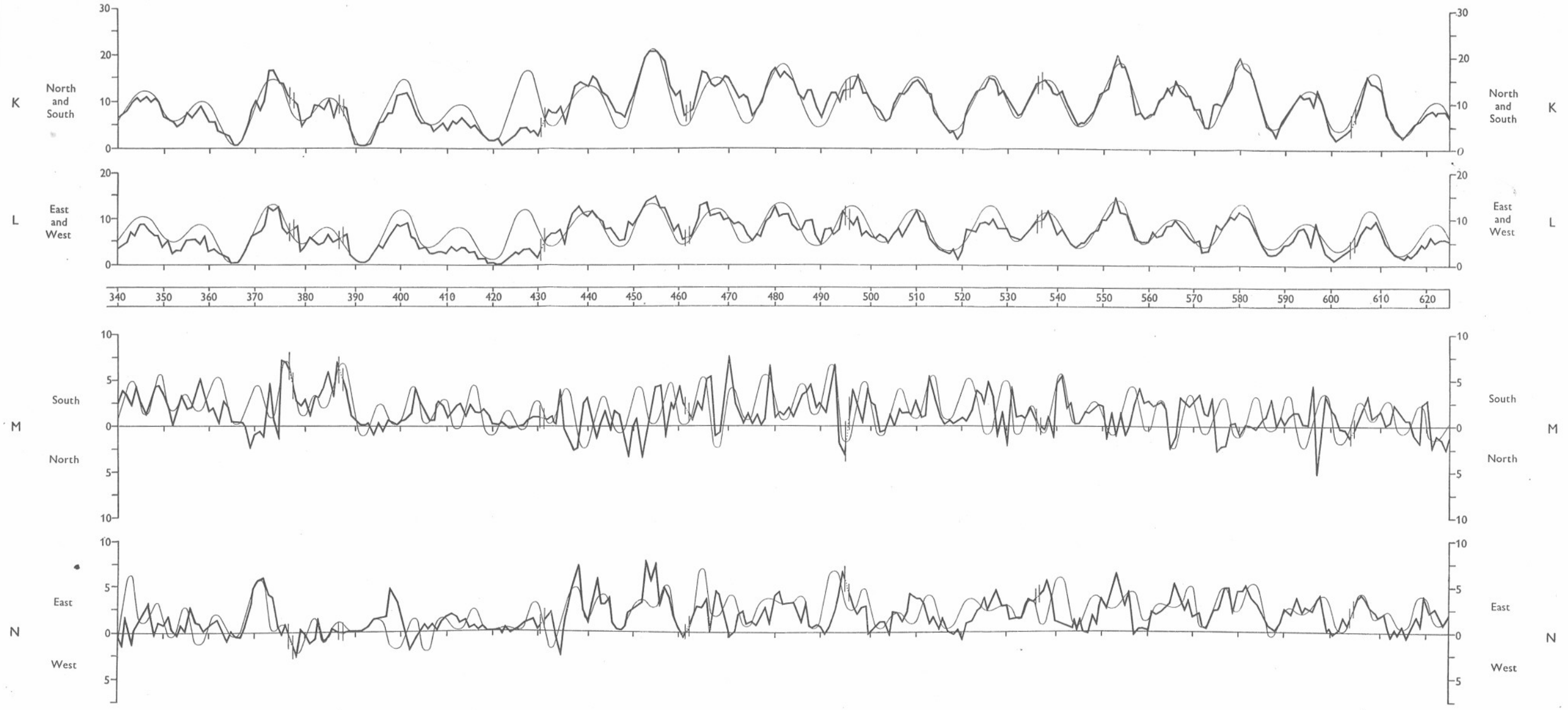
190 200 210 220 230 240 250 260 270 280 290 300 310 320 330 340


K
North and South
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SEASONAL CHANGES IN THE PHYTOPLANKTON AS INDICATED BY CHLOROPHYLL ESTIMATIONS

By W. R. G. Atkins, Sc.D., F.R.S. and Mary Parke, D.Sc.

From the Plymouth Laboratory

Introduction

When studying the suspended matter in sea water Armstrong & Atkins (1950) filtered carboys of sea water taken from the surface at the International Hydrographic Station, England No. 1, about 10 miles south-west of the Eddystone. The samples averaged 22 l., filtered through a Whatman No. 50 paper, 11 cm. diameter, on a Buchner funnel with the water pump. The first 10 l. was always re-filtered. The results for the suspended matter were shown to be only about 4% less than when filtration was through 'Gradocol' collodion membranes of average pore diameter 1·09 micron. The removal of the phytoplankton should thus be more complete than when the finest bolting silk is used, for according to Harvey (1945) the mesh apertures of the latter average $42 \times 50\,\mu$ when wet and swollen. Since there are many flagellates and non-motile forms less than $5\,\mu$ in length it is obvious that the net may let through much that is retained by the cellulose or collodion filters.

The suspended matter thus obtained gave us the opportunity of following the changes in the phytoplankton in the surface water, by extracting the pigments with acetone—a method introduced by Kreps & Verjbinskaya (1930), and by Harvey (1934*a*) with more accurate measurement of the volume filtered by the nets. Riley (1938–41) filtered surface samples through paper, as did Graham (1943). Krey at Kiel (1939) used 'cella'—presumably collodion—filters for water from 0–30 m. Cole & Jones (1949) also have made plankton counts using collodion filters.

Before proceeding it is appropriate to consider the known plastid pigments of the phytoplankton and their abundance in typical species.

The Plastid Pigments of the Phytoplankton

In recent years these have received much attention. According to Rabinowitch's summary (1945), the chlorophylls constitute about two-thirds of the total plastid pigments, the remaining third consisting of carotenoids, of which one-fifth contains orange red carotenes, polyene hydrocarbons, and four-fifths consists of their oxygen derivatives, namely yellowish xanthophylls. The amounts vary with species and environment, but the relative proportions are fairly constant in growing cultures. Chloroplasts often appear yellowish

or brown, rather than green, apparently due to the physical state of the plastid rather than to the preponderance of the yellow pigments.

According to Manning & Strain (1943), diatoms contain chlorophyll *a* and a little chlorophyll *c*, with carotenes and xanthophylls, mainly fucoxanthin, also diadinoxanthin and some diatoxanthin. The diatoms and brown algae have similar chlorophylls and xanthophylls. Pace (1941), however, did not find fucoxanthin in *Nitzschia closterium*, but it has been proved by Whitford (1947) to exist in the Chrysophycean *Phaeosphaera perforata*. Calculated on the dry weight of *Nitzschia closterium*, Pace found 2·17% chlorophyll *a* and 0·155% chlorophyll *b*, also β-carotene, cryptoxanthin, lutein, isolutein and two xanthophylls. The chlorophyll-carotenoid ratio was 3·77.

The presence of the xanthophylls and carotenes, and sometimes of other pigments, makes direct colorimetric comparisons useless for the estimation of the mixed chlorophylls. Of these, Strain (1949) summarizes the absorption-band measurements, and for chlorophyll *a*, $C_{55}H_{72}O_5N_4Mg$, reports principal bands at 440 and 660 mμ; for chlorophyll *b*, $C_{55}H_{70}O_6N_4Mg$—which may constitute 20–40% of the chlorophyll of the Chlorophyta—the bands are at 480 and 650. In red algae and diatoms, however, Manning & Strain (1943) found that *b* was less than 0·3% of *a*. The position of the bands varies somewhat according to the solvent used.

The formula and molecular structure of *c* is unknown, but it is found in small amounts along with chlorophyll *a* in diatoms, dinoflagellates and brown algae; the absorption maxima, in ether, are given as 446, 579·5 and 627 mμ (Strain, Manning & Hardin, 1944).

Chlorophyll *d* is found in very small amounts, with *a*, in red algae, though up to 25% is *d* in *Rhodochorton rothii*. It contains magnesium, but its formula is unknown. In ether its principal bands are at 445 and 686 mμ, and at about 457 and 698 mμ in methanol (Manning & Strain, 1943).

The Colorimetric Estimation of Chlorophyll and the Preparation of Extracts of Plastid Pigments from Phytoplankton

On viewing acetone solutions of a bought dry solid chlorophyll and of various extracts from algal cultures and sea water with a hand spectroscope, the absorption in the red gave a well-marked band. By inserting the Schott RG1 filter a spectrum of longer wave-length than 600 mμ is obtained, between which and the end of the visible red the band may reduce the light very markedly, and so permit of colorimetric comparisons without interference from the yellow pigments. A Kober colorimeter (by Klett) was used for this work.

There is, however, an uncertainty in the composition of chlorophyll powder, such as that from the British Drug Houses. Nettle leaves may be used as a

source. Though there are a number of chlorophylls and these have labile isomers the net effect of such changes as occur appears to be of no great importance as regards the absorption bands in the red; such small shifts in the bands would not seriously affect the colorimetric comparisons. Care should be taken to avoid errors due to evaporation of the acetone during the comparisons.

The aqueous acetone extracts from pure cultures of species selected from the phytoplankton (Parke, 1949) were thus compared among themselves and with chlorophyll standards. The cell numbers were counted in the haemocytometer field. Table 1 shows the numbers of algal cells from active cultures of measured average size which yield 1 mg. of chlorophyll.

The solvent used was of 'analytical reagent' quality and was added to the wet filter-paper on which the algal cells had been collected and washed with distilled water. If necessary, to keep in solution the salts of sea water liberated from the cells, a little distilled water was added till the cloudiness in the acetone vanished.

The chlorophyll-bearing cells, from cultures or from sea water, vary in size down even to one micron in diameter, as we have found recently. They are accordingly too small to be retained quantitatively on filter-paper, such as Whatman No. 42, intended for the finest precipitates. The filtration of large volumes on the 4 cm. diameter collodion membranes is very tedious and the membranes have to be changed frequently as they become choked. Centrifuging, even with tubes containing 250 ml. is unsatisfactory, and slow, though according to H. W. Harvey (private communication) dead cells are deposited better than are living. The simplest method is to add 5 ml. of a 1% solution of potassium aluminium sulphate crystals to about a litre of culture or sea water. The samples are usually at about pH 8, or over. The acid alum solution brings this nearer to neutrality; the reaction should be tested with bromthymol blue. If it is necessary to add more alum, for a very thick culture, the reaction may go slightly below neutrality, pH 7. If it is much below—in a fresh water—it can be restored by adding a little sodium bicarbonate. This is not done to precipitate the aluminium hydroxide which comes down from pH 3·5–5, but to avoid any possible effect of acid on the pigments. According to Atkins (1922) the reaction of algal cells is close to neutrality, whereas land plants are often markedly acid. Trouble arises more frequently in dense cultures through the reaction of the water being too alkaline, pH 9 or over. The aluminium does not then form a good floc, but either remains in solution or in a very fine suspension. The alkalinity may be reduced by passing in carbon dioxide, or by the cautious addition of very dilute acetic acid, till the pH is brought slightly below 7, and a yellowish green is given with bromthymol blue. This should be done before the addition of the alum solution, and it is advisable to allow the floc, with algae, to settle in weak light before filtration. It is often possible to pour off liquid over the floc, thus reducing time of filtration. Filtration

may then be effected on an 11 cm. Buchner funnel, with the filter pump. The rate should be low at first till the aluminium hydroxide floc has sealed the pores, when the suction may be increased. Unless too much alum has been added filtration proceeds at a reasonable rate. Algae from cultures are thus obtained for pigment studies, or it is possible to get the phytoplankton from 1 or 2 l. of sea water to follow the rate of production in the sea; smaller volumes should suffice when plankton is abundant.

Algae carried down in the transparent floc are readily seen under the microscope. *Dicrateria inornata* was perfectly visible and only by very careful adjustment of the light was it possible to discern the floc. Cells of *Chlamydomonas* were observed to be actively motile after two filtrations with too little alum or with too alkaline a solution for effective flocculation.

The weight of the aluminium hydroxide floc which is effective is amazingly small; a 1% solution of potassium aluminium sulphate crystals contains only 0·82 mg. of the hydroxide in 5 ml. Yet in 100 ml. of sea water this gives a marked turbidity in a few minutes and a sediment about 4 mm. in height in the measuring cylinder. Settling is naturally slower in a litre vessel, and as much as 15 ml., namely about 2·5 mg., may give with a culture a slowly filtering slime.

The chlorophyll content of pure algal cultures

A *Gymnodinium* culture contained 144 cells/mm.^{3}, (144 million/l.) The cell numbers per milligram of chlorophyll were obtained as follows. A freshly diluted chlorophyll solution contained 16·0 mg./l. Of this 50·0 matched 35·8 of a *Gymnodinium* extract, as read on the Kober scale, using filter RG 1. The extract, therefore, contained 22·3 mg./l., and as its volume was 27·6 ml., which had been used in successive small portions to extract the algae filtered from 250 ml. of culture, the culture contained 2·46 mg./l., in 144 million cells. So 58·5 million cells contain 1·0 mg. The results for a number of species are given in Table I which include determinations on three species of diatom by Krey, Pace and Graham.

Differences in the volumes of the cells appear to account for the major differences in the milligram counts. One may not appreciate that, for example, the average volume of *Coscinodiscus centralis* is fourteen thousand times that of *Dicrateria inornata*.

To separate the pigments we tried aluminium oxide (Kahlbaum) specially prepared for such work. A blue green chlorophyll band was retained near the top; below this came one, or usually two, bands, orange red, and presumably carotenes. The liquid which came through was yellowish and appeared to be a xanthophyll, or several mixed perhaps. The above were obtained with the pigments in petroleum ether b.p. 40–60° C. after evaporation of the acetone on a water-bath. Whitford (1947) has reviewed previous work; he separated

the pigments on a starch column and with suitable solvent mixtures obtained bands for chlorophyll and two xanthophylls, the carotene coming through.

The separation of the chlorophylls can thus be readily effected and could be used as a check on the colorimetric comparison in the red.

TABLE I. NUMBER OF CELLS FROM ACTIVE ALGAL CULTURES WHICH YIELD 1 MG. OF CHLOROPHYLL. COLOUR REFERS TO EXTRACTS

	Size		Mg. count
	Mean (μ)	Range (μ)	
Chlorophyceae			
Order VOLVOCALES			
Chlamydomonas I, pure green. *By* F. Gross	10×5	8×4–12×6	202×10^6
Chlamydomonas III, pure green. *By* Mrs Föyn	8×6	6×4–12×8	109×10^6
Order CHLOROCOCCALES			
Chlorella I, yellowish green	$3{\cdot}5d$	$2{\cdot}5$–$4{\cdot}5d$	2400×10^6
Chrysophyceae			
Order CHRYSOMONADALES			
Dicrateria inornata Parke, yellowish green	$4d$	3–$5{\cdot}5d$	563×10^6
Bacillariophyceae			
Order CENTRALES			
Coscinodiscus centralis Ehr., yellowish green. *By* R. Bainbridge	$110d \times 50t$	$105d \times 35t$ / $140d \times 60t$	74×10^3
Chaetoceros gracilis Schütt (Krey, 1939)	$8 \times 6b$	—	286×10^3
C. vanheurckii Gran (Graham, 1943)	24–$28w$	—	170×10^3
Thalassiosira gravida Cleve, yellowish green	$22d \times 12t$	$20d \times 10t$–25×14	123×10^6
Order PENNALES			
Nitzschia closterium (Ehr.) W.Sm. forma *minutissima*. *By* Allen and Nelson; pure green	30×3–$8 \times 3b$	25×3–35×4	743×10^6
N. seriata Cleve (Pace, 1941)	100×6	—	$1{\cdot}25 \times 10^6$
Cryptophyceae			
Order CRYPTOMONADALES			
Hemiselmis rufescens Parke, almost pure green with insoluble red	$7 \times 4 \times 3$	$4 \times 3{\cdot}5 \times 2$–$8{\cdot}5 \times 5 \times 3$	3260×10^6
Dinophyceae			
Order DINOFLAGELLATA			
Gymnodinium sp. very close to *G. simplex*, yellowish green	15*	10–22	58×10^6

Notes: *b*, body, without spines; *d*, diameter; *t*, thickness; *w*, width of cell; * sphaeroidal; *By*, isolated by and maintained since at Plymouth.

THE SEASONAL CHANGES IN THE PHYTOPLANKTON

These have for many years been studied by the changes in concentration of phosphate and other nutrient salts. A number of isolated measurements have been made, as mentioned previously, but Harvey (1934*b*) followed the changes at a station, L 4, inside the Eddystone using a net filtering measured volumes of water and an arbitrary colorimetric scale compounded with potassium chromate and crystalline nickel sulphate.

There is, however, an uncertainty in the number of molecules of water of crystallization even in the 'analytical reagent' quality. The figure is between $6H_2O$, taken by Harvey, and $7H_2O$. The uncertainty is 6%. A solution of

known nickel content may, however, be prepared by dissolving nickel wire. The nickel chromate standards have been considered to be a tolerably good colour match for acetone extracts of plankton. We are indebted to Dr Harvey for kindly comparing an extract from plankton filtered from a carboy taken on 30 November 1949 (Table II). This he assessed as corresponding to 10–15 units in 10 ml., but the extract was far more yellow than the standard, so a closer match was not possible. Viewing the tubes through the filter RG 1, the sample was rather under 8 units, possibly as low as 6 units. Taking into account the volumes of extract and of water this corresponds to 1·39–1·04 mg. of chlorophyll/m.^{3}, using Harvey's value, based on Guthrie's work, of 0·3 μg. of chlorophyll/unit. The result found by comparison with a chlorophyll standard with the RG 1 filter was 1·43 mg./m.^{3}. It seems possible that the yellower colour of the November extract may have been due to the presence of a larger number of flagellates than are ordinarily found in the net plankton to estimate which the colour units were devised.

Riley (1938) estimated chlorophyll from algae by comparison with a chlorophyll prepared by Dr C. G. Deuber of Yale. He separated the chlorophyll from the yellow pigments by saponifying it and removing the carotenoids in ethyl ether. He found 1 unit of the Harvey scale to correspond to 0·88 $\pm$ 0·01 μg. chlorophyll. There was good agreement between the dry organic matter and the chlorophyll content, but only in the upper layers of the water. Paper filtration (Whatman No. 44) was found to give up to seven times as much chlorophyll extract as did bolting silk, and use of collodion membrane produced about 6% more than did paper in Long Island Sound (1941 *a*). Using the same method for removing the yellow pigments Riley tabulated Harvey units against chlorophyll for his Long Island work and the mean showed 0·26 μg./unit. This is much below his earlier value, but agrees tolerably well with Harvey's estimated value 0·3 μg., which seems to accord reasonably well with the single comparison already quoted in this paper when the red filter was used. Riley also records that 17·44 mg. chlorophyll corresponded to 600 mg. dry organic matter, namely the chlorophyll was 2·91%. This is close to Pace's value 2·32% for the sum of chlorophyll *a* and *b* in *Nitzschia closterium*, in which a lower value is to be expected as the analysis refers to a silica-bearing organism only.

The extracts made during 1948 and 1949 from suspended matter filtered on collodion from water from Station E 1 (which was selected to be beyond the range of fluctuation due to land drainage) were compared among themselves without the red filter and, using the filter, with chlorophyll solutions of suitable strength. The results are shown in Table II, together with the sea temperature, the suspended inorganic matter and ash after incineration (S.I.M.A.) and the percentage of silica contained in the latter, in order to see whether any relation existed between these and high chlorophyll values. No such relation is, however, observable. Thus 2020 and 1190 mg./m.^{3} S.I.M.A. both have 44%

of silica and correspond respectively to 1·05 and 1·43 mg. of chlorophyll/m.^{3}. Furthermore, 490 mg./m.^{3} S.I.M.A. had 43% of silica, but only 0·17 mg./m.^{3} of chlorophyll.

In 1948 the chlorophyll content was much as would be expected from the phosphate studies, with a well-marked maximum in April, and a lesser crest in October, separated by the year's minimum in mid-August. As always, a larger number of observations would have been better. For 1949 the April figure observed was only half that of 1948, but this was, after a drop, followed by a large outburst in June and a high maximum in July, leading, after fluctuations to a late November outburst rather greater than that observed in April. It must be remembered, however, that these observations are on

TABLE II. CHLOROPHYLL CONTENT, WITH ACCOMPANYING SURFACE TEMPERATURE, SUSPENDED INORGANIC MATTER AND ASH (S.I.M.A.), AND SILICA CONTENT OF THE LATTER

Chlorophyll and S.I.M.A in mg./m.^{3} sea water (parts per thousand million). Silica in percentage of S.I.M.A.

DATE 1948	Chlorophyll	°C	S.I.M.A.	SiO_2%	DATE 1949	Chlorophyll	°C	S.I.M.A.	SiO_2%
Jan.	—	—	—	—	5 Jan.	0·61	11·2	760	21
11 Feb.	—	10·1	—	—	1 Feb.	0·86	10·2	1600	26
10 Mar.	0·92	9·3	—	—	1 Mar.	0·58	10·1	740	21
12 Apr.	2·84	10·2	—	—	13 Apr.	1·37	9·9	800	37
10 May	—	12·4	—	—	9 May	0·57	11·5	800	31
9 June	0·73	12·6	1140	54	9 June	3·40	13·9	1360	52
15 July	0·82	14·7	2770*	25	8 July	4·30	16·5	1880	41
Aug.	—	—	—	—	8 Aug.	0·36	15·3	450	18
16 Aug.	0·17	15·4	890	43	17 Aug.	1·05	16·0	2020	44
31 Aug.	—	16·8	—	—	29 Aug.	0·51	19·4	800	42
4 Oct.	1·22	14·7	490	44	6 Oct.	—	16·4	590	43
30 Nov.	0·30	13·2	950	17	8 Nov.	1·43	14·0	1190	44

* 70% of this was calcium carbonate probably precipitated out of the water.

surface water and there is now evidence from several sources that the surface is the seat of a large amount of suspended matter. None the less, the surface outbursts in June and July are remarkable.

When these figures 0·17–4·3 mg./m.^{3} chlorophyll are compared with values recorded by other workers, it is better to neglect the early net-filtered results, which are clearly low. The numerous measurements by Riley, filtering through the finest paper, would be low if the small flagellates were an important constituent. For surface samples from the North Atlantic he gives (1939) as mean 1·2 and maximum 3·6 mg./m.^{3}, with 5·6 and 27·2 for George's Bank (1941*b*) also 17·4 and 62·0 for Long Island Sound. Riley has recently (1949) given an extensive review of the subject. For La Jolla, Graham (1943) gives 0·77 and 1·86 maximum. His results appear to be low, as he reports no chlorophyll found in a sample in which *N. seriata* constituted 83% of the catch. His method of estimating the chlorophyll avoids errors due to the yellow pigments, for he used a visual spectrophotometer set at 668 mμ. with slit width

0·4 mm. Krey (1939) used a 'cella' (collodion) filter and for 0–30 m. at Kiel got a mean of 2·00 mg./m.^{3} and a maximum of 5·00.

It has been customary for biologists to count microscopic organisms on the ruled squares of the Thoma haemocytometer, the side of the ruled area being 1 mm. and the depth one-tenth thereof. The volume is one-tenth of a cubic millimetre. It may serve to show how sparsely populated sea water is by recalling that the simultaneous utilization of all the phosphate present at the winter maximum in the English Channel suffices to produce *N. closterium* at a density of 2·7 per haemocytometer field (Atkins, 1923). One milligram of phosphorus suffices for 2050×10^6 cells of *N. closterium* var. *minutissima*. When compared with the production of 743×10^6 cells for 1 mg. of chlorophyll (Table I) we see that the chlorophyll to phosphorus ratio is 2·76 in this species, weight for weight.

TABLE III. NUMBER OF CELLS IN A HAEMOCYTOMETER FIELD DERIVABLE FROM THE OBSERVED MAXIMUM 4·3 MG. OF CHLOROPHYLL PER CUBIC METRE, ASSUMING ALL TO BE OF ONE SPECIES AS LISTED

Species	Cells per field
Coscinodiscus centralis	$0{\cdot}32 \times 10^{-4}$
Thalassiosira gravida	0·053
Nitzschia closterium var. *minutissima*	0·32
Dicrateria inornata	0·24
Isochrysis galbana	0·27
Hemiselmis rufescens	1·40
Chlamydomonas I	0·087
Chlamydomonas II	0·047
Chlorella I	1·03
Gymnodinium sp.	0·025
Human red blood corpuscles	450×10^3

Table III shows the number of cells per field which would be produced if the maximum amount of chlorophyll recorded in Table II, namely 4·30 mg./m.^{3}, were all produced by the single species listed. It may be seen that, for *Nitzschia*, the observed maximum is only about one-eighth of the possible, were the winter maximum of phosphorus to give one crop without any intermediate grazing down; thus in a pure culture the chlorophyll produced by water of this composition would be about $4{\cdot}3 \times 8{\cdot}4$, namely 36 mg./cm.^{3}.

The figures in the Table indicate the difficulty of making direct counts.

SUMMARY

The pigments of pure cultures of algae, of known number per volume, have been extracted with aqueous acetone after separation by filtration. The extracts were compared in a Kober colorimeter with standard solutions of a preparation of bought chlorophyll. The number required to give 1 mg. of chlorophyll was thus determined.

The algae studied included: Chlorophyceae, two species of *Chlamydomonas* and one *Chlorella* not yet described; Chrysophyceae, *Dicrateria*

inornata Parke; Bacillariophyceae, *Coscinodiscus centralis* Ehr., *Thalassiosira gravida* Cleve and *Nitzschia closterium* (Ehr.) W.Sm. forma *minutissima*; Cryptophyceae, *Hemiselmis rufescens* Parke; Dinophyceae, *Gymnodinium* sp. The numbers per milligram of chlorophyll varied from 74×10^3 for *Coscinodiscus* to over 3200×10^6 for *Hemiselmis rufescens*. Of the nine cultures, six were between 50 and 750×10^6. The volume of the cell is the decisive factor in the milligram count.

Filtration of these and of sea-water samples was made through either collodion membranes of known average pore diameter, supplied by courtesy of the Director of the Department of Pathology, St Mary's Hospital, London, or through the finest grade of Whatman filter-paper. To retain the algal cells on paper about 5 ml. of a 1% solution of alum was added. The transparent floc serves to entangle the cells. They are thus ready for examination under the microscope, and motile organisms are slowed down or brought to rest. The floc will settle down in a cylinder. The water should be close to pH 7 before addition of the alum.

Colorimetric estimation of chlorophyll can be made even with extracts which are yellowish green or yellow by using a red colour filter Schott RG1 cutting off close to 0·6 μ, which is placed over the eyepiece of the colorimeter.

The seasonal changes in the chlorophyll content of water in the English Channel, about 20 miles off Plymouth, were followed from March 1948 to November 1949 inclusive, by filtering surface water. The spring maxima in April were respectively 2·84 and 1·37 mg./m.^{3}, and the autumn maxima 1·22 and 1·43. The yearly minima were in August, 0·17 and 0·36. But most unexpectedly June and July 1949 gave 3·40 and 4·30 respectively. Such figures are comparable with those of Krey, for Kiel, 2 mg. mean and 5 mg. maximum, and of Riley, for North Atlantic, 1·2 mean and 3·6 maximum.

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THE BIOLOGY OF *ASTERIAS RUBENS* L. II. PARASITIZATION OF THE GONADS BY THE CILIATE *ORCHITOPHRYA STELLARUM* CÉPÈDE

By H. G. Vevers, M.A., D.Phil.

Zoologist at the Plymouth Laboratory

(Plate I)

CONTENTS

Introduction

The astomatous holotrich ciliate, *Orchitophrya stellarum*, was originally described and named by Cépède (1907*a*, *b*), who found it in the gonads of only three males out of a total of over 6000 *Asterias rubens* of both sexes. These starfishes were taken by him from the Boulogne and Wimereux area. There was no trace of the parasite in any ovaries, but he noticed that it caused a partial and direct castration of its male host. *Orchitophrya* was found by Piatt (1935) in the testes of *Asterias forbesi* in Long Island Sound, where Burrows (1936) observed that the percentage of parasitized males varied from 1 to 20% according to the locality. Burrows also found that a small number of the female starfishes (about 1%) were infected. Smith (1936) recorded the parasite in the ovaries of about 25% of the females of *A. vulgaris* from oyster beds in Malpeque Bay, Prince Edward Island. Eggs taken from these infected ovaries appeared normal and were fertilizable.

I am indebted to Mr Y. R. Tripathi for assistance in the original identification of the parasite, and to Dr J. S. Alexandrowicz for making the photomicrographs.

Distribution of the Parasite off Plymouth

During the years 1946–50 large numbers of *A. rubens* have been trawled from different localities in the Plymouth area. In the course of investigations on the reproductive cycle in these localized populations, smears have been taken

from the gonads of each starfish and transverse sections cut of a number of selected gonads. In March 1947 trawling was commenced on the Outer Grounds, to the south and south-west of Eddystone. The differences between the starfish from this area and those from the more northerly Rame-Eddystone Grounds have already been described (Vevers, 1949). *Orchitophrya stellarum* was found in a varying percentage of the males from all the six trawl hauls taken in spring 1947 on the Outer Grounds. In the early months of the years 1948, 1949 and 1950 the parasite was again found in male starfishes from these Grounds and also in a population of *Asterias rubens* trawled from Asia Shoal, Plymouth Sound. The parasite has never been found in starfishes from the geographically intermediate Rame-Eddystone Grounds. The significance of this

TABLE I. ANALYSIS OF PARASITE OCCURRENCES IN STARFISH FROM HAULS FROM OUTER GROUNDS AND PLYMOUTH SOUND

Date	Total in haul	Total males	No. of males parasitized	Approx. percentage of males parasitized
		(*a*) Outer Grounds		
20. iii. 47	33	12	3	25
9. iv. 47	29	11	3	27
17. iv. 47	44	17	4	24
18. iv. 47	50	25	7	28
25. iv. 47	175	66	16	24
23. v. 47	57	17	2	12
15. i. 48	29	15	1	7
12. iii. 48	38	15	1	7
14. iv. 48	103	50	6	12
13. v. 48	231	87	1	1
10. ii. 49	63	26	2	8
15. iii. 49	46	17	1	6
14. ii. 50	41	23	2	9
9. iii. 50	79	32	3	10
		(*b*) Plymouth Sound (Asia Shoal)		
16. iv. 48	100	52	3	6
20. iv. 49	25	10	1	10
10. iii. 50	80	37	1	3

distribution will be discussed later. Table I gives a synopsis of the occurrences of *Orchitophrya stellarum* in *Asterias rubens* from the Plymouth area.

The occurrence of the parasite is strictly seasonal. It has only been found near Plymouth during January to May (inclusive) when the host's testes are either ripe or nearly ripe. Smith (1936) and Burrows (1936) both record it as occurring during 'summer'.

The absolute number of parasitized starfishes caught in any one haul is necessarily small and so it is difficult to obtain a figure representing the true percentage of males infected. However, the data given in Table I show clearly that the percentage infected was much greater in 1947 than in any of the three succeeding years. The catches taken from the Outer Grounds in March and April 1947 gave very constant percentages of infected males. A month later

SEASONAL CHANGES IN THE PHYTOPLANKTON AS INDICATED BY CHLOROPHYLL ESTIMATIONS

By W. R. G. Atkins, Sc.D., F.R.S. and Mary Parke, D.Sc.

From the Plymouth Laboratory

Introduction

When studying the suspended matter in sea water Armstrong & Atkins (1950) filtered carboys of sea water taken from the surface at the International Hydrographic Station, England No. 1, about 10 miles south-west of the Eddystone. The samples averaged 22 l., filtered through a Whatman No. 50 paper, 11 cm. diameter, on a Buchner funnel with the water pump. The first 10 l. was always re-filtered. The results for the suspended matter were shown to be only about 4% less than when filtration was through 'Gradocol' collodion membranes of average pore diameter 1·09 micron. The removal of the phytoplankton should thus be more complete than when the finest bolting silk is used, for according to Harvey (1945) the mesh apertures of the latter average $42 \times 50\,\mu$ when wet and swollen. Since there are many flagellates and non-motile forms less than $5\,\mu$ in length it is obvious that the net may let through much that is retained by the cellulose or collodion filters.

The suspended matter thus obtained gave us the opportunity of following the changes in the phytoplankton in the surface water, by extracting the pigments with acetone—a method introduced by Kreps & Verjbinskaya (1930), and by Harvey (1934*a*) with more accurate measurement of the volume filtered by the nets. Riley (1938–41) filtered surface samples through paper, as did Graham (1943). Krey at Kiel (1939) used 'cella'—presumably collodion—filters for water from 0–30 m. Cole & Jones (1949) also have made plankton counts using collodion filters.

Before proceeding it is appropriate to consider the known plastid pigments of the phytoplankton and their abundance in typical species.

The Plastid Pigments of the Phytoplankton

In recent years these have received much attention. According to Rabinowitch's summary (1945), the chlorophylls constitute about two-thirds of the total plastid pigments, the remaining third consisting of carotenoids, of which one-fifth contains orange red carotenes, polyene hydrocarbons, and four-fifths consists of their oxygen derivatives, namely yellowish xanthophylls. The amounts vary with species and environment, but the relative proportions are fairly constant in growing cultures. Chloroplasts often appear yellowish

or brown, rather than green, apparently due to the physical state of the plastid rather than to the preponderance of the yellow pigments.

According to Manning & Strain (1943), diatoms contain chlorophyll *a* and a little chlorophyll *c*, with carotenes and xanthophylls, mainly fucoxanthin, also diadinoxanthin and some diatoxanthin. The diatoms and brown algae have similar chlorophylls and xanthophylls. Pace (1941), however, did not find fucoxanthin in *Nitzschia closterium*, but it has been proved by Whitford (1947) to exist in the Chrysophycean *Phaeosphaera perforata*. Calculated on the dry weight of *Nitzschia closterium*, Pace found 2·17% chlorophyll *a* and 0·155% chlorophyll *b*, also β-carotene, cryptoxanthin, lutein, isolutein and two xanthophylls. The chlorophyll-carotenoid ratio was 3·77.

The presence of the xanthophylls and carotenes, and sometimes of other pigments, makes direct colorimetric comparisons useless for the estimation of the mixed chlorophylls. Of these, Strain (1949) summarizes the absorption-band measurements, and for chlorophyll *a*, $C_{55}H_{72}O_5N_4Mg$, reports principal bands at 440 and 660 mμ; for chlorophyll *b*, $C_{55}H_{70}O_6N_4Mg$—which may constitute 20–40% of the chlorophyll of the Chlorophyta—the bands are at 480 and 650. In red algae and diatoms, however, Manning & Strain (1943) found that *b* was less than 0·3% of *a*. The position of the bands varies somewhat according to the solvent used.

The formula and molecular structure of *c* is unknown, but it is found in small amounts along with chlorophyll *a* in diatoms, dinoflagellates and brown algae; the absorption maxima, in ether, are given as 446, 579·5 and 627 mμ (Strain, Manning & Hardin, 1944).

Chlorophyll *d* is found in very small amounts, with *a*, in red algae, though up to 25% is *d* in *Rhodochorton rothii*. It contains magnesium, but its formula is unknown. In ether its principal bands are at 445 and 686 mμ, and at about 457 and 698 mμ in methanol (Manning & Strain, 1943).

The Colorimetric Estimation of Chlorophyll and the Preparation of Extracts of Plastid Pigments from Phytoplankton

On viewing acetone solutions of a bought dry solid chlorophyll and of various extracts from algal cultures and sea water with a hand spectroscope, the absorption in the red gave a well-marked band. By inserting the Schott RG1 filter a spectrum of longer wave-length than 600 mμ is obtained, between which and the end of the visible red the band may reduce the light very markedly, and so permit of colorimetric comparisons without interference from the yellow pigments. A Kober colorimeter (by Klett) was used for this work.

There is, however, an uncertainty in the composition of chlorophyll powder, such as that from the British Drug Houses. Nettle leaves may be used as a

source. Though there are a number of chlorophylls and these have labile isomers the net effect of such changes as occur appears to be of no great importance as regards the absorption bands in the red; such small shifts in the bands would not seriously affect the colorimetric comparisons. Care should be taken to avoid errors due to evaporation of the acetone during the comparisons.

The aqueous acetone extracts from pure cultures of species selected from the phytoplankton (Parke, 1949) were thus compared among themselves and with chlorophyll standards. The cell numbers were counted in the haemocytometer field. Table 1 shows the numbers of algal cells from active cultures of measured average size which yield 1 mg. of chlorophyll.

The solvent used was of 'analytical reagent' quality and was added to the wet filter-paper on which the algal cells had been collected and washed with distilled water. If necessary, to keep in solution the salts of sea water liberated from the cells, a little distilled water was added till the cloudiness in the acetone vanished.

The chlorophyll-bearing cells, from cultures or from sea water, vary in size down even to one micron in diameter, as we have found recently. They are accordingly too small to be retained quantitatively on filter-paper, such as Whatman No. 42, intended for the finest precipitates. The filtration of large volumes on the 4 cm. diameter collodion membranes is very tedious and the membranes have to be changed frequently as they become choked. Centrifuging, even with tubes containing 250 ml. is unsatisfactory, and slow, though according to H. W. Harvey (private communication) dead cells are deposited better than are living. The simplest method is to add 5 ml. of a 1% solution of potassium aluminium sulphate crystals to about a litre of culture or sea water. The samples are usually at about pH 8, or over. The acid alum solution brings this nearer to neutrality; the reaction should be tested with bromthymol blue. If it is necessary to add more alum, for a very thick culture, the reaction may go slightly below neutrality, pH 7. If it is much below—in a fresh water—it can be restored by adding a little sodium bicarbonate. This is not done to precipitate the aluminium hydroxide which comes down from pH 3·5–5, but to avoid any possible effect of acid on the pigments. According to Atkins (1922) the reaction of algal cells is close to neutrality, whereas land plants are often markedly acid. Trouble arises more frequently in dense cultures through the reaction of the water being too alkaline, pH 9 or over. The aluminium does not then form a good floc, but either remains in solution or in a very fine suspension. The alkalinity may be reduced by passing in carbon dioxide, or by the cautious addition of very dilute acetic acid, till the pH is brought slightly below 7, and a yellowish green is given with bromthymol blue. This should be done before the addition of the alum solution, and it is advisable to allow the floc, with algae, to settle in weak light before filtration. It is often possible to pour off liquid over the floc, thus reducing time of filtration. Filtration

may then be effected on an 11 cm. Buchner funnel, with the filter pump. The rate should be low at first till the aluminium hydroxide floc has sealed the pores, when the suction may be increased. Unless too much alum has been added filtration proceeds at a reasonable rate. Algae from cultures are thus obtained for pigment studies, or it is possible to get the phytoplankton from 1 or 2 l. of sea water to follow the rate of production in the sea; smaller volumes should suffice when plankton is abundant.

Algae carried down in the transparent floc are readily seen under the microscope. *Dicrateria inornata* was perfectly visible and only by very careful adjustment of the light was it possible to discern the floc. Cells of *Chlamydomonas* were observed to be actively motile after two filtrations with too little alum or with too alkaline a solution for effective flocculation.

The weight of the aluminium hydroxide floc which is effective is amazingly small; a 1% solution of potassium aluminium sulphate crystals contains only 0·82 mg. of the hydroxide in 5 ml. Yet in 100 ml. of sea water this gives a marked turbidity in a few minutes and a sediment about 4 mm. in height in the measuring cylinder. Settling is naturally slower in a litre vessel, and as much as 15 ml., namely about 2·5 mg., may give with a culture a slowly filtering slime.

