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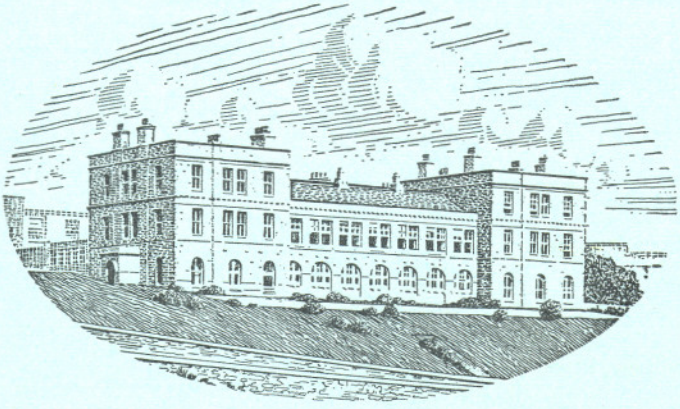

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OBSERVATIONS ON LUMINESCENCE IN *NOCTILUCA*

By J. A. C. Nicol
The Plymouth Laboratory

(Text-figs. 1–9)

Noctiluca miliaris Suriray is a well-known luminescent organism, and its light emission has been studied repeatedly. Hitherto, however, no attempt has been made to record the luminescent flashes of this species, either under normal conditions, or after experimental treatment. With the sensitive photoelectric recording methods now available it has become possible to subject the luminescent flashes of *Noctiluca* to experimental analysis, and with this end in view the present study of *Noctiluca* was undertaken.

Noctiluca is a dinoflagellate approximately spherical in shape and 0·2–1·2 mm in diameter. It possesses a single stout tentacle and a small flagellum by which it executes a limited amount of slow movement. The specific gravity of *Noctiluca* is less than that of sea water so that it tends to float at the surface. The explanation of this low density is still uncertain (Davis, 1953). The interior of the cell is highly vacuolated and contains fine cytoplasmic strands which radiate outwards from the region of the nucleus to the periplast. E. N. Harvey (1952) has reviewed previous literature dealing with the luminescence of *Noctiluca*.

MATERIAL AND METHODS

During July and August 1955 there were large numbers of *Noctiluca* in the surface plankton off Plymouth, and abundant material became available for studies of luminescence. Dr M. W. Parke was successful in culturing *Noctiluca* in Erdschreiber solution. These cultures were supplied with *Isochrysis galbana* for food, and were subcultured at intervals. From them *Noctiluca* cells were removed for study when required. Further supplies of *Noctiluca* were obtained in June 1957, in the Bay of Douarneney (48° 18·5′ N., 5° 13′ W.) and the Bay of Concarneau (47° 51′ N., 3° 58′ W.) (R.V. 'Sarsia' cruise 3 of 1957).

The luminescent flashes of *Noctiluca* were detected by means of a photomultiplier tube. The photocurrent was passed through a 500 kΩ resistor, and voltage changes were amplified (DC amplifier) and recorded by means of cathode-ray oscilloscope and camera. The photomultiplier was an E.M.I. type no. 6685, with an end-window 9 mm in diameter. This photomultiplier

has 14 stages and was operated at voltages up to 1800 V. The Sb-Cs cathode possesses maximal sensitivity in the violet and blue; the relative spectral sensitivity curve, as determined by the National Physical Laboratory, is shown elsewhere (Nicol, 1958*a*, p. 34, fig. 2, curve A). The specimens of *Noctiluca* were placed in a small container closely underneath the end-window of the photomultiplier and all leads were screened to eliminate a.c. interference. For the majority of records, vertical deflexions of the oscilloscope spots were photographed on moving paper; a few photographs on film were also made of single and repeat sweeps of the oscilloscope when triggered by the stimulator.