The chlorophyll content of pure algal cultures

A *Gymnodinium* culture contained 144 cells/mm.^{3}, (144 million/l.) The cell numbers per milligram of chlorophyll were obtained as follows. A freshly diluted chlorophyll solution contained 16·0 mg./l. Of this 50·0 matched 35·8 of a *Gymnodinium* extract, as read on the Kober scale, using filter RG 1. The extract, therefore, contained 22·3 mg./l., and as its volume was 27·6 ml., which had been used in successive small portions to extract the algae filtered from 250 ml. of culture, the culture contained 2·46 mg./l., in 144 million cells. So 58·5 million cells contain 1·0 mg. The results for a number of species are given in Table I which include determinations on three species of diatom by Krey, Pace and Graham.

Differences in the volumes of the cells appear to account for the major differences in the milligram counts. One may not appreciate that, for example, the average volume of *Coscinodiscus centralis* is fourteen thousand times that of *Dicrateria inornata*.

To separate the pigments we tried aluminium oxide (Kahlbaum) specially prepared for such work. A blue green chlorophyll band was retained near the top; below this came one, or usually two, bands, orange red, and presumably carotenes. The liquid which came through was yellowish and appeared to be a xanthophyll, or several mixed perhaps. The above were obtained with the pigments in petroleum ether b.p. 40–60° C. after evaporation of the acetone on a water-bath. Whitford (1947) has reviewed previous work; he separated

the pigments on a starch column and with suitable solvent mixtures obtained bands for chlorophyll and two xanthophylls, the carotene coming through.

The separation of the chlorophylls can thus be readily effected and could be used as a check on the colorimetric comparison in the red.

TABLE I. NUMBER OF CELLS FROM ACTIVE ALGAL CULTURES WHICH YIELD 1 MG. OF CHLOROPHYLL. COLOUR REFERS TO EXTRACTS

	Size		Mg. count
	Mean (μ)	Range (μ)	
Chlorophyceae			
Order VOLVOCALES			
Chlamydomonas I, pure green. *By* F. Gross	10×5	8×4–12×6	202×10^6
Chlamydomonas III, pure green. *By* Mrs Föyn	8×6	6×4–12×8	109×10^6
Order CHLOROCOCCALES			
Chlorella I, yellowish green	$3{\cdot}5d$	$2{\cdot}5$–$4{\cdot}5d$	2400×10^6
Chrysophyceae			
Order CHRYSOMONADALES			
Dicrateria inornata Parke, yellowish green	$4d$	3–$5{\cdot}5d$	563×10^6
Bacillariophyceae			
Order CENTRALES			
Coscinodiscus centralis Ehr., yellowish green. *By* R. Bainbridge	$110d \times 50t$	$105d \times 35t$ / $140d \times 60t$	74×10^3
Chaetoceros gracilis Schütt (Krey, 1939)	$8 \times 6b$	—	286×10^3
C. vanheurckii Gran (Graham, 1943)	24–$28w$	—	170×10^3
Thalassiosira gravida Cleve, yellowish green	$22d \times 12t$	$20d \times 10t$–25×14	123×10^6
Order PENNALES			
Nitzschia closterium (Ehr.) W.Sm. forma *minutissima*. *By* Allen and Nelson; pure green	30×3–$8 \times 3b$	25×3–35×4	743×10^6
N. seriata Cleve (Pace, 1941)	100×6	—	$1{\cdot}25 \times 10^6$
Cryptophyceae			
Order CRYPTOMONADALES			
Hemiselmis rufescens Parke, almost pure green with insoluble red	$7 \times 4 \times 3$	$4 \times 3{\cdot}5 \times 2$–$8{\cdot}5 \times 5 \times 3$	3260×10^6
Dinophyceae			
Order DINOFLAGELLATA			
Gymnodinium sp. very close to *G. simplex*, yellowish green	15*	10–22	58×10^6

Notes: *b*, body, without spines; *d*, diameter; *t*, thickness; *w*, width of cell; * sphaeroidal; *By*, isolated by and maintained since at Plymouth.

THE SEASONAL CHANGES IN THE PHYTOPLANKTON

These have for many years been studied by the changes in concentration of phosphate and other nutrient salts. A number of isolated measurements have been made, as mentioned previously, but Harvey (1934*b*) followed the changes at a station, L 4, inside the Eddystone using a net filtering measured volumes of water and an arbitrary colorimetric scale compounded with potassium chromate and crystalline nickel sulphate.

There is, however, an uncertainty in the number of molecules of water of crystallization even in the 'analytical reagent' quality. The figure is between $6H_2O$, taken by Harvey, and $7H_2O$. The uncertainty is 6%. A solution of

known nickel content may, however, be prepared by dissolving nickel wire. The nickel chromate standards have been considered to be a tolerably good colour match for acetone extracts of plankton. We are indebted to Dr Harvey for kindly comparing an extract from plankton filtered from a carboy taken on 30 November 1949 (Table II). This he assessed as corresponding to 10–15 units in 10 ml., but the extract was far more yellow than the standard, so a closer match was not possible. Viewing the tubes through the filter RG 1, the sample was rather under 8 units, possibly as low as 6 units. Taking into account the volumes of extract and of water this corresponds to 1·39–1·04 mg. of chlorophyll/m.^{3}, using Harvey's value, based on Guthrie's work, of 0·3 μg. of chlorophyll/unit. The result found by comparison with a chlorophyll standard with the RG 1 filter was 1·43 mg./m.^{3}. It seems possible that the yellower colour of the November extract may have been due to the presence of a larger number of flagellates than are ordinarily found in the net plankton to estimate which the colour units were devised.

Riley (1938) estimated chlorophyll from algae by comparison with a chlorophyll prepared by Dr C. G. Deuber of Yale. He separated the chlorophyll from the yellow pigments by saponifying it and removing the carotenoids in ethyl ether. He found 1 unit of the Harvey scale to correspond to 0·88 $\pm$ 0·01 μg. chlorophyll. There was good agreement between the dry organic matter and the chlorophyll content, but only in the upper layers of the water. Paper filtration (Whatman No. 44) was found to give up to seven times as much chlorophyll extract as did bolting silk, and use of collodion membrane produced about 6% more than did paper in Long Island Sound (1941 *a*). Using the same method for removing the yellow pigments Riley tabulated Harvey units against chlorophyll for his Long Island work and the mean showed 0·26 μg./unit. This is much below his earlier value, but agrees tolerably well with Harvey's estimated value 0·3 μg., which seems to accord reasonably well with the single comparison already quoted in this paper when the red filter was used. Riley also records that 17·44 mg. chlorophyll corresponded to 600 mg. dry organic matter, namely the chlorophyll was 2·91%. This is close to Pace's value 2·32% for the sum of chlorophyll *a* and *b* in *Nitzschia closterium*, in which a lower value is to be expected as the analysis refers to a silica-bearing organism only.

The extracts made during 1948 and 1949 from suspended matter filtered on collodion from water from Station E 1 (which was selected to be beyond the range of fluctuation due to land drainage) were compared among themselves without the red filter and, using the filter, with chlorophyll solutions of suitable strength. The results are shown in Table II, together with the sea temperature, the suspended inorganic matter and ash after incineration (S.I.M.A.) and the percentage of silica contained in the latter, in order to see whether any relation existed between these and high chlorophyll values. No such relation is, however, observable. Thus 2020 and 1190 mg./m.^{3} S.I.M.A. both have 44%

of silica and correspond respectively to 1·05 and 1·43 mg. of chlorophyll/m.^{3}. Furthermore, 490 mg./m.^{3} S.I.M.A. had 43% of silica, but only 0·17 mg./m.^{3} of chlorophyll.

In 1948 the chlorophyll content was much as would be expected from the phosphate studies, with a well-marked maximum in April, and a lesser crest in October, separated by the year's minimum in mid-August. As always, a larger number of observations would have been better. For 1949 the April figure observed was only half that of 1948, but this was, after a drop, followed by a large outburst in June and a high maximum in July, leading, after fluctuations to a late November outburst rather greater than that observed in April. It must be remembered, however, that these observations are on

TABLE II. CHLOROPHYLL CONTENT, WITH ACCOMPANYING SURFACE TEMPERATURE, SUSPENDED INORGANIC MATTER AND ASH (S.I.M.A.), AND SILICA CONTENT OF THE LATTER

Chlorophyll and S.I.M.A in mg./m.^{3} sea water (parts per thousand million). Silica in percentage of S.I.M.A.

DATE 1948	Chlorophyll	°C	S.I.M.A.	SiO_2%	DATE 1949	Chlorophyll	°C	S.I.M.A.	SiO_2%
Jan.	—	—	—	—	5 Jan.	0·61	11·2	760	21
11 Feb.	—	10·1	—	—	1 Feb.	0·86	10·2	1600	26
10 Mar.	0·92	9·3	—	—	1 Mar.	0·58	10·1	740	21
12 Apr.	2·84	10·2	—	—	13 Apr.	1·37	9·9	800	37
10 May	—	12·4	—	—	9 May	0·57	11·5	800	31
9 June	0·73	12·6	1140	54	9 June	3·40	13·9	1360	52
15 July	0·82	14·7	2770*	25	8 July	4·30	16·5	1880	41
Aug.	—	—	—	—	8 Aug.	0·36	15·3	450	18
16 Aug.	0·17	15·4	890	43	17 Aug.	1·05	16·0	2020	44
31 Aug.	—	16·8	—	—	29 Aug.	0·51	19·4	800	42
4 Oct.	1·22	14·7	490	44	6 Oct.	—	16·4	590	43
30 Nov.	0·30	13·2	950	17	8 Nov.	1·43	14·0	1190	44

* 70% of this was calcium carbonate probably precipitated out of the water.

surface water and there is now evidence from several sources that the surface is the seat of a large amount of suspended matter. None the less, the surface outbursts in June and July are remarkable.

When these figures 0·17–4·3 mg./m.^{3} chlorophyll are compared with values recorded by other workers, it is better to neglect the early net-filtered results, which are clearly low. The numerous measurements by Riley, filtering through the finest paper, would be low if the small flagellates were an important constituent. For surface samples from the North Atlantic he gives (1939) as mean 1·2 and maximum 3·6 mg./m.^{3}, with 5·6 and 27·2 for George's Bank (1941*b*) also 17·4 and 62·0 for Long Island Sound. Riley has recently (1949) given an extensive review of the subject. For La Jolla, Graham (1943) gives 0·77 and 1·86 maximum. His results appear to be low, as he reports no chlorophyll found in a sample in which *N. seriata* constituted 83% of the catch. His method of estimating the chlorophyll avoids errors due to the yellow pigments, for he used a visual spectrophotometer set at 668 mμ. with slit width

0·4 mm. Krey (1939) used a 'cella' (collodion) filter and for 0–30 m. at Kiel got a mean of 2·00 mg./m.^{3} and a maximum of 5·00.

It has been customary for biologists to count microscopic organisms on the ruled squares of the Thoma haemocytometer, the side of the ruled area being 1 mm. and the depth one-tenth thereof. The volume is one-tenth of a cubic millimetre. It may serve to show how sparsely populated sea water is by recalling that the simultaneous utilization of all the phosphate present at the winter maximum in the English Channel suffices to produce *N. closterium* at a density of 2·7 per haemocytometer field (Atkins, 1923). One milligram of phosphorus suffices for 2050×10^6 cells of *N. closterium* var. *minutissima*. When compared with the production of 743×10^6 cells for 1 mg. of chlorophyll (Table I) we see that the chlorophyll to phosphorus ratio is 2·76 in this species, weight for weight.

TABLE III. NUMBER OF CELLS IN A HAEMOCYTOMETER FIELD DERIVABLE FROM THE OBSERVED MAXIMUM 4·3 MG. OF CHLOROPHYLL PER CUBIC METRE, ASSUMING ALL TO BE OF ONE SPECIES AS LISTED

Species	Cells per field
Coscinodiscus centralis	$0{\cdot}32 \times 10^{-4}$
Thalassiosira gravida	0·053
Nitzschia closterium var. *minutissima*	0·32
Dicrateria inornata	0·24
Isochrysis galbana	0·27
Hemiselmis rufescens	1·40
Chlamydomonas I	0·087
Chlamydomonas II	0·047
Chlorella I	1·03
Gymnodinium sp.	0·025
Human red blood corpuscles	450×10^3

Table III shows the number of cells per field which would be produced if the maximum amount of chlorophyll recorded in Table II, namely 4·30 mg./m.^{3}, were all produced by the single species listed. It may be seen that, for *Nitzschia*, the observed maximum is only about one-eighth of the possible, were the winter maximum of phosphorus to give one crop without any intermediate grazing down; thus in a pure culture the chlorophyll produced by water of this composition would be about $4{\cdot}3 \times 8{\cdot}4$, namely 36 mg./cm.^{3}.

The figures in the Table indicate the difficulty of making direct counts.

SUMMARY

The pigments of pure cultures of algae, of known number per volume, have been extracted with aqueous acetone after separation by filtration. The extracts were compared in a Kober colorimeter with standard solutions of a preparation of bought chlorophyll. The number required to give 1 mg. of chlorophyll was thus determined.

The algae studied included: Chlorophyceae, two species of *Chlamydomonas* and one *Chlorella* not yet described; Chrysophyceae, *Dicrateria*

inornata Parke; Bacillariophyceae, *Coscinodiscus centralis* Ehr., *Thalassiosira gravida* Cleve and *Nitzschia closterium* (Ehr.) W.Sm. forma *minutissima*; Cryptophyceae, *Hemiselmis rufescens* Parke; Dinophyceae, *Gymnodinium* sp. The numbers per milligram of chlorophyll varied from 74×10^3 for *Coscinodiscus* to over 3200×10^6 for *Hemiselmis rufescens*. Of the nine cultures, six were between 50 and 750×10^6. The volume of the cell is the decisive factor in the milligram count.

Filtration of these and of sea-water samples was made through either collodion membranes of known average pore diameter, supplied by courtesy of the Director of the Department of Pathology, St Mary's Hospital, London, or through the finest grade of Whatman filter-paper. To retain the algal cells on paper about 5 ml. of a 1% solution of alum was added. The transparent floc serves to entangle the cells. They are thus ready for examination under the microscope, and motile organisms are slowed down or brought to rest. The floc will settle down in a cylinder. The water should be close to pH 7 before addition of the alum.

Colorimetric estimation of chlorophyll can be made even with extracts which are yellowish green or yellow by using a red colour filter Schott RG1 cutting off close to 0·6 μ, which is placed over the eyepiece of the colorimeter.

The seasonal changes in the chlorophyll content of water in the English Channel, about 20 miles off Plymouth, were followed from March 1948 to November 1949 inclusive, by filtering surface water. The spring maxima in April were respectively 2·84 and 1·37 mg./m.^{3}, and the autumn maxima 1·22 and 1·43. The yearly minima were in August, 0·17 and 0·36. But most unexpectedly June and July 1949 gave 3·40 and 4·30 respectively. Such figures are comparable with those of Krey, for Kiel, 2 mg. mean and 5 mg. maximum, and of Riley, for North Atlantic, 1·2 mean and 3·6 maximum.

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THE BIOLOGY OF *ASTERIAS RUBENS* L. II. PARASITIZATION OF THE GONADS BY THE CILIATE *ORCHITOPHRYA STELLARUM* CÉPÈDE

By H. G. Vevers, M.A., D.Phil.

Zoologist at the Plymouth Laboratory

(Plate I)

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Introduction

The astomatous holotrich ciliate, *Orchitophrya stellarum*, was originally described and named by Cépède (1907*a*, *b*), who found it in the gonads of only three males out of a total of over 6000 *Asterias rubens* of both sexes. These starfishes were taken by him from the Boulogne and Wimereux area. There was no trace of the parasite in any ovaries, but he noticed that it caused a partial and direct castration of its male host. *Orchitophrya* was found by Piatt (1935) in the testes of *Asterias forbesi* in Long Island Sound, where Burrows (1936) observed that the percentage of parasitized males varied from 1 to 20% according to the locality. Burrows also found that a small number of the female starfishes (about 1%) were infected. Smith (1936) recorded the parasite in the ovaries of about 25% of the females of *A. vulgaris* from oyster beds in Malpeque Bay, Prince Edward Island. Eggs taken from these infected ovaries appeared normal and were fertilizable.

I am indebted to Mr Y. R. Tripathi for assistance in the original identification of the parasite, and to Dr J. S. Alexandrowicz for making the photomicrographs.

Distribution of the Parasite off Plymouth

During the years 1946–50 large numbers of *A. rubens* have been trawled from different localities in the Plymouth area. In the course of investigations on the reproductive cycle in these localized populations, smears have been taken

from the gonads of each starfish and transverse sections cut of a number of selected gonads. In March 1947 trawling was commenced on the Outer Grounds, to the south and south-west of Eddystone. The differences between the starfish from this area and those from the more northerly Rame-Eddystone Grounds have already been described (Vevers, 1949). *Orchitophrya stellarum* was found in a varying percentage of the males from all the six trawl hauls taken in spring 1947 on the Outer Grounds. In the early months of the years 1948, 1949 and 1950 the parasite was again found in male starfishes from these Grounds and also in a population of *Asterias rubens* trawled from Asia Shoal, Plymouth Sound. The parasite has never been found in starfishes from the geographically intermediate Rame-Eddystone Grounds. The significance of this

TABLE I. ANALYSIS OF PARASITE OCCURRENCES IN STARFISH FROM HAULS FROM OUTER GROUNDS AND PLYMOUTH SOUND

Date	Total in haul	Total males	No. of males parasitized	Approx. percentage of males parasitized
		(*a*) Outer Grounds		
20. iii. 47	33	12	3	25
9. iv. 47	29	11	3	27
17. iv. 47	44	17	4	24
18. iv. 47	50	25	7	28
25. iv. 47	175	66	16	24
23. v. 47	57	17	2	12
15. i. 48	29	15	1	7
12. iii. 48	38	15	1	7
14. iv. 48	103	50	6	12
13. v. 48	231	87	1	1
10. ii. 49	63	26	2	8
15. iii. 49	46	17	1	6
14. ii. 50	41	23	2	9
9. iii. 50	79	32	3	10
		(*b*) Plymouth Sound (Asia Shoal)		
16. iv. 48	100	52	3	6
20. iv. 49	25	10	1	10
10. iii. 50	80	37	1	3

distribution will be discussed later. Table I gives a synopsis of the occurrences of *Orchitophrya stellarum* in *Asterias rubens* from the Plymouth area.

The occurrence of the parasite is strictly seasonal. It has only been found near Plymouth during January to May (inclusive) when the host's testes are either ripe or nearly ripe. Smith (1936) and Burrows (1936) both record it as occurring during 'summer'.

The absolute number of parasitized starfishes caught in any one haul is necessarily small and so it is difficult to obtain a figure representing the true percentage of males infected. However, the data given in Table I show clearly that the percentage infected was much greater in 1947 than in any of the three succeeding years. The catches taken from the Outer Grounds in March and April 1947 gave very constant percentages of infected males. A month later

(23 May 1947) the percentage infected had dropped to half; probably because most of the males had spawned in the meantime, leaving fewer ripening testes available for the parasites. In January-April 1948 the percentage infected was, on the average, 10, and again there was a sharp drop in percentage to less than 2 in May. There were only two infected catches in 1949 from the Outer Grounds, one in February and one in March, and the percentage with parasites was less than 10. The same was found in the two catches for 1950.

In the Plymouth Sound starfish population *Orchitophrya* has been found only in small numbers in one catch in each of the years 1948, 1949 and 1950.

The percentage of males infected was proportionately much greater in the size classes 10·0–19·9 cm. than in the size classes 5·0–9·9 cm. and 20·0–25·9 cm. (Table II). In the lower-size classes (5·0–9·9 cm.) the scarcity of parasitized individuals is understandable, since some, at least, of these starfishes were definitely juvenile with testes which showed no signs of ripening at the time of observation.

TABLE II. SIZE DISTRIBUTION OF INFECTED MALES IN THE POPULATION (OUTER GROUNDS)

Size class in cm.	Total males	Infected males	Percentage infected
5·0–9·9	35	2	6
10·0–14·9	162	29	18
15·0–19·9	181	19	11
20·0–25·9	35	1	3

The very low percentage of infections in the highest size classes (20·0–25·9 cm.) suggests that there may be a certain resistance to the parasites with increased host size. There is, however, no direct evidence for this interpretation.

DISTRIBUTION OF THE PARASITE WITHIN THE HOST

Burrows (1936) noted variation in the amount of parasites within the individual, including cases where some gonads were parasitized and others were normal. Similar conditions were found in the present investigation, thus in starfish 3076 (16 April 1948) there was a very heavy infection of the testes in arm II/interradius 2/3, while all the rest of the testes showed mobile spermatozoa and no parasites. In starfish 3087 (16 April 1948) there were medium infections in two testes in non-contiguous arms and no parasites in the other eight gonads. At the time these starfishes were caught, in mid-April, most of the starfishes on the Outer Grounds were ripe, but few had spawned. In the previous year larger catches of starfishes were made, and among these were a few in which ripe, spawned and parasitized testes were

found in the same animal. Thus in starfish 998 (23 May 1947) the condition of the gonads was:

Arm	Interradius	Condition of gonad
I	5/1	Spawned, re-ripening
	1/2	Spawned
II	Arm missing	
III	2/3	Spawned
	3/4	Mobile sperm distally, rest spawned
IV	3/4	Few parasites
	4/5	Few parasites
V	4/5	Mobile sperm distally, rest spawned
	5/1	Spawned

There is no doubt that the main centre of infection is in the testes, although the parasites can sometimes be found in other organs. In starfish 640, for instance, *Orchitophrya* was found in the gut and coelomic fluid as well as in the testes, but not in the digestive coeca or tube feet. These are probably chance infections from lesions in the testis and are not considered to be of any importance.

Effect of the Parasite on the Testes of *Asterias rubens*

Cépède (1910) gives a good description of the morphology and life cycle of the parasite, and he noted that it caused partial or direct castration of the host. His material was very limited and neither he nor subsequent workers have recorded the histological changes which occur in testes infected with *Orchitophrya*. With the large number of infected males available from the Plymouth grounds, it has now been possible to obtain further information on this subject.

In the early stages of infection the testes still have well developed spermatogonial ridges, with numerous spermatocytes and spermatids filling the lumen of each tubule. As the parasites increase in number, the sexual products in the lumen disappear and a transverse section then shows that each tubule has distinct spermatogonial ridges and its lumen is filled with parasites. The ridges become progressively smaller and the parasites increasingly crowded (Pl. I, fig. 1). The nutrient medium in which the parasites are living is that of the ripening germ cells, and as the latter disappear so does the food supply of the parasites. When this happens the parasites start to decrease in numbers and the gonad tubules show only a very thin layer of genital epithelium (Pl. I, figs. 2 and 4). In this stage the connective tissue sheath begins to thicken, probably due to a shrinking of the whole tubule, as it becomes less distended with parasites.

Finally, very few parasites are left in the tubule lumina, there is little or no trace of genital epithelium and all that remains are the thick shrunken sheaths of the original testis tubules (Pl. I, fig. 3).

Discussion

The spread of the parasite would appear to be greater in starfish populations which are relatively crowded, for the largest percentages of infected males occurred on the Outer Grounds in 1947. During this year the number of starfishes caught on these grounds in comparable hauls was larger than in subsequent years, and in addition the values for their mean individual body and testes sizes and available food supply were also higher. It has already been found (Vevers, 1949) that a numerically rich population, with abundant food supply, has a large mean body and gonad size. From the present observations it appears that rich and 'successful' populations (as on the Outer Grounds and on Asia Shoal, Plymouth Sound) were also characterized by the presence of a varying percentage of males with ciliate-infected testes. Conversely, a starfish population with small numbers, and low mean body and gonad size (as on the Rame-Eddystone Grounds) showed no trace of the parasites, although many starfishes from these grounds were examined.

Testes containing *Orchitophrya* never showed mobile sperms, even when the infection was relatively light, and there is little doubt that once it has been infected a testis ceases to function as a reproductive organ during that season. Although sometimes ripe, spawned and infected testes were found in the same starfish, it was more common to find all the testes of a starfish infected in some degree. In a population where over 20% of the males were infected (as in the Outer Grounds in March-April 1947) the intensity of reproduction, measured as the number of potential gametes, would necessarily be reduced by at least a similar amount, since the same number of predators and adverse factors would be preying on a reduced number of gametes. On theoretical grounds this check to reproduction should be reflected in a reduced population in subsequent years. There was, in fact, an observed reduction in the population of *Asterias rubens* on the Outer Grounds in 1948, 1949 and 1950 as compared with 1947 (Vevers, unpublished data). As it is not possible to follow the fate of broods which go through a pelagic phase one cannot gather direct evidence to show the causes of such a population reduction. On the Outer Grounds any reduction in population following on a year of heavy testis parasitization could easily be masked by immigration from neighbouring areas. There are also other factors, such as movement of food supply, which might reduce the population in numbers and mean body size. The observed population reduction since 1947 is probably the result of many factors, but it is considered that the parasitic castration of over 20% of the males in this population during 1947 must have played a definite part, and that it did, in practice, act as a natural check to a crowded population, a view which is supported by the observations of Galtsoff & Loosanoff (1939) on *A. forbesi*.

Summary

The parasitic astomatous holotrich ciliate, *Orchitophrya stellarum* Cépède, has been found in the testes of starfishes (*Asterias rubens*) in the Plymouth area. It was found only in starfishes from numerically rich and well-fed populations, which also showed large gonad growth. In such populations it occurred in up to 28% of the males during March-April 1947, and in lower percentages during the spring of the three following years. The parasite was never found in a geographically adjacent population containing smaller numbers of poorly fed starfishes. The parasite was found to be relatively more common in the testes of medium-sized starfishes than in those of large and small starfishes.

Presence of the parasite causes a complete breakdown of all the germinal tissue of the testes, so that most of the infected starfishes suffer complete castration. This involution of the testicular tissue has been studied, and photomicrographs are given which show a number of stages in the process.

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Explanation of Plate I

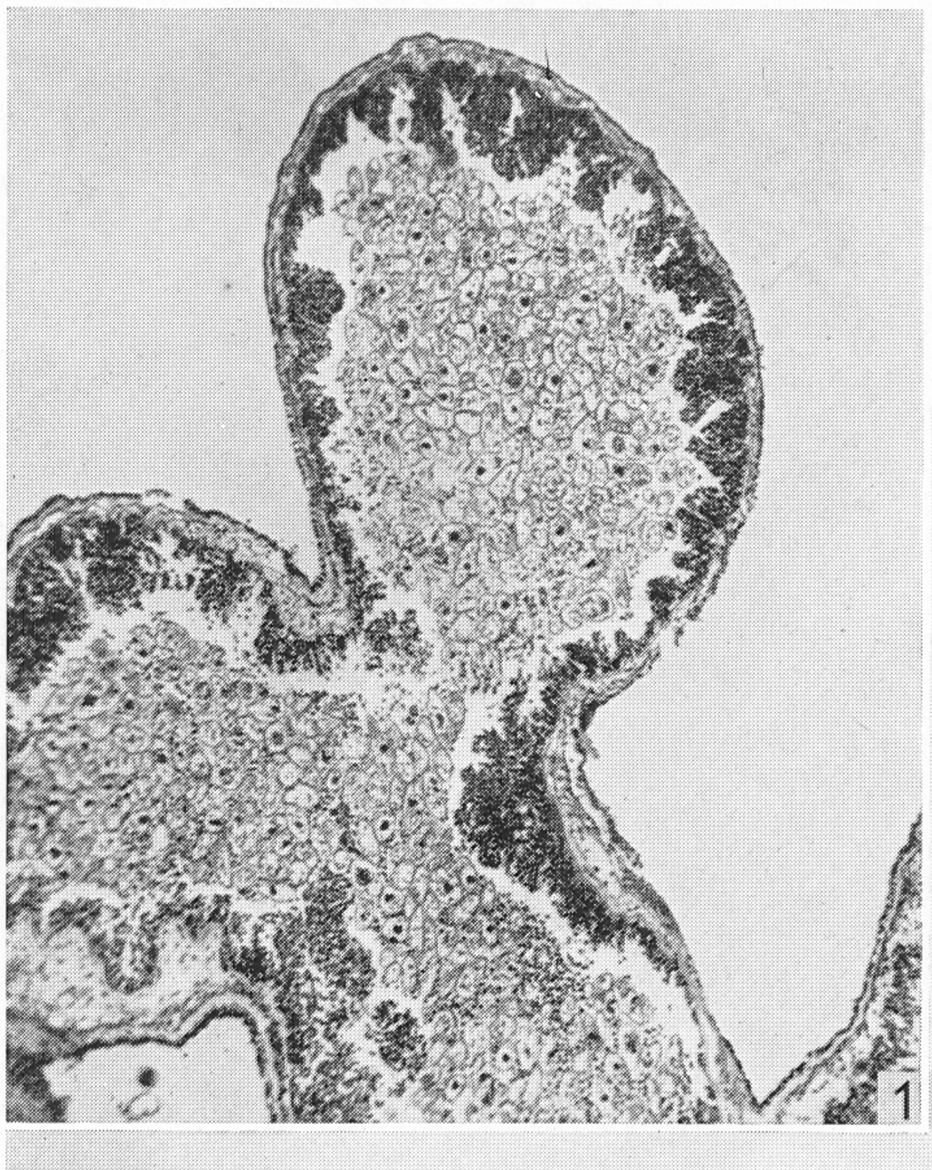
Photomicrographs of transverse sections of *Asterias rubens* testes showing stages of infection by *Orchitophrya stellarum*.

Fig. 1. Numerous parasites free in the lumen of a gonad tubule. Spermatogonial ridges still distinct.

Fig. 2. Parasites starting to decrease; spermatogonial ridges have disappeared.

Fig. 3. Final stage in the involution of the testis, with genital epithelium destroyed and gonad only represented by the thick shrunken connective tissue sheath. Very few parasites remain.

Fig. 4. Enlargement of part of fig. 2 to show parasites (cut at different angles) completely filling the lumen of the testis tubule. Very few germinal cells remain among the parasites.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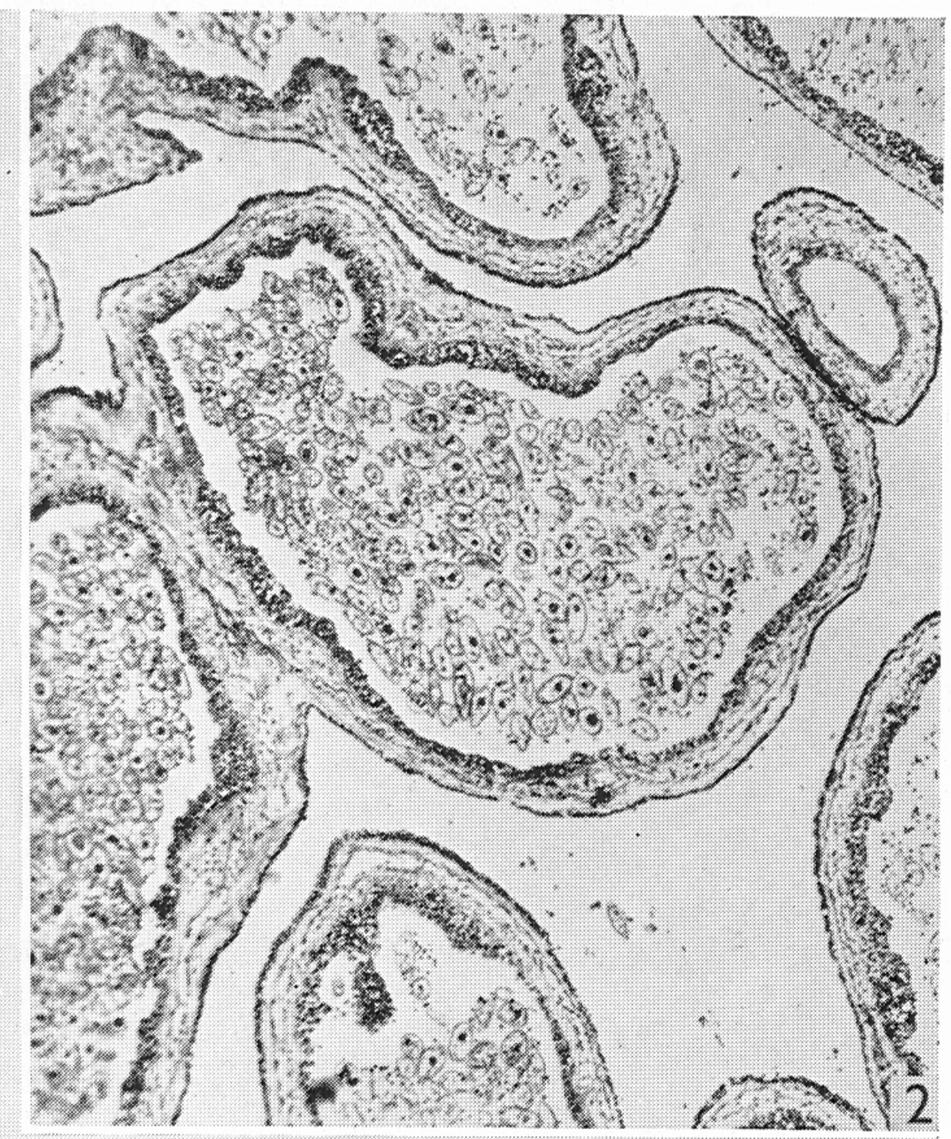
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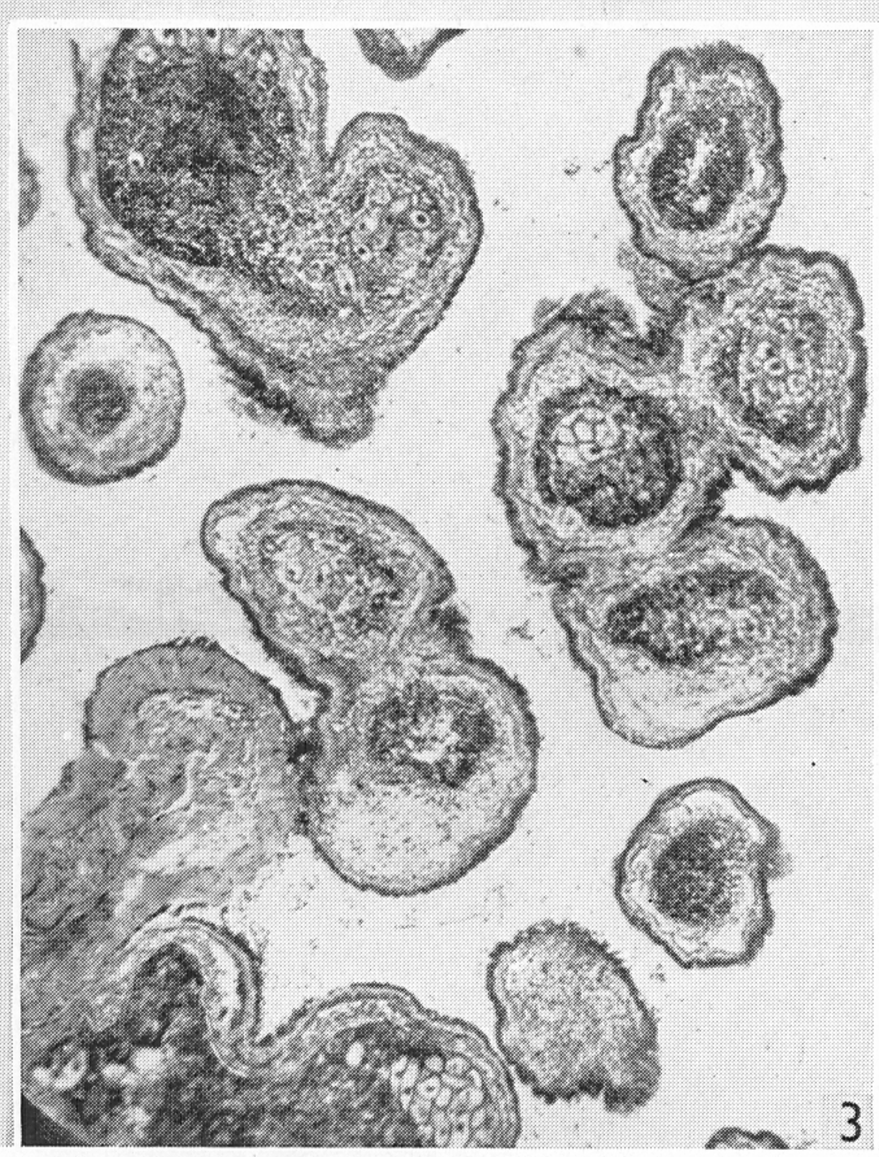
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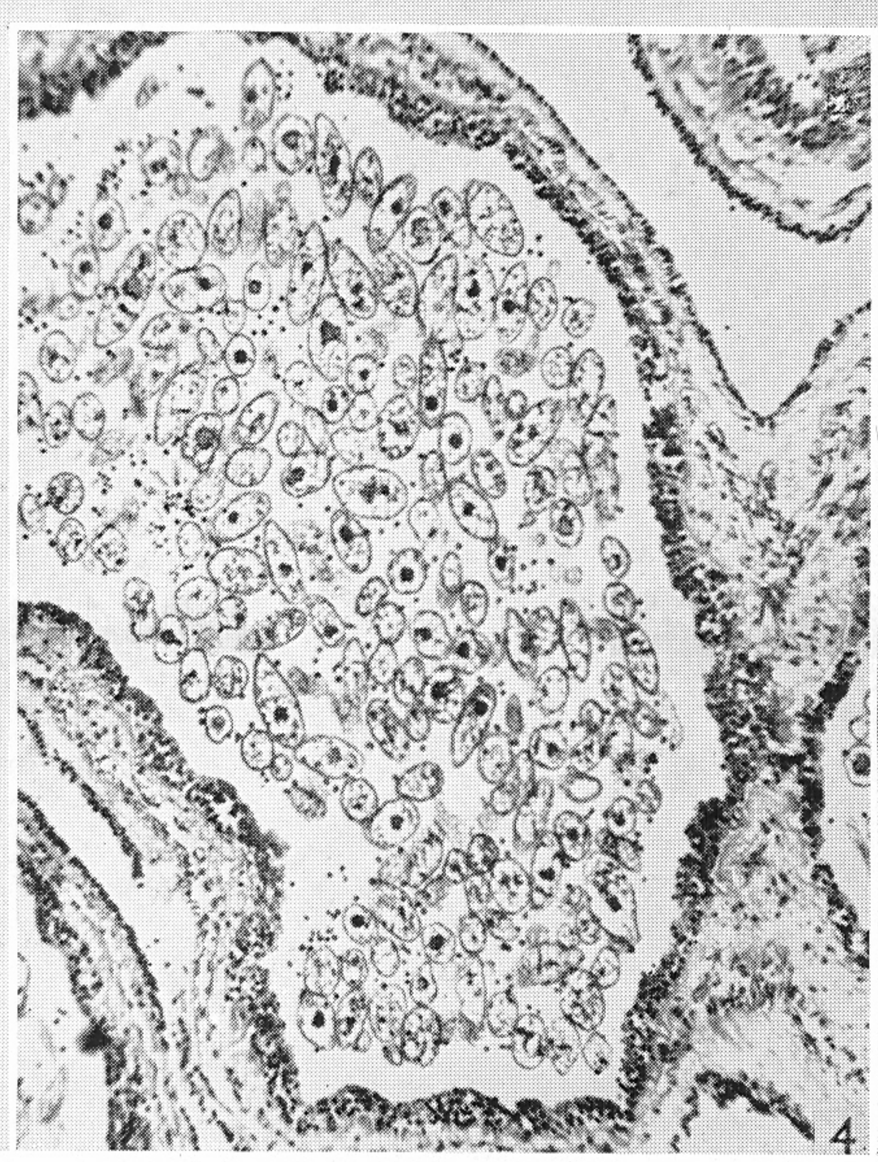
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Figs. 1–4.

OBSERVATIONS ON THE SPAWNING BEHAVIOUR OF *SACCOGLOSSUS HORSTI* BRAMBELL & GOODHART, AND OF OTHER ENTEROPNEUSTA

By C. Burdon-Jones

Department of Zoology, University College of North Wales, Bangor

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INTRODUCTION

A survey of the literature reveals few observations on the spawning behaviour of the Enteropneusta. Those existing are confined to descriptions of various continental species.

Bateson (1884, 1886) suggested that *Saccoglossus kowalevskyi* Agassiz from Chesapeake Bay released its sperm and ova by a rupturing of the body wall, the former dehiscing as lobate spermatophoric masses. Ritter & Davis (1904) studied *S. pusillus* Ritter at San Pedro, California, and stated that 'sperm is discharged in a delicate milky stream through the pores of the ripe genital lobes', and similarly the ova. They discovered eggs and embryos within a burrow, and concluded that that was their normal place of release and development. Davis (1908) collected all his material for a study of the embryology of *S. pusillus* from the burrows. Heider (1909) recorded a clump of eggs of *Balanoglossus clavigerus* Delle Chiaje amongst specimens received from Grado. Stiasny (1913) also worked on this species, and made observations on the method of spawning, fertilization and breeding season. A spawning male specimen of *Glossobalanus marginatus* was described by Meek (1922). This had been dredged from a depth of 52 fm. off the Farne Islands in the North Sea. Dawydoff (1928) described the egg masses of *Glossobalanus minutus* Kowalevsky at Naples. Laboratory records were made at Tortugas by Payne (1936) for *Ptychodera bahamensis* Spengel. Probably the most complete account of

spawning as yet recorded, for any species, is that of Kirk (1937, 1938), for *Saccoglossus otagoensis* Benham, found near Wellington, N.Z. This is a rock-pool inhabitant, and has a comparatively specialized mode of spawning. During their study of *S. pygmaeus*, Hinrichs & Jacobi (1938) noted some fertilized eggs in their aquaria, but they did not give many details.

The recent discovery of *S. cambrensis* in the Menai Straits (Brambell & Cole, 1939), and *S. horsti* in the Solent (Brambell & Goodhart, 1941), provided an opportunity for a study of their development. The spawning behaviour will be dealt with here, and the development described in subsequent papers. The following account is, in the main, confined to *S. horsti* on which the majority of the observations were made, with appropriate references to other species.

I am greatly indebted to Prof. F. W. Rogers Brambell, F.R.S., and Dr T. B. Reynoldson, of the Department of Zoology, University College of North Wales, for their continued interest and encouragement throughout this work. Also to Dr E. W. Knight Jones of the Marine Biological Station, University College of North Wales, and Prof. J. E. G. Raymont of the Department of Zoology, The University College of Southampton, whose information concerning the Solent grounds greatly facilitated the collection of material. These collections, and others referred to in the text, were made possible by a grant from the Browne Research Fund of the Royal Society. The air and sea temperatures quoted for the Southampton area were very kindly provided by Lieut.-Commander D. H. Macmillan, R.N.R., Hydrographic Surveyor to the Southampton Harbour Board.

Habitat of *Saccoglossus*

S. horsti was originally described as occurring in deep grey mud, of a glutinous type, from just above low-water mark spring tides to a little way above low-water mark neap tides. Subsequent exploration of the Solent area revealed a marked preference for areas of comparatively clean sand containing a smaller proportion of clay, silt, organic carbon and shell debris than was given in the original analysis. Such areas were invariably saturated, the water table lying above, or immediately below the surface of the sand. Shallow pools and streams of drainage water from neighbouring beds of *Spartina townshendii* Groves, and the upper reaches of the shore helped to maintain this saturated condition during the ebb tide. Regions were noted, however, where the water table was often 6 in. below the surface at the time of extreme low water. Surface casts and holes indicated that the number of specimens in these comparatively dry areas was less than in the others. A substrate of gravel, comparable to that so characteristic of the *Saccoglossus cambrensis* beds, was noted in many well-populated regions of the shore.

The animals live in reasonably well defined, irregularly coiled burrows, lined with mucus, and extending 4–8 in. below the surface.

Field Observations on *Saccoglossus horsti*

Spawning of Females

Collections were made on the Solent beds during all the workable tides of June 1946, May 1947, 1948, 1949 and May–June 1950, but it was not until the last two years that any spawning was observed in the field.

The area worked during these years covered several acres of the shore, and surface casts averaging over 500 per m.^{2} were common in the more densely populated parts. Observations were made throughout every tide during the period 12–16 May 1949, 28 May–2 June 1950 inclusive. On both occasions ripe adults were extremely abundant and extraordinarily difficult to remove from their burrows without damaging them. Such pronounced ripeness had not been encountered in previous years. The condition was general.

Whilst making field notes on the evening ebb of 15 May 1949, the first indications of spawning were observed. Particles of detritus had been seen passing in a constant stream into a burrow, when the continuity of the flow was interrupted, became spasmodic, and was finally reversed. Detrital material which had just passed into the burrow was expelled. Almost immediately after this, a continuous flow of viscous, perfectly transparent mucus was seen to be exuding slowly from the burrow. Its refractive index was such as to make it almost invisible under the overlying water, but the movement of sand particles and detritus around its margin and settling on it from above indicated its shape and movement. When it first appeared this mucus was too viscous to be drawn up into a pipette of 1·5 mm. bore, but it became progressively less viscous after a period of exposure to the surrounding water. Light grey ovoid eggs then began to appear, embedded in a 'mucus cord', which coiled upon itself around the mouth of the burrow. The eggs were sparse at first, but soon the mucus cord was uniformly speckled with them. The cord was about 3 mm. in diameter, the eggs about 0·25 mm. and spaced roughly 0·5 mm. apart. Occasionally they lay in rows 4 or 5 deep, but this arrangement was rapidly destroyed as the cord coiled upon itself and adjacent portions tended to fuse. The production of the egg mass usually went on steadily for 5–10 min., but sometimes it was rather erratic and more prolonged. The grey colour of the egg masses made them easily visible against the yellow of the sand. Spawning commenced about 30 min. after the shore had been exposed by the receding tide. Within an hour the entire bed was 'splashed' with egg masses, each some 7–8 cm.^{2} in area. The number of specimens spawning at a time increased to a maximum during this period, and then gradually decreased. After 2 hr., the rate of production of new egg masses had declined considerably, and within 2½ hr. there was no evidence of any being formed. Although no accurate counts were possible in the field, it was estimated that each egg mass contained some 2500–3000 eggs. These were contained in cords some 15–20 cm. long. Extension of the cord was, however, impossible, for the overlapping coils adhered tenaciously to

each other immediately on contact, and the whole mass coalesced within minutes of its formation. The resultant mass resembled miniature frog's spawn in many respects, notably in its elastic and slippery nature, a property which made collection extremely difficult.

Spawning of males

Approximately 20 min. after the first egg mass was seen, pale pink and milky white blotches began to appear amongst them. These were dense clouds of sperms issuing from the burrows of the males in much the same manner as that described for the eggs. The enveloping mucus was, however, less viscous, and in consequence the sperm clouds were slowly carried away and dispersed by the currents in the overlying water. These blotches, at first some 20–30 cm.^{2} in area, thus became thin streaks of pink or milky translucency, and extended for 30–40 cm. from the burrow mouth before becoming so diffuse as to be invisible to the naked eye.

These observations are similar to those recently made by Newell (1948) on *Arenicola marina L.*

Although the area where this spawning took place had been carefully scrutinized for the entire period of its exposure during the morning and evening ebbs of the previous seven tides, and the subsequent one, the phenomenon was not repeated. Neither was there any evidence of it when the shore was examined during the ebb on the following morning.

Fertilization

Egg masses in the immediate vicinity of the sperm clouds erected their fertilization membranes rapidly, thereby increasing their diameter fourfold. Others, apparently upstream and beyond the visible range of dispersal of the sperms, also showed signs of fertilization, suggesting that it was not wholly dependent on the currents in the overlying water.

The process of fertilization was accompanied by a gradual reduction in viscosity of the enveloping mucus as it was dissociated by the surrounding medium. Whereas there was evidence of disintegration of the egg mass prior to the fertilization of its constituents, there was no doubt that dissociation of the enveloping mucus took place rapidly once the fertilization membranes had been erected. The outermost eggs were fertilized first and soon detached themselves from the underlying ones. This process continued until the entire mass had been fertilized, and the eggs had been carried away by the currents in the overlying water, or remained in a loose cluster around the mouth of the burrow, to be subsequently dispersed by the incoming tide.

Partially fertilized egg masses, with the fertilized eggs as yet undetached, were observed in the direct flow of the sperms from the burrows. Such egg

masses were pink or white with sperms, but the preponderance of male elements did not seem to affect the normal progress of fertilization and erection of membranes of the unfertilized eggs. Whereas the unfertilized eggs released by dissociation of the enveloping mucus either lay in crevices amongst the sand grains, or were slowly rolled away by the over-running stream, the more buoyant fertilized ones were carried away without any difficulty. This indicated that the specific gravity of the latter had been considerably reduced by the erection of their fertilization membranes. Crude artificial fertilizations carried out with freshly spawned eggs and sperm, in the field, indicated the existence of a maturation period comparable to that noted in the laboratory. The eggs were placed in about 500 c.c. of clean sea water in a collecting jar, and a few drops of sperm added. After gentle stirring they were allowed to stand undisturbed for 30 min. When examined at the end of this period few of the eggs had been fertilized, but on further examination after an hour had elapsed the majority of the eggs had erected their fertilization membranes. These eggs remained in almost permanent suspension in the water when disturbed by stirring. The few remaining, unfertilized eggs settled rapidly. Although no control was possible under the circumstances, it seemed fairly certain that the eggs were impregnated by the sperms added, and not by any already present in the water.

Mechanism of Spawning

Since it was not possible to see the animals spawning, except for occasional glimpses of a proboscis at the burrow mouth, the behaviour of the animals during this period must be deduced from the way the genital products are forced out on to the surface.

The gradual outflow of detritus from the burrow prior to the appearance of mucus and, subsequently, of eggs or sperms, indicates a movement of the occupant towards the surface preparatory to spawning. The mucous glands secrete a larger quantity of mucus than usual. Probably the collar contributes a high proportion of the mucus, assisted by the large clusters of glandular cells in the genital and post-genital regions. When the release of the eggs and sperms has begun the animal is thought to retreat slowly to the lower regions of the burrow, continuing to produce large quantities of mucus, and spawning as it does so. After a short period the movement is reversed, and the animal now proceeds to force the mucus along with the enveloped eggs or sperm out of the burrow. This would explain the initial smooth outflow of the mucus cord from the burrow. Eggs and sperms were absent from the first few centimetres of this, possibly because the mucus comprising them was produced by the regions anterior to the gonads, viz. the proboscis, collar and the anterior branchial region of the trunk. The slow rhythmic flowing of the cord, referred to earlier, was probably due to the worm repeating the process. The even rather than patchy distribution of the sexual elements within the mucus indicates that

they are released in an orderly manner and not cataclysmically. This suggests release through the genital pores, rather than by a rupturing of the body wall, a suggestion supported by the absence of evidence of disintegration in any spent specimens examined.

Complete discharge of the genital products does not take place, since the ovaries of adults always contain some large eggs. Specimens might thus spawn more than once in a season. Some were noted where the gonads were asymmetrically placed, an arrangement which might be due to one side discharging its products before the other. The remarkable synchronization between the times of release of the female and male elements indicated that this was an instance of induced spawning. Similar instances of induced spawning have been quoted, and described by Thorson (1946). Whereas the literature revealed the rule that ripe females of various invertebrates will not spawn unless induced to do so by the presence of the active sperm of their own species, the ripe females of *Saccoglossus horsti* spawned first, and seemed to induce the males to spawn. Other marine animals have been known to behave in a similar manner, e.g. *Perinereis marionii* (Herpin, 1925) and *Ostrea virginea* (Galtsoff, 1940), but they are comparatively few in number. Whether or not the inducement subsequently became mutual, as noted by Coe (1947) for *Tivela stultorum*, was not evident, but the result was an 'epidemic' spawning such as that described by Hargitt (1910) for *Hydroides dianthus*, and those quoted by Thorson (1950) for other polychaetes and certain molluscs. The chances of all the eggs spawned being fertilized were thus greatly increased because they were present simultaneously with enormous quantities of sperm in a comparatively small volume of water. Unfertilized eggs were very scarce at the onset of the flood, so that the mode of spawning was seemingly an extremely efficient one.

Laboratory Observations on *Saccoglossus horsti*

Over the past 4 years some 200 mature specimens of *S. horsti*, along with a considerable quantity of their native mud and sand, were transported to Bangor and maintained in a healthy condition for periods of varying duration up to 6 months. This material was required for embryological purposes, so that observations on spawning were incidental. Nanoplankton cultures were provided as food. The aquaria were aerated.

After an acclimatization period of 1 or 2 days, the specimens settled down in burrows which they frequently made along the glass sides of the aquaria. Observation of their behaviour was thus greatly facilitated.

The surface of the mud, particularly in the immediate vicinity of burrows known to be occupied by females, and the interiors of any burrows alongside the walls of the aquaria, were carefully scrutinized at regular intervals daily, for the first 6 weeks after the collection and at less frequent intervals afterwards. Since the aquaria were situated in reduced light, well away from any

sunshine, eggs were difficult to see against the mud and silt which invariably settled in the aquaria. Some illumination was essential, and a small spot-light electric torch proved extremely useful. The beam from this could be directed in through the sides of the aquaria, and along the surface of the mud. Egg clusters illuminated in this way could be seen clearly against the dark substrate. It was also useful for the examination of the remoter regions of the burrows.

Although the author was never fortunate enough to observe any spawning within the 'open' burrows along the walls of the aquaria, several instances of spawn issuing from the burrows were recorded. Although these were in the main exactly as observed in the field, occasions were noted when fertilized and unfertilized eggs were seen to be exuding from the burrows. They flowed out in a manner which suggested that the female was pushing them, for her proboscis appeared at the mouth of the burrow from time to time, as more and more eggs were forced out on to the surface. The tip of the proboscis was observed once, under similar circumstances, in the field.

The enveloping mucus of the egg masses seemed to dissociate more rapidly in the aquaria. Several times eggs were found lying loose on the surface, with no evidence of any mucus around them. Some 50% of these were fertilized when discovered. This suggested that the dissociation of the mucus was not due to the action of the sperm alone, but to other factors, possibly the pH of the surrounding medium.

Sperm clouds observed in the laboratory were dispersed by the aeration currents and were similar to those seen in the field. Microscopic examination of a sample taken from one of these clouds showed that the sperms were solitary, and very active. Isolated samples of naturally and artificially released sperms maintained their vigour for several hours. One sample accidentally raised to 29° C. still contained numerous active sperms.

Fertilizations were carried out with naturally spawned eggs, and artificially as well as naturally released sperms. Freshly spawned eggs did not erect their membranes, after the addition of sperms, as rapidly as those which had been spawned for some time. At 16–17° C. a maturation period of 30 min. to 1 hr. ensued before impregnation could be effected. The eggs remained fertilizable for periods varying from 6 to 10 hr. Mature eggs, released some 2–3 hr. prior to the addition of sperms, erected their fertilization membranes within 10–15 min. On one occasion a few drops of a sperm suspension were injected into the burrows of several ripe females, and small clusters of eggs were observed around the mouths of many of these burrows the following morning, some 10 hr. later. No further experiments of this nature were carried out, but this single observation suggested that the females were induced to spawn by the presence of sperm.

Breeding Season of *Saccoglossus horsti* and *Saccoglossus cambrensis*

Collections were made in the Solent area during the periods 14. vi. 46–16. vi. 46; 20. v. 47–23. v. 47; 7. v. 48–12. v. 48 and 11. v. 49–16. v. 49. Some 400 specimens were examined in all. Collections could not be made earlier than May, but from the general condition of the gonads, and the paucity of spent or partially spent specimens, it was concluded that the first three collections had been made prior to the main spawning crisis for those years, and during the first main crisis for the latter. This conclusion is borne out by subsequent records of spawning in the aquaria, for apart from those stimulated to spawn by the 'shock' of collection, the majority spawned during the following 4–6 weeks. Whilst recognizing that the artificial conditions under which the animals were maintained may influence their behaviour, it is felt that the records of spawning, thus obtained, give some indication of the duration of the breeding season and the conditions under which it probably takes place.

Spawning was first recorded in the laboratory by Dr E. W. Knight Jones on 20. v. 46, and subsequently by the author from 17. vi. 46 to 15. vii. 46; 25. iv. 47 to 30. v. 47; 18. v. 48 to 1. vi. 48, and on three occasions 15. v. 49, 1. vi. 50 and 2 .vi. 50 in the field. These records were mainly of one, often two, rarely three specimens spawning in any one day. There was never any indication of a concerted effort comparable to the field records.

Temperature records show that specimens will spawn over a fairly wide range, from 13·5 to 21·0° C. A temperature rise prolonged over 2 or 3 days invariably resulted in some specimens spawning. Some 60% of the records were made at 16–17° C., 30% below, and the remainder above. Many eggs were spawned at comparatively low temperatures (14·5° C.) and failed to develop beyond the 3rd or 4th cleavage. Others spawned at higher temperatures (20° C.) suffered the same fate, but those produced between 16 and 17° C. developed normally and the larvae were successfully reared until they had several pairs of gill-apertures.

The occurrence of several spent specimens amongst those examined from the Solent collections of June 1946 indicated that some spawning had already taken place, probably during the previous spring tides. Air and sea temperatures in the area for this period were suitable, and rose from 11·1 to 15·6° C. during the period 27. v. 46–30. v. 46, whilst the main Southampton water was *c.* 14·4° C. Inshore temperatures would have been proportionately higher, particularly in the sheltered regions, and thus ideal for spawning.

In the collections of May 1947 a fairly high proportion of immature specimens was noted, and the impression gained was that spawning had not yet commenced for that season, but it did so in the laboratory some 4–5 days later.

Specimens collected during May 1948 were extremely ripe, and very difficult to handle without causing injury. Several hot days followed their

transfer to the laboratory, and spawning commenced on the 18th, a week after they had been collected. The extreme ripeness of the numerous specimens observed in the field indicated the imminence of a spawning crisis, possibly the first of the season, for spent specimens were very rare. Air temperatures for the period 7. v. 48–11. v. 48 rose from 11·1 to 15·6° C., the sea temperature rising from 12·2 to 14·4° C., but the air temperature dropped to 13·3 °C. the next day, and subsequently to 10° C. for the 13th and most of the 14th. This might well have delayed the spawning until the next temperature rise took place during the afternoon of the 14th, when it rose to 16·7° C., and then to 20° C. on the 15th. Temperatures remained at about this level throughout the next few days, but since the tides had lapsed into neaps during this period it is thought that the full effect of the rise would not be felt, and that in all probability spawning did not start until the onset of the next series of spring tides when there were several warm days and maximum air temperatures varied from 19 to 22° C.

At the time of the mass spawning in the Solent (15. v. 49) the temperature of the shallow surface water in the inlet during the ebb was 17·5° C., and that of the sand varied from 15 to 16° C. according to the degree of exposure to the sun. The temperature at a depth of 6 in. in the sand was some 2° C. below that recorded at the surface. The sea temperature[1] was at 12·8° C. on that day, having risen steadily from 11·6° C. recorded on 8. v. 49, whilst the air temperature had risen with slight fluctuations from 7·8° C. at 18.00 hr. on 11. v. 49 to 14·4° C. at 12.00 hr. and to 16·7° C. at 18.00 hr. on 15. v. 49. The phenomenon was repeated on two successive occasions during the spring tides of June, 1950. The beds had been examined during the ebb tides of the previous four days, but it was not until the afternoon ebb of 1st June that spawning commenced. In every respect the progress of events was comparable to those observed in 1949. Spawning began some 30 min. after the tide had receded, and was mainly confined to those areas of the beds which were covered by shallow pools. The temperature of the water in these pools was 21° C., and that of the underlying sand was 17° C. at a depth of 6 in. below the surface. Although several egg masses were observed within a few minutes of the discovery of the first it was some time before the first sperm cloud was seen. The intensity of spawning was greater than that experienced previously, and an arbitrarily chosen square metre of the shore contained 125 casts, 21 egg masses and 5 sperm clouds. The production of egg masses reached its climax some $1\frac{1}{2}$–2 hrs. after the tide had ebbed, whilst the production of sperm clouds continued vigorously until the flood had commenced, when it abated markedly. Examination of the area at 6 a.m. the following morning failed to reveal any traces of the spawning. The water in the surface pools at this hour had fallen to 17·2° C., but that of the sand remained at 17·0° C. During the afternoon

[1] The sea temperatures quoted are for the main Southampton Water, unless otherwise stated.

ebb of this day the water temperature rose to 21·5° C. and that of the sand to 17·5° C., and spawning commenced as on the previous day.

Since similar weather and tidal conditions prevailed for the succeeding two days it is likely that the intermittent spawning would continue until the tides lapsed into neaps. A temperature rise seems to have played a major part in initiating the mass spawning observed on these three occasions, for they all occurred after the shore had been subjected to hours of fairly intense sunshine over a period of several days. Orton (1920) and Thorson (1946, 1950) have shown that temperature influences the spawning of numerous marine invertebrates. Korringa (1947) cites several examples where tidal influences also play an important part. It would seem that both factors are probably concerned in the spawning of *S. horsti*.

Specimens of *S. cambrensis* have been examined at all times of the year, and whereas they were apparently always ripe, there was very little evidence of any spawning. A close inspection of the more densely populated areas in the Menai Straits made during the spring tides of June and July 1949, yielded several empty egg cases. These were discovered in the sand around the mouths of burrows. They were very similar to those of *S. horsti*, but in the absence of any embryos the identification must remain uncertain. One egg contained a cream-coloured ovoid embryo which was densely ciliated, and very like the late gastrula stage of *S. horsti*. It rapidly disintegrated in the laboratory, so that little else can be said about it. Tow-nettings with a no. 15 bolting silk net were made over the surface of the sand just prior to its exposure by the receding tide. These yielded several more empty egg cases, all of the same size and appearance. Since these were discovered within a short period of the mass spawning in the Solent, and under comparable weather conditions, it is possible that a spawning had already taken place in the Menai Straits and that the egg cases were the remnants of eggs which had hatched either in the burrows and were subsequently expelled, or in amongst the sand grains on the surface. Some fifty specimens of a *Saccoglossus* species (Burdon-Jones, 1950*b*) examined in the Sound of Mull, during the spring tides of August 1948, revealed that ripe females and, to a lesser degree, ripe males, were comparatively rare. Numerous specimens were difficult to sex because they were either spent, or immature. The impression gained was that the main spawning, for that year, had already taken place. Numerous adult specimens of a species of *Protoglossus* (Burdon-Jones, 1950*a*) were examined during August, September and October 1949, and although mature specimens of both sexes were collected, they were very much in the minority, the paucity being most pronounced amongst the females. These observations, once more, suggest a breeding season at some time during the preceding few months, viz. May to July.

It would seem that the main spawning season for the British species of the Harrimanidae is mainly during the months of May to July. Mass spawning comparable to that described for *Saccoglossus horsti* is likely to be common to them all and to take place under similar climatic and tidal conditions.

Discussion

In the light of this new information, it remains for us to examine what is known of the spawning behaviour in the other species of Enteropneusta.

Bateson (1884) suggested that in *Saccoglossus kowalevskyi* the eggs and sperms, the latter aggregated in lobate masses, were released by a rupturing of the body wall. Spengel (1893) pointed out the improbability of this, basing his arguments on the mode of maturation of the gonads. His comments were borne out by the discovery of large genital apertures in mature *Glossobalanus ruficollis*, which Willey (1899) noted would enable eggs to be released without any difficulty. There was no evidence of rupturing in *Saccoglossus horsti*, or any evidence of increased mortality amongst spawning specimens in the laboratory or in the field. Rupturing and spermatophoric masses have been observed only in one other species, viz. *S. otagoensis* (Kirk, 1937, 1938), but this is a rock-pool inhabitant, and has a specialized mode of spawning in keeping with its habitat.

For *S. pusillus* Ritter & Davis (1904) recorded mature specimens in August, and suggested that the breeding season extended over at least 4 months. Davis (1908) discovered that the main breeding season was in January and February. The genital products were released through the genital apertures as in *S. horsti*, but the eggs were discovered closely packed and somewhat flattened, and adhering to the walls of inhabited burrows. Their appearance and situation suggests that they were not expelled with the main clutch, but had been pressed into the mucus lining of the burrow whilst spawning was taking place. In this position they could be fertilized by sperms carried into the burrow by the aerating currents of the animal within it, and thus aerated and protected they would develop. In the light of the observations on *S. horsti* however, these eggs might be regarded as a remnant of the main egg mass which had been expelled from the burrow and probably washed away by the tide, or camouflaged by silting. Since the habitat was a muddy one, this could easily have occurred and, in consequence, the eggs might well have been overlooked.

Stiasny (1913) made comparable observations on *Balanoglossus clavigerus*. It is significant that he noticed eggs were easily overlooked within the burrows because their colour closely resembled that of the sand. Under such circumstances it is probable that they might also be overlooked if lying on the surface.

On this interpretation, spawning of *Saccoglossus pusillus* may be comparable to that noted in *S. horsti*, and so also might that of *Balanoglossus clavigerus*, for Heider (1909) recording observations made on specimens in the laboratory noted:

> Am 12. Juni, um 6 Uhr nachmittags fand sich an der Mündung einer solchen Wohnröhre ein schleimiger Laichklumpen von etwa Nussgrösse. Der Schleim, in welchem Hunderte von Eiern eingeschlossen waren, ist ungemein zerfliesslich, und nachdem der Laich herauspipettiert war und das Gefäss in welchem er sich nun befand, einigem Schütteln ausgesetzt war, löste er sich scheinbar vollständig auf.

Because the observations were made on specimens in an aquarium, van der Horst (1927–39) queried the probability of such egg masses occurring in the field. Nevertheless, they occurred in *Saccoglossus horsti*, both in the laboratory and on the shore, so that we must regard Heider's observations as being indicative of a similar occurrence in *Balanoglossus clavigerus*, although this was never confirmed by Stiasny.

Kowalevsky (1866) made the supposition that, 'Es ist wahrscheinlich, dass der *Balanoglossus* Eierschnüre legt, in der Art, wie es die meisten Nemertinen und viele Anneliden thun', but Agassiz (1872) failed to find any whilst working on *Saccoglossus kowalevskyi*. Subsequently, this theory was strongly deprecated by Spengel (1893) on the grounds that the gross morphology of the gonads would make it impossible. The observations on *S. horsti* tend to invalidate this statement, for when first expelled from the burrow the eggs of this species are in a cord which coils on itself and rapidly fuses into a single mass. The existence of such cords is not necessarily universal, but they have also been described in *Glossobalanus minutus* (Dawydoff, 1928). The persistence of the cord undoubtedly depends on the conditions under which it is expelled from the burrow. Certain specific variations might well occur.

From the above observations and those of Russell (1925) and others, on the seasonal occurrence of enteropneust larvae in the English Channel, North Sea and various parts of the world, and the large numbers of Tornaria larvae of the same size that are often found together, it might be concluded that an 'epidemic' spawning comparable to that described for *Saccoglossus horsti*, and initiated and perpetuated in a similar manner, is common to all the littoral and possibly some sub-littoral species of the families Ptychoderidae and Harrimanidae.

Summary

The genital products of *Saccoglossus horsti* are discharged within the burrows and expelled after the tide has ebbed. They are not retained in the burrows for any length of time.

Fertilization occurs mainly in the overlying surface water, or during the flood.

An 'epidemic' spawning was observed on three occasions in the field.

A rise of temperature to about 16° C. is regarded as the essential factor primarily responsible for initiating the spawning.

The females were observed to spawn before the males. Some reciprocal inducement might have occurred.

The breeding season in the Solent area is mainly confined to the months of May, June and July, and is seemingly dependent on climatic and tidal conditions during these months.

The spawning behaviour of other species of the Enteropneusta is discussed.

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THE IDENTIFICATION OF BRITISH SPECIES OF THE GENUS *ENSIS* SCHUMACHER (LAMELLIBRANCHIATA)

By N. A. Holme, B.A.

Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1–5)

Introduction

Winckworth (1932) lists three British species in the genus *Ensis* Schumacher. Two of these, *E. ensis* (L.) and *E. siliqua* (L.), are recorded by Linnaeus in the genus *Solen*; the third, *E. arcuatus* (Jeffreys), was considered by Jeffreys (1863) to be a variety of *E. siliqua*. Winckworth has, however, raised it to specific rank, without giving any reasons. In the present paper Winckworth's classification is followed, a note on the validity of the species appearing at the end.

Examination of specimens in various collections has revealed the confusion that has arisen in the identification of the species of *Ensis*: consequently many records are unreliable. Identification has proved difficult partly on account of a dearth of good illustrations of the three species, and also through the lack of any diagnostic distinguishing characters. Although *E. siliqua* is illustrated in many works, there are few good drawings of *E. ensis*, and some (Sowerby, 1887, for example) have illustrated *E. arcuatus* as *E. ensis*. Forbes & Hanley (1853) have an engraving of *Solen ensis* var. *magna* (=*E. arcuatus*), but failed to illustrate *Ensis ensis*.

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I am grateful to the Linnean Society of London for allowing me to examine type specimens; and to Dr R. Tucker Abbott, Division of Mollusks, U.S. National Museum, for kindly supplying photographs of Jeffreys' original specimens of *E. arcuatus*.

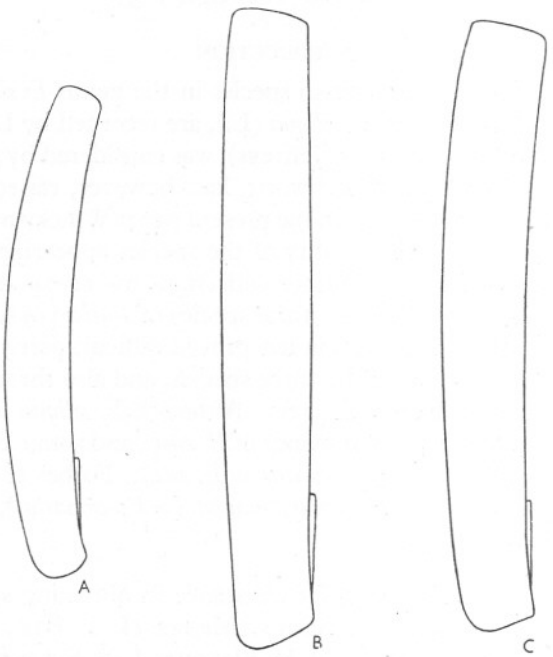
The Genus *Ensis*

The genus *Ensis* comprises lamellibranchs with elongate equivalve shells, gaping at either end. The anterior end of the shell is not constricted, and the

hinge is terminal, having two teeth in the left valve, between which fits the single tooth of the right valve. There is a long external ligament. The two siphons are short and are surrounded by cirri. A fourth pallial aperture is present.

Distinguishing Characters

In several of the distinguishing characters to be described there is some overlap owing to variation among individuals of a species. Consequently it is often necessary to employ all the available characters before a 'difficult' specimen can be identified.



Text-fig. 1. Outline of *Ensis* shells, ×3/5. A, *E. ensis*; B, *E. siliqua*; C, *E. arcuatus*.

The Shell

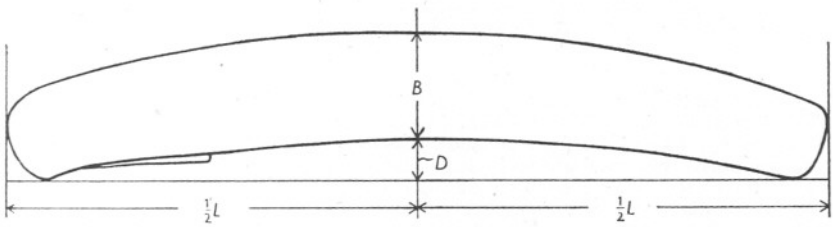
This remains the primary means of identification, both of the genus and species. The shell of *Ensis* is elongated along its anterior-posterior axis. Hence the pedal end is morphologically anterior, and the siphonal end is posterior. The long edge bearing the hinge is dorsal.

Length. The length attained by adult specimens differs in the three species. *E. siliqua* reaches a maximum of 20 cm., while *E. arcuatus* and *E. ensis* attain 15 and 10 cm. respectively. In many populations, however, these lengths are not reached, and Text-fig. 3 gives some indication of the lengths usually encountered.

Length/breadth ratio. Measurements of shell breadth are made as shown in Text-fig. 2. Results obtained from measurements of about 100 specimens from different localities are shown in Text-fig. 3, and summarized in Table I. The mean ratio is 6·80 in *E. siliqua*, 7·18 in *E. arcuatus*, and 7·80 in *E. ensis*. The range in proportions within each species is such, however, that there is some overlap between the species. In *E. siliqua* the shell tends to broaden in larger sizes, in *E. arcuatus* it remains fairly constant, whereas in *E. ensis* there is a tendency for it to become narrower.

Ford (1925) found a difference in the proportions of very small specimens of *E. ensis* and *E. arcuatus*. (He does not state, however, at what point the shell breadth was measured.) In *E. arcuatus* ranging from 7·5 to 21·0 mm. in length the mean ratio was 5·08, and in *E. ensis* ranging from 5·0 to 22·5 mm. the mean ratio was 6·44. Here again there was some overlap between the two species.

Thus the length/breadth ratio is not a reliable distinguishing character where only a few specimens from a population are available.



Text-fig. 2. Method of measuring breadth (*B*) and curvature (*D*) of an *Ensis* shell.

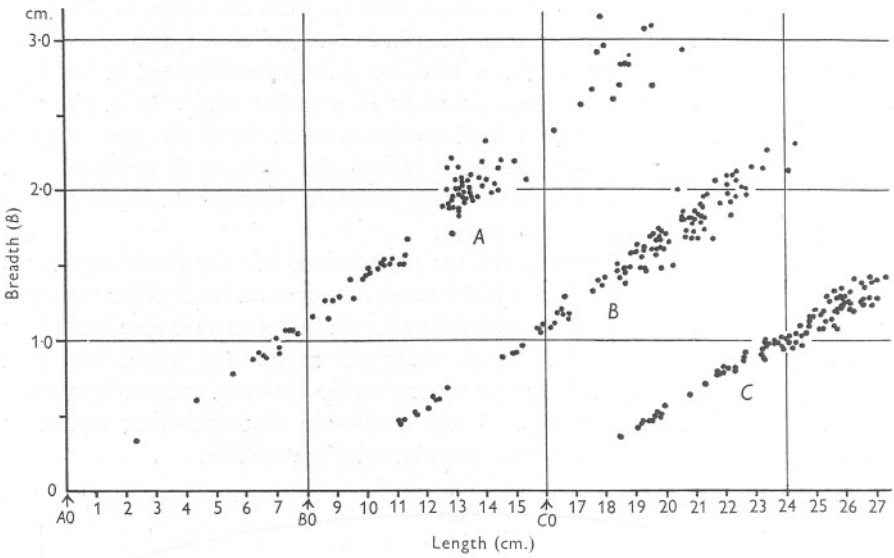
Curvature. The most obvious difference between the species is in the shell curvature. A measure of the curvature of the dorsal edge of the shell is obtained as shown in Text-fig. 2. The dorsal edge of a single valve is placed against a straight edge on a special measuring board, so that the two ends touch the edge. The ligament is cut away as necessary to allow this. In *E. siliqua* the shell usually touches at the anterior end and at a point just behind the mid-region, as the shell is often slightly convex on the dorsal surface. The distance $B+D$ is measured by a vernier calliper, as is the breadth (B). 'D' is then obtained by subtraction.

In *E. siliqua* most specimens are straight or slightly convex, (Text-fig. 4) giving a 'D' of zero. 'D' is not more than 0·1 cm. in normal specimens. Two very small specimens show some degree of curvature; this results in a slight curvature in the hinge region in adult specimens.

In *E. arcuatus* curvature is variable, some being as straight as slightly curved specimens of *E. siliqua*.

In *E. ensis* curvature is greater than in *E. arcuatus*, the plots of the two species scarcely overlapping.