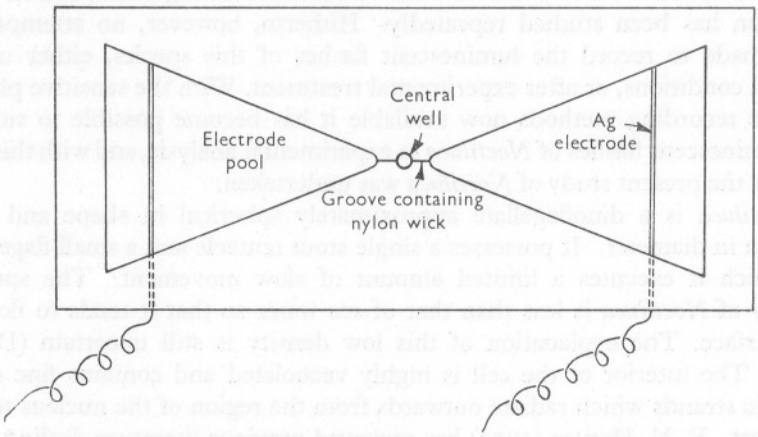

Fig. 1. Diagram of the chamber used for electrical stimulation of *Noctiluca*. Modified from Chang (1954).

For electrical stimulation *Noctiluca* was placed in a Perspex chamber, provided with two silver electrodes and shaped as in Fig. 1. The Noctiluca cell lay in the small central well, which was connected with two large lateral wells by narrow slits; the latter were filled with wet threads or agar. The whole chamber was flooded with sea water and was covered with a glass or perspex plate to prevent evaporation. Electrical stimuli consisted of condenser-discharges or square waves from electronic apparatus. Electrical stimuli were signalled on the second beam of the oscilloscope. A time signal was provided by the periodic flashing of a small lamp, controlled by a Palmer relay (this set-up was used with moving paper); or by an A.F. oscillator (used with sweeps and stationary film). Room temperatures at which the experiments were carried out varied from 18° to 19° C (shore laboratory) and 20° to 23° C (ship's laboratory).

OBSERVATIONS

MECHANICAL STIMULATION

The natural stimulus evoking luminescence in *Noctiluca* is mechanical. Placed in a vessel, Noctilucae assemble at the top, especially about the margin of the vessel. Upon agitating the container, many of the cells respond by a bright flash. Similarly, moving an object through the water, or blowing a jet of air on the surface, agitates the cells and causes them to flash. Animals moving through the water also disturb the Noctilucae, and make them luminesce. In a breffit containing a large number of Noctilucae and some *Calanus* it was observed that whenever a *Calanus* invaded the superficial Noctiluca layer, it gave rise to a bright glow in a circumscribed area, owing to agitation of a group of Noctiluca cells.

When a single cell is mechanically stimulated by agitating the container in which it lies, it is found that the intensity of the flash depends on the vigour of stimulation, a slight shake giving a faint flash, a brisk shake a stronger flash (Fig. 2*a*, *b*). At a temperature of 17° C the flash duration varied from 22 to 95 msec (a bright flash possessing a longer duration). The flash of a single cell, lasting 95 msec, had the following temporal characteristics: time to maximum, 20 msec; time to half maximum, 10 msec; decay time from maximum, 70 msec; time of half decay, 20 msec.

These figures for response characteristics are presented to give some idea of the magnitudes involved. With present recording technique they make no claim to absolute accuracy, since they depend on the amplification characteristics of the apparatus. At high amplification, threshold for measurable deflexion of the oscilloscope beam is lowered, and the response appears to start sooner, and last longer, than at low amplifications. The apparent duration of a flash, therefore, depends on the amplification-factor. (This effect has been analysed in the responses of cells stimulated electrically, and is discussed on p. 541.)

Various methods were tried to obtain more accurate regulation of mechanical stimulation than could be achieved merely by manual operation. This proved difficult because the *Noctiluca* is buffered by the pool of sea water in which it floats and because, when disturbed, it sinks and changes position. Some records were obtained by stimulating Noctilucae mechanically by means of a loud speaker. Condenser shocks, fed into the speaker, shook the dish and caused the Noctilucae to flash.

From a group of about 10 cells the following response parameters were determined for a flash lasting 120 msec (17° C). Rise to maximum occupied 43 msec; half maximum, 30 msec; decay from maximum occupied 80 msec; half decay, 20 msec. Latency from time of condenser-discharge varied from 10 to 30 msec.