It will be noticed that 'D' becomes proportionately greater in large specimens. This is to be expected if the shells are growing in a curve approximating

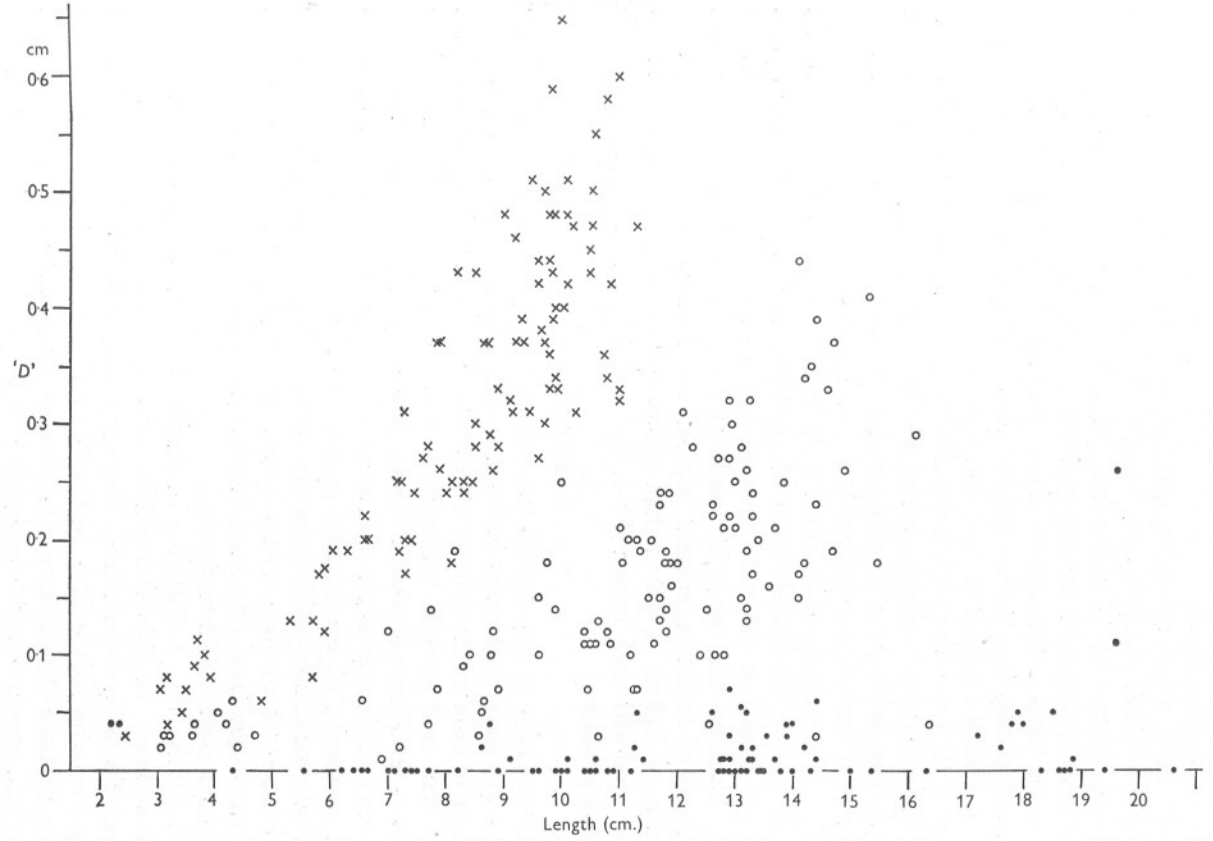


Text-fig. 3. Length-breadth relations of shells of *Ensis*: *A*, *E. siliqua*, 95 specimens from Broadsands, Torbay (6); Dale Roads, Milford Haven (6); Helford river, Cornwall (3); Millport (9); Paignton (59); Polesands, Exmouth (7); Salcombe (5). *B*, *E. arcuatus*, 112 specimens from Derbyhaven, Isle of Man (4); Eddystone shell-gravel (1); Grouville Bay, Jersey (10); Mewstone shell-gravel, Plymouth (1); Millport (3); Newton Haven, Northumberland (2); Salcombe, (52); Tresco, Scilly Is. (16); Yealm river (23). *C*, *E. ensis*, 101 specimens from Broadsands, Torbay (6); washed up on Dawlish Warren Beach (44); Grouville Bay, Jersey (5); St Aubin's Bay, Jersey (26); Salcombe (20). All shells are from material collected alive, except for some of those from Dawlish Warren Beach.

Note that the plots of *A*, *B* and *C* have different origins (indicated by arrows).

TABLE I

	Shell length (cm.)	Number examined	Length/breadth ratio		
			Mean	Maximum	Minimum
E. siliqua	0 – 4·0	1	7·06	—	—
	4·1– 8·0	13	7·09	7·72	6·28
	8·1–12·0	21	7·06	7·54	6·74
	12·1–16·0	44	6·67	7·50	5·84
	> 16·0	16	6·55	7·26	5·66
	All sizes	95	6·80	7·72	5·66
E. arcuatus	0 – 4·0	6	6·92	7·16	6·49
	4·1– 8·0	12	7·23	7·61	6·65
	8·1–12·0	46	7·20	8·29	6·71
	12·1–16·0	46	7·17	8·17	6·20
	> 16·0	2	7·32	7·56	7·08
	All sizes	112	7·18	8·29	6·20
E. ensis	0 – 4·0	11	7·20	7·64	6·83
	4·1– 8·0	28	7·66	8·39	7·20
	8·1–12·0	62	8·01	9·07	7·25
	All sizes	101	7·80	9·07	6·83



Text-fig. 4. Measurements of shell curvature ('*D*', Text-fig. 2) against shell length. The shells are those used for breadth measurements in Text-fig. 3. ×, *E. ensis;* ○, *E. arcuatus;* ●, *E. siliqua.*

to an arc of a circle. The points would then form part of an ellipse, the proportions of which would naturally vary according to the scale adopted for the two axes of the graph.

Taper. In *E. siliqua* the dorsal and ventral edges are almost parallel, with little taper at either end (Text-fig. 1 and Pl. I, fig. 1). In *E. arcuatus* there is some slight taper at the posterior end. In *E. ensis*, however, the ventral edge approaches the dorsal in the posterior third of the shell, producing a most pronounced taper. Although no measurements of taper have been made it would appear that the degree of taper in extreme specimens of *E. arcuatus* is similar to that of a typical *E. ensis*, and vice versa.

Shape of the ends. The posterior end of the shell in all three species is truncated, that of *E. ensis* being if anything a little more rounded than in the other two. The anterior ends of *E. siliqua* and *E. arcuatus* are similarly truncated, but that of *E. ensis* is rounded, as shown in Text-fig. 1.

Colour. The outside of the shell is divided diagonally into two areas of a different colour. The dorsal area is white or liver-coloured, while the ventral area varies from pale yellow to chestnut brown in colour. *E. ensis* is usually lighter in colour than the other species, but all shades from yellow to dark brown may be found in different populations of all three species. Small individuals are lighter in colour than adults from the same locality, and are often spotted with dark brown (Pl. I, fig. 2). The spots disappear or become indistinct in adults.

Soft Parts

Bloomer (1901–2) has studied the anatomy of *E. ensis* and *E. siliqua*. He found only minor differences between them, of little value in identification. Mr Bloomer informs me that his specimens were obtained from the Specimen Department at Plymouth. Since *E. ensis* is rare at Plymouth, most of the records in the *Plymouth Marine Fauna* (Marine Biological Association, 1931) being incorrect identifications of *E. arcuatus*, it seems possible that Bloomer was in fact comparing *E. arcuatus*, not *E. ensis*, with *E. siliqua*.

The internal anatomy of *Ensis* has not been examined in any great detail. The gross anatomy of all three species is very similar. Sections of the gills failed to show any significant differences in structure. Two characters have, however, been found useful for identification.

Colour of the foot. A difference in the colour of the foot has been noted by several authors. In *E. siliqua* and *E. arcuatus* it is creamy white in colour, reticulated with fine brown lines. The colour varies with the degree of distension or contraction of the foot. In *E. ensis* the foot is a pale reddish brown, and is also reticulated. The difference in colour is not great, but is useful in sorting out a mixed population of *E. ensis* and *E. arcuatus*.

The fourth aperture. In the posterior half of the body the mantle edges are fused ventrally, but anteriorly fusion is very weak, so that the mantle folds may be readily separated back as far as a small opening, the fourth aperture

(Text-fig. 5,A). The weak fusion is brought about by a cuticular junction of the mantle edges (Atkins, 1937).

Yonge (1948) believes the aperture to be a 'safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement'.

The aperture is bordered by a row or rows of papillae, which interdigitate when the shell is closed. The papillae occur in about equal numbers on each side of the aperture. There is considerable variation in the number of papillae in each species, but *E. siliqua* tends to have more than the other two:

E. siliqua. Thirty-four specimens from Paignton, Devon. Number of papillae on one side of the opening: mean, 20·9; maximum, 40; minimum, 9.

E. arcuatus. Forty-two specimens from Tresco, Scilly Isles. Mean, 10·5; maximum, 26; minimum, 5.

E. ensis. Twelve specimens from St Aubin's Bay, Jersey. Mean, 12·0; maximum, 15; minimum, 8.

The species differ more in the form than in the number of papillae. In *E. siliqua* the papillae occur in more than one row, in a staggered arrangement. In small specimens they are simple (Text-fig. 5,G) but in those over about 7 cm. in length they are branched, or compound (Text-fig. 5,B, E and F). In side view they often resemble molar teeth. The form of the papillae can be distinguished with a lens in living specimens. Those illustrated in Text-fig. 5 are preserved in alcohol; the papillae do not seem to contract to any great extent in preserved specimens.

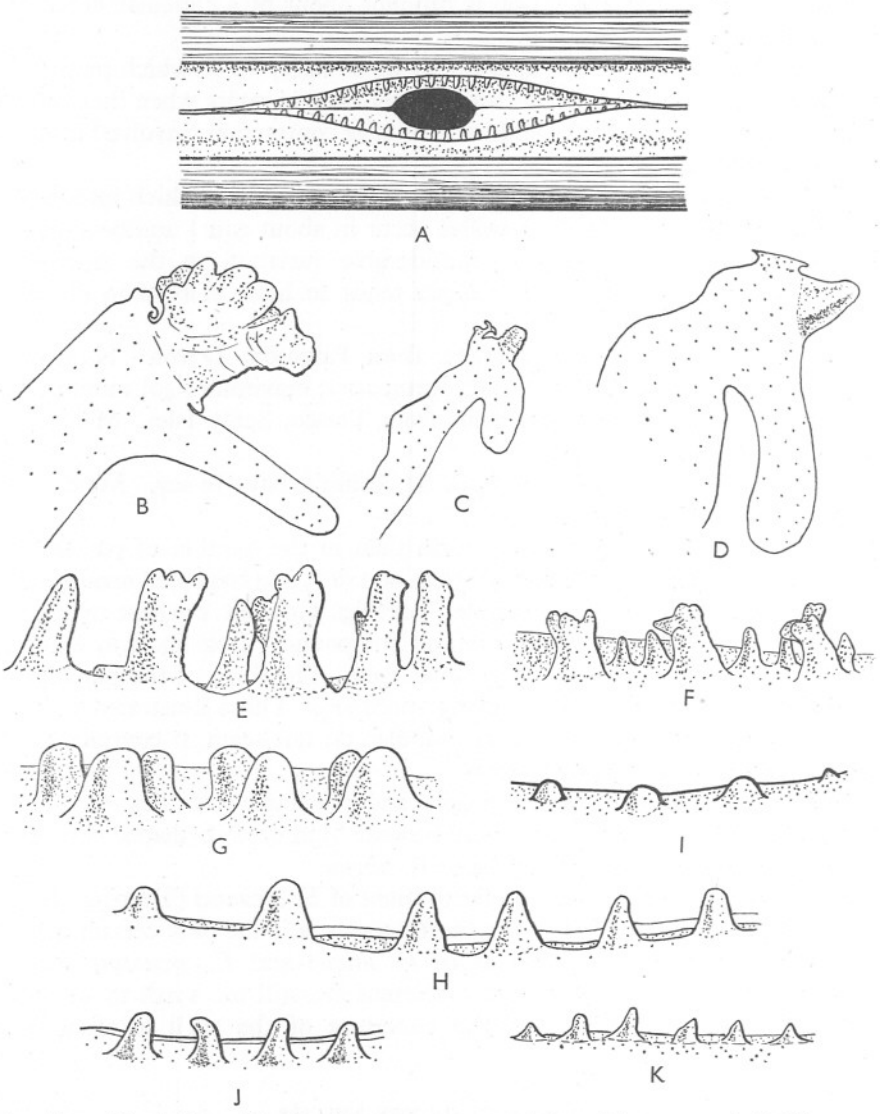
In *E. arcuatus* the papillae are simple, and in a single row (Text-fig. 5,H, I). Rarely, in large specimens, they may become bifid or club-shaped, but never assume the compound form typical of *E. siliqua*.

In *E. ensis* the papillae are similar to those of *E. arcuatus* (Text-fig. 5,J, K).

The form of the papillae of the fourth aperture is the only certain method of distinguishing adult specimens of *E. siliqua* and *E. arcuatus*. Certain separation is more difficult where specimens are still too small to show differences in these papillae, but the curvature of the shell is often some guide.

Validity of the Species

Constant morphological differences have been found between the three species of *Ensis*. These differences are slight however, and might be attributable to the effect of environment on a single species. *E. siliqua* occurs in clean sand at L.W.S.T., extending a little below extreme low-water mark. *E. arcuatus* lives in coarse sand or fine gravel at L.W.S.T., and extends out into deeper water. *E. ensis* inhabits bottoms of fine, sometimes slightly muddy, sand; rarely occurring on the shore. Thus the three species are not often found living together.



Text-fig. 5. Morphology of the fourth aperture. A, ventral view of the aperture in *E. siliqua*, × 4. The shell is shown slightly gaping to reveal the mantle folds surrounding the opening. The anterior end is to the left. B–D, thick sections through the edge of the mantle opposite the aperture, the latter being on the right of the lip (lower right). A papilla (compound in *E. siliqua*) is shown top right. B, *E. siliqua*; C, *E. ensis*; D, *E. arcuatus*. All are × 19·5. E–K, papillae viewed from inside the aperture, looking outwards: E, *E. siliqua*, length 15·0 cm., × 19·5; F, *E. siliqua*, length 13·7 cm., × 19·5; G, *E. siliqua*, length 7·0 cm., × 59; H, *E. arcuatus*, length 14·75 cm., × 19·5 (all papillae on one side shown); I, *E. arcuatus*, length 7·9 cm., × 19·5; J, *E. ensis*, length 10·05 cm., × 19·5; K, *E. ensis*, length 4·52 cm., × 19·5.

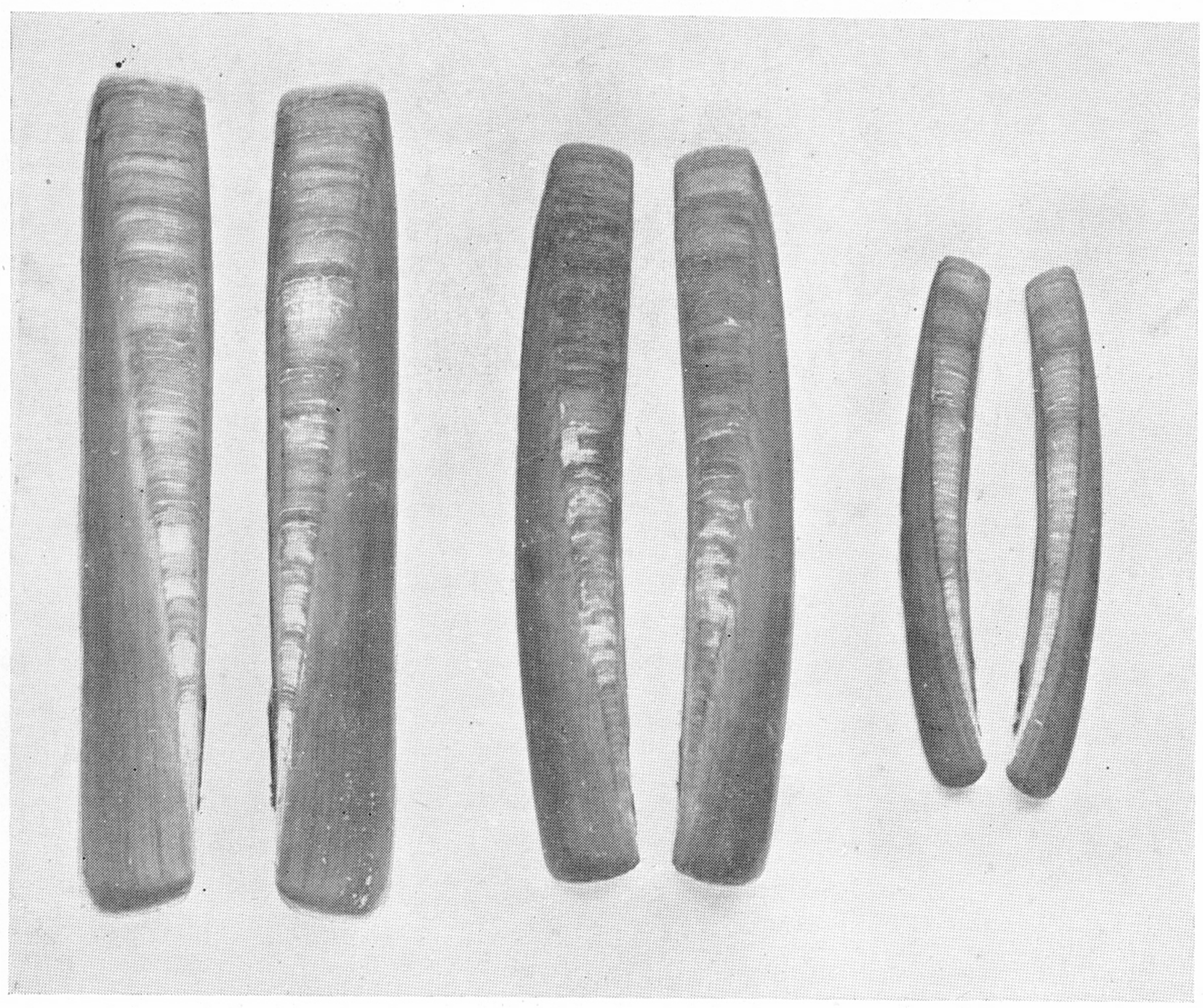


Fig. 1. Shells of adult *Ensis*. ×0·47. Left to right: *E. siliqua*, *E. arcuatus*, *E. ensis*.

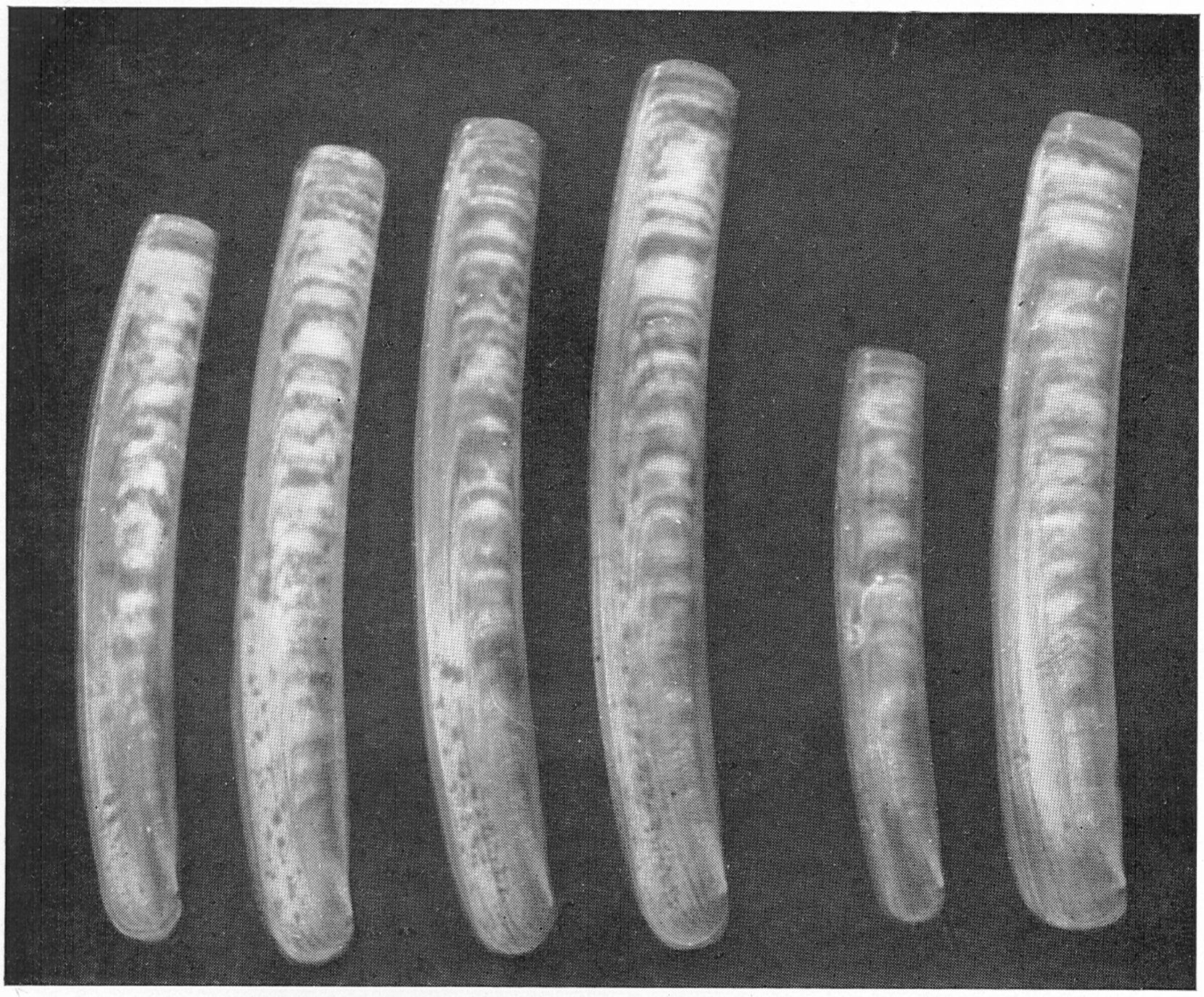


Fig. 2. Small individuals of *Ensis*. ×2·4. Left: four specimens of *E. ensis* dredged in Whitsand Bay. Right: two specimens of *E. arcuatus* from the same locality. The foot may be seen projecting beyond the end of the shell in some of the specimens.

Occasionally, however, mixed populations have been found living in the same grade of soil in one locality. The following instances have been recorded:

E. siliqua living with *E. ensis*: Broadsands, Torbay, in fine sand.

E. siliqua living with *E. arcuatus*: south side of Millbay, Salcombe, in fine sand; Jeffreys (1863) records both species from Belgrave Bay, Jersey.

E. arcuatus living with *E. ensis*: in sand in St Aubin's Bay and Grouville Bay, Jersey, in Whitsand Bay, and in coarse muddy sand at Millbay, Salcombe.

Since the three forms maintain their distinctive characters when living together, it seems probable that they are separate species.

Summary

The diagnostic characters of the British species of *Ensis* are described. The shell remains the primary means of identification, but additional characters in the soft parts are necessary for certain recognition. The three forms of *Ensis* described are considered to be valid species.

Table II. Summary of Distinguishing Characters

	E. siliqua	*E. arcuatus*	*E. ensis*
Length of shell	20 cm.	15 cm.	10 cm.
Shell curvature	Straight	Slightly curved	More curved than in *E. arcuatus*
Taper of posterior end	None	Slight	Marked taper
Anterior end	Truncated	Truncated	Rounded
Foot colour	Cream-white	Cream-white	Pale red-brown
4th aperture:			
Rows of papillae	Staggered	1 row	1 row
Shape of papillae	Compound	Simple	Simple

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A STATISTICAL STUDY OF VARIABILITY IN CATCH OBTAINED BY SHORT REPEATED TRAWLS TAKEN OVER AN INSHORE GROUND

By H. Barnes and T. B. Bagenal

The Marine Station, Millport

(Text-figs. 1–3)

Introduction

The numerous quantitative studies on various types of fishing gear have always been chiefly directed to the relation between the proportion of size-groups in the sample and in the population, and to the effect of mesh size on this relation. There have been only a small number of controlled experiments on the variability of replicate samples. While the former type of information is fundamental in fishery investigations, the latter, equally necessary, becomes an essential preliminary in a detailed ecological approach to fishery problems, for it is then necessary to know whether hauls taken at different times or in different places have given significantly different catches.

Thompson (1928) considered sampling problems in his extensive haddock investigations. Data are given from two series of hauls (using a 60 or 50 ft. otter trawl), each series extending over several days; and he points out that these samples (1 hr. trawling, *c.* 350 fish per catch) gave an adequate representation of the proportion of size-groups. Using logarithmic values of his catches (see below) the coefficients of variation were 27 and 51 % for the two series.

Hickling (1933), using a full-sized trawl and working on hake, also gives data for repeated hauls taken under various conditions, although like Thompson he was more particularly concerned with the size-frequencies in his samples. The coefficient of variation for catches (log values) of hake varied from 25 to 88 %, this range including results from R. V. *George Bligh* and from commercial trawlers.

Gardiner & Graham (1925) have considered the working error of Petersen's young fish trawl, and the design of these experiments was similar to that of the present work. They counted a number of species in ten replicate hauls and they give coefficients of variation calculated on actual numbers varying from 27 % for *Euthemisto compressa* to 54 % for *Aglantha digitalis*. The analysis of variance of their data (log values) using those animals occurring in all samples is given in Table I.

The mean square for hauls is significant when tested against $H \times S$ and the estimated log standard deviation for a single observation $\sqrt{s_H^2 + s_{HS}^2}$ is 0·1936, corresponding to a coefficient of variation of 56%.

TABLE I

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	9	0·9835	0·1093
Species (S)	6	28·2730	4·7120
Residual			
$H \times S$	54	1·3792	0·0255
Total	69	—	—

This present work consists of the analysis of the variability of a series of replicate hauls taken over a prescribed ground with the same gear and as far as possible under controlled conditions. In order that the results shall be of value to other workers it is necessary to describe both the gear and working conditions in some detail.

METHODS

The Gear and Method of Working

A standard type V.D. trawl, as described by Davis (1936, p. 104), was used, the detailed specifications being as follows: doors, 7 ft. 3 in. × 3 ft. 10½ in.; bridles, 20 fathoms; headline (fitted in part with Phillips's patent plane floats), 54 ft.; foot rope, 72 ft.; size of meshes, wings 5 in., square 5 in., belly 3½ in., cod-end 3 in.

The trawl was shot and hauled in the usual manner (Davis, 1936) from the M.V. *Calanus* under the supervision of Captain R. Souter.

The Ground and Working Conditions

The area trawled was an inshore ground on the east side of Bute, in the vicinity of Scoulag Point (full Kilometre National Grid Reference 26/1160–1159). A dan buoy was laid down and each haul was made on a somewhat elliptical course over the ground, starting and returning to the buoy. Positions were also checked by conspicuous objects on the shore. The bottom, which is here a sandy mud at 20 fathoms, shelves towards the centre of the channel. Tidal currents in this area are of the order of 1½ knots. During the trawling echo-soundings were taken, and are shown in Fig. 1, which indicates that each set of hauls was consistently taken over similar ground.

Three series of four replicate hauls were taken. Each haul lasted 30 min.; including shooting and hauling, each set of four hauls, all taken between 10.30 and 14.30 hr., occupied 3 hr. The weather conditions during all three series were moderate to good.

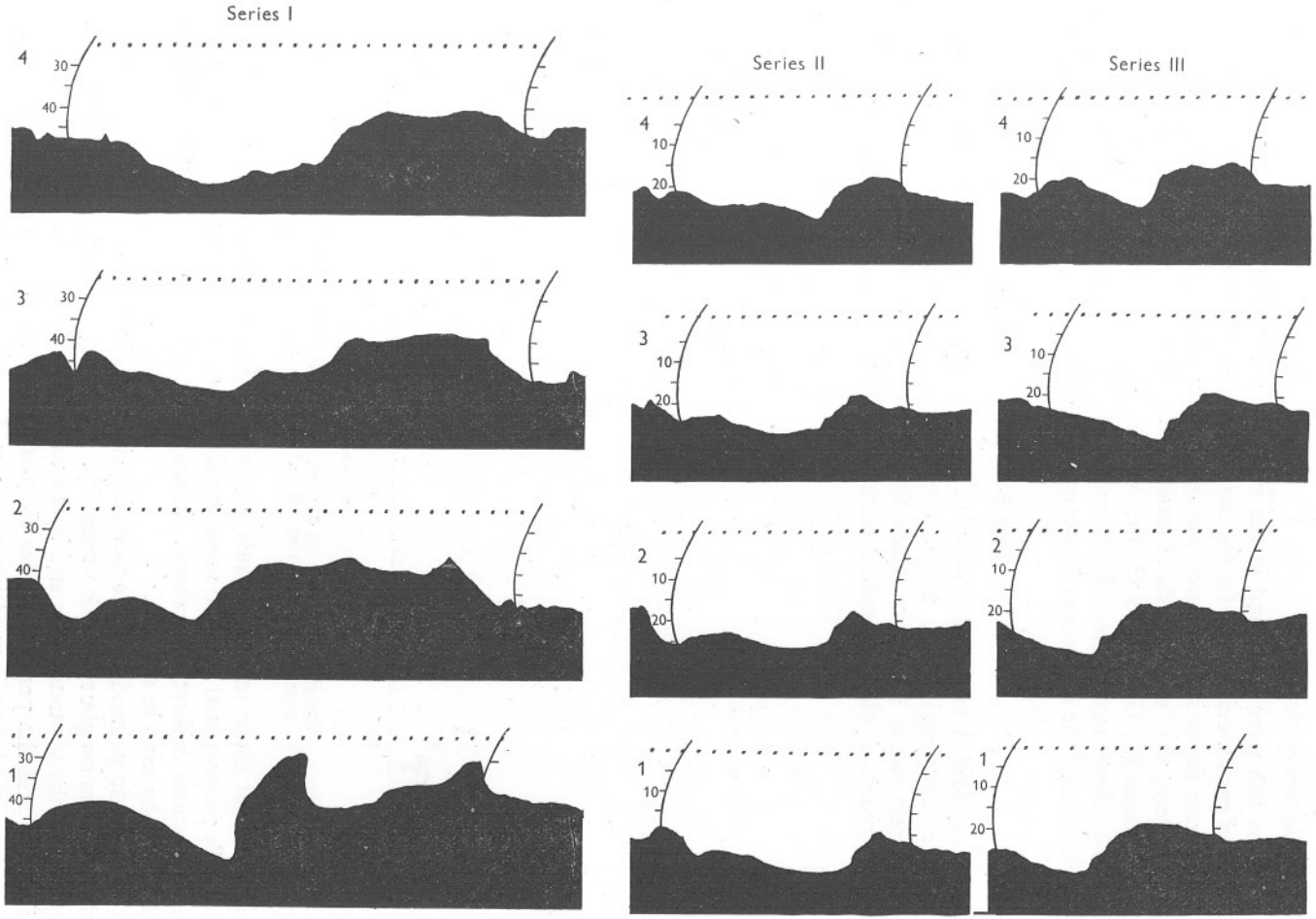

Fig. 1. Echo-soundings for hauls 1–4, series I–III. Series I time-marks at minute intervals; depth in metres. Series II (the echo-sounder was changed during the experiments) and III time-marks at 2 min. intervals; depth in fathoms. Marks at shooting and hauling.

The Collection of the Data

All the fish were measured in the standard manner, and a representative sample of each species taken for the examination of the stomach contents. The invertebrate fauna in each catch was also identified and counted. The major species were, the 'round' fish, *Acanthias vulgaris* Risso, *Gadus callarias* L., *G. merlangus* L., *G. minutus* O. Fr. Müller, *Merluccius merluccius* (L.); the 'flat' fish, *Pleuronectes platessa* L., *P. cynoglossus* (L.), *Drepanopsetta platessoides* (O. Fabricius); the crustacean *Nephrops norvegicus* L.

The Results

If the standard deviation of a series of catches is roughly proportional (as in plankton sampling) to the mean, a transformation from actual catches to logarithmic values should be made for the analysis of variance (Winsor & Clarke, 1940). A plot of standard deviation against mean catch for all species

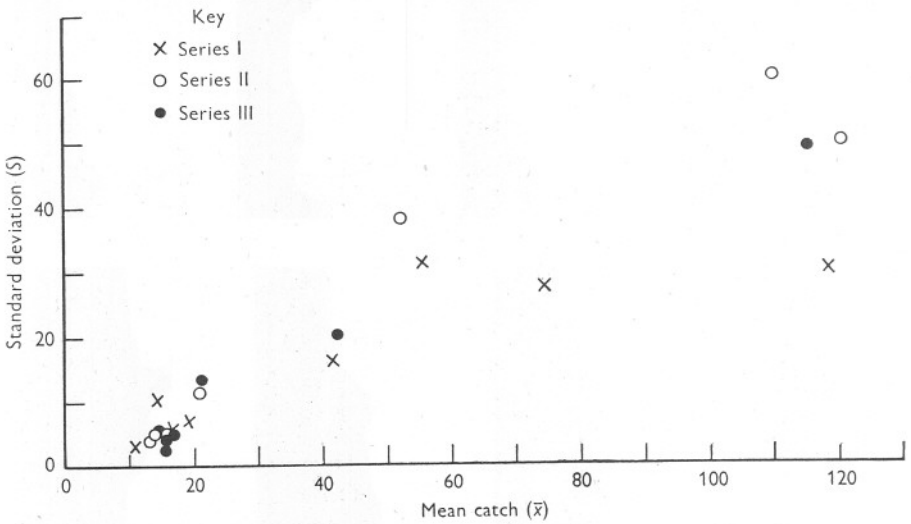

Fig. 2. Standard deviation (s) plotted against mean catch ($\bar{x}$) for each separate species from all the hauls of series I–III.

taken in all three series of hauls is given in Fig. 2. The two values are roughly proportional and the same trend is seen in the results of the earlier investigations referred to above. Logarithmic values of the catches will therefore be used in analysis.

As already pointed out, the work is primarily directed to a comparison of the numbers caught and their variability. However, the mean length for each species in the separate hauls and in the total catch are shown for all series in Table II and the percentage size frequency curves are given in Fig. 3, for some species present in moderate numbers. Since in some the number caught

TABLE II. THE MEAN LENGTH AND GRAND MEAN LENGTH (CM.) FOR SPECIES IN THE SEPARATE HAULS COMPRISING SERIES I–III

Species	Series I					Series II					Series III				
	Haul				Grand mean	Haul				Grand mean	Haul				Grand mean
	1	2	3	4		1	2	3	4		1	2	3	4	
Dogfish	—	—	—	—	—	61·8	60·4	61·9	59·2	60·8	—	—	—	—	—
Cod	40·0	36·5	45·7	48·9	43·8	45·0	47·6	47·7	51·5	48·0	49·9	48·7	45·4	35·8	45·0
Whiting	24·1	23·8	24·4	22·7	23·8	22·0	22·8	24·3	24·6	23·4	24·6	23·3	23·6	22·5	23·5
Poor Cod	18·3	16·3	14·2	16·0	16·2	15·3	19·0	19·0	17·8	17·8	—	—	—	—	—
Hake	37·6	36·2	39·1	27·8	35·2	—	—	—	—	—	39·0	35·9	35·1	37·1	36·8
Plaice	38·1	36·1	36·8	38·0	37·3	40·9	41·0	38·5	39·1	39·9	39·7	37·4	37·2	34·3	37·2
Witch	29·4	28·4	27·1	29·2	28·5	—	—	—	—	—	28·9	26·4	26·6	26·6	27·1
Long Rough Dab	20·0	20·2	20·2	19·4	20·0	18·1	18·9	20·0	19·9	19·2	19·0	20·5	20·2	20·9	20·2
Nephrops	16·5	15·5	14·2	14·1	15·1	14·0	14·1	14·0	14·2	14·1	15·0	14·9	15·5	15·7	15·3

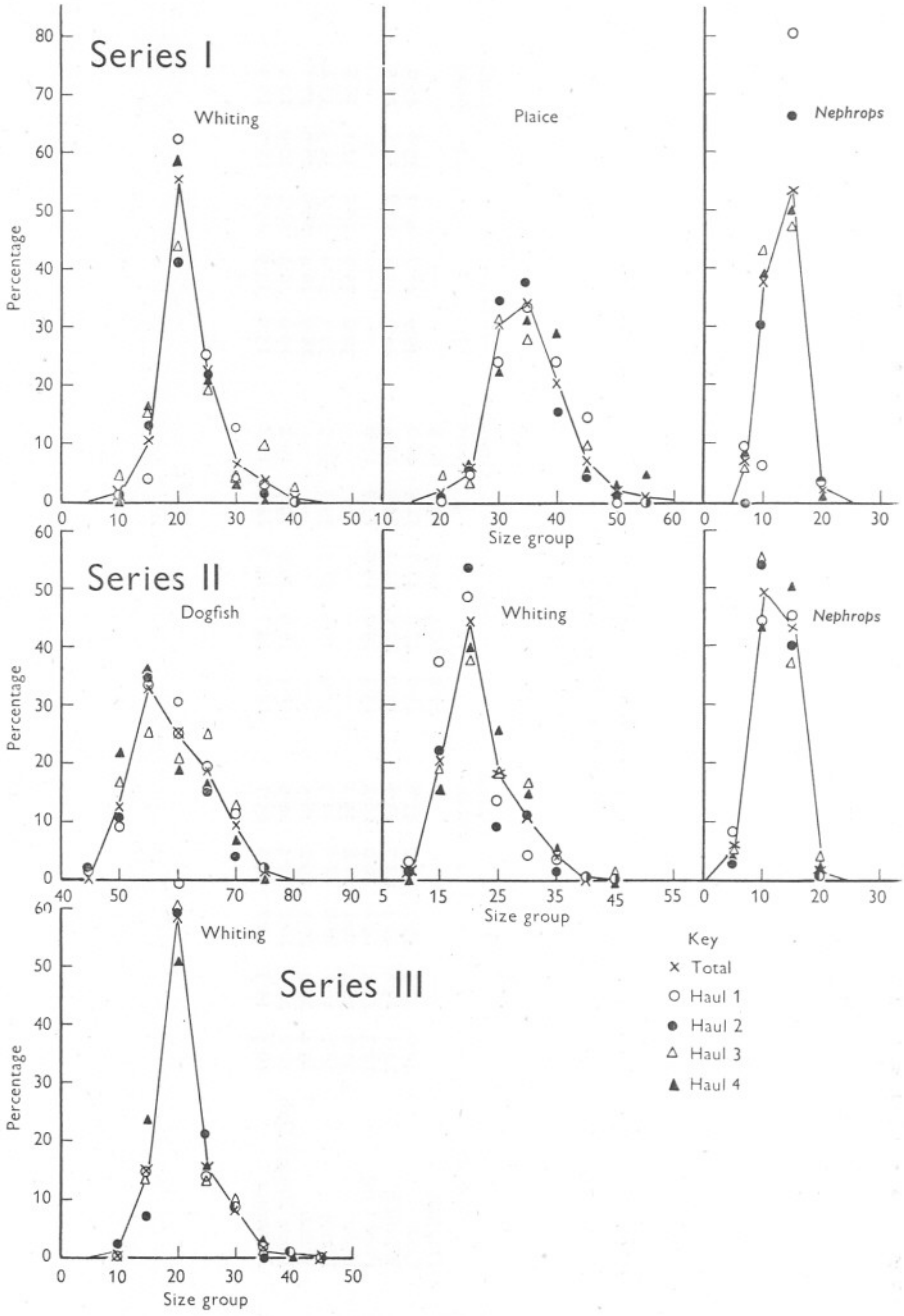

Fig. 3. Percentage frequency distribution of size-groups. Values shown for totals and separate hauls of a given series.

was small and since in others more than one population (as regards size-groups) was sampled in one haul, quantitative deductions regarding size-frequency in sample and in population have not been made. It is clear, however, that the figure and table strongly suggest that a similar population as regards size-distribution was being sampled throughout any given series.

Series I

In series I the species caught in adequate numbers for analysis were the 'round' fish (cod, whiting, poor cod, hake) and the 'flat' fish (plaice, witch, long rough dab) together with *Nephrops*.

In haul 1 of this series a moderate number of haddock was taken (39), although in subsequent hauls the numbers of this fish were very small (2, 3, 0). It is suggested that during part of the first haul a somewhat different ground had been sampled; this suggestion is substantiated both by the occurrence in

TABLE III

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·1088	0·0363
Species (S)	3	1·6688	0·5563
Residual			
$H \times S$	9	0·5334	0·0593
Total	15	—	—

TABLE IV

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·4521	0·1507
Species (S)	3	0·9466	0·3155
Residual			
$H \times S$	9	0·3985	0·0443
Total	15	—	—

this haul only of large numbers of *Asterias rubens* and *Metridium* sp., indicating somewhat harder ground, and by the echo-sounding records seen in Fig. 1, where the trace of haul 1 is somewhat different. It is therefore of interest to note that the stomach contents of the haddocks caught in this first haul consisted largely of the remains of *Ophiura* sp., indicating hard-ground feeding, whereas in contrast, the stomach contents of the species common to all the hauls correspond to the invertebrate fauna of the sandy mud.