Mechanical latency of the system was slightly less than 1 msec; and maximal movement occurred 23 msec after condenser-discharge. Owing to

inertia of the system it is not possible to cite a value for true latency of the cell. However, the shortest interval measured from the beginning of mechanical stimulation (viz. 10 msec) shows that latency following mechanical stimulation may be of the same order of magnitude as that following electrical stimulation (viz. 9 msec).

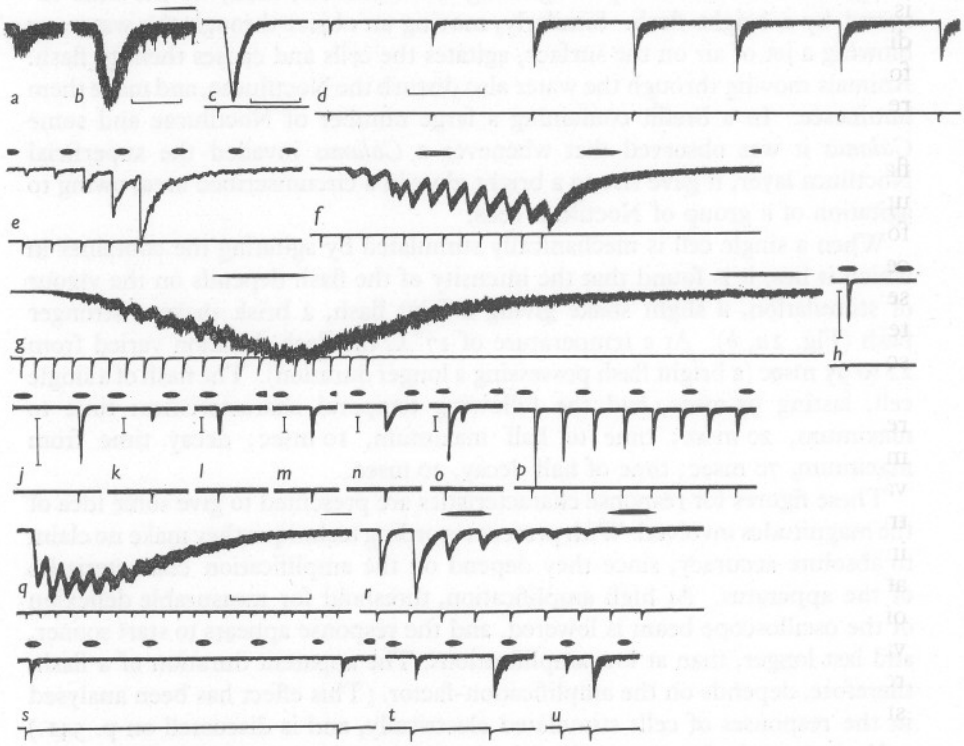

Fig. 2. Oscilloscope records of the flashes of a single Noctiluca cell. Photographs on moving paper of vertical excursions of the oscilloscope beams. *a*, *b*, flashes of a Noctiluca cell in response to mechanical stimulation (agitation of the container). *a*, strong; *b*, weak stimulus. The response is registered as a downward deflexion of the trace and is superposed on background noise. Time scale, 10 msec. Temp. 17° C. *c*, response of a Noctiluca cell to a single electrical shock. Time scale, 10 msec. Temp. 19° C. *d–g*, electrical stimulation of a Noctiluca cell at various frequencies. *d*, burst of shocks at 48/min. Time scale, 1 sec. Temp. 21° C. *e*, burst of 5 shocks at 2/sec (background noise reduced with a low band-pass filter). *f*, burst of 12 shocks at 9/sec. *g*, burst of 20 shocks at 28/sec; fusion of individual responses almost complete, long after-glow. Temp. *e*, *f*, *g*, 20° C. *h–o*, effect of increasing strength of stimulus on intensity and characteristics of the responses. *h–n*, responses of the same cell to pulses of increasing duration (shocks from 0·023, 0·5, 0·72, 1, 1·95, and 4μF condensers, respectively). Relative amplification shown to the left of each record. Note lengthening of the pulse in record *n*. *o*, double flash induced by a pulse at voltage 3 × threshold. Temp. 19° C. *p*, *q*, *r*, different patterns of responses under repetitive electrical stimulation. *p*, intervals 0·5 sec; *q*, 0·03 sec; *r*, 0·2 sec. Temp. 19° C. *s–u*, electrical stimulation of a single Noctiluca cell. Paired shocks at intervals of 5·5, 1·4 and 0·5 sec. Temp. 20·4° C. Time scale *e–p*, *r–u*, 1/sec; *q*, 0·1 sec. Electrical stimuli shown on lower lines of records *c–u*.

It may be noted that it proved impossible to make satisfactory observations on *Noctiluca* at sea when the ship was under way. The vibration of the vessel produced continuous excitation, and fatigued the luminescent response.

Fatigue

As others have observed before (e.g. Gosse, 1853), the flashing of *Noctiluca* is subject to fatigue. When one or a few Noctilucae are placed in a small dish and the dish is repeatedly shaken the cells flash several times, but after four or five flashes the light becomes weaker and disappears. Following a rest period of several minutes the cells recover and flash brightly once more.

Similar fatigue is shown under repetitive electrical stimulation, when the flashes decline in intensity, either initially from the first flash, or subsequent upon build-up to a plateau level (cf. histograms in Figs. 3 and 4). The time for recovery of full strength of response was determined by stimulating a cell at various intervals. The procedure was to give a pair of stimuli at some selected interval, and then to allow a rest period of 5–10 min before administering another pair of stimuli. The rest period of 5–10 min was chosen after some preliminary trials had shown that recovery occurred in that time.

With electrical stimulation it was found that recovery of full flash-intensity required an interval of about 2 min (19° C). Data obtained from one experiment in which a single cell was stimulated with pairs of shocks at given intervals are plotted in Fig. 5. Despite the scatter of observations, a general trend towards recovery of full luminescent intensity with lengthening of interval is apparent. The distribution of points representing flash-intensity at the 5 min level also gives some idea of the variation of response-intensity of a rested cell under electrical stimulation. It is uncertain whether this variability is intrinsic, or whether it is due to variation in apparent threshold resulting from small movements of the *Noctiluca* in the central well of the stimulating-chamber.

ELECTRICAL STIMULATION

A single electrical shock, above threshold-strength, elicits a flash of light from the cell or cells in the current-field (Fig. 2*c*). To bursts of shocks, a cell flashes repetitively, one flash per stimulus (Fig. 2*d–f*). With fast stimulation (> 3/sec), some fusion of consecutive responses occurs, the effect becoming more pronounced as the frequency is raised (Fig. 2*e–g*). Fusion is nearly complete at a frequency of 28/sec (interval of 36 msec). This interval slightly exceeds the time required to reach maximal response-intensity, viz. 26 msec (latent period + rise time). Following bursts of high-frequency stimulation, there is usually a prolonged after-glow, lasting as long as $\frac{3}{4}$ sec (Fig. 2*g*).

Temporal characteristics

Single flashes, induced by electrical stimulation of resting cells, vary in duration from 69 to 830 msec. A flash lasting 145 msec has the following

temporal characteristics: rise time, 17 msec; time to ½ maximum, 8 msec; time of ½ decay, 12 msec. Latent period, measured in records at maximal amplification, is 9 msec (temp. 19° C). Apart from latent period, these values agree reasonably well with those of responses evoked by mechanical

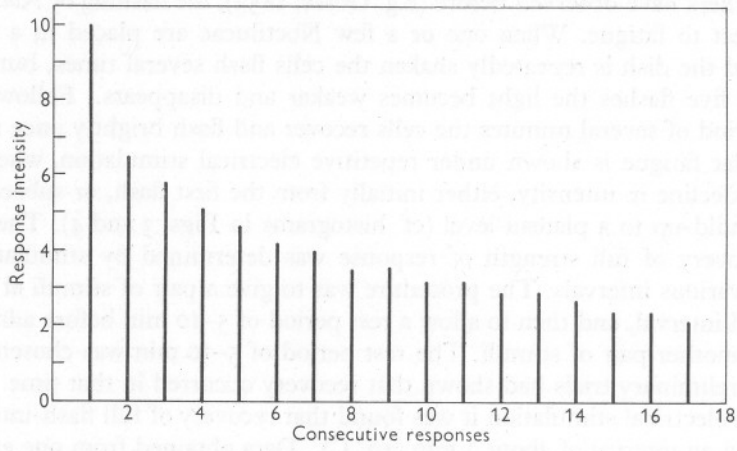

Fig. 3. Fatigue of photogeny in a Noctiluca cell. The cell was stimulated with a burst of 17 electric shocks at a frequency of 2/sec. Note progressive decline in height of responses. Ordinates, luminescent intensities in arbitrary units. Temp. 19° C.