The 'round' fish and 'flats' (together with *Nephrops*) are considered separately. The analysis of variance for 'round' fish is given in Table III. The error variance of a single observation (H is less than $H \times S$) is 0·0593 corresponding to a log standard deviation of 0·2436 or a coefficient of variation of 75·3%, for a given species.

For the second group, 'flat' fish plus *Nephrops*, the analysis is given in Table IV. The mean square for hauls is not significant and an estimate of the error variance is obtained by pooling H and $H \times S$. This gives the variance of a single observation as 0·0708 or a log standard deviation of 0·2663, corresponding to a coefficient of variation of 84·7 %.

The catches of *Nephrops* were more irregular than the 'flat' fish, and analysis of the latter separately gives a coefficient of variation of 59·7 %. There were large enough numbers of witch in this series to consider two separate size-groups, namely greater and less than 25 cm. An analysis of variance of these two size-groups considered by themselves gives a coefficient of variation of 48·9 %.

Series II

In this series, taken 6 days later, there was some change in the major species caught. The hake were negligible, whilst large numbers of spur-dogs were taken. The division into 'round' (which includes the latter) and 'flats' plus

TABLE V

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·3293	0·1098
Species (S)	3	1·8083	0·6028
Residual			
$H \times S$	9	0·3596	0·0400
Total	15	—	—

TABLE VI

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·1178	0·0393
Species (S)	2	2·1836	1·0918
Residual			
$H \times S$	6	0·1428	0·0238
Total	11	—	—

Nephrops has been maintained. For the 'round' fish the analysis of variance is shown in Table V. Again pooling H with $H \times S$ since the former is not significant, gives a mean square of 0·0574, or a log standard deviation of 0·2396 corresponding to a coefficient of variation of 73·7 %.

For the second group ('flat' fish plus *Nephrops*) the analysis of variance is shown in Table VI. The value for H is not significant; pooling gives an estimated error variance of a single observation of 0·0290, a log standard deviation of 0·1703 and a coefficient of variation of 48 %.

Series III

In this set dogfish were again absent and haddock were very few, the remaining species being as before, with a noted absence of hard-bottom fauna. Analysis of the 'round' fish is given in Table VII. Again the value for hauls is not significant; the variance of a single observation after pooling is therefore given by 0·0203, a log standard deviation of 0·1425 and a coefficient of variation of 39%.

TABLE VII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·0786	0·0262
Species (S)	2	1·8816	0·9408
Residual			
$H \times S$	6	0·1041	0·0174
Total	11	—	—

TABLE VIII

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Hauls (H)	3	0·0968	0·0323
Species (S)	3	0·5172	0·1724
Residual			
$H \times S$	9	0·3006	0·0334
Total	15	—	—

The analysis with the 'flats' plus *Nephrops* is given in Table VIII. The value for hauls is less than that for interaction so that the latter may be taken as the required error variance; this is equivalent to a log standard deviation of 0·1828 corresponding to a coefficient of variation of 52%.

DISCUSSION

The coefficient of variation, which although in the first instance is strictly applicable only to the present results, has been found to vary from 40 to 85% and this includes values for both 'round' and 'flat' fish. There is no reason, however, to believe that the value is other than adequately representative of this type of sampling of inshore populations. As Winsor & Clarke (1940) pointed out, with such high log standard deviation it is usually better to work on log values throughout, but if 2σ limits are set from these logarithmic values (see Silliman, 1946, for pilchard eggs), then taking 75% as a representative value for the coefficient and converting to actual catches the fiducial limits would be 30–300% for a single observation from a single haul. The catches of a given species from two separate hauls could not, on this basis, be considered significantly different unless one was less than a third or greater than three times the other. In attempting to 'contour' fish populations these limits would also be observed.

The mean catches for all the more abundant species for the three series are given in Table IX. In series I an invasion of haddock into the area, or sampling from a somewhat different ground, has been noted. In the second series there was an incursion of dogfish on to the grounds, the fish being present in reasonable numbers in all four hauls; in contrast to the haddock in series I these dogs were therefore distributed over the whole sampling area. The stomach contents were in an advanced state of digestion, suggesting that they had not been recently feeding on this ground. The cod, whiting, poor cod and hake of the

TABLE IX. MEAN CATCHES OF CHIEF SPECIES IN SERIES I–III

	I	II	III
Dogfish	0	52·3	(1)
Cod	16·5	13·8	16·5
Whiting	74·5	110·0	115·3
Poor Cod	11·0	21·0	(12)
Hake	14·5	(9)	15·8
Plaice	56·5	14·0	42·5
Witch	41·8	(8)	14·5
Long Rough Dab	19·3	15·8	16·0
Nephrops	118·5	120·5	21·3

TABLE X

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects			
Dates (*D*)	2	0·1423	0·0712
Hauls (*H*)	3	0·0108	0·0036
Species (*S*)	3	5·2682	1·7561
First-order interactions			
$D \times H$	6	0·1106	0·0184
$D \times S$	6	0·5190	0·0865
$H \times S$	9	0·2347	0·0261
Residual			
$D \times H \times S$	18	1·1577	0·0643
Total	47	—	—

'round' fish have shown a constant population over the whole sampling period of 4 weeks. This is indicated by the results in Table IX, and confirmed by analysis (Table X), using the catches for the three separate dates.

The second-order interaction is high; none of the first-order interactions are significant, and the mean squares for dates and hauls are not significant. The population can therefore be considered unchanged throughout the period. The small value for hauls indicates that no significant changes took place as a result of successive hauls over the 'same' ground.

The greatest differences are shown in the two 'flat' fishes, plaice and witch, and the crustacean *Nephrops*. The catch of plaice showed a significant fall in series II. Examination showed that the gonads were almost ripe and that the fish had not been feeding; and it was suspected at the time that, as might be

expected at this season, the fish were moving to deeper water for spawning. However, the catches rose again in series III, and this 'recovery' was maintained in later hauls not given. A similar 'recovery' was also found in the witch and *Nephrops*. The reason for these changes is not clear, since when compared with the 'round' fish less mobility would be expected in bottom-living species.

These results give no evidence on the origin of the variability in replicate hauls, that is, how much is due to inadequacies of technique and how much is inherent in sampling variation dependent upon the population distribution. It is of interest to note that as with plankton sampling, the standard deviation is roughly proportional to the mean, whilst the variance is greater than and increases with the mean. This suggests that the population is aggregated into groups, so that much of the sampling variation may be inherent in the population distribution, and this problem is now under consideration.

For ecological work, in order to investigate a particular habitat it may be desirable to sample a large number of small areas in a short time. It was for this reason that half hour hauls were made. Comparison of such short hauls has been made with hour hauls, alternating the order of trawling. In view of the high variability of results it is clear that in order to compare the ratio with that expected (1:2) it is necessary to have a number of counts. Using the results from a number of trawls, with thirty-two separate values of the ratio the mean was 1:1·96. Clearly this value is within the limits expected.

It should be emphasized that the results refer to variations with the *same* gear tested under as far as possible similar working conditions; it might be expected that the variability with a modified gear would be of the same order. The results provide no information regarding the variations which result when different or modified gear is used over the same ground.

Summary

The variability in catch of a series of hauls with a V.D. trawl taken under, as far as possible, controlled working conditions has been determined.

For analysis the species were divided into 'round' fish and 'flat' fish together with *Nephrops*; for both groups the coefficient of variation varied from 40 to 85%. Taking 75% as a representative value, the 2σ fiducial limits are 30–300% for a single species from a single haul of half an hour duration.

It has been found that the standard deviation is roughly proportional to the mean, and that the variance is greater than the mean and increases with the mean. This suggests aggregation of the population.

The species are considered over the whole sampling period (4 weeks). Except for haddocks and dogfish the 'round' fish constituted a constant population. Changes were found in the other groups and their origin is discussed.

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SPONTANEOUS ACTIVITY PATTERNS IN ANIMAL BEHAVIOUR: THE IRRIGATION OF THE BURROW IN THE POLYCHAETES *CHAETOPTERUS VARIOPEDATUS* RENIER AND *NEREIS DIVERSICOLOR* O. F. MÜLLER

By G. P. Wells and R. Phillips Dales

From the Departments of Zoology, University College, and Queen Mary College, London

(Text-figs. 1–8)

The water movements by which many polychaete worms irrigate their burrows are easy to record kymographically. It has been shown, by these means, that the common lugworm, *Arenicola marina*, tends to settle down to a characteristic pattern, in which the water is driven in vigorous bursts, separated by periods of gentler irrigation or of rest. The bursts are not reflexly produced, as one might perhaps suppose, by O_2 lack or CO_2 accumulation in the burrow, but are due to a spontaneously rhythmic pacemaker system internal to the worm (Wells, 1949*a*, *b*; Wells & Albrecht, 1951). The experiments to be described were made on polychaetes of other families, to find out whether equally characteristic patterns appear, and, if so, to what extent they depend on external conditions.

Our main interest lies, not so much in the respiratory and feeding mechanisms of the species concerned, as in a more general problem. The irrigation of a burrow is closely akin to locomotion. One has only to consider those Crustacea which swim to filter-feed, rather than to get anywhere, to see how the two are connected. Now the rate of locomotion of an animal varies in response to external conditions, and also, as far as one can see, spontaneously—a fact of which anybody who has attempted experiments on taxes and kineses is aware. Sometimes the variations are very regularly cyclic, as with many medusae. We believe that the study of irrigation rhythms has a useful contribution to make to the wider problem of activity variations in animal behaviour. It has the great advantages, that a water current is easily recorded, and the conditions are easily controlled; the investigator avoids the technical problems set by an animal which moves from place to place.

The experiments were done at the Plymouth Laboratory, in January, March and April, 1950, at temperatures ranging from 11° to 16° C.—those on *Chaetopterus* by G. P. W. and those on *Nereis* by R. P. D. We wish to thank Mr N. A. Holme, who first pointed out to us the suitability of *Chaetopterus* for work of this kind.

Methods

Modified versions of the apparatus previously described for *Arenicola marina* were used.

Method for Nereis

The results on this species were got with a rather generalized apparatus, that would probably give good results with many burrowing polychaetes (Fig. 1, left-hand side).

The apparatus is immersed in a tank of circulating sea water to the level *A*. The worm is in U-tube *B*, whose diameter can be chosen to suit the species to be used. The right-hand end of the U opens into the outer tank, and the left into wide cylinder *C* (internal diameter 31 mm.). The cylinder communicates with the outer tank through capillary *D* (internal diameter about 1 mm.). Owing to the resistance of *D*, the pumping movements of the worm cause slight variations in the level of the sea water in *C*. These are recorded by means of a lever connected to 'float' *E*, made of paraffin wax moulded on to a silver disk (diameter, before thinly coating with paraffin, 29 mm.). The 'float' really sinks, but is held in the required position relative to the meniscus by counterweight *F*. The water movements are traced by frontal writing point *G*.

In certain of the experiments, the circulation was closed, so that the worm had access only to a limited volume of non-aerated water. This can be done by means of a glass T-piece connected to rubber tubes *H*, *I*, *K*; *H* is connected to *B* and *I* to *D*. Tube *K* is 40–50 cm. long and opens into the outer tank. The fitting can therefore be attached without interrupting or defacing the tracing. When this has been done, the worm can circulate the water contained in *B*, *C*, the T-piece and the connecting tubes, but the system is now practically closed. Only very small amounts of O_2 or CO_2 will pass between *C* and the closely fitting 'float'. Recording occurs as before, and the variation in the volume of water in *C* which this entails is compensated by an ebb-and-flow movement in *K*. Owing to the capacity and form of the dead space which the latter presents, there will be little renewal from this source.

Method for Chaetopterus.

The apparatus just described was modified in three respects, as shown on the right in Fig. 1.

(i) Because of the great vigour of the currents produced by *Chaetopterus*, capillary *D* is replaced by glass tube *L*, drawn out to a jet of internal diameter 1·5–2 mm. (ii) Tubing *H* is replaced by the second wide cylinder *M*, to allow of feeding experiments (see below). The level in *M* is held constant by open tube *K*. (iii) The worm is mounted in its own parchment-like tube *N*. The narrow ends of the tube are cut off, and the rest is tied on to a pair of glass tubes, sleeved by rubber tubing of suitable size.

For closed-circulation experiments, cylinder *M* is sealed with liquid paraffin, as shown in the figure. The circulation can now be closed when desired, by passing rubber tube *I* over jet *L*. For feeding experiments, the

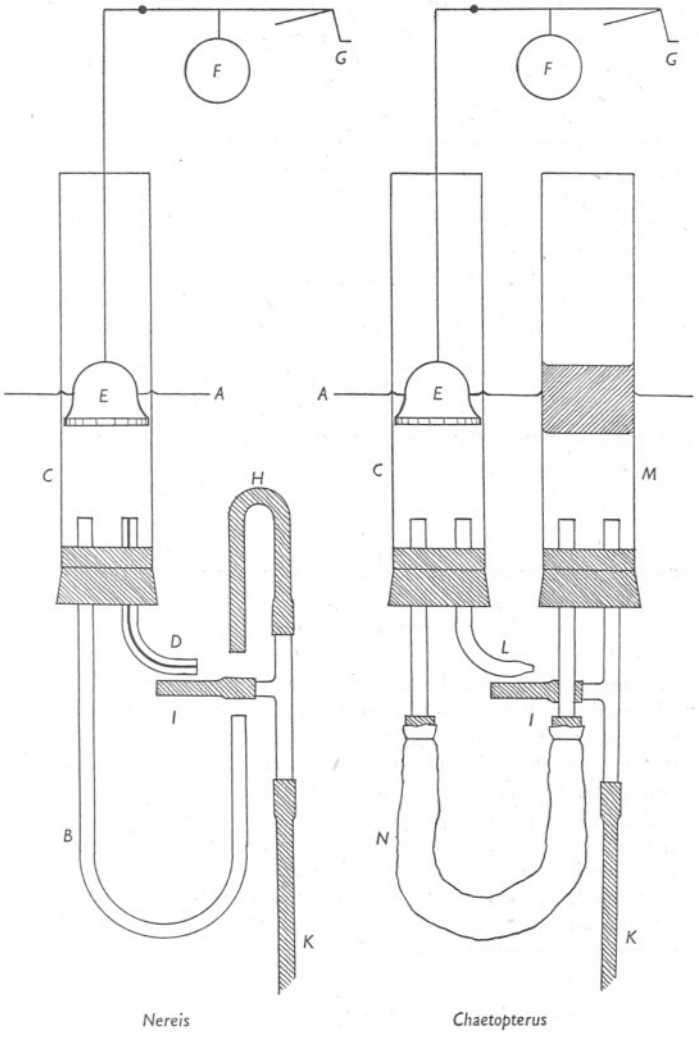

Fig. 1. Apparatus for recording the irrigation currents (see text).

paraffin seal is omitted, *M* is stirred and aerated by an air-jet, and *I* is kept permanently on *L*. The effect of adding diatom cultures, tow-nettings, etc., to *M* can now be recorded.

Calculation of flow rates from the records

The main objective of the experiments was to get a picture of the worm's activity cycles over long periods of time. The records were therefore taken on slowly moving surfaces (at 1 to 6 cm./hr.). This means that they are unsuitable for the measurement of the amounts of water propelled by the worms, except during sustained spells of steady pumping. The general method for deriving flow rates from the tracings is as follows.

(i) *The flow rate through the capillary or jet.* This is proportional to the difference of pressure between the ends of the capillary and therefore to the excursion of the writing point, provided that the temperature is constant and that a certain critical flow rate is not exceeded. We will assume at first that these conditions are satisfied.

The capillary constant j is defined as the flow rate through the capillary in c.c./min. when the pressure difference across it is 1 cm. water. Let amplification factor of lever $= k$, diameter of cylinder $C = d$ cm., velocity of writing surface $= v$ cm./min.

If at any moment the writing point is w cm. from the null position, then the flow rate through the capillary at that moment is

$$\frac{j}{k} w \text{ c.c./min.}$$

If over any period of time the area between the tracing and the null line is a cm.^{2}, then the total flow through the capillary in that period is

$$\frac{j}{kv} a \text{ c.c.}$$

The constant j could be calculated from the equation:

$$j = 25600 \frac{\rho}{\eta} \frac{r^4}{l} \text{ cm.}^2\text{/min.}$$

where ρ, η are respectively the density and coefficient of viscosity of the sea water, and r, l are the radius and length of the capillary in centimetres. In practice, owing to the difficulty of measuring r with sufficient accuracy, the value of j is best determined by setting up the apparatus without a worm, allowing sea water to flow into C through B at a known constant rate (from a graduated Mariotte bottle) and recording the excursion of the writing point. The dependence of j on viscosity necessitates a careful watch on the temperature, not only during calibration but throughout the work, since the Q_{10} of the viscosity of sea water is about 1·3.

At a certain critical flow rate the flow becomes turbulent and the linear relation between pressure and flow rate breaks down. The critical pressure difference h_c necessary to produce turbulent flow is given very approximately in cm. of sea water by the equation

$$h_c = 8 \frac{\eta^2}{\rho^2} \frac{l}{r^3} \text{ cm.}$$

Inserting the following rough but reasonable values: $\eta = 0{\cdot}012$, $\rho = 1$, $l = 5$, $r = 0{\cdot}07$, we get a value of 16·5 cm. for h_c. This is of course very much greater than the height to which the level in C can rise, so we may conclude that the linear relation will always hold when a capillary of dimensions suitable for such worms as *Arenicola* or *Nereis* is on the apparatus. However, h_c falls rapidly with an increase in r, and it also falls (through η) as the temperature rises. Where doubt exists, the linearity of the relation

between pressure and flow rate can easily be checked during calibration. We found that the jets used for *Chaetopterus* gave turbulent flow even under ordinary working conditions, so we derived the flow rates for this worm from curves made by recording the lever excursions at various known flow rates.

The critical flow rate above which turbulence occurs is jh_c c.c./min., and inspection of the above equations shows that this product is proportional to r but independent of l. In other words, when choosing capillaries for recording rapid rates of flow, a long, wide tube should in general be preferred to a short, narrow one giving the same value of j.

(ii) *The output of the worm.* The volume of water in cylinder C varies with the position of the writing point. This means that the output of the worm is equal to the flow through the capillary or jet whenever the tracing is running parallel to the null line. If the two lines are diverging, the worm's output exceeds the return rate through the capillary; if they are converging, it is less.

If at any moment the tracing slopes away from the null line at an angle θ, the worm's output exceeds the flow through the capillary by

$$\frac{\pi d^2 v}{4k} \tan \theta \text{ c.c./min.}$$

The total flow through the worm tube over any period is equal to that through the capillary, if the distance between the two lines is the same at the beginning and end of the period. An increase of δw cm. in the distance between the lines means that the worm pumped, during the period in question, a volume of water which exceeded that flowing through the capillary by

$$\frac{\pi d^2}{4k} \delta w \text{ c.c.}$$

For reasons already given, our records are not suitable for the accurate measurement of the slope of the tracing, or (unless it is running nearly parallel to the null line) of the area under it. We have therefore restricted our calculations to estimates of peak velocities and of amounts pumped during spells of steady activity. To do more than this would require records taken on a rapidly moving surface.

CHAETOPTERUS VARIOPEDATUS

Chaetopterus variopedatus is a specialized polychaete living in a roughly U-shaped tube of parchment-like material which it secretes. It is generally found below low-tide mark, though in certain localities it can be collected from the lowest part of the beach. The water currents through the burrow are driven by the three muscular 'fans' or 'palettes'. Each fan is derived from the dorsal wall and notopodia of a single segment. The three fans are borne on segments xiv, xv and xvi.

Two published accounts of the movements of the fans are of great importance in the present context. They are by Enders (1909), who described many aspects of the worm's behaviour, and MacGinitie (1939), who gave a detailed account of a method of feeding.

The fans normally drive water in a tailward direction, the only exception so far recorded occurring when irritating matter is being expelled from the tube (see below). The worm can reverse itself very rapidly in the tube, and produce

a change in the direction of flow by this means; according to Enders, turning round can be completed in from 10 to 20 sec.

The main functions of the water currents, as described by Enders and by MacGinitie, will now be summarized.

Feeding. The gut contents include mud and sand particles, diatoms, foraminifera, shells of mollusc embryos, skeletons of copepods and young Crustacea, and eggs of *Chaetopterus* itself (Joyeux-Laffuie, 1890; Enders, 1909). The collection of fine carmine suspensions and of diatoms was watched by Enders, who describes their trapping in mucous strands running along ciliated grooves on certain of the appendages of the anterior end; the strands are carried along a dorsal ciliated groove to the mouth, where they are either swallowed or rejected: 'This has the appearance of a selective response on the part of the cilia.' Further details of the processes of swallowing and rejection are given by Faulkner (1931). A different mechanism is described by MacGinitie, who writes: 'No paper that I have seen has given the correct method of feeding of this animal.' According to MacGinitie, a mucous bag is secreted across the lumen of the tube, and water is driven through the tube for some time, during which suspended particles are filtered out by the bag. The bag is finally rolled up into a bolus, passed along the dorsal ciliated groove to the mouth, and swallowed. A new bag is then secreted, and so on. The following details of the timing of the performance are taken from MacGinitie (1939) and from MacGinitie & MacGinitie (1949): 'From the beginning of the spinning of the mucous bag to the ingestion of the bolus of food required, on the average, 17 minutes, and varied only plus or minus 1 minute from this average'; during filtration, the fans beat about once per second; 'this ceases while the pellet of food is being propelled to the mouth'. Our views on the question whether either method of feeding is more correct than the other are given below.

Expulsion of irritating matter. A number of interesting responses to the introduction of coarse carmine granules or sand are described by Enders. The first response to the presence of such particles in the tube is cessation, then reversal, of the direction of beat of the fans; the headward strokes may be performed 'with such energy that the irritating material is expelled to a distance of several centimetres above the end of the tube'. With more severe stimulation, other responses appear. They result in a tailward expulsion of the particles, the worm reversing itself for the purpose if necessary. Tailward expulsion is sometimes remarkably vigorous: Enders describes the driving of sand up to a water surface 30–45 cm. above the opening of the burrow.

Expulsion of faeces. MacGinitie makes no mention of defaecation, and the following details are taken from Enders. The faecal masses 'are sometimes discharged from the anus singly, but more frequently by twos and threes... they remain until a fairly constant number has been discharged, then the palettes vibrate more strongly and expel them to the exterior. When the small specimens upon which I have made observations were well fed they expelled

from ten to twenty masses at intervals of four minutes. The faeces are expelled with considerable force.' Even if the animal receives very little food, it produces faeces consisting largely of mucus. It is rather remarkable that the forcible performance described by Enders was not recorded by MacGinitie; the point is returned to below.

Other functions. According to MacGinitie & MacGinitie (1949): 'When the worm is not feeding, the fans may beat to supply a current for respiration, but this beating is intermittent and arhythmic.' A comparatively gentle background of activity is apparently adequate to supply O_2 and wash away CO_2 and the nephridial excretions, in the absence of the more vigorous currents described above. As the intestine loops up into each fan, irrigation presumably influences the movement of food along the gut.

Irrigation patterns

Our experiments on *Chaetopterus* were begun at the suggestion of Mr N. A. Holme, who showed us a living specimen which had made its burrow in a glass jar. The jar had been dredged up during an Easter Class excursion, and the worm subsequently lived over a year in one of the aquarium tanks. The circulating sea water in the Plymouth Laboratory therefore contains enough suspended matter to supply the animals' needs.

Our records of worms in their own tubes were taken from twelve individuals each one kept in the apparatus for from 2 to 6 days, and yielding a total of thirty-seven recorded 'worm-days'. Experimental tests (closure of the circulation, feeding) were made from time to time on five of these worms; the rest were left in peace.

Portions of the records are chaotic, but the greater part of the material can be grouped into one or other of four main patterns. Each of these was seen in several worms, and most of the worms gave at least two of the patterns, registering one of them for a few hours and then changing, apparently spontaneously, to another. The patterns are as follows.

(*a*) *Expulsion behaviour* (Fig. 2).

The worm traces brief but very violent outbursts, during which the writing point moves up and down over a wide distance and with impressive speed, its strokes evidently corresponding to the 'kicks' of the fans. Between these bursts the worm is nearly or quite motionless. The bursts may follow each other fairly rapidly (as in the first part of Fig. 2), or at longer, and sometimes rather regular, intervals (as at the end of Fig. 2). The worm often reverses itself while registering this type of behaviour (this occurs four times in the first half of Fig. 2). The quantities of water driven during the outbursts can only be estimated very roughly from the records. The writing point, in the example of Fig. 2, often moved over 2 cm. at each stroke of the fans; this means an increase

of the amount of water in the float chamber, at each stroke, of about 3 c.c. The strokes follow each other at intervals of about a second. We have named this pattern 'expulsion behaviour' because it appears to correspond with the violent ejections of irritating suspensions described by Enders. Its occurrence may be

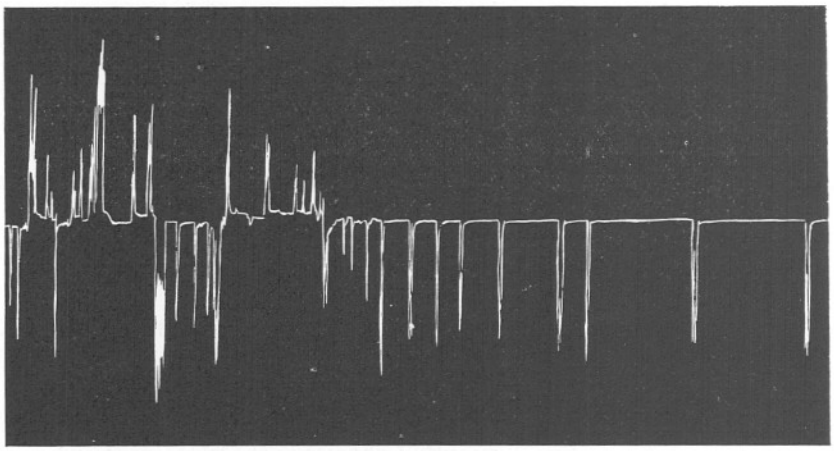

Fig. 2. *Chaetopterus variopedatus*. Irrigation record. The printed extract is 3 hr. long, and begins 1½ hr. after the tube was mounted on the apparatus. *Read all records from left to right.*

due to some disturbing mechanical or chemical factor. It was often seen at the beginning of an experiment, i.e. just after the tube had been tied to the apparatus, but it occasionally appeared later, without evident cause, after the worm had traced other patterns for many hours.

(*b*) *Periodic reversal* (Fig. 3, middle line).

The worm irrigates continuously but rather irregularly, and reverses itself every 20–40 min. This may be a second type of response to irritating conditions, as it appeared very constantly when the circulation was closed (see below), but it often appeared when no evident change in the conditions had occurred. The flow rates in the extract of Fig. 3 gradually fall from about 10 to about 5 c.c./min. In some cases, expulsion outbursts were superimposed on a periodic reversal trace like that of Fig. 3. The first part of Fig. 2 shows periodic reversal in which the continuous irrigation background is very slight compared with the superimposed outbursts.

(*c*) *Mucous-bag feeding* (Fig. 3, upper line).

This pattern was traced from time to time by five of the worms. The base-line is given by the tips of the regularly spaced 'peaks', in the upper extract of Fig. 3. The worm is irrigating very steadily, except for brief pauses at the

'peaks', when the lever returns to the null position. The intervals between pauses average 18 min. The pattern agrees excellently with MacGinitie's account of mucous-bag feeding as summarized above, which it undoubtedly represents. A mucous bag is passed forwards to the mouth and swallowed at each pause. The following quantities can be got from Fig. 3. The flow rate, during the filtration periods, is 16 c.c./min., and the volume of water passed through each bag is about 290 c.c.

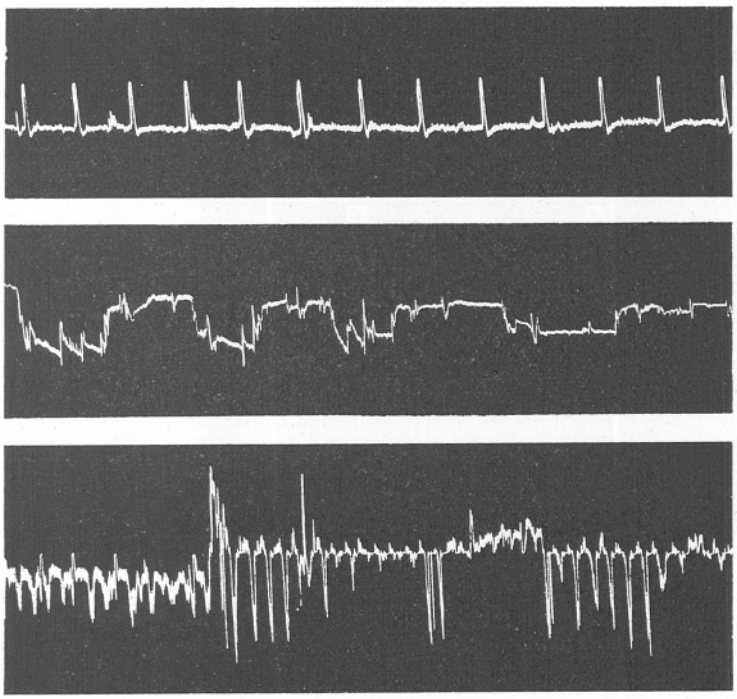

Fig. 3. *Chaetopterus variopedatus*. Extracts from the irrigation records of three individuals, all taken with the same lever magnification factor. Each extract is 4 hr. long.

Unfortunately, the paper was moving too slowly for the individual fan strikes to be counted, but the whole picture agrees so well with MacGinitie's account that his figure, of about 1 stroke per sec., can probably be applied to the activity in Fig. 3. This means that the fans were propelling about 0·27 c.c. of water per stroke, or less than 10% of what they can drive when taking vigorous ejection action.

(*d*) *Five-minute cycle* (Fig. 3, lower line).

There is fairly continuous activity on which a cycle is evidently superposed, having a period of about 5 min. (5·3 min. in the extract of Fig. 3). The cycle

varies somewhat in its expression, as the extract shows, but it often appears as a series of brisk, but by no means maximal, outbursts of the expulsion type. The picture agrees reasonably well with Enders's account of the forcible ejection of faeces from the tube every 4 min., as summarized above.

Now a striking feature of the upper line of Fig. 3 is the absence of anything which could be interpreted as faecal ejection, neither does MacGinitie mention such an act as interrupting the mucous-bag feeding process. On the other hand, the description of Enders is very clear and convincing. The available facts suggest that *Chaetopterus* has more than one method of feeding. We know that *Nereis diversicolor* can take relatively large pieces of animal or plant material with its jawed proboscis, or ingest the surface mud, or filter-feed with a mucous plankton net (Linke, 1939; Harley, 1950); and there seems no reason why *Chaetopterus* should not ring the changes too. Perhaps the MacGinitie method is chiefly

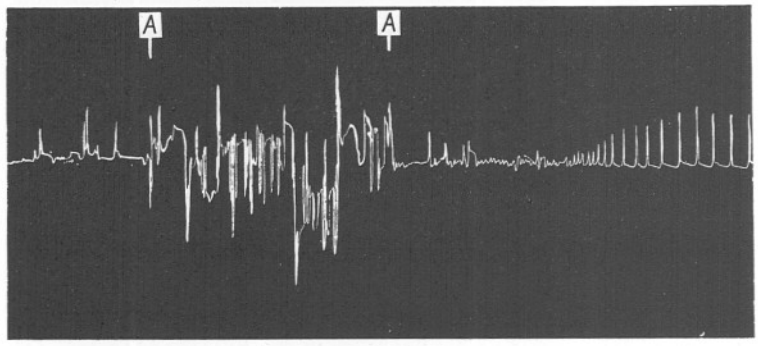

Fig. 4. *Chaetopterus variopedatus*. Irrigation record. The circulation was closed for 3 hr., between the marks *A*. Total length of extract, 10 hr.

used when the suspended particles are few and fine, and the Enders method when they are coarser and more numerous; the first might result in the production of light, mucoid faeces which would drift away with the filtration current, and the latter of heavier ones which would have to be kicked out.

Response to closure of the circulation

As described on p. 663, the circulation could be closed in such a way that the worm had access to only about 90 c.c. of water, including the volume contained in its tube, with little opportunity for the entry of additional O_2 or the escape of CO_2 or other metabolites. This was done in seven experiments, made on four worms, the period of closure varying from 3 to 7 hr.

The effect of closure was to produce a sharp increase in the water currents, which lasted during the whole closure period (Fig. 4). The movements consist in the main of violent expulsion bursts, superimposed on periodic reversal in the tube; that is to say, they suggest a generalized state of irritation rather than

a specific increase of respiratory irrigation. Re-opening of the circulation was invariably followed by a prolonged period in which the water movements were very slight, or even ceased altogether.

These responses afford a great contrast to those of *Arenicola marina*, as described elsewhere (Wells, 1949*a*). The lugworm irrigates its tube in powerful bursts. If the circulation is closed, the bursts appear with about the same timing as before, but with greatly diminished vigour, and they now seem to serve as a periodic testing of the conditions. When the circulation is opened again, the irrigation is enormously increased, as if the animal were paying off an oxygen debt run up during the period of closure. Now the lugworm typically inhabits tidal sand and mud flats. At low tide, the burrows may lie exposed for hours, and, on a hot summer day, the surface water which often covers them may warm up to temperatures high enough to injure the worm (Linke, 1939; Wells, 1949*a*). An automatic acceleration of irrigation in response to O_2 shortage or CO_2 accumulation would be harmful under these conditions; but the ability to suspend external respiration for some hours, together with testing behaviour when conditions are unfavourable, followed by compensatory hyper-irrigation when the returning tide removes the danger, would clearly tend towards survival. *Chaetopterus*, on the other hand, though it sometimes occurs in the lower part of the tidal zone, is typically found at greater depths, and will seldom, if ever, be exposed to these dangers. The circulation through its burrow might become closed from various causes, such as the settling of some object over the two openings of the burrow. Should this occur, it will be better for the worm to respond in such a way as to remove the obstruction, or to minimize its effects, rather than to wait until the situation should mend itself.

Response to 'feeding'

The effect of adding small volumes of dense suspensions of organisms, by the means described on p. 663, was tried three times, on two worms. A typical response is shown in Fig. 5, when the addition consisted of tow-nettings (from which the larger organisms had been removed with a 1 mm. screen) enriched with diatom cultures (*Biddulphia sinensis*, *Thalassiosira gravida*, *Coscinodiscus centralis*, *Nitzschia closterium*). A prompt and sustained increase in activity can be seen, but the patterns do not resemble those identified above with feeding. They consist in the main of expulsion outbursts. Similar effects were produced by diatoms alone. The type of response suggests that the added organisms were simply irritating, like the sand or coarse carmine in Ender's experiments. Confirmation comes from a single experiment in which a very similar response to that shown in Fig. 5 was given to a suspension of Kieselguhr. Perhaps our additions resulted in too great a density of suspended matter. As already stated, the water circulating in the Plymouth tanks contains sufficient particles to keep *Chaetopterus* alive for over a year.

Dependence of the patterns on external conditions

The following conclusions can be drawn from the results described above.

(i) *Chaetopterus* can exhibit any one of several characteristic irrigation patterns.

(ii) Its choice of pattern at any time depends, to some extent at least, on external conditions. There is evidence that the expulsion bursts, and periodic reversal, appear as responses to irritation. It was suggested, in discussing feeding, that at least two methods of collecting particles are available, and that the particular method employed may be influenced by the nature of the suspended matter in the water.

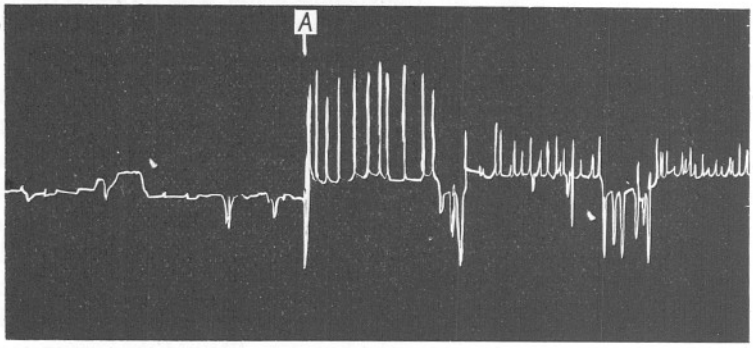

Fig. 5. *Chaetopterus variopedatus*. Irrigation record. A suspension of organisms was added at *A*. Total length of extract, 10 hr.

(iii) Though the choice of pattern can be environmentally determined, intrinsic factors are largely responsible for the forms of the patterns themselves. Periodic reversal appears whenever the circulation is closed, but there is no periodic change in the external conditions which would account for each act of reversal. We seem to be concerned here with the release of an internal rhythmic pattern during the period of action of a constant irritant. The lower line of Fig. 3 strongly suggests that a spontaneous pacemaker is at work, discharging every 5·3 min., but producing movements whose vigour varies from time to time, much as the vigour of the movements evoked by the oesophageal pacemaker of *Arenicola marina* can vary (Wells, 1937*a*). The very regular and invariable pattern which is traced during mucous-bag feeding, as in the upper line of Fig. 3, again suggests the existence of an internal, spontaneous timing mechanism.[1]

[1] During filtration, the bag is continually being secreted round its rim by the aliform notopodia, and rolled up at its apex by the dorsal cupule, in which its substance collects as a pellet. The timing of the cycle might here depend on a relation between secretion rate and the capacity of the cupule.

Behaviour of isolated fan segments

The complex irrigation patterns could conceivably be due to the modulation of a simple inherent rhythmicity of the fan-bearing segments by influences coming from other parts of the worm. To test this possibility, we took a number of records from single fan segments. It was already pointed out by Berrill (1927) that isolated fan segments will beat in sea water for 4 or 5 weeks, and that their movements depend on the presence of the nerve ganglia. In our experiments, the worm was ligatured in front of one of the fans, the ends of the thread were tied into a loop, and the segment was isolated by transecting the worm in front of the ligature and behind the fan. The preparation was mounted in sea water, by passing the loop over a horizontal glass rod, and a fine hook passed through the tip of the fan was connected to a light isotonic lever (pull on the preparation, 0·4 g.).

Segments set up in this way remain vigorously active for at least 24 hr., but their behaviour is surprisingly variable. The extracts in Fig. 6 show not only several behaviour-rhythms of different frequencies, but also striking and apparently spontaneous changes of pattern. The sudden increase in activity, seen in the last third of the upper extract, is a typical example.

Accustomed, as one becomes in the classroom, to the steady performance of such material as the heart of the frog, or the gill cilia of *Mytilus*, one naturally looks for external causes to explain these sudden changes of pattern. However, if two or three isolated segments are recorded simultaneously, in the same vessel of sea water, they change their patterns at different times, and quite independently of each other. If external causes were responsible, their behaviour might be expected to be parallel. The causes of the fluctuations are apparently internal to the preparations themselves.