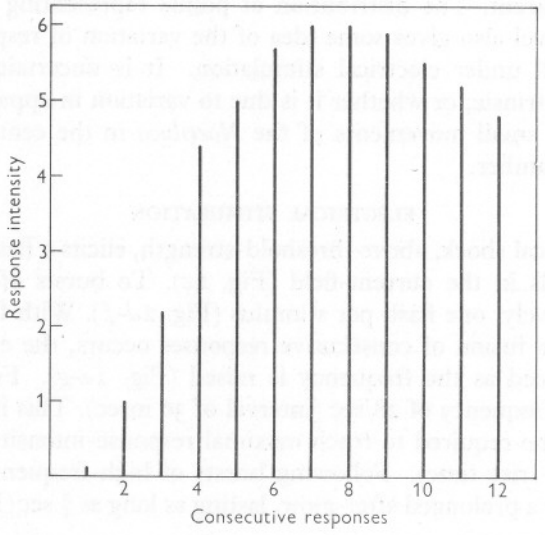

Fig. 4. Histogram showing facilitation and fatigue of consecutive responses in *Noctiluca*. A cell was stimulated with a series of 12 shocks at a frequency of 9/sec. Each vertical line represents the intensity of a flash measured from the level of luminescence (if any) existing at the beginning of that response. Intensities (ordinates) in arbitrary units. Temp. 20° C.

stimulation (p. 537). The latency after mechanical stimulation is discussed on p. 538.

The apparent duration of the flash as measured in the photographic records is influenced by the amplification of the apparatus. To determine the magnitude of this effect, flashes of a single cell were recorded at various amplifications and at fast paper speed. Since amplification of the apparatus varied in a linear manner, the responses at high amplification passed off the paper, and

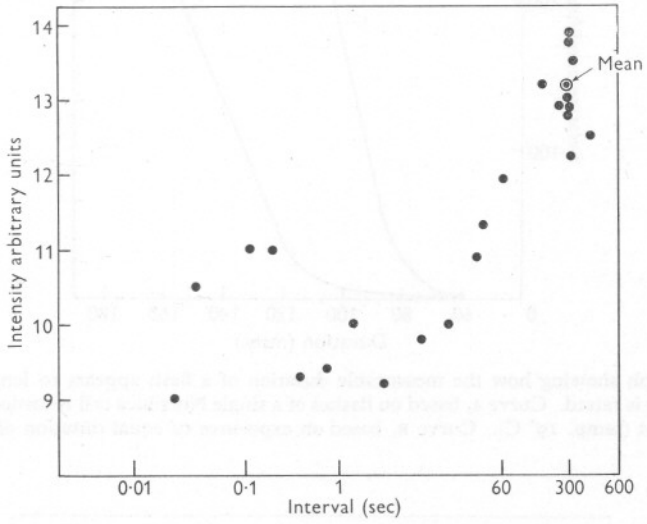

Fig. 5. Recovery of luminescence in a Noctiluca cell following electrical stimulation. Each point represents the intensity of a flash after a rest-period of selected duration since the last flash. Ordinates, intensities of response in arbitrary units. Abscissae, intervals in sec between 2 shocks (log $_{10}$ scale). Temp. 19·4° C.

it was possible only to measure latent period and total duration of these responses. In order to secure a series of responses of approximately the same intensity, a rest period of 2 min was allowed between each flash, and conditions of stimulation were kept constant. The amplification factor was varied from 0·3 to 100.

The results are plotted in Fig. 6A, in which it appears that the measurable duration of a flash is a high function of the amplification used. In the same figure there is a curve (B) showing apparent increase in duration of a brief flash from an artificial light source: actual exposures (flashes) had the same length (regulated by a mechanical device). When the amplification is increased by a factor of 100, the response-duration appears to be lengthened two-fold. The maximal response-duration in this series of records was 182 msec (19° C). The response-duration of 145 msec, mentioned on p. 539, was determined with an amplification-factor of 3. At maximal amplification of 100, this would appear 80 msec longer (i.e. 225 msec).

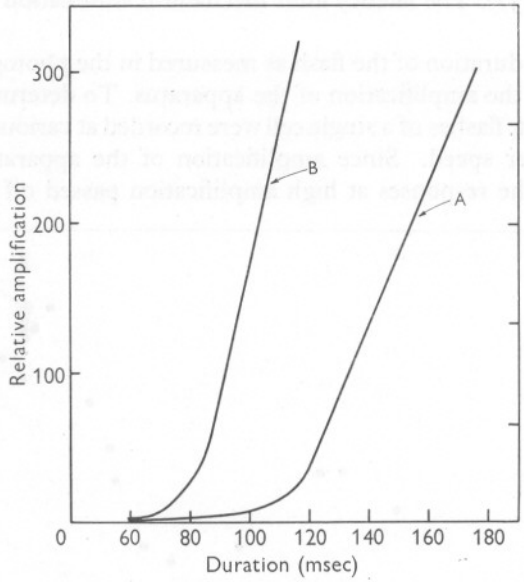

Fig. 6. Graph showing how the measurable duration of a flash appears to lengthen as the amplification is raised. Curve A, based on flashes of a single Noctiluca cell recorded at different amplifications (temp. 19° C). Curve B, based on exposures of equal duration of an artificial light source.

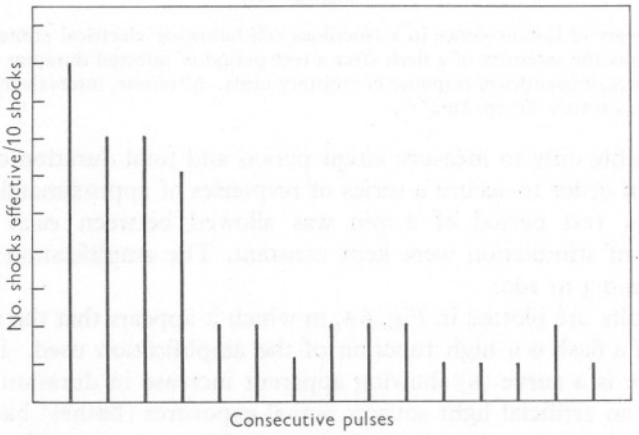

Fig. 7. Fluctuation of threshold. A Noctiluca cell was stimulated with a burst of 150 electrical pulses at a frequency of 3/sec. On the ordinates are plotted the number of stimuli effective in each consecutive series of 10 shocks (total scale = 10). With continued stimulation, fewer pulses were effective, until only each 4th or 5th shock produced a flash. Temp. 19° C.

Effect of increasing stimulus-strength

The intensity of a flash produced by *Noctiluca* depends on the strength of stimulus. This was determined either by varying the voltage, or by switching to different stimulating capacitors. When the current was gradually increased above threshold level, it was found that the response increased correspondingly (Fig. 2*h–n*). By doubling the stimulating voltage, the intensity of the luminescent flash was increased fivefold. A plateau-level of response was finally reached, above which further increment of stimulus-strength produced no further increase in flash-intensity.

At maximal stimulus-intensities the flashes were usually prolonged in duration as well as increased in intensity (Fig. 2*n*). Strong flashes, several times threshold-strength, sometimes gave rise to double flashes in quick succession (Fig. 2*o*). Continued stimulation at high voltages produced depression of the response, and finally extinction. The effect was irreversible, and indicative of cellular injury.

After a prolonged period of electrical stimulation it was usually found that the threshold was raised. This was also exhibited by giving a series of shocks at threshold-strength. During such a series occasional shocks became ineffective (Fig. 7). No evidence was found for summation of subthreshold stimuli: bursts of subthreshold shocks at various frequencies failed to elicit a response.

Facilitation

Noctiluca cells often but not invariably show facilitation under electrical stimulation. This is a phenomenon in which each stimulus engenders a persistent excitatory state which, when added to that produced by the next stimulus, augments the intensity of the next response. Under repetitive stimulation the successive flashes of a Noctiluca cell sometimes increase in intensity (Fig. 4).