The isolated oesophagus of *Arenicola marina* exhibits at least three types of spontaneous activity: (i) a simple rhythmic alternation of contraction and relaxation, following each other at intervals of a few seconds; (ii) cyclic alternation of periods of rhythmic activity and periods of rest, the whole cycle lasting for a few minutes; (iii) superimposed disturbances, often coming very regularly at intervals of the order of 1 hr. (Wells, 1937*a*; Wells & Albrecht, 1951). At least the first two of these are functionally normal, and not experimental artefacts. Perhaps the changes of pattern shown in Fig. 6 would appear cyclically, if the preparations could be kept going for many days and recorded on even slower drums. In any case, the segments evidently show spontaneous behaviour patterns of much greater elaboration than those shown by isolated hearts, and the same is true of many invertebrate preparations, including extroverts and body-wall strips of several polychaete species (Wells, 1937*b*, 1939; Wu, 1939; Wells & Ledingham, 1940). It may be the simple regularity of the heart which is the more specialized, since it has obvious functional value.

We have not traced any detailed correspondence between the time-patterns

of the isolated fan segments and those of the intact worm; but it seems clear that the former afford a good supply of material from which the latter could be constructed. There is also, of course, the likelihood of other spontaneous centres, elsewhere in the nervous system.

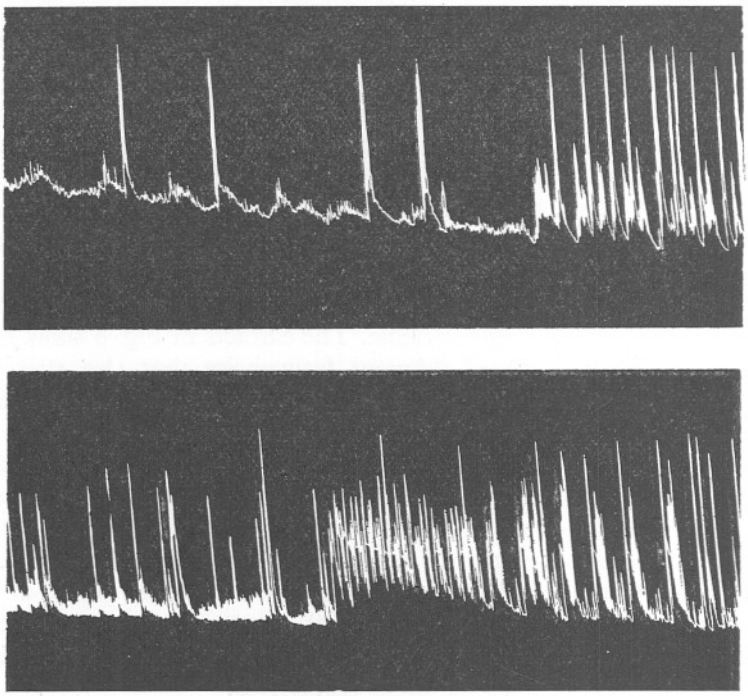

Fig. 6. *Chaetopterus variopedatus*. Movements of the isolated 14th segment, recorded with a light isotonic lever. Each extract is from a different individual. Duration of extracts, 4 hr.

Nereis diversicolor

Our experiments on *Nereis* arose from the coincidence at Plymouth of R. P. D., who was studying the ecology of this species, and of G. P. W., who was completing the work on *Chaetopterus*. A small number of records were taken from *Nereis*, to compare (*a*) its irrigation patterns in aerated sea water, and (*b*) its responses to closure of the circulation, with those of *Arenicola* and *Chaetopterus*.

Unlike *Chaetopterus*, *Nereis diversicolor* is almost entirely restricted to the littoral zone. It lives in mud or sand, in a fairly permanent burrow; this may be a simple U, but often it is complicated by the presence of additional branches with openings to the surface (Linke, 1939).

Until recently *N. diversicolor* was described as feeding partly on such objects as algal fragments and dead Crustacea or molluscs, and partly by swallowing the

surface mud around the opening of the burrow (Thamdrup, 1935; Linke, 1939). The water current, which it drives through its burrow, was therefore mainly respiratory; as a secondary function, it could bring chemical stimuli to the worm, and so inform it of the presence of suitable food (Copeland & Wieman, 1924). Browsing on the mud has frequently been watched by R. P. D. on many beaches, and is undoubtedly of great importance. However, Harley (1950) has shown that the worm can also use a filter-feeding mechanism, like that of *Chaetopterus*, in which water is driven through a mucous net across the burrow. Harley's observations were made on worms in glass tubes, as ours were; there is as yet no information about the importance of the process in the everyday life of the animal.

The waves producing the irrigation current are dorsiventral, while those which accompany locomotion are lateral. It follows that irrigation must be interrupted by acts involving locomotion, such as the backward excursions to the surface for defaecation. Apart from this, the irrigation of worms in glass tubes is always intermittent, periods of undulation alternating rather irregularly, and without visible cause, with periods of rest.

The irrigation waves invariably travel along the body in a head-to-tail direction. The worm can turn rapidly round in the tube, and so reverse the direction of the water current.

Irrigation patterns on open circulation

Our material was obtained from 4 worms, recorded continuously for 21, 22, 39 and 42 hr. The circulation was closed twice with one worm, for 4 and $7\frac{3}{4}$ hr., and once in each of the others, for $10\frac{1}{2}$ and $12\frac{1}{2}$ hr.

The irrigation of the worms, on open circulation, was never steadily sustained, but consisted of short bursts, between which the lever usually returned momentarily to the base-line. In two worms irrigation was often interrupted by periodic rests of about 10–15 min. duration; several such rests are seen in the 3 hr. before the circulation was closed in Fig. 7. They are reminiscent of the pauses studied by Lindroth (1938) and by van Dam (1937, 1938) in *Nereis virens*, but their timing is rather different from that which Lindroth gives as typical for the latter species. 'Ventilationsperioden von etwa 5 Minuten Länge' he writes 'werden von Ruheperioden von 20 bis 30 Minuten abgelöst', whereas in our own records the pauses are relatively brief interruptions of irrigation.

All of the worms showed spells, of several hours' duration, during which the pattern reversed itself at intervals of 15 to 45 min.; examples of this periodic reversal, which is due to the worm turning in the tube, are seen at the beginning and end of Fig. 8. This might be a response to unfavourable conditions, as in *Chaetopterus*; on the other hand, if the water current serves for chemical testing of the surroundings of the burrow, it will clearly be of advantage for each of the openings to act in turn as a nostril.

The filter-feeding of *Nereis*, as described by Harley (1950), is very much less regular than that of *Chaetopterus*. The process of secreting a mucous net, driving water through it, and then swallowing it, may take anything from a little over 1 min. to nearly 7 min., according to her figures, and she writes: 'The cycles of feeding may follow rapidly one after the other with a few short breaks, or they may occur with intervals of several minutes, or irregularly, for a total period of about two hours.' Some of the rapid oscillations in our tracings—for instance, those which occur in a continuous series, about one-third of the way across the upper part of Fig. 8—might be due to this cause, and it is difficult to see what other functional significance they could have; but the pattern as described by Harley is so variable, that the identification cannot be made with any certainty.

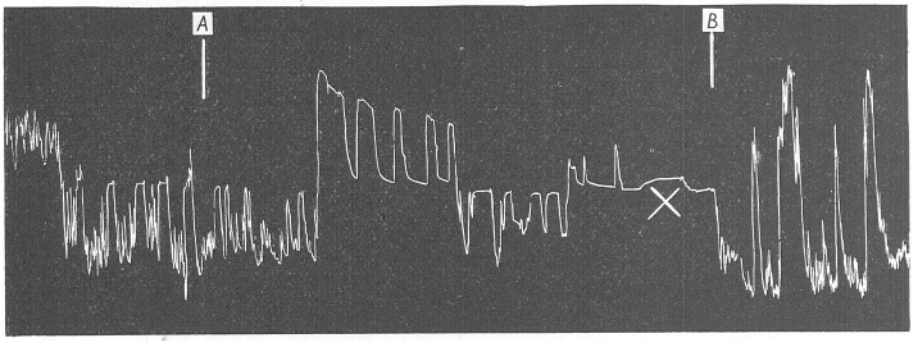

Fig. 7. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 22 hr.; length from *A* to *B*, 12½ hr. The slight rise at *X* is an artefact due to a temporary change in level of the water in the outer tank.

It will at least be clear, from the illustrations, that there are several distinct behaviour patterns in this species, and that, as in *Chaetopterus*, they may suddenly replace each other without evident external cause. Moreover, the patterns traced by *Nereis* are different from those of *Chaetopterus*, or of *Arenicola*. It is as if each species had its own handwriting.

Response to closure of the circulation

The response of *Nereis diversicolor* to closure of the circulation is as follows. There is little change in behaviour for 2–3 hr., then the rapid activity oscillations are replaced by long spells of relatively steady irrigation separated by equally long, or longer, periods of complete rest. Irrigation activity gradually decreases, and after many hours of closure it has fallen practically to zero (Figs. 7, 8). Re-opening of the circulation is followed by a prompt resumption of irrigation, and the amounts of water passed are well above normal for a considerable time.

The sudden change of pattern produced by closure, shown very clearly in Fig. 7, is arresting. Evidently, the outbursts of irrigation cannot be direct responses to O_2-exhaustion or to CO_2-accumulation in the tube, for after closure the irrigation would then become more and more powerful, and more and more continuous, and it would rapidly decrease on re-opening the circulation. We seem to be concerned once again with the sudden release, under the closure conditions, of a pattern whose detailed characteristics are part of the make-up of the worm.

The responses to closure and re-opening are on the whole similar to those of *Arenicola* and opposite to those of *Chaetopterus*. The difference in reaction between those species was related above to their difference in habitat, and it is

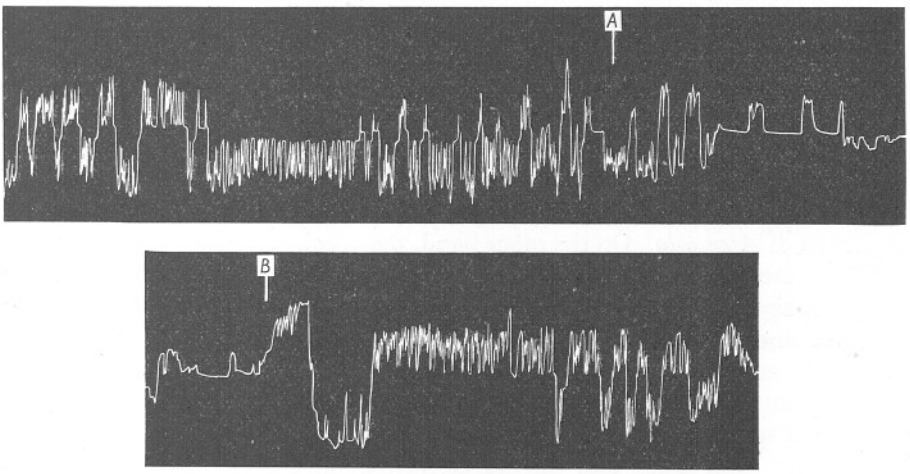

Fig. 8. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 38 hr.; length from *A* to *B*, 10½ hr.

at first sight tempting to accept as confirmation the fact that closure depresses, while re-opening increases, the irrigation of *Arenicola* and *Nereis*, both of which are inhabitants of littoral sand and mud flats. On reflexion, however, it will be seen that the agreement is not really so good. *Arenicola* responds to closure, not by a complete change of pattern, but by an immediate reduction in the amount of water pumped at each irrigation outburst. In *Nereis*, on the other hand, large amounts of water are pumped through the burrow in the sustained irrigation outbursts before activity dies away. Clearly, an interpretation in terms of the avoidance of dangerous surface water (as was advanced for *Arenicola*, on p. 671) is inadmissible. Now *Nereis diversicolor* is exceptionally resistant to adverse conditions. Its powers of osmoregulation are well known; its long survival under conditions of practically complete oxygen lack was described by Hecht (1932); and, in the matter of temperature, Linke (1939)

writes of worms that were seen crawling and swimming in surface pools at 30–35° C., though they could have cooled themselves to 20° C or less by simply withdrawing into the underlying mud. These facts suggest that *Nereis* could safely irrigate a burrow when *Arenicola* on the same beach could not, and so its failure to respond to adverse conditions, as *Arenicola* does, by a prompt cutting down of irrigation becomes more intelligible.

Specificity of the irrigation patterns

A more detailed functional interpretation of the irrigation patterns of *Nereis* is hardly possible at present, because the behaviour and conditions of life of the worm in its natural habitat are insufficiently well known. In any case, we are in some doubt as to the extent to which the principle that behaviour is adjusted to habitat can usefully be pressed.

An analogy can perhaps be drawn between the time-patterns which form the subject of this paper, and the space-patterns with which the morphologist and the systematist are concerned. Considering, for example, the variations of shape of the parapodium in polychaetes, one finds a number of obviously adaptive modifications, such as the fans and suckers of *Chaetopterus*, the elytra of *Aphrodite*, or the ring-like parapodia which embrace the more anterior segments of *Arenicola*. On the other hand, the species, especially in the errant families, are often distinguished by slight but constant differences in the proportions of the various parts of the parapodium to which, in spite of their elegance and their value to the systematist, a functional interpretation can hardly be attached. In the same way, though there are certain fairly clear fitnesses in the irrigation patterns (for instance, the 3-phase outburst of *A. marina* serves to integrate the irrigation of the burrow with the periodic defaecatory excursions, and can be converted, in certain circumstances, to a method of aerial respiration), the finer peculiarities which distinguish the tracings of one species from those of another (such as the particular frequency with which a filter-feeding *Chaetopterus* or *Nereis* replaces its mucous nets) may well be functionally meaningless. The metaphor was used above, that each species has its own handwriting, and the detailed characteristics of a handwriting are only of use in establishing the identity of the writer.

Summary

Simple methods for recording the water currents, which many polychaetes drive through their tubes, are described. The circulation may be either open (the worm having access to large amounts of well-aerated sea water) or closed (in which case the worm can circulate a small volume only, and there is no oxygenation or removal of excretory products).

When on open circulation, both *Chaetopterus variopedatus* and *Nereis diversicolor* often trace quite regularly cyclical patterns for hours at a stretch.

Each species has several possible patterns, and may change from one to another without evident external cause. The tracings of each species differ from those of the other, and also from those of *Arenicola marina*, which were described elsewhere.

The details of the patterns traced, on open circulation, by *Chaetopterus* and by *Nereis* are described, and their functional significance is discussed, in the text.

The effect of closure of the circulation is quite different in the two species. *Chaetopterus* responds by an increase in irrigation, the particular patterns traced suggesting a generalized reaction to irritating conditions rather than a specifically respiratory one. *Nereis* responds, first by the appearance of a special pattern (in which long spells of steady irrigation alternate with equally long, or longer, periods of rest), and then by the gradual decrease, which may lead to total cessation, of irrigation.

If the circulation is re-opened after a period of closure, *Chaetopterus* responds by a great decrease, or total cessation, of irrigation, while *Nereis* responds by a prompt return of irrigation activity, the amounts of water pumped being at first much greater than normal.

The movements of isolated fan segments of *Chaetopterus* were recorded with light isotonic levers. They give complicated tracings in which several periodicities can be detected, and they may suddenly, and apparently spontaneously, change their pattern during the course of an experiment.

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THE RESPIRATION OF SOME PLANKTONIC COPEPODS

By J. E. G. Raymont, B.Sc., A.M.
University College, Southampton
and D. T. Gauld, B.Sc., Ph.D.
Marine Station, Millport

(Text-figs. 1, 2)

The respiratory rates of zooplankton organisms are of considerable interest, if only in so far as they permit an assessment of the metabolic requirements of the zooplankton, which forms a vital link in the economy of the sea. Yet very little information is available on the respiratory rates even of copepods, which usually comprise the bulk of a zooplankton community. Data exist only for a few species of copepods, and even then only for a few stages in the life histories of the species. The first measurements of the respiration of a selected species, as distinct from mixed plankton catches, were made by Marshall, Nicholls & Orr (1935). They worked with *Calanus finmarchicus* (Gunner), adults (male and female) and Stage V. In 1939, Clarke & Bonnet published a further series of measurements of the respiration of Stage V *C. finmarchicus*, giving figures slightly higher than those of Marshall *et al.* Zeuthen (1947) included some observations on copepods in his study of size and metabolic rates, but he determined the species of only a few of the animals he used.

In this paper the study of respiration in the Copepoda has been extended to a species much larger than *Calanus*, viz. *Euchaeta norvegica* Boeck, and to two smaller species, *Centropages typicus* Kroyer and *C. hamatus* (Lilljeborg), and in the two larger species, *Calanus* and *Euchaeta*, an additional copepodite stage has been included. In this and further papers a survey will be made of the respiration of the more important species of planktonic copepods, throughout their life histories and under varying environmental conditions. In this way, in time, a picture may be built up of the food requirements of the planktonic population in the sea.

The authors would like to thank Mr E. Ford, the Director of the Marine Station, Millport, for his interest and encouragement in the work.

Material and Methods

Copepods were taken by townet in the Fairlie Channel, or off Garroch Head, both grounds within half an hour's run from the laboratory. The tow-nettings were well diluted for transport. In the laboratory, with the larger forms,

vigorous specimens of the desired species and stage were picked out as soon as possible and put in jars of sea water filtered through Whatman No. 1 filter-papers. The labour of sorting individually large numbers of *Centropages hamatus* was very great; and for them, after the larger copepods and any possible predators such as medusae had been picked out, the townettings were well diluted with filtered sea water, and the *Centropages* picked out only as required. The jars were kept in a sink of running water where the temperature rarely changed by more than 1° C. in 24 hr. No copepods were used until at least the day following capture. An attempt was made not to use the same catch for more than 2 days, but unfortunately rough weather prevented fresh hauls being taken on several occasions, and, especially at the end of the experiments, copepods had to be used that had been captured 4–5 days before.

Respiration was measured manometrically, in Dixon-Haldane constant pressure respirometers, the apparatus being arranged as outlined by Dixon (1943). Clarke & Bonnet (1939), who used this apparatus for their measurement of the respiration of *Calanus*, found that the presence or absence of KOH in the flasks had no effect on the readings observed. We were not satisfied on this point and KOH was always used in the annular cup in the neck of the flask. The respiration flasks were completely immersed in a bath of running water, as no means of maintaining a water-bath at constant temperatures below room temperature was readily available. It was possible by this means to keep the temperature well below 20° C. The maximum range of temperature observed in the bath during any experiment was 0·5° C., which was sufficiently constant to have no disturbing effect on the accuracy of the readings. The greatest disadvantage of this arrangement was the day-to-day variation in the temperature which fell more or less steadily from 19° C. at the beginning of the series of experiments to 15·5° C. towards the end.

The respirometers were attached to a Barcroft shaking-apparatus and shaken with an amplitude of 2 cm. at a frequency of 100 per min. Contrary to the observation of Clarke & Bonnet (1939), this shaking appeared to have no ill effect on the copepods, which survived well—only 10 out of a total of over 600 copepods used in the experiments died during the experiment, and the vast majority of them were alive and active the day following the experiment in which they had been used. However, in view of Clarke & Bonnet's experience, copepods were never used a second time for normal experiments. After closing the respirometer taps, readings were made every 30 min. for 3 hr. and the total change was converted to volume of dry gas at N.T.P. In the first nine measurements, where the respirometer taps were closed 5 min. after the flasks had been attached, as recommended by Dixon, it was found that the first reading of the manometer, 30 min. after the taps were closed, showed a very large change—sometimes two or three times that found for the subsequent 30 min. periods. The period of equilibration was therefore increased to 15 min., and the large initial change was eliminated. In the early experiments where the

equilibration period was only 5 min., and an abnormally large change was recorded in the first 30 min., the first half hour has been neglected and the calculations have been based on the last $2\frac{1}{2}$ hr. experiment.

The respiration flasks usually contained 5 ml. of filtered sea water, but the number of copepods varied with their size—usually 2–5 *Euchaeta*, 10 *Calanus* (adults, Stage V and Stage IV), 20–25 *Centropages typicus* and 50 *C. hamatus*.

For each experiment the copepods were picked out of the jars by eye, but when there was any doubt in identification they were checked under a low-power microscope before being counted into the respiration flasks. In the experiment with *C. hamatus*, in order to save time and damage to the animals, they were sorted by eye only, but were fixed in formalin at the end of the experiment for checking and counting. Any animals which were to be measured after an experiment were similarly fixed and measured with an eyepiece micrometer.

Results

In all, sixty-five separate determinations of respiration were made, and results are listed in Table I. In the table, the fifth column gives the amounts of oxygen in microlitres consumed by one copepod in 1 hr., for the temperature at which the experiment was made. A correction for temperature was made from the curve of respiration of *Calanus* with temperature, given by Marshall *et al.* The sixth column shows the data for respiration corrected to 17° C. Table II gives the mean values for each of these groups of observations, together with the standard deviation of the observations from their mean; the second figure in each pair is that obtained from the data corrected to 17° C. In the discussion which follows reference will be made only to the figures corrected to 17 °C.

More determinations were made on the respiration of *Calanus* Stage V than on any other form, and they include two small groups in which the conditions were changed. In the first special group (Exps. 36–39) the experiments were conducted in the dark, and in the second (Exps. 40–42) the respiration flasks were not shaken at all during the experiment. The group of experiments done in the dark give a mean respiration rate of 0·54 μl./cop./hr. as compared with 0·53 μl./cop./hr. for those in the light; there is no significant difference between these two means ($d/\sigma_d = 0{\cdot}11$). This confirms the finding of Marshall *et al.* that the respiration of *Calanus* Stage V is not affected by light. The mean respiration rate when the respirometers were not shaken was 0·67 μl./cop./hr.; this is significantly higher than that for the rest of the measurements ($d/\sigma_d = 3{\cdot}14$). The number of observations on *Calanus* adult males and on the stages of *Euchaeta* was severely limited by the difficulty of obtaining material; nevertheless, it was decided that the data obtained were worth including.

It has already been explained that, owing to the difficulty of identifying rapidly the stages of *Centropages*, almost all the experiments on *C. hamatus*

TABLE I. LIST OF EXPERIMENTS AND RESPIRATORY RATES OBTAINED

Exp. no.	Number and stage	Date	Temp. (° C.)	Respiratory rate (μl./cop./hr.)	Corrected respiratory rate (17° C.) (μl./cop./hr.)
		Euchaeta norvegica			
1	2 adult females	15. ix.	15·85	4·284	4·785
2	4 adult females	10. ix.	16·35	3·077	3·277
3	4 adult females	10. ix.	16·35	2·999	3·194
4	4 Stage V	15. ix.	16·0	2·137	2·351
5	5 Stage V	15. ix.	15·85	2·326	2·598
6	2 Stage IV	15. ix.	16·0	1·069	1·175
		Calanus finmarchicus			
7	10 adult females	27. viii.	18·95	(0·429)	(0·362)
8	8 adult females	8. ix.	16·65	0·759	0·785
9	7 adult females	8. ix.	16·65	0·751	0·777
10	9 adult females	11. ix.	16·0	0·728	0·801
11	10 adult females	11. ix.	16·0	0·967	1·064
12	6 adult males	8. ix.	16·65	0·841	0·870
13	10 Stage V	24. viii.	19·0	0·550	0·426
14	,,	24. viii.	19·0	0·513	0·431
15	,,	24. viii.	19·0	0·844	0·708
16	,,	25. viii.	18·9	0·735	0·622
17	,,	25. viii.	18·9	0·478	0·404
18	,,	25. viii.	18·9	0·542	0·458
19	,,	26. viii.	18·8	0·512	0·437
20	,,	26. viii.	18·8	0·505	0·432
21	,,	26. viii.	18·8	0·551	0·471
22	,,	28. viii.	18·25	0·645	0·577
23	,,	28. viii.	18·25	0·615	0·550
24	,,	28. viii.	18·25	0·676	0·571
25	,,	30. viii.	18·2	0·615	0·552
26	,,	30. viii.	18·2	0·717	0·644
27	,,	30. viii.	17·9	0·521	0·479
28	,,	30. viii.	17·9	0·613	0·568
29	,,	30. viii.	17·9	0·490	0·451
30	,,	31. viii.	17·8	0·493	0·458
31	,,	31. viii.	17·8	0·524	0·486
32	,,	31. viii.	17·8	0·585	0·544
33	,,	1. ix.	17·5	0·643	0·614
34	,,	1. ix.	17·5	0·487	0·466
35	,,	1. ix.	17·5	0·548	0·525
36	,,	1. ix.	17·5	0·609	0·583 Dark
37	,,	1. ix.	17·5	0·457	0·437 Dark
38	,,	1. ix.	17·5	0·579	0·553 Dark
39	,,	2. ix.	16·9	0·578	0·583 Dark
40	,,	9. ix.	16·4	0·682	0·722
41	,,	9. ix.	16·4	0·617	0·654
42	,,	9. ix.	16·4	0·586	0·621 Dark
43	15 Stage IV	6. ix.	17·9	0·262	0·242
44	,,	6. ix.	18·0	0·198	0·180
45	,,	6. ix.	18·0	0·187	0·170
46	,,	11. ix.	16·0	0·270	0·297
47	,,	14. ix.	15·9	0·326	0·362
		Centropages typicus			
48	32♀	8. ix.	16·55	0·317	0·332
49	18♀	9. ix.	16·2	0·273	0·295
50	12♀, 5♂, I..V	9. ix.	16·2	0·222	0·240
51	9♀, 4♂ I..V	9. ix.	16·2	0·308	0·332
52	25♀	12. ix.	15·9	0·167	0·186
53	25♀	12. ix.	15·9	0·158	0·175
54	20♀	13. ix.	15·6	0·187	0·215
55	20♀	13. ix.	15·6	0·172	0·187
56	20♀	14. ix.	15·8	0·169	0·190
57	20♀	14. ix.	15·8	0·110	0·124
58	29♀	14. ix.	15·9	0·222	0·247
		Centropages hamatus			
59	26♀ 10♂, 64 V	2. ix.	16·85	0·079	0·082
60	17♀	2. ix.	16·85	0·125	0·135
61	13♀, 16♂, 31 V	2. ix.	16·85	0·066	0·068
62	15♀, 11♂, 29 V	5. ix.	17·25	0·107	0·105
63	35♀, 5♂, 17 V	5. ix.	17·25	0·112	0·110
64	22♀, 7♂, 5 V	6. ix.	18·0	0·118	0·108
65	15♀, 8♂	8. ix.	16·55	0·134	0·140

and the earlier ones on *C. typicus* were done on groups of animals which included adult males, females and Stage V. The data concerning *C. typicus* fall into two well-marked groups, but for reasons other than this mixing of adults and Stage V. Exps. 48–51 and 58 form one group in which there is a range in the rate of respiration from 0·24 to 0·33 μl./cop./hr. (mean = 0·29), and Exps. 52–57 form a second group in which the rate of respiration is much lower, ranging from 0·12 to 0·22 (mean = 0·18). This difference in respiration rate cannot be explained as a consequence of a difference in the proportionate number of adult and Stage V animals used in the different experiments, since in Exps. 48, 49 and 58 of the first group, and in all the Exps. 52–57 of the second group, the animals were exclusively adult females, yet the rate of respiration was high in the first group and low in the second. Or again, within the first

TABLE II. MEAN VALUE OF RESPIRATORY RATE

Species	Stages	Respiratory rate (μl.O_2/cop./hr.)		Standard deviation σ	
		Observed	Corrected to 17° C.	Observed	Corrected to 17° C.
Euchaeta norvegica	Adult ♀	4·284	4·785	—	—
	Adult ♂	3·038	3·235	—	—
	V	2·232	2·474	—	—
	IV	1·069	1·157	—	—
Calanus finmarchicus	Adult ♀	0·801*	0·857	0·111	0·139*
	Adult ♂	0·814	0·870	—	—
	V (13–35)	0·578	0·517	0·089	0·080
	V (36–39)	0·556	0·539	0·067	0·069
	V (13–39)	0·578	0·521	0·090	0·076
	V (40–42)	0·628	0·666	0·049	0·051
	IV	0·249	0·250	0·057	0·081
Centropages typicus	A (48–51, 58)	0·268	0·289	0·031	0·044
	B (52–57)	0·161	0·180	0·025	0·030
C. hamatus		0·106	0·107	0·025	0·026

* Omitting Exp. 7.

group itself, the rate of respiration in Exps. 50 and 51 in which animals were not all adult females was not significantly different from that in Exps. 48, 49 and 58 in which only adult females were present.

Originally it was thought that the lower rate of respiration in the second group of experiments might be due to starvation of the copepods used, with a consequent reduction in metabolism. In the first four, Exps. 48–51, the measurements of respiration were all made on animals caught during the previous day, whereas in Exps. 52–57 carried out on 12–14 September, the animals used had been caught on 10 September. Those used in Exps. 52 and 53 had been kept for 48 hr. in filtered sea water and had therefore not fed for this period; those in Exps. 54 and 55 had been picked out of the diluted townet catches that had been standing in running water for 72 hr., and although there may have been some phytoplankton in the diluted townetting for the copepods to eat, the

amount may well have been inadequate. The animals used in the four experiments, Exps. 52–55, were therefore transferred to a jar containing a thick suspension of a culture of *Chlamydomonas* and on the following day, after having been fed for 20 hr., the most active of these were picked out and used for Exps. 56 and 57. At the same time Exp. 58 was carried out with fresh animals picked out from a townetting taken the previous day (i.e. 13 September) and fed for 20 hr. The respiration rates in Exps. 56 and 57 were no different from those in Exps. 52–55; in Exp. 58 it was distinctly higher and agreed well with the rates observed in Exps. 48–51 (Table I). It is apparent therefore that starvation was not the cause of the lower respiration rate, or that, if starvation was the causative factor, one day's feeding in a rich suspension of food was insufficient for recovery.

It might be suggested that the lower rate of respiration was due to a size difference in the copepods, but it is unlikely that the animals caught on 10 September were for any reason smaller than those caught at other times. In the first place they were caught in the same locality, and, in the absence of currents passing through the area, there is no reason to expect that they came from a population different from those caught on 9 September. Secondly, the two species of *Centropages* were always separated initially by the naked eye without difficulty, since the greater size of *C. typicus* clearly distinguished it from *C. hamatus*. It is shown later that the respiratory rate is roughly proportional to the square of the length. If the observed difference in the rate of the two groups of *C. typicus* were due to size, those copepods caught on 10 September should have had a mean length of *c.* 1 mm., as compared with a mean length of 1·25 mm. for those caught on 9 September. But *C. typicus* of mean size 1 mm. would be no different in size from *C. hamatus*, and the normal separation of the two species on 10 September without microscopical examination would have been impossible.

It is clear that the two groups of *C. typicus* did not differ appreciably in mean length, and it is more likely that marked differences in respiratory rate are in some way correlated with the handling and retention of the copepods in the laboratory. It may be suggested, and support for this suggestion will be given in a later section, that the lower rate of respiration is the more correct one and that *Centropages* takes longer to regain its normal respiratory rate after the excitement of capture and handling than does *Calanus* for which 24 hr. appears to be sufficient.

These differences in the respiratory rates of *Centropages typicus* adult females necessitated a careful scrutiny of the earlier observations in order to see whether such differences could be detected in any other species. Only one result was clearly anomalous, namely Exp. 7 with *Calanus* females (27 September) where the respiratory rate was 0·36 μl./cop./hr. as compared with a mean for the other four experiments on adult females (Exps. 8–11) of 0·86 μl./cop./hr. Again the animals used in Exps. 7 had been kept for more than 24 hr. before the measure-

ments were made. On the other hand, all the experiments done with Stage V *Calanus* from 28 August up to and including 1 September were done with animals taken from an unusually good townetting taken on 27 August, and no significant decline of the respiration rate is detectable in this group (cf. Table I, col. 5, Exps. 22–35). It may be incorrect, however, to compare Stage V *Calanus* with adult copepods. Stage V copepodites may be better able to maintain a constant metabolic rate under conditions of stress, for it must be remembered that Stage V copepodites obtained in late summer were part of an overwintering stock (cf. Marshall *et al.* 1934) which pass into deep water and possibly live at a lowered metabolic level (cf. Gross & Raymont, 1942).

TABLE III. LENGTH MEASUREMENTS

Species and stage (no. of observations)	Total length		Cephalothorax	
	Mean	σ	Mean	σ
Euchaeta norvegica:				
Female (2)	7·45	0·038	5·10	0·0
Male (8)	6·14	0·259	4·36	0·184
Stage V (5)	5·75	0·148	4·15	0·121
Calanus finmarchicus:				
Female (19)	3·12	0·118	2·45	0·091
Stage V (19)	2·66	0·225	2·06	0·175
Stage IV (31)	2·03	0·138	1·63	0·226
Centropages typicus:				
Female (37)	1·86	0·111	1·25	0·095
Male (8)	1·74	0·089	1·21	0·040
Stage V (2)	1·66	0·186	1·21	0·074
Stage IV (1)	1·32	—	0·95	—
Centropages hamatus:				
Female (10)	1·47	0·096	1·06	0·097
Male (8)	1·29	0·089	0·94	0·076
Stage V (1)	1·16	—	0·79	—

Table III gives the mean lengths of the groups of copepods measured. Two measurements are given for each group: (1) the length of the cephalosome and metasome, i.e. the 'cephalothorax'; and (2) the total length including the urosome. The advantages of measurements of the 'cephalothorax' are threefold: it is the bodily dimension that is easiest to measure accurately; it is the dimension most commonly used in measuring copepods; and thirdly, if the respiration rate is to be related to any power of a linear dimension, it will be more closely associated with some power of the length of the cephalothorax than with a power of the total length, since the cephalothorax makes up by far the greater part of the bulk of the animal. Our measurements agree reasonably well with previous measurements of copepods in the Clyde area (Marshall 1933, 1949; Nicholls, 1934).

DISCUSSION

The measurements made of the respiratory rate of *Calanus finmarchicus* agree well with those determined previously by Marshall *et al.* (1935), and by Clarke & Bonnet (1939). On both previous occasions measurements were

given in ml./1000 cops./hr.; these are numerically the same when expressed in μl./cop./hr. Marshall *et al.* made no observations at 17° C., but their curve for the relationship between temperature and respiratory rate gives a value of 0·44 μl./cop./hr. for *Calanus* Stage V, which does not differ significantly from the mean value of our measurements, 0·52 μl./cop./hr. ($d/\sigma_d = 1{\cdot}05$). Clarke & Bonnet's experiments at 16·8° C. give a rather higher respiration rate, (0·80 μl./cop./hr.), the difference from that given by the present observation being statistically significant ($d/\sigma_d = 3{\cdot}4$). However, the order of magnitude is the same, and in the present poor state of knowledge of the physiology of plankton, the agreement can be regarded as reasonably satisfactory. The respiration rates for male and female *Calanus* found by us were both higher than those given by Marshall *et al.*, that for females (0·86 as compared with 0·66 μl./cop./hr.) being significantly so, but again the agreement is reasonably good.[1]

Zeuthen (1947) quotes one measurement of the respiration of *Centropages hamatus*, giving a mean respiration rate of 0·08 μl./cop./hr. at 16° C. This agrees fairly well with the measurements here recorded which have a mean of 0·11 μl./cop./hr. This agreement too becomes even closer when account is taken of the size of the animals: Zeuthen's copepod was 0·86 mm. long (presumably total length) compared with the mean total length of 1·30 mm. for the *C. hamatus* given here.

Marshall *et al.* (1935) found marked falling off in respiration with time after capture, especially between the time of capture and 24 hr. later. Clarke & Bonnet (1939) found no such decline but their results are hardly comparable, as they did not use animals until the day after capture—the practice followed in the experiments reported here. Zeuthen (1947), citing a single measurement of the respiratory rate of *C. hamatus*, found a decline during the course of his experiment. In the present series of observations, there was no very obvious decline during the course of individual experiments. However, if the mean oxygen consumption is calculated at the end of each 30 min. period for the experiments with *Calanus* Stage V, the rate of consumption appears to fall (Fig. 1), since the points for times shorter than the mean time (1·75 hr.) lie above and two of those for longer times lie below the straight line drawn from the origin through the means (1·75 hr. and 11·38 μl. O_2 consumed). But closer examination shows that only one of the means differs from the corresponding point on the straight line by as much as its standard error, and the deviation of this one, that for the second group, is less than three times its standard error so that the differences are insignificant. It is therefore improbable that there was any real falling off in the respiration rate during our experiments.

[1] Comparison is made more difficult by the fact that the curve drawn by Marshall *et al.* showing the relationship between temperature and respiratory rate appears to be based on a single experiment, while different respiratory rates are given for other experiments at a given temperature. Thus the respiratory rates of female *Calanus* at 15° C. is given on p. 8 as 0·57, on p. 12 as about 0·70 (for normally saturated sea water), while on p. 15 a value of 0·74 is given for a temperature of only 12° C.

It is generally true that the respiratory rate of animals is related approximately to their surface area. Hence, since the copepods used in the experiments described above are all closely comparable in shape, some relationship may

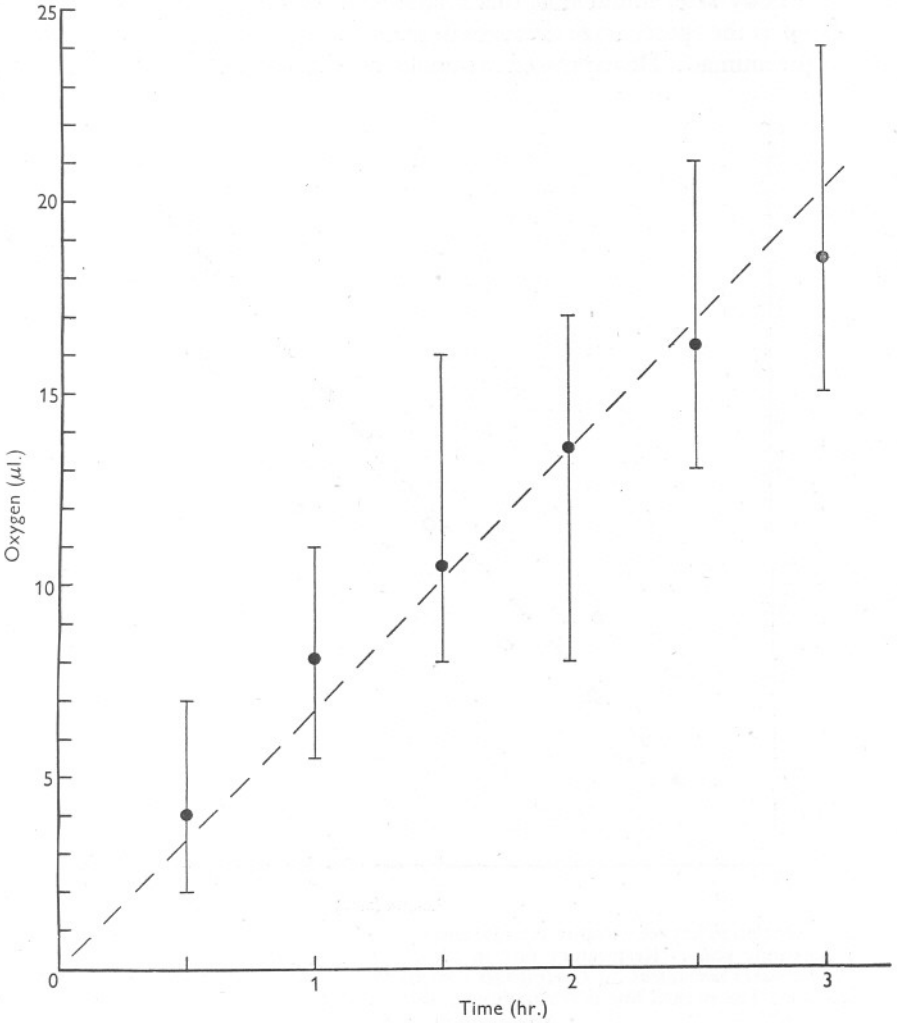

Fig. 1. Oxygen consumption by ten copepods at half-hourly intervals after start of an experiment.

be expected between their respiratory rate and the square, or some power close to the square, of their length. In Fig. 2 the respiratory rate is plotted against the length, on logarithmic co-ordinates, and it can be seen at once that the observed values lie very nearly on a straight line. The calculated regression line of the logarithm of the respiratory rate (R) on the logarithm of the length (L) is

$$\log R = 2{\cdot}193 \log L - 0{\cdot}9278,$$

from which it can be seen that in these measurements the respiratory rate was related to the length to the power of 2·19.

Zeuthen (1947, p. 81), in his analysis of the relationship between respiratory rate and body size, found that this relationship could be most satisfactorily expressed as the 'percentage decrease in metabolic rate at ten times magnification of the animal'. He expressed metabolic rate in terms of oxygen consumed

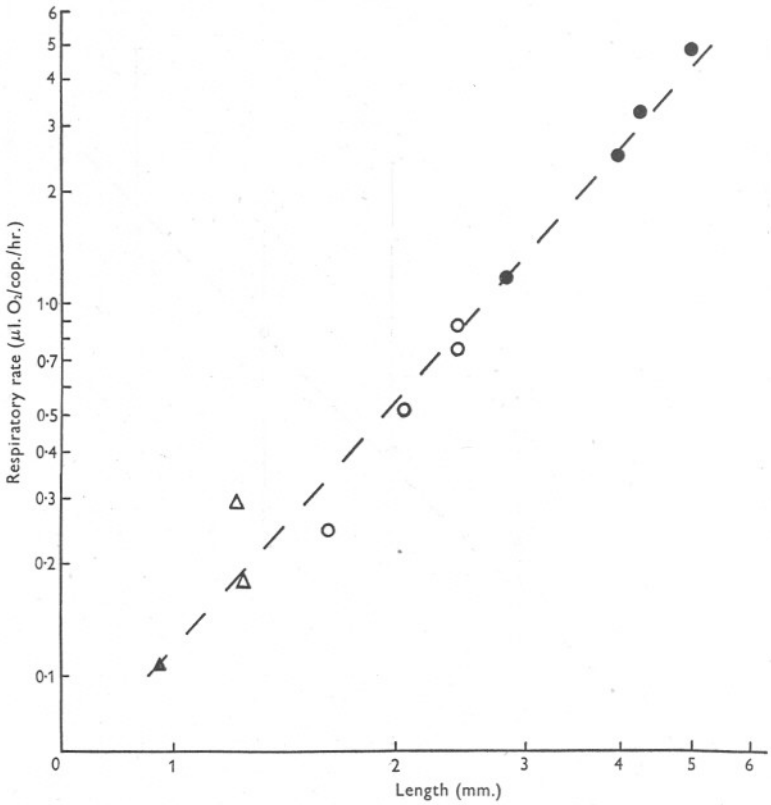

Fig. 2. The relation between respiratory rate and size of different copepods, plotted on a double logarithmic scale. (Respiratory rate in μl. O_2 per copepod per hour; length in mm.) ○, *Euchaeta norvegica*; △, *Centropages typicus*; ●, *Calanus finmarchicus*; ▲, *Centropages hamatus*. The pecked line is the regression line, given by

$$\log R = 2{\cdot}19 \log L - 0{\cdot}928.$$

per unit nitrogen content $\left(\frac{\mu\text{l. } O_2 \times 10^{-2}/\text{hr}}{\gamma N}\right)$ or per unit of weight, and showed that for a ten times magnification of the body size, the percentage decrease declined fairly steadily from *c.* 52 % for medium-sized animals (10 g.–1000 g. wt.) to only *c.* 20 % for small copepods. The percentage decrease for animals of the size range used in this present investigation he found to be

30–40 %. In the experiments described here no measurements of weights or nitrogen contents were made, but weight is usually closely proportional to the cube of the length for animals of similar shape so that a rough comparison with Zeuthen's results can be made by expressing metabolic rate as rate of oxygen consumption divided by the cube of the length.

In the measurements made above there are three pairs of figures from which percentage decrease in the metabolic rate for a ten-times magnification of size can be calculated. *Euchaeta* females are very nearly ten times the size (as given by the cube of the length) of *Calanus* females, *Euchaeta* males are just less than ten times the size of *Calanus* Stage V and *Calanus* Stage V are nearly ten times the size of *Centropages hamatus*. The decreases in metabolic rate (expressed by respiratory rate divided by the length cubed) found for these pairs are 30, 35·75 and 49·75 % respectively, with a mean of 38·5 %. The decrease in metabolic rate for a ten times increase in size calculated from the regression of respiratory rate on length given above is 46 %. These figures agree very well with Zeuthen's figure of 30–40 % for animals of the range of size represented by the copepods used in the present experiment.

The difference between the respiratory rates of the two groups of experiments with *C. typicus* has been discussed above. The distribution of the observed points given in Fig. 2 suggests that the lower value might be the more correct one, or at least that corresponding to the figures found for the other species. The deviation of the higher value (0·29 μl. O_2/cop./hr.) from the regression line

$$\log R = 2{\cdot}193 \log L - 0{\cdot}9278$$

is 0·19, twice the standard error of estimate (0·09), whereas that for the lower value (0·18 μl. O_2/cop./hr.) is only 0·03. The agreement of the lower rather than the higher respiratory rate for *C. typicus* with those for the other species is made even clearer by calculating a regression omitting the higher value. This makes a slight but not clearly significant improvement in the correlation coefficient and gives regression equation

$$\log R = 2{\cdot}302 \log L - 0{\cdot}9901.$$

The deviation of the higher respiratory rate from this line is more than three times the standard error of estimate, i.e. this value almost certainly differs from the group of values represented by this regression line, while the deviation of the lower value is less than half the standard error of estimate.

Several suggestions could be made to account for an enhanced respiratory rate in *Centropages* as found in Exps. 48–51 and 58—for instance, that *C. typicus* is excited more easily than other species by handling or by light, but in the absence of any information about the factors which might have produced the increase of the respiratory rate, further discussion is not profitable.

The question as to which of the two respiratory rates found for *C. typicus*

represent the 'true' value leads to the wider question, namely how far the rates as determined for the other species (*Calanus*, *Euchaeta*, *Centropages hamatus*) are true for these copepods living under natural conditions in the sea. Any future discussion of nutritional requirements based on respiratory rates (cf. Pütter, 1909) must imply that the metabolic rates determined in the laboratory are true for the copepods under natural conditions. The curve given by Marshall *et al.* (1935) for respiration and temperature would permit us to calculate approximately the respiration rates for the various temperatures at which the different species are living over the seasons of the year. But there are many other factors apart from temperature that might also affect respiration. Of these some attention has been given to such internal factors as sex and developmental stage. As regards environmental conditions, there are indications that light has little effect on Stage V *Calanus* (cf. also Marshall *et al.*), though no experiments were made using bright sunlight. However, the precise effects of light as well as of such factors as feeding, season, etc., must await further study.

There remains the very pertinent question as to how far the experimental conditions in a closed respirometer may modify the metabolic rate. The experiments on *Calanus* by Marshall *et al.* seemed to show that lowered O_2 tension had little or no effect unless the concentration fell below about 3 ml. O_2/l.—a value which would never even be approached in our 3-hourly experiments. There is also the possible disturbing effect on metabolism of handling the animals. This would appear to be slight (with the possible exception of *Centropages typicus*) in view of the fact that no clear reduction in respiratory rate with time was observed in our experiments, and also since our results (for *Calanus*) agree very well with those of Marshall *et al.* who employed the Winkler technique where animals were left undisturbed for relatively much longer periods of time. From the results of a few experiments with Stage V *Calanus* (Table I, Exps. 40–42) where shaking was limited to a few minutes immediately prior to final reading of the manometers, it is apparent that shaking depressed the respiratory rate of the copepods. But no permanent injury appears to have been caused by it, since the great bulk of our experimental copepods were active and healthy after being in the respirometers, and indeed, if used for a second experiment, gave a result usually showing good agreement with the original determination. The shaking of the respirometers may have reduced respiration by interfering with the physical activity of the copepods in the respirometer flask rather than by injury of the animal.

It is obvious, of course, that we were measuring the respiratory rates of the copepods in a state of activity, but how far their activity in the respirometer corresponds to their normal activity in the sea is not easy to determine. In these measurements, as in those of Marshall *et al.* and Clarke & Bonnet, the copepods were enclosed in a very small volume of water, of the order of 1 ml. per copepod, while in the sea the water in which the copepod is swimming is

effectively infinite and its distance from its nearest neighbour is probably of the order of ten or possibly a hundred times as great as it is in the respirometer. In consequence the probability of contact with the walls of the respirometer or with other copepods is very much greater than it is in nature. This repeated stimulus of contact may keep the copepods in a comparatively excited condition and this may produce a rise in the respiratory rate.

Summary

The respiratory rates of four species of planktonic copepods were measured. In two of the species measurements were made with two copepodite stages, and with adult male and female specimens.

The rate for *Calanus finmarchicus* Stage V at 17° C. was found to be 0·52 μl./cop./hr., a figure which agreed with previous measurements.

For all the species and stages studied the respiratory rate was found to be closely proportional to the length to the power of 2·2.

The relevance of such measurements to conditions in the sea is briefly discussed.

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THE GRAZING RATE OF PLANKTONIC COPEPODS

By D. T. Gauld, B.Sc., Ph.D.

Department of Zoology, University of Edinburgh, and the Marine Station, Millport

(Text-figs. 1–4)

Introduction

The source of the food of planktonic animals has been frequently discussed since, on the basis of his calculations of food requirements, Pütter proposed in 1907 that the particulate food available to them was quite inadequate for their needs and that they must therefore derive the greater part of their nourishment from organic substances dissolved in the water. Critical study of Pütter's experiments showed that they were unreliable, and his calculations were made generally invalid by the publication in 1908–11 of Lohmann's work on the nanoplankton in sea water. In these studies Lohmann drew attention to the existence in the sea of enormous numbers of organisms, mainly unicellular algae, from 1 to 25 μ in diameter and length, and too small to be captured by plankton nets. He was also able to show that the Appendicularia obtained their food from these minute organisms and were able to filter in an hour a volume of water many thousand times their own size. Pütter tried to show that even here the amount of plankton filtered was inadequate. Krogh (1931) pointed out that Pütter based his calculations on the numbers of organisms found in the filters, and overlooked the fact that the contents would be emptied into the gut at regular intervals, and he commented (p. 415): 'It must however be admitted that Lohmann on his side did not prove the sufficiency of the nanoplankton food for the Appendicularia.'

Pütter (1909, 1925) included Copepoda among the animals which would be unable to obtain enough particulate food from sea water. As Krogh (1931) remarked, the existence in these animals, as in others, of a well-developed gut and a complex apparatus adapted to the acquisition of particulate material is itself evidence that the bulk of their food is particulate, and examination of the contents of the gut shows the presence of particulate food (Dakin, 1908; Esterly, 1916; Lebour, 1922; Marshall, 1924). Even Pütter himself mentions 'eine grüne Masse' which was undoubtedly made up of nanoplankton flagellates. But no attempt was made to find out whether the copepods could obtain a sufficiently large quantity of food by collecting the minute organisms present in the water until 1936, when Fuller & Clarke measured the filtering rate of *Calanus finmarchicus*.

The amount of food which a filter-feeding animal can obtain in a given time is determined by the volume of water which it can filter in that time, the concentration of suitable food particles in the water, and the efficiency of the filtering mechanism. The filtering rate, i.e. the rate at which water is passed through the food-catching apparatus, is independent of the concentration of the food particles, but is dependent, like any other biological process, on the physical and chemical conditions of the environment and on the activity of the animal. For example, filtering may be discontinuous and in consequence the filtering rate during active feeding may be considerably greater than that indicated by measurements made over longer periods which include periods of inactivity. The efficiency of the filtering apparatus will depend on the size of the particles, being greatest for those which are neither so small that they are able to pass through the apertures of the filter, nor so large that they obstruct the filtering apparatus. It is possible, however, that, even with particles of uniform size, the efficiency of the filter may be variable, and may be under some kind of control by the animal.

The measurements of Fuller & Clarke (1936) and those of Fuller (1937) seemed to show that the animal's power of catching particulate food was quite inadequate for its needs. Fuller & Clarke found that *Calanus*, a large copepod, could sweep clear of carmine particles 4·5 ml. of water per day. At the same time they estimated that in order to supply its needs it would have to sweep clear about 72 ml. of water containing a rich natural diatom population. In 1937, estimating the food requirements on a different basis, Fuller stated that even with the maximum rates of filtering in his experiments (2·88 ml. per day) *Calanus* would have obtained, in water where it is known to thrive, less than one-tenth of the required amount of its food from particulate matter. On the other hand, Harvey (1937) reports a small number of experiments in which he found far more rapid filtering rates for *Calanus*, 2–4 ml. swept clear per hour with *Lauderia borealis*, a medium-sized diatom, and 7–10 ml. per hr. with the larger *Ditylium brightwelli*.

In his measurements of filtering rates, Fuller (1937) found no correlation between the concentration of food and the filtering rate, and concluded that *Calanus* obtained its food by filtering particles from a stream of water passed through the setae of the posterior cephalic appendages, and made his investigation on this assumption. However, Lowndes (1935), basing his views on anatomical grounds and on the fact that crustacean remains have been reported from the gut, states (p. 702) 'It is difficult to see any justification for describing the feeding of *Calanus finmarchicus* as being either automatic or non-selective', and implies that the bulk of its food is obtained by seizing and chewing up larger particles, especially other crustaceans.

The experiments which are to be described below throw some light on the question of filter-feeding by copepods and of the magnitudes of the filtration rate.

Acknowledgements

The author is indebted to Prof. J. Ritchie, of the Department of Zoology, University of Edinburgh, for his interest in the work and for his careful reading of the manuscript, and to Mr E. Ford, Director of the Marine Biological Station, Millport, for his helpful criticism during the last part of it. Some of the work was done while the author held a Jacobsson Fellowship at the Oceanographic Institute at Göteborg, and he would like to thank Prof. Hans Pettersson and the Board of the Göteborgs Sjöfartsmuseum for giving him the opportunity of doing this work. Finally, he acknowledges the assistance of the late Dr F. Gross, who supplied the cultures with which the experiment started and who gave ready help and advice throughout the work.

Material and Methods

The experiments to be described fall into three groups; (i) those done in the Department of Zoology, Edinburgh University (Series A and D); (ii) those done in the Oceanographic Institute, Göteborg (Series B and C); and (iii) those done at the Marine Station, Millport (Series E–G). On arrival at the laboratory the copepods were sorted and transferred to cooled sterile sea water in 'breffit' jars, and at Edinburgh and Göteborg kept in a refrigerator the upper temperature limit of which was set at 10° C. At Millport the jars in which the copepods had been placed were kept in running water to cool them. Some preliminary experiments were done with the diatom *Skeletonema costatum* as food. In these experiments the diatoms occasionally settled to the bottom of the dish during the experiments, especially in experiments done in darkness. In consequence these experiments had to be abandoned, and the *Skeletonema* culture was replaced by one of a species of *Chlamydomonas*. *Chlamydomonas* is an actively motile flagellate; its approximate dimensions are: length 9·5–13·8 μ, diameter 6–8·4 μ (Raymont & Gross, 1942) and no evidence was ever seen of its settling or being unevenly distributed in any way.

For the experiments a culture of *Chlamydomonas* was diluted with sterile sea water, and divided among a number of beakers or large crystallizing dishes, each one receiving 100 or 150 ml. of this experimental medium. In some of the jars one or more, according to their size, healthy active copepods were placed; others were kept as controls. The concentration of the suspension of the food organism was estimated at the beginning of the experimental period, usually about 24 hr., and again at the end. Usually at the end of one experiment the copepods were transferred into a second set of vessels and a new experiment started.

In the first two series of experiments (A and D) the concentration of the culture of the food organism was measured by its extinction of light in a 'Unicam' photometer. This method was satisfactory only if the concentration of the food organism was rather high—very much higher than likely to occur in nature.

There was a possibility therefore that the behaviour of the copepods might be abnormal in such conditions, so that this method was later abandoned in favour of counting. In all the other experiments the concentrations were measured by counting the *Chlamydomonas* cells on a Fuchs-Rosenthal counting slide—four millimetre squares from each of five drops, making a total of four microlitres, were counted from each experimental vessel. The agreement between the counts of different drops and between the counts of different squares from the same drop was generally good.

If it is assumed that a copepod is a filter-feeding animal, then in an experimental vessel where the physical and chemical conditions are kept constant, the concentration of food particles in the presence of a steadily grazing copepod will decline exponentially, and at any given time it is given by the expression

$$C_t = C_0 e^{-kt}, \tag{1}$$

where C_t is the concentration after time t, and C_0 the initial concentration.

Further if v is the volume of water per animal, then vk is the volume of water swept free by one animal in unit time, so that the filtering rate (F) is given by

$$F = vk. \tag{2}$$

This expression can be evaluated from (1) in the form

$$F = v \frac{\log_{10} C_0 - \log_{10} C_t}{t \log_{10} e}. \tag{3}$$

The results of the experiments to be described were evaluated from this formula (3) and expressed as millilitres of water swept clear by one copepod in the period covered by the experiment, usually 18 or 24 hr.

Experiments

A summary of the experiments and their results is given in Table I, and Figs. 1–3 show the results in greater detail. In the figures, the volume swept clear is plotted against the concentration of the control cultures.

Fig. 1 gives the results of the experiments done with *Pseudocalanus*. The results of experiments with *Temora* and *Centropages* are given in Fig. 2 and those with *Calanus* in Fig. 3.

Of the experiments with *Calanus* Stage V (Series E), and Stage IV (Series F), most were done over 18 hr., starting at about 16.00 hr. and finishing about 10.00 hr. the following day, i.e. the experimental period included the hours of darkness. But in Series E six experiments were continued for 24 hr. and eight for only 12 hr. The means of these two groups were respectively 82·31 and 73·62 ml. swept clear, in comparison with 69·66 ml. swept clear for the

TABLE I

Series	No. of experiments in series	Species	No. of copepods per vessel	Volume of vessel (ml.)	Duration (hr.)	Temperature (° C.)	Mean volume swept clear per copepod (ml.)	Standard deviation σ
A	21	*Pseudocalanus minutus*	1	10	24	10	4·28	1·46
B	45	*Temora longicornis*	10	150	24	10	8·38	1·91
C	8	*Centropages hamatus*	10	150	24	10	12·99	1·20
D	19	*Calanus finmarchicus* stage V	1	100	24	12·5	64·36	11·63
E	77	*C. finmarchicus* stage V	1	100	18	17	71·03	13·17
F	25	*C. finmarchicus* stage IV	2	100	18	17	36·65	8·75
G	13	*C. finmarchicus* stage III	3	100	18	17	22·24	5·58

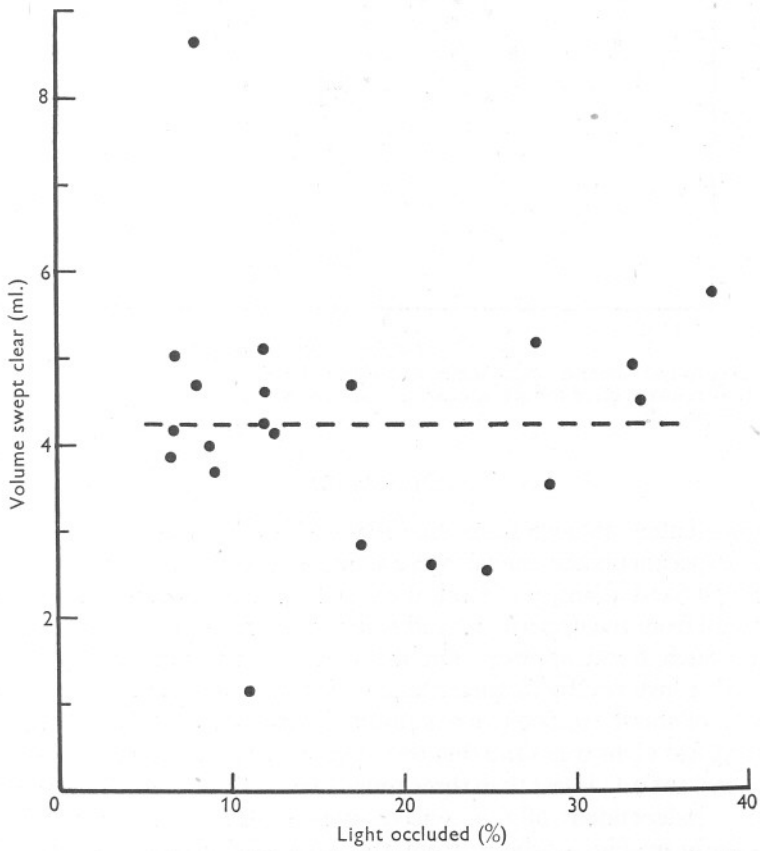

Fig. 1. *Pseudocalanus minutus*. Volume (ml.) of culture swept clear compared with the concentration of the control culture, measured by the percentage of light occluded.

remainder measured over 18 hr. The difference between the volumes swept clear in 12 and 18 hr. is not significant. The increased volume swept clear in 24 hr. is possibly significant, but only just so ($D/\sigma_m = 2{\cdot}1$).

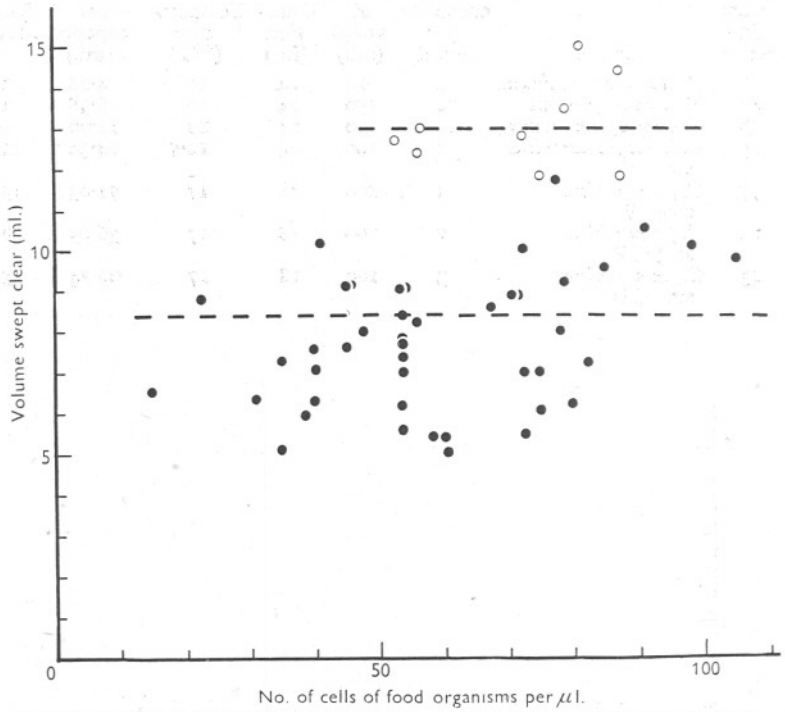

Fig. 2. *Centropages hamatus* (open circles) and *Temora longicornis* (black circles). Volume (ml.) of culture swept clear compared with the concentration of the control culture, measured as cells per μl.

Discussion

It is immediately obvious from the scatter of the points in the diagrams that in these experiments the animals were acting as filter-feeders. If they had been collecting a fixed quantity of food, the scatter of the points would have shown some trend from the upper left-hand side of the figure to the lower right-hand side: no such trend appears. On the contrary, the number of *Chlamydomonas* cells consumed by *Calanus* Stage V (Series E), for example, ranges from a minimum of about 250,000 to a maximum of 2,000,000, i.e. the largest amount consumed was eight times the smallest. On the other hand, the largest volume swept clear, 101 ml., is less than three times the smallest, 42 ml. That the volume filtered is independent of the concentration of the food particles is shown more clearly in Fig. 4 where, from the data of Series C, the difference in the concentration produced by one *Temora* in 24 hr. is plotted against the

concentration of the initial cultures. Here there is a very clear trend from lower left-hand side to the upper right-hand side of the figure, and the broken line in the figure is the graph of the difference produced by a steady filtration rate of 8·38 ml. in 24 hr., the mean of the observed rates. Similar figures could be drawn for the other series of experiments. These findings are therefore in agreement with Fuller's that there is no correlation between the concentration of the food particles and the filtering rate.

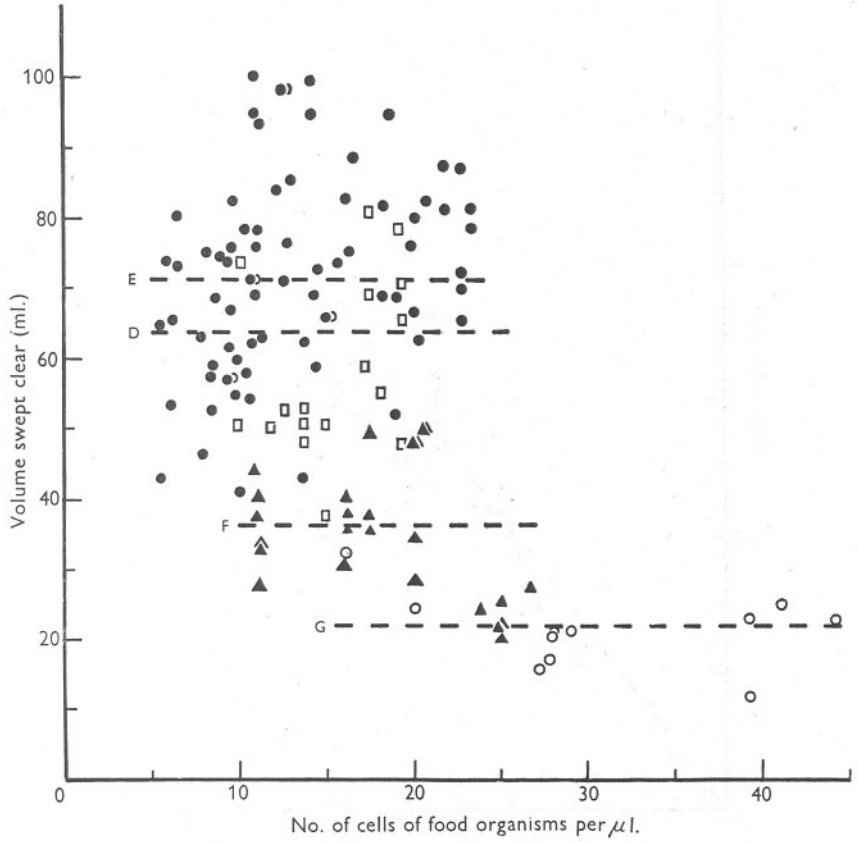

Fig. 3. *Calanus finmarchicus*. Volume (ml.) of cultures swept clear compared with the concentration of the control culture, measured as cells per μl. □, Series D, Stage V; ●, Series E, Stage V; ▲, Series F, Stage IV; ○, Series G, Stage III.

It may be objected that, while these figures (like Fuller's) show that the animals collected all the food from a given volume of water, they do not prove that it was collected by filtration although they make it more likely. However, the total number of particles consumed can readily be calculated and those for *Calanus* Stage V have already been mentioned. If it is assumed that the copepods worked continuously for the whole period of the experiment, although

it has been suggested that this may not be so, it is possible to calculate how many particles were collected in unit time. In the experiments with *Calanus* Stage V (Series E) this works out at nearly 4 per sec. from the lowest figure to over 30 per sec. from the highest. Similar collecting rates apply to the other experiments; *Temora*, for instance, collected particles at a rate of from $1\frac{1}{2}$ to 9

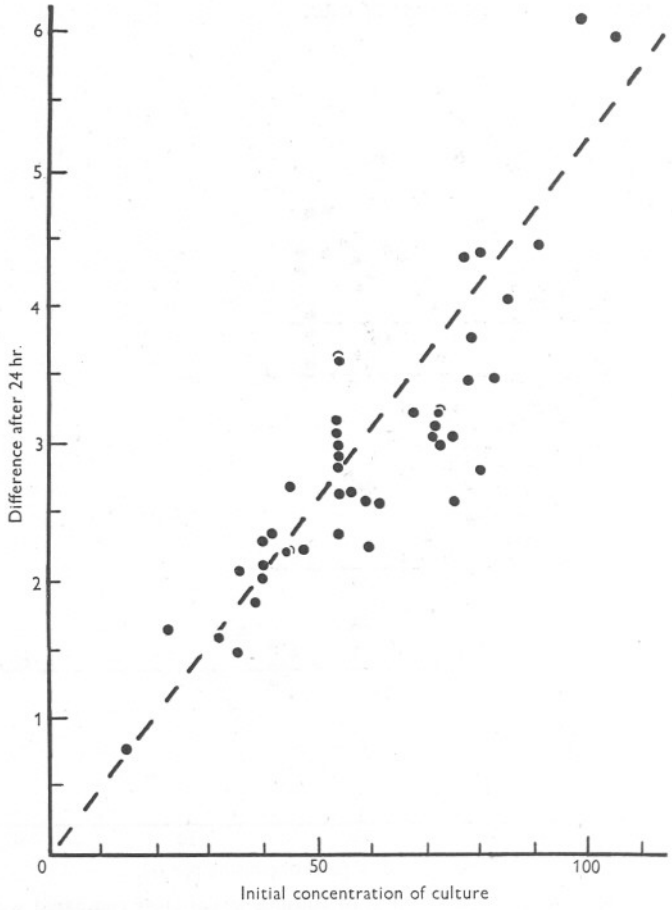

Fig. 4. *Temora longicornis*. Difference in the concentration of food organisms produced by one copepod in 24 hr. plotted against the concentration of the initial culture. Units are cells per μl.

particles per sec. in the experiments in Series C. It is difficult to imagine any way in which the animals could collect particles so rapidly except by filtration, especially since it is probable that the copepods fed actively during a part only of the experimental period and so must have collected their food even more rapidly than the figures show.

The magnitude of the filtering rates found here for *Calanus* is much greater than those found by Fuller & Clarke (1936) and Fuller (1937). The 1936 measurements were made by estimating the rate at which carmine particles were removed from the water. Some of the carmine was definitely ingested but it is possible that the bulk was rejected after it had been collected on the filtering apparatus and that the apparently low filtering rates were due to return to the water of the particles so rejected. Fuller (1937) measured the filtering rate by estimating the change in the concentration of cultures of the diatom *Nitzschia closterium* (Plymouth strain), and found rather smaller filtering rates than Fuller & Clarke. *A priori*, *Nitzschia* might appear to be suitable for such measurements since *Calanus* has been reared on cultures of this diatom (Crawshay, 1915), but the experiments of Harvey (1937) seem to show that for some reason it is unsuitable, since he found very low filtering rates with *Nitzschia* although with other diatoms, *Ditylium* and *Lauderia*, he obtained very much higher rates. One criticism may be made of Fuller's experiments. The measurements were made in vessels in which three copepods were confined in 15 ml. of water. In view of the size and activity of *Calanus* this seems to be a very small amount of water for each animal, and indeed it is difficult to see how volumes swept clear much larger than 5 ml. per animal could be measured in such experiments.

The measurements of Harvey (1937) are of the same order of magnitude as those recorded here for *Calanus*, but immediate comparison cannot be made because his experiments covered variable and rather short periods and the results are given as filtering rates per hour. If it is true that *Calanus* filters intermittently, results based on short periods of observation are liable to be misleading, since an experiment which covers a period of a few hours may or may not include part of a period of active filtration. Two of Harvey's experiments however covered a 24 hr. period and the volumes swept clear in these were 74 and 94 ml. per *Calanus*. One experiment of 48 hr. showed a total filtration of 96 ml. per copepod, and of the measurements made over periods of less than 24 hr. none exceeded 70 ml. These results therefore do not contradict the hypothesis that *Calanus* filters a volume of about 70 ml. per 24 hr., but that the greater part of this filtration is confined to a relatively short period.

Riley, Stommel & Bumpus (1949) calculated the filtering rates of mixed plankton populations, and found filtering rates of 80–110 ml. swept clear per day for each milligram (wet weight) of zooplankton. Bogorov (1934) gives the wet weight of *Calanus* Stage V as varying between 0·35 and 0·70 mg. with a mean value of 0·53 mg. From these figures the filtering rate of *Calanus* Stage V can be calculated, giving an overall range of from 28 to 77 ml. swept clear per day, values which agree very well with those found in the present experiments, in spite of the roundabout way in which they have been reached.

Fuller (1937) found that the diatom concentration in his experimental vessels often remained stationary for a day or more, showing that feeding was

not a continuous process, and in some of his experiments he reported a diurnal feeding rhythm in which the diatoms were removed more rapidly at night. Such a rhythm is suggested by the observation in the present experiments that there is little difference between the amount of grazing in 12, 18 or 24 hr., but sufficient evidence is not available to show the period, or periods, during which grazing was most active, or the causes of the rhythm.

Comparison of the filtering rates found for the different species and stages is difficult because the experiments were carried out at different temperatures. If, however, it is assumed that the relation between temperature and filtration rates is the same as that between temperature and respiratory rate, and the observed rates are all corrected for a single temperature (10° C.), it can be shown that the filtering rates are approximately related to the squares of linear dimensions. (The correlation coefficient between the filtration rate and the square of the length is 0·84.) However, the range of size covered by these experiments is small and the variation in the observed values of the filtering rates rather large, so that more detailed mathematical investigation of this relation is not justified without further evidence.

In discussing Harvey's results, Fuller (1937) suggested that *Calanus* was better able to retain large particles on its filtering surface than small ones, and that the low filtering rates found by Harvey and himself with *Nitzschia* were due to the small cells of *Nitzschia* passing through the filter. But Harvey's observation (Exp. C, p. 98) that, in a mixed suspension of *Lauderia borealis* and a species of *Chaetoceros*, *Calanus* reduced the concentration of *Lauderia* from 13 to 1·9 per ml. in 48 hr. 'without any considerable reduction in the *Chaetoceros* population', cannot be explained in this way. The species of *Chaetoceros* used in this experiment was almost certainly larger than *Nitzschia closterium* forma *minutissima*, which Harvey found to be removed in appreciable amounts, though much more slowly than *Lauderia* in Exp. N 90. Wilson (1946) states that this form of *Nitzschia* is 3–4 μ in diameter and 25–35 μ in length. It is impossible to be certain of the size of the *Chaetoceros* species used, but none of the measurements given in Lebour (1930) for any species of *Chaetoceros* is less than 4 μ broad. In addition, *Nitzschia closterium* is a solitary species while the species of *Chaetoceros* nearly all form chains and the spines characteristic of the latter genus might increase the effective diameter of a chain of cells, possibly to five times that of the cells. Riley *et al.* (1949) suggested that the result of Harvey's experiment was due to the rejection by *Calanus* of *Chaetoceros* 'which in chains would presumably be larger than *Ditylium*' (p. 64), and implied that *Chaetoceros* in chains was too large to be eaten by *Calanus*. This is not so since *Calanus* is known to feed on *Chaetoceros* (Marshall, 1924; Raymont & Gross, 1942). That chains of *Chaetoceros* cells may be larger than a *Ditylium* cell is probably unimportant since diatom chains are readily broken up, much more so than the cells of *Ditylium* which *Calanus* cannot swallow whole but has to break up, as it does many large diatoms

(Marshall, 1924). If the size of the particles were the only factor in the selection of food by copepods as Fuller and Riley *et al.* suggest, Harvey's grazing rates suggest that the optimum size of particle is one about the size of a *Ditylium* cell or a *Lauderia* chain which would be about the same size and shape, approximately a cylinder 40–50 μ in diameter and 100–200 μ long. *Chlamydomonas*, the food organism used in the experiments described in the present paper, is a solitary flagellate, entirely without projections of any kind, and its linear dimensions are nearly ten times smaller than *Ditylium* and of the same order as those of *Nitzschia*. Raymont & Gross (1942) give its dimensions as 6–8·4 μ by 9·5–13·8 μ, and a small number of measurements made recently agree closely with those. Yet in the experiments described here *Calanus* filtered the *Chlamydomonas* at the same rate as Harvey found with *Lauderia*, and nearly twenty times as fast as it filtered *Nitzschia*. It is clear that selection is not merely a matter of size, and some more active mechanism of selection may be involved, but sufficient evidence is not available for further discussion to be profitable.

Fuller & Clarke (1936) and Fuller (1937) attempted to relate the filtering capacity of *Calanus* to its food requirements. Fuller & Clarke computed the volume an individual *Calanus* would require to filter in Vineyard Sound in July in order to obtain its minimum food requirements as 72 ml. per day. From a different estimate of the available food, Fuller calculated that a single *Calanus* would need a minimum filtering rate of the order of 30 ml. per day. If this latter estimate is correct, the filtering rate found in the present experiments is quite adequate. But since the amount of food provided by the phytoplankton at any time and place is still uncertain, and the daily requirements of a copepod are difficult to assess, further attempts to relate filtering rate and food requirements can have little value until more evidence is available.

Summary

The filtering rate of four species of marine planktonic copepods was measured by estimating the rate at which they consumed cultures of *Chlamydomonas*.

The filtering rate was independent of the concentration of the food organism and it is concluded that the copepods were acting as filter feeders.

The filtering rates were much greater than those reported by Fuller & Clarke (1936) and Fuller (1937), but agreed with those reported by Harvey (1937).

Some evidence was obtained that grazing was restricted to some only of the 24 hr., most probably to the hours of darkness.

The filtering rates were approximately proportional to the square of the linear dimensions of the copepod.

The purely mechanical selection suggested by Fuller (1937) to account for differences in filtering rates obtained with different species of diatoms cannot account for all the differences which have been observed.

It is probable that the copepods could obtain sufficient particulate food in the sea by filtering a daily volume of water corresponding to the filtering rates found.

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THE STATUS OF THE COMMON SEAL (*PHOCA VITULINA* L.) ON THE EAST ANGLIAN COAST

By D. E. Sergeant

Department of Zoology, University of Cambridge

(Text-fig. 1)

From time to time over a number of years the Fisheries Laboratory at Lowestoft has been asked to investigate aspects of the problem of the alleged harm to fisheries caused by the common seal. There are numerous colonies of these animals off the East Anglian coast, frequenting especially the sandbanks of the Wash, which dry out at low water, and therefore form secluded resting places.

It would be a major undertaking to make a full estimate of damage done by the seals, whether this is large or small; but evidence on which a judgement can be based has been collected, and is given in the following pages. This evidence is often inconclusive, but in one locality it clearly shows harm done by the seals, and in the author's opinion it would be prudent from time to time to reduce the number of seals, incidentally finding a commercial use for the meat and hides.

The evidence comes from an investigation of the food of the seals, and of their numbers, to which are added some notes on their biology.

This work was carried out in the summer of 1947 and the spring of 1948 at the Fisheries Laboratory, Lowestoft, and grateful acknowledgement is made of help given by members of the staff of the laboratory in its progress. I am particularly indebted to the director, Mr Michael Graham, for allowing me to incorporate the results of his own earlier investigations in this paper, for reading through the manuscript and suggesting improvements, and for encouraging its publication.

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Finally, I am indebted to Prof. James Gray for permission to submit the paper for publication while I have been engaged on other research work under his supervision.

Food

Altogether 194 stomachs of seals obtained in the Wash district during 1947 were examined, 2 of these with the complete gut. In addition, 6 stomachs from the Blakeney district of the Norfolk coast, and 2 unpreserved stomachs from

seals killed on the Scroby Sand, off Yarmouth, were examined. The last were sent by Messrs Pettit of Reedham. All the rest were sent by the Eastern Sea Fisheries Joint Committee, while a scheme was in operation under which fishermen received a bounty for each stomach collected and preserved in formalin. These were forwarded to the Fisheries Laboratory in milk-cans for examination.

To supplement the results of these examinations a 3-day visit was made by the author in April 1948 to King's Lynn and the coast of North Norfolk as far east as Sheringham, and inquiries were made of fishermen at Lynn, Wells, Brancaster, Blakeney and Sheringham. These inquiries yielded eye-witness accounts of the feeding of seals and the stomach-contents in freshly killed seals. The author has, in addition, observed seal herds in the Wash on several occasions, and has been able to study the bottom fauna brought up by the trawls of shrimping vessels in that estuary, as an indication of the food available to the seals there.

Of the 202 stomachs examined, all came from seals killed between June and September, with the exception of the two from Scroby Sand which had been killed in March. Thus the results do not indicate a complete year's feeding habits, and more spring-killed seals would have been desirable, for example, to examine for remains of sea-trout (which appear to be caught off the Norfolk coast by the fishermen in May).

Only date and position of capture were given with the stomachs, with no information available as to the size or sex of the seals from which they had been taken. However, it was possible to distinguish the young and first-winter animals by the small size and thinness of their stomachs. All other stomachs are labelled 'adult'. Of this total of 202 stomachs, 106 were those of young seal pups, containing (if anything) only milk. Of the remaining 96, only 25 contained recognizable food remains; so that the number does not permit of a quantitative evaluation of the food eaten. However, it has been possible to confirm the results from earlier work, previously unpublished, carried out by Mr M. Graham from 1926 to 1930 on the food of seals in this region. These results are included in the tables (see Table I separately and together with the results of the present investigations.

To account for the small percentage of stomachs containing any food remains at all it is presumed that most of the seals were killed while resting on sand-banks at low water, some time after their last meal. Digestion in these animals is very rapid, all traces of food having left the stomach within 3 hr., according to Havinga (1933).

From the data available, the food of seals frequenting the Wash may be summarized as follows:

The pups are suckled for at least a month. Havinga (1933) gives 6 weeks from birth to weaning, and my results indicate about the same time—all pups were feeding on milk up to 10 July, and some were still unweaned by the 25th.

However, some began to feed on shrimps about 12 July onwards, and these became the predominant food until about the middle of October. Havinga also found, from analyses of stomach contents, that young seals on the Dutch coast fed largely on shrimps in their first autumn.

TABLE I. SUMMARY OF FOOD FOUND IN STOMACHS OF SEALS FROM THE WASH (ADULT AND IMMATURE), 1929 AND 1947

	No. of stomachs in which found			Total number of individuals of species		
Species	Graham 1929	D.E.S. 1947	Total	Graham 1929	D.E.S. 1947	Total
Fish:						
Flatfish (*Pleuronectes* spp.)	5	2	7	*c.* 15	2	*c.* 17
Whiting (*Gadus merlangus*)	2	1	3	2	1	3
Sand eel (*Ammodytes* sp.)	1	—	1	1	—	1
Salmonid (?)	—	1	1	—	1	1
Pipefish (*Syngnathus* sp.)	—	1	1	—	15	15
Unidentified	1	1	2	1	1	2
Mollusca:						
Common whelk (*Buccinum undatum*)	17	6	23	158	14	172
Squid (*Loligo* sp.)	—	3	3	—	5	5
Mussel (*Mytilus edulis*)	—	3	3	—	8	8
Cockle (*Cardium edule*)	4	2	6	4	2	6
Crustacea:						
Common shrimp (*Crangon vulgaris*)	5	9	14	110	245	355
Prawn (*Pandalus montagui*)	1	—	1	50	—	50
Crabs (*Carcinus* or *Portunus* sp.)	—	1	1	—	1	1
Hermit crabs (*Eupagurus* spp.)	1	1	2	1	1	2
Unidentified	1	—	1	2	—	2

Totals calculated by weight at time of assimilation, including shell weight for the Mollusca: all fish 4%, Mollusca 92%, Crustacea 4%.

There is thus after weaning a transitional shrimp-eating stage. Then, in their first winter, the seals become more omnivorous and eat fish, crabs, etc., as well as shrimps. As may be seen from Table I, the food of adult seals in the Wash appears to be predominantly the Common Whelk (*Buccinum undatum* L.), the opercula of which were found alone and in some numbers in many stomachs, in both investigations. Fish are not a large item, but flatfish (*Pleuronectes* spp.), whiting (*Gadus merlangus* L.), pipefish (*Syngnathus* sp.), and salmonid remains were identified from whole remains, otoliths, or vertebrae. Other food includes squids (*Loligo*, sp.), shrimps, hermit crabs (*Eupagurus* sp.), true crabs (*Carcinus maenas* Penn. and *Portunus* sp.), and small mussels (*Mytilus*).

The sample from Blakeney shows a complete contrast. The number of stomachs was relatively small, but most were full, and showed an overwhelming preponderance of fish-remains. Reports from fishermen confirm these piscivorous tendencies. Apart from flatfish (Pleuronectids) and gobies (*Gobius*

minutus Gmelin) which were found in the stomachs sent in, soles, eels, mackerel and sea-trout are said to have been found in stomachs opened by the fishermen themselves in the past, and in addition seals have been watched feeding on skates and cod.

No food remains were found in the two intestines examined.

It is possible that the percentage of fish has been underestimated, since (i) the small fish otoliths would pass out of the stomachs more rapidly than the larger whelk opercula, etc., and (ii) the heads of fish may, according to eye-witnesses, be bitten off, and rejected, leaving only the more rapidly digested vertebral column for recognition.

TABLE II

A. FOOD FOUND IN STOMACHS OF SEALS FROM BLAKENEY (SIX STOMACHS, THREE CONTAINING FOOD REMAINS, OCTOBER–DECEMBER, 1947)

Species	No. of stomachs	No. of individuals	Remarks
Dab (*Pleuronectes limanda*)			
Plaice (*P. platessa*)	3	*c.* 90	All 10–12 cm. in length
Flounder (*P. flesus*)			
Common goby (*Gobius minutus*)	2	*c.* 12	—
Unidentified elasmobranch	1	1	—
Shrimp (*Crangon*)	2	2	—
Hermit crab (*Eupagurus bernhardus*)	2	2	—
Crab (*Portunus* sp.)	1	8	—
Mussel (Mytilus)	1	1	—

B. FOOD FOUND IN STOMACHS OF SEALS FROM SCROBY SAND (TWO STOMACHS, APRIL 1948)

(i) 1 pleuronectid (ii) 3 shrimps (*Crangon*)

Some of the smaller invertebrates may have been taken as secondary food, i.e. that eaten by the seal's prey; but this has been considered for each individual, e.g. small worms (*Lagis* sp.) associated with flatfish were certainly the food of the latter, but crabs with a carapace width of *c.* 25 mm. in the same stomach could not have been so. The whelks must certainly have been taken directly, as they were never associated with any fish remains.

Thus the results for adult seals from the Wash contrast strongly with those from the open coast at Blakeney. Examinations of shrimpers' catches in the Wash show that shrimps form the great bulk of the free bottom fauna, while fish of any size are rare. Small flatfish of 2–3 in. in average size, small gadoids and the common goby are the principal small fish brought up in these fine-meshed trawls, together with occasional sprats (*Clupea sprattus* L.), the sea-snail (*Liparis montagui* Don.), and the armed bullhead (*Agonus cataphractus* L.). Whelks are presumably common: although the trawls do not take them, there are local fisheries for whelks at Brancaster and Wells just outside the bay of the Wash. In the Wash there are no inshore fisheries dependent on fish, as there

are on the open coast. All the boats at Lynn and Boston are used either for shrimp-trawling, or for gathering cockles (*Cardium edule* L.) or mussels from the beds in the Wash. The evidence suggests, therefore, that the common seal in this district has catholic tastes in its choice of food, fish comprising the normal or 'first-class' food, and invertebrates predominating when fish are difficult to secure. All of the animals upon which the seals feed, with the exceptions of the squids, are bottom-living. The substratum in shallow water along the coast and in the outer part of the channels of the Wash is clean sand, grading into mud, and finally into heavy estuarine clays in the river-channels of the Great Ouse, Nene, Welland and Witham.

Havinga found the seals of the Dutch coast to be feeding almost exclusively on fish, which together accounted for about 97 % by weight of the total food. The most important species, in descending order, were: flounder (*Pleuronectes flesus* L.) 30 %, whiting (*Gadus merlangus* L.) 17 %, herring (*Clupea harengus* L.) 15 %, and the bullheads (*Cottus scorpius* L. and *Agonus cataphractus* L.) together 16 %. Shrimps, eaten mainly by the young seals, made up the bulk of the remaining 3 % of invertebrate food, which also included a few cuttlefish (*Sepia officinalis* L.). Whelks were not recorded at all, and Havinga was sceptical of the earlier findings, then unpublished, which have been included in this paper. But as he used exactly the same methods of computation after analysis of stomach contents, one can only conclude that whelks are a food taken but locally. The seals on the Dutch coast, which included herds both on the open coast and in the channels of the Scheldt-Maas estuary, were thus found to have a diet resembling in a general way that of seals on the Norfolk coast, directly across the North Sea, as far as one can say from the relatively few data available from the English side. No doubt a more extensive investigation would show a more detailed correlation with the relative abundance or scarcity of individual food species in different areas and at different seasons. However, it seems strange, when one considers how much richer are the inshore waters of the Dutch coast than those of the opposite North Sea coast in young plaice, to find that this species comprised only some 3 % of the total fish-food in Havinga's investigations.

Scheffer & Sperry (1931) (and see also Scheffer & Slipp, 1944), studied the food of the subspecies *Phoca vitulina richardii* (Gray) on the Pacific north-west coast of the United States. Their results, based on analysis of eighty-one stomachs with food-remains, were as follows: fish 93·6 % by volume, mollusca 5·8 %, and Crustacea 0·6 %. The most important fish were: Pleuronectidae, various gadoids, the Pacific herring (*Clupea pallasii*), and various Cottidae, in that order; the Mollusca: squids, an octopus, and a bivalve (*Yoldia myalis*); the Crustacea: shrimps (*Crago* spp.), crabs, and the burrowing prawns *Upogebia* and *Callianassa*. These data show a striking similarity to those of Havinga (with respect to the principal families and genera, though not of course, the species, of the fish) and to the data here presented, with respect to the

available invertebrates. Thus it seems that within a wide range of available food animals certain types seem to be preferred. The most easily available of these in any one locality and at any given season will then bulk largest in the diet, and the seals may (as in the Wash) adapt themselves permanently to feeding almost exclusively on one or two of these forms.

This adaptiveness in feeding-habits agrees well with what one knows of the highly developed adaptive behaviour of the common seal in other ways, for instance its rapid learning of relative safety or danger in different circumstances. It will also mean that food is not likely to be a limiting factor in the distribution of the species.

In fact, *Phoca vitulina* on the coasts of Europe ranges from the Mediterranean and Portugal to Iceland and the White Sea (Doutt, 1942), and within the British Isles where it is widespread the range of habitats is a wide one, not apparently related to any particular type of coast. Thus, common seals are found in the sea lochs of the Western Highlands and the Hebrides, and along the exposed coasts of the Shetlands, as well as in estuaries and on sandy coasts as in the east of England and Scotland. The only general preference that can be noted is for sandy coasts, with sandbanks or low islets on which the herds can haul out at low tide.

By contrast, the grey seal (*Halichoerus grypus* F.) keeps to more remote islands and coasts, always on exposed shores. It appears to be a more specialized fish-feeder (as one might guess from comparing its sharply pointed teeth with the more lobose cusps of the common seal's), and it hunts especially the Gadidae and other inshore fish of rocky coasts (Darling, 1948, p. 222). However, it is a species which is very vulnerable at the breeding season, since the young cannot swim until some days after birth, and do not naturally enter the water for some weeks. Persecution by man has undoubtedly confined it to the more remote islands.

Of other members of the genus *Phoca*, the harp seal (*P. groenlandica* Müll.) of the Arctic feeds on pelagic crustacea and fish (Sivertsen, 1941), as does the ringed seal (*P. foetida* Müll), which was found by Dunbar (1941) to feed in the Canadian Arctic chiefly on the amphipod *Themisto libellula*.

Population

An inquiry was carried out in the spring and summer of 1948, with the help of local fishery officers of the Eastern Sea Fisheries Joint Committee, in order to find the approximate numbers of seals along the east coast from south Lincolnshire to Suffolk. Officers were asked to count the herds on sandbanks frequented by seals in their respective districts, where possible on several dates as a check. The response was good, the whole coast from Skegness to Yarmouth being covered, and the writer wishes to express his thanks to the fishery officers concerned for this information. The counts were made chiefly between

April and June, i.e. at a time when the population, prior to breeding, should be at a maximum, while as yet no young would be present to complicate the estimate.

Details of the counts, with previous counts and estimates of the total number of seals in the Wash and of the number killed in each of these years, are given in Table III. Data for years other than 1948 were taken from unpublished records in the possession of the Fisheries Department.

The accompanying map shows the approximate positions of herds located in 1948.

TABLE III. SUMMARY OF DATA ON SEAL POPULATION IN VARIOUS YEARS, FROM 1912 TO 1948

Sand	1912	1920	1924	1928	1947	1948*
Scroby Sand	—	—	—	—	—	120–140
Blakeney Point	—	—	—	—	—	*c.* 150
Burnham Overy	—	—	—	—	—	10–20
Total for open coast	—	—	—	—	—	280–310
Woolpack Middle Sand	—	—	*c.* 50	—	—	*c.* 150
Blackguard Sand	—	—	—	—	(18 killed)	40
High Soft or Seal Sand	—	—	—	—	(19 killed)	40–50
Thief Sand	—	—	—	—	(21 killed)	150
Inner Westmark Knock	—	—	—	—	250	20–30
Old South	—	—	—	—	(53 killed)	80–120
Gat Sand	—	—	—	—	(4 killed)	—
Hook Hills	—	—	—	—	—	10–14
Black Buoy Sand	—	—	—	—	(1 killed)	—
Roger Sand	20	30–40	200	—	(3 killed)	28–34
Ants	—	50	—	—	—	30
Long Sand	300	50	—	—	—	'Hundreds' 40 (Sept.)
Inner Dog's Head	350	400	300	—	—	100 (Sept.)
Inner Knock	50	100	100	—	—	30 (Sept.)
Wainfleet Mains	—	—	—	—	—	43 (Sept.)
Total for Wash	'2000'	750 counted	'Very abundant'	750–1000	—	750–850
Total killed in Wash	*c.* 100	—	150	200?	300	100

* All counts in 1948 were made between April and June unless otherwise stated.

The totals given by these counts for the year 1948 are: 750–850 for the herds in, and on the margins of, the Wash, and 300 for the herds along the Norfolk coast, giving a total of between 1050 and 1150 seals. In spite of the usual human tendency to estimate too high, this is probably an underestimate, since (i) the number counted on a sand at any time is unlikely to include all the seals in the vicinity (some being in the water may easily be missed); and (ii) a herd or two probably went unrecorded. Repeated counts over a period of some weeks at several sands showed that these herds did not fluctuate greatly in numbers, and therefore probably remained as fairly static units which did not move about to different sands to be recorded more than once. I would therefore estimate about 850 seals as the approximate population in the Wash. This is of

the order of magnitude of earlier estimates, e.g. 750 counted in 1913, and 750–1000 estimated by Mr Graham during the 1928 investigations. The annual toll of seals in the Wash has varied from about 100 to 300, with an average of (say) 200. Havinga (1933) concluded that in Holland an average toll of 1000 per annum was maintained for many years from a computed stock of 4000; but his graph, in fact, shows a slight decline, and a later rise after 3 years of diminished killing during the First World War.

On this basis the Wash population (excluding the Norfolk coast herds), averaging between 800 and 1000, would remain more or less constant with an average kill of about 200. The number killed in 1947 was well over 300. In 1948 about 100 seals from the Yarmouth, Boston and Stiffkey (Blakeney) districts were received by a Norfolk firm, and doubtless the total number killed was considerably greater.

We may therefore give the total normal population in the whole area of the census as between 1000 and 1500 animals. Clearly the census method used is by no means an ideal one for this species. Counting from slow-flying planes should be a method eminently suitable for herds spread out on these flat sand-banks; not only would there be less disturbance, but the whole area could be surveyed over a short period during one low tide, thus eliminating the risk of duplicating counts in individual herds.

Biological Notes

Havinga, with Scheffer & Slipp, have summarized most of what is known of the life history and ecology of *Phoca vitulina* in two widely separated sections of its range; but a few points of interest may be noted from the present inquiry.

There are said to be fewer seals in the Wash during the winter. This may represent merely a splitting up of the herds into smaller groups—a decreased gregariousness—or it may represent a partial migration to the outer coast, occasioned by the migration to deeper water of the bottom fish and invertebrates (e.g. the decapod Crustacea) which is known to occur in winter. The former seems the more likely explanation, since should the latter be true the herds along the coast might be expected to increase in size, or at least to be unaffected, by contrast, which is not so. The herds increase in numbers in the spring, and reach a maximum in June, when the young are born. Scheffer & Slipp mention similar fluctuations on the coast of Washington.

In 1948 the first young were seen, at different sands, on 17 and 18 June; in 1947 young seals were killed in numbers from 23 June. To the writer's knowledge, no one has observed the actual process of birth in this species; should it occur on the tidal sandbanks it must presumably occur at low water, although the pups can swim immediately after birth.

It will be noted from the map that the Norfolk coast herds are larger, while

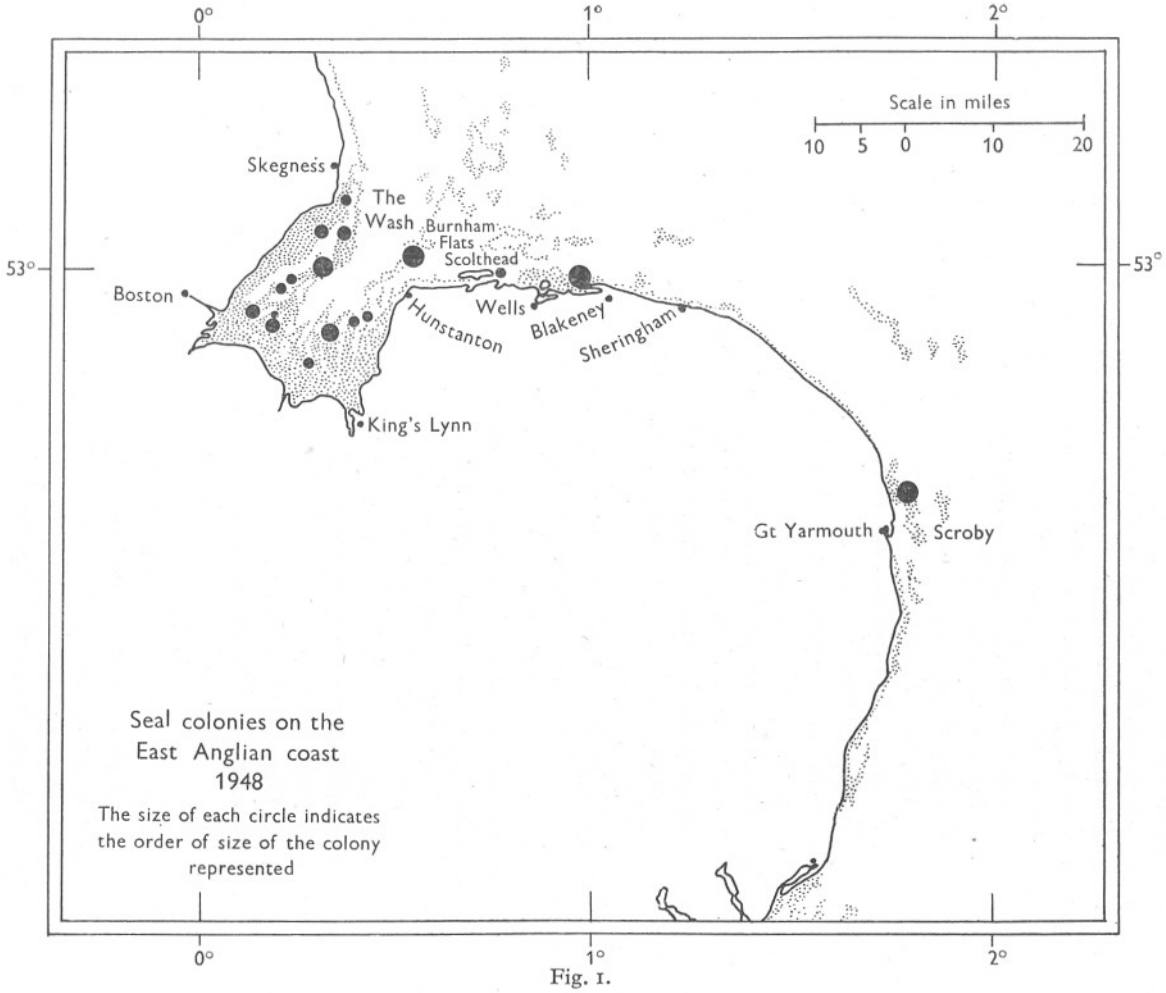
0°
1°
2°
53°
Scale in miles
10 5 0 10 20
Skegness
The Wash
Burnham Flats
Scolthead
Boston
Wells
Blakeney
Hunstanton
Sheringham
King's Lynn
Gt Yarmouth
Scroby
Seal colonies on the East Anglian coast 1948
The size of each circle indicates the order of size of the colony represented

Fig. 1.

farther apart from each other, than those in the Wash. This is no doubt due to the scarcity of suitable sands along the outer coast, which leads to local concentration. These herds probably disperse farther to feed; seals are reported frequently all along the coast, as at Brancaster harbour and the west end of Scolt Head Island, in and outside the harbour at Wells, off Sheringham, and off Winterton and Palling 'especially when the herring drifters are about'. Reports of seals, including single females with pups, off Orfordness and in the Suffolk estuaries may represent incipient colonization in this region or merely an occasional drift down the coast from the Scroby herd off Yarmouth.

These coast herds seem to have increased considerably of recent years; thus according to one observer the colony on the Woolpack Sand numbered some 50 in 1925, while it is now given as 150, and in spite of persecution the Blakeney herd has steadily increased in numbers. It seems likely that these increases have been due in part to recruitment from elsewhere, but it is impossible to say how static and isolated the separate colonies really are until marking experiments have been carried out on these seals. It should be possible to mark the pups successfully. In the White Sea, pups of *Phoca groenlandica* were marked with aluminium disks pierced through the web of the tail in a similar manner to plaice-marking, and their movements traced from subsequent recoveries (Sivertsen, 1941).

In many parts of its range the common seal is known to ascend rivers to a considerable distance from the sea. Records of seals in the fenland rivers are not uncommon; one was shot in the Great Ouse at Hemingford Abbots (45 miles up the river and just below the first lock) on 16 January 1947, and one frequented the Yare between Reedham and Surlingham from late September to early November, 1947 before it was killed. These and other similar records have all been of immature seals in autumn and winter (August to January), which may indicate that seals of this age wander more than the adults. They cause considerable damage to the stocks of fresh-water fish in such small rivers, and rarely survive for long.

Dr Fraser Darling informs me that the young of grey seals are likewise more prone to wander than the adults.

Summary

A study has been made of the food, population, and some aspects of the ecology of the common seal (*Phoca vitulina* L.) along the East Anglian coast.

Examination of stomach contents of 194 seals killed in the Wash in 1947 confirms earlier evidence that the species here feeds largely on whelks (*Buccinum undatum*). The food is estimated by weight as 92 % molluscs, 4 % fish and 4 % Crustacea. Young seals for 2–3 months after weaning feed almost exclusively on shrimps (*Crangon vulgaris*).

Data derived from six stomachs, together with verbal reports, suggest that

seals on the open coast feed more exclusively on fish, chiefly pleuronectids. This agrees with the findings of other workers in Holland and Washington State, U.S.A., that fish are the primary food animals. It is therefore suggested that in the Wash, where suitable breeding sands are common, the seals have become adapted to feeding on a 'second-class' food in the absence of dense stocks of fish.

Counts of all the seal herds located between Skegness in Lincolnshire and Yarmouth in Norfolk in the summer of 1948 gave as an estimate of the total population 1000–1500 individuals. This agrees broadly with the figure deduced from the number of seals killed annually. Comparison with estimates over the last 25 years shows that the species maintains its numbers in spite of intense persecution, several large herds on the Norfolk coast having in fact noticeably increased.

The herds appear to be sedentary, though a slight spring increase in size, probably due to a more marked gregariousness, has been noted. Immature seals frequently ascend rivers and may therefore be more prone to wander than adults.

The young are born from mid-June in this region.

It is concluded from the results of the food investigations that there is local damage to inshore fisheries, though the main part of the stock probably does not have any serious effect on fisheries for shrimps and shellfish.

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THE SCOTTISH SEAWEED RESEARCH ASSOCIATION

By F. N. Woodward, B.Sc., Ph.D., F.R.I.C., F.R.S.E.

Institute of Seaweed Research, Musselburgh

The production of chemicals from the brown seaweeds is one of the oldest branches of the chemical industry, having its origin as far back as 1720 when soda was first produced from kelp in France, and soon after taken up in Ireland, Scotland and Norway. Until the early nineteenth century this was the only source of this chemical on which the glass and soap industries were built up. When the cheap Leblanc soda later became competitive the industry was able to switch to potash and iodine production, a demand for which had arisen about the same time. This industry reached sizeable proportion, as is evidenced by the fact that in 1820 more than 20,000 tons of kelp were produced in the Outer Hebrides, involving the collecting and burning of about a million tons of cast weed.

History repeated itself again, however, as in the middle of the century cheaper sources of potash and iodine were found, and by about 1870 the industry was struggling for survival. Foreseeing the end, E. C. C. Stanford, the chief chemist of the principal company operating in this field, investigated that part of the seaweed which had been burnt during the previous 150 years in the hope that it might contain further chemicals of potential value to industry. As a result, he discovered alginic acid in 1883, suggested a constitution, and found it to be a colloid not unlike cellulose in composition and properties. Stanford was, however, fifty years in advance of the times and the industry virtually came to an end before the close of the century without any use having been made of his discovery.

As kelp production in the Outer Hebrides and Orkney had been the principal means of livelihood of the inhabitants of these islands, the loss of markets resulted in considerable depopulation, a trend which has continued until recent times.

Many efforts have been made during recent years, however, to prevent this decline and various projects have been suggested to afford the crofters a means of obtaining a livelihood sufficiently attractive not only to stop depopulation but, if possible, to reverse the trend. One obvious possibility was to attempt the establishment of a new industry based on the Islands' seaweed resources, although it was quite obvious that any attempted revival of the old industry to produce the inorganic chemicals soda, potash and iodine would not meet the case. Several things had happened, however, since the demise of the old

industry which suggested that a new one could be built up on modern lines, provided fundamental data were obtained and new techniques developed.

In 1929, C. W. Bonniksen, who was then working in the Chemistry Department of University College, London, reinvestigated the alginic acid discovered by Stanford fifty years earlier, and he conceived the idea that it might be possible to produce cellophane-like material from this algal chemical. In pursuance of this idea, he and a number of his university colleagues formed a company for the purpose of collecting brown seaweed, extracting alginic acid therefrom and converting it into cellophane, Despite almost insuperable difficulties some measure of success had been achieved by 1939, when a small factory was in operation at Bellochantuy on the Mull of Kintyre, although the outbreak of the war put a stop to the commercial fruition of this project. However, the earlier work was not wasted, as after two or three years of war it became obvious to the Government that a substitute for jute hessian required for camouflage purposes was urgently needed; furthermore, it was abundantly clear that the basic starting material would have to be found in Britain.

The Ministries of Supply and Home Security therefore set in train a number of projects and collaborative investigations aimed at developing a camouflage textile from alginic acid which it was hoped could be obtained in adequate quantities from indigenous seaweed. This development involved the design and construction of three factories for the production of alginic acid; the responsibility of establishing these and operating them on behalf of the Government was given to Bonniksen and his colleagues. At the same time, fundamental and technical investigations were carried out in several University and Government laboratories and in the laboratories and workshops of a number of textile firms, aimed at the production first of a yarn from alginic acid and subsequently the fabrication of a textile suitable for camouflage purposes.

Success followed their combined efforts, although by the time that the work was complete the need for this material had decreased, as the Japanese were then being pushed back and their threat to the Indian jute supplies minimized.

As a direct outcome of this wartime work there were three large and well-equipped factories established on the west coast of Scotland, but once the wartime need for alginate fabrics lapsed there was a very grave risk that the new seaweed chemical industry would, after all, fail to become established on a permanent basis. The wartime investigations had revealed many gaps in our knowledge. For instance, little was known about the type, location and availability of the brown seaweeds growing in Scottish inshore waters. Next to nothing was known about the chemical composition of even the common species, and no methods for harvesting the sublittoral brown algae had been developed.

The Scottish Seaweed Research Association was therefore formed towards the end of 1944 at the instigation of the Scottish Council on Industry, the Ministry of Supply, the Scottish Office, the Department of Scientific and Industrial

Research, the Marine Stations, and semi-official and independent organizations interested in seaweed utilization, to provide the basic information on which it was hoped that non-governmental interests could build up an industry based on Scottish seaweed, primarily with a view to bringing useful employment to the crofter population of the Scottish Highlands and Islands.

From the outset it was realized that a combined sociological and applied marine biological experiment of this magnitude required an unconventional approach on the widest possible basis, and the pattern which has been followed is probably unique in the annals of marine science or industrial development.

A programme of research and development was outlined and the problems there defined have subsequently been investigated by the Association's own staff of botanists, chemists, chemical engineers and engineers, and by fifteen University and Government or state-aided laboratories, in close collaboration with the interested industry and the appropriate Government departments and Ministries.

The Seaweed Research Association's early operations were based on accommodation made available by the Chemistry Department of the University of Edinburgh, but the growth of the Association's activities and the University's need for all its laboratory facilities at the termination of hostilities resulted in accommodation having to be found elsewhere. Since 1947 the Association's headquarters have been the Institute of Seaweed Research at Inveresk Gate, an old mansionhouse standing in 11 acres of land which has been converted to house chemical, botanical and engineering laboratories and workshops and the necessary library and office facilities. In addition, four outstations at Oban and Dunbar on the mainland, Kirkwall in Orkney, and Lochmaddy in North Uist, have been set up from which the survey and experimental vessels have operated.

Although the original research and development programme has not yet been completed, considerable progress has been made both by the Association's staff and by its extra-mural collaborators.

Investigations so far completed have covered the development of methods for the quantitative survey of brown seaweed beds (Walker, 1947*a*), and their application to the Scottish littoral (Walker, 1947*b*; Gibb, 1950) and sublittoral zones (Walker, 1947*a*, 1950); the study of ecological factors (Walker, 1948; Moss, 1948, 1950*a*, *b*; Black, 1950*b*; Black & Dewar, 1949), and the determination of optimum conditions of weed growth by controlled culture (Smith & Walker, 1948).

With a view to developing new and extended uses of seaweed and seaweed products, studies of the chemistry of algal chemicals have been made (Percival & Ross, 1948*b*, 1949, 1950*a*, *b* 1951; Chanda & Percival, 1950; Connell, Hirst & Percival, 1950), methods of analysis developed (Cameron, Ross & Percival, 1948; Percival & Ross 1948*a*; Black, Cornhill, Dewar, Percival & Ross, 1950), and determinations of the chemical composition of the

principal indigenous brown algae and its variation with species, season, age, environment, etc., carried out (Black, 1948*a*, *b*, *c*; 1949; 1950*a*, *c*).

Methods have also been developed for the production of such constituents and their derivatives as are found to be of potential technical value (Bashford, Thomas & Woodward, 1950; Black, Dewar & Woodward, 1951), and the value of seaweed as a component of animal feed and as a fertilizer assessed.

As the ultimate success of an industry based on seaweed must depend upon adequate supplies at a reasonable cost, the efforts of the engineering staff have been largely directed to the development of economic harvesting techniques (Mackenzie, 1947; Jackson, 1951) and the determination of optimum conditions of drying, grinding and handling.

The Association is not a commercial organization, but is so constituted that any individual or organization in Britain in any way interested in the utilization of seaweed can become a member by payment of a nominal fee. By this means scientific and technical data as it becomes available can be and is made use of with the minimum of delay by the universities, research organizations and by industry.

The Board of Management of the Scottish Seaweed Research Association has always realized however, that, in addition to being responsible for providing the basic information on which a rural industry can be established, it has the far more important and exacting task of ensuring that this is understood and applied in such a manner as will benefit the rural community without spoliation of any of the nation's natural marine resources.

This has involved the putting into effect of a sizeable public relations and educational programme by means of wide circulation of technical and progress reports, press releases, and semi-popular articles (cf. Jackson 1948), the production and display of informative films and the giving of lectures, radio talks, demonstrations, exhibitions and discussions, and the holding of informal meetings at which the need for balanced conservation techniques has been stressed.

This programme, amongst other things, has been aimed at showing both the crofter and lay public and the interested industry that, largely because of increasing population pressure and consequent depletion of the country's non-renewable mineral reserves, increasing use will inevitably have to be made of our renewable resources (Woodward, 1950*a*, *b*). As Britain's agricultural and forestry techniques are as advanced as any in the world, and as a very high proportion of the land area is already under extensive cultivation, the sea is virtually the only untapped indigenous source of new organic material.

That the operations of the Association and those associated with it have not been without success is indicated by the fact that its original membership has doubled since its formation in 1944; whereas in 1944 there were no companies specifically harvesting seaweed, now there are two about to commence operations. In 1944 there were five companies in Britain using seaweed for

chemical production or agricultural use, now there are eight. There has, in addition, been a significant expansion within the industry during this time, and as a result cast weed is now collected in S. Uist, N. Uist, Benbecula, Barra, Lewis, Tiree, the Orkneys and in the Fraserburgh and Peterhead areas. The total tonnage of seaweed collected in Scotland has increased sevenfold in the last five years, and the total number of collectors has increased sixfold during that time. As a direct outcome of this expansion in the industry there is now no male unemployment in S. Uist.

Alginate production is at the time of writing Britain's major seaweed industry, and this chemical now sells in twenty countries abroad as well as in the home market. British agar production has similarly developed since the end of the war. Whilst accurate figures for the output of the five British alginate and agar-producing firms are not available, it is fairly certain that the industry is producing these chemicals to the value of about £700,000 per annum at the present time, a not inconsiderable portion of which represents wages paid to the seaweed collectors and the operatives employed in the four Scottish seaweed processing factories located near Girvan, Oban and Lochboisdale. As this industry, which is still expanding, has virtually been built up since the war, it can reasonably be claimed that the £120,000 so far provided by the Treasury from the Development Fund, together with the additional £11,500 subscribed by industry and private interests to further the work of the Association, has been a sound investment, for only as the result of this research and development work and that of the Association's member firms has this been made possible.

Much, however, still remains to be done, as commercial outlets for algal chemicals other than alginic acid and agar have yet to be established, and the mechanical harvesting of Scotland's 10,000,000 tons of brown seaweed and adequate resources of red weed have yet to be carried out on the commercial scale.

A list of publications so far issued or submitted for publication under the auspices of the S.S.R.A. (up to October 1950) is herewith appended.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

THE EQUILIBRIUM FUNCTION OF THE OTOLITH ORGANS OF THE THORNBACK RAY

By Otto Lowenstein and T. D. M. Roberts

Journ. Physiol., Vol. 110, 1949, pp. 392–415.

In the labyrinth of *Raja* the otolith organs in the utriculus, sacculus and lagena contain sense-endings with equilibrium function. The discharge frequencies from these sense-endings undergo changes when the skull is tilted.

In some endings each position of the skull is associated with a characteristic discharge frequency regardless of the direction from which this position is reached (stato-receptors proper).

In other endings the succession of frequencies and the position of maximum activity was found to be dependent on the direction of tilting, but the discharge activity reverted to some constant value when and wherever the skull was brought to rest (out-of-position receptors). Single functional units were generally found to respond to lateral as well as to fore-and-aft tilting.

The ranges of response types for the utriculus and sacculus overlap. Two types may be distinguished: those with their maximum frequency of discharge in the 'side-up' and 'nose-up' positions, and those with maximum frequency in 'side-up and 'nose-down'. The absence of stato-receptor preparations with a maximum frequency of discharge in the 'side-down' position is unexpected.

In the lagena the maximum frequency was always in or near the normal position, the frequency falling off fairly sharply on either side of the maximum (into level receptors). This organ is thus particularly suited for mediating stabilization around the normal position. O.L.

THE CONTROL OF RETINAL PIGMENT MIGRATION IN *LEANDER SERRATUS*

By Francis G. W. Knowles

Biol. Bull. Woods Hole, Vol. 98, 1950, pp. 66–80.

A study was made of the relative importance of hormonal control and a direct response to illumination in the movements of the distal and proximal retinal pigments in *Leander serratus*. Animals from which the sinus glands had been

BOOK REVIEW

NETS. HOW TO MAKE, MEND AND PRESERVE THEM

By G. A. Steven

Routledge & Kegan Paul Ltd., 1950. Price 5*s*.

Mr Steven has well earned the thanks of all who work with, or are interested in, nets and netting. His brilliant little manual should be welcomed by Libraries, Technical Institutes, Sea Scouts, and Fishermen, whether amateurs, learners, or professionals. The most experienced trawlerman will find in it much interest, and fresh knowledge. Coming as it does from a practical scientist on the staff of the Laboratory of the Marine Biological Association, with a background of experiments with net preservatives, must stamp the book with the highest of hall-marks. Mr Steven's travels and his work on colonial fisheries' development have enabled him to bring to his book fresh angles and methods. In simple language he takes one through the routine of net-making, mounting, and mending; he has a chapter on knots and hitches, another on preservation and even one on how to make such things as rabbit purse nets, garden hammocks, tennis nets and a lady's shopping bag.

I found the book, once picked up, difficult to put down. I seldom remember having seen so good a 5*s*. worth.

With some 160 simple and clear illustrations this little manual might well be described as the perfect *vade mecum* on nets. M.H.N.

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) and Vol. XXVII (p. 761) 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 two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

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

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

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

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