Facilitatory increment occurred at intervals up to 1·4 sec, too long to allow fusion of separate responses, and increased at shorter intervals (Fig. 2*d*, *e*, *f*, *s*, *t*, *u*). During a long burst of stimuli, facilitation was evident initially for the first eight or so responses, whereupon the responses reached plateau level, which was briefly maintained and followed by a decline of response-intensity (Fig. 4). It has already been noted that the luminescent responses of *Noctiluca* are fatigued by repetitive stimulation at short intervals, recovery requiring some 2 min. This recovery period, during which the flash-intensity is depressed below normal, far exceeds the maximal interval at which facilitation is operative (viz. *ca.* 1·5 sec).

It is concluded, therefore, that facilitatory increment is partly masked by fatigue, i.e. the height of each facilitated response is the resultant of two conflicting factors, increment of excitation and temporary depression of the photogenic system.

In some other instances, facilitation was shown only in the second of a series of flashes, the third and subsequent flashes progressively decreasing in intensity (Fig. 2*q*, *r*). Again, there were many records in which the first flash of a series was maximal, and the subsequent flashes diminished in intensity (Figs. 2*p*, 3). This progressive diminution of successive flashes has been alluded to previously as fatigue (p. 539). I was unable to discover any apparent reason for this variability in the responses of different cells. The existence of facilitation in many cells, however, was well established, and is of intrinsic interest.

Illumination without effect

Exposure to light is said to cause inhibition of luminescence in *Noctiluca* (Henneguy, 1888) as well as certain other species (dinoflagellate *Gonyaulax* and ctenophores) (Harvey, 1952; Haxo & Sweeney, 1955). In view of the reported sensitivity of *Noctiluca* to light, it was decided to re-investigate the phenomenon. The procedure was as follows. A single Noctiluca cell or a group of cells was maintained in the dark for an hour, and then stimulated with an electrical shock to record the level of a normal response. The cell or cells were then exposed to a daylight tungsten bulb for 10–30 min at illumination levels up to *ca.* 1 kilolux. After extinguishing the light the Noctilucae were again stimulated electrically. The responses recorded were no weaker than those elicited before illumination. This result agrees with the observations of E. N. Harvey (1926) who found that daylight was without effect in suppressing the luminescence of *Noctiluca*. Massart (1893) reported a diurnal rhythm of luminescence in *Noctiluca* in continual darkness. I did not observe that the cells which I studied gave any brighter flashes by night than by day.

SPECTRAL COMPOSITION OF THE LIGHT

Dense layers of *Noctiluca* were obtained from plankton hauls, and the light produced by mechanical agitation of these samples was sufficiently bright and persistent for determination of its spectral composition. As an initial attempt, I examined the light of *Noctiluca* visually through a series of glass and gelatine filters (Chance, Ilford and Kodak), so as to judge the efficiency of the recording system. Filters used were purple (transmitting in the blue and red), green, yellow, orange, and red. The light of *Noctiluca* was largely eliminated by red and orange filters (transmitting above 590 mμ), faintly visible through blue and green filters (transmitting in the range 400–610 mμ). From these observations it appears that the light of *Noctiluca* has a spectral distribution between about 400–600 mμ. This range is in the spectral region to which the photomultiplier is most sensitive.

Relative spectral emission was determined quantitatively, as follows. The light from Noctilucae was passed through coloured spectral filters, and the

resultant electrical responses were estimated by measuring oscilloscope deflexions. The spectral filters were mounted in openings about the margin of an opaque disc, which rotated beneath the photomultiplier. The speed of the disc was slightly faster than 1 rev./sec. Light was produced by discharging a suspension of Noctilucae from a pipette into a vessel lying below the disc. The experimental arrangement is depicted diagrammatically in another paper (Nicol, 1957*c*, fig. 1), where the method is described in more detail.

Two discs were used, each containing 8 or 9 different kinds of spectral filters. These are tabulated in another paper (Nicol, 1958*c*).

The filters were slightly wider than the diameter of the photomultiplier end-window. An opaque blank space between two contiguous filters allowed the responses of the individual filters to be distinguished; and a double blank at one place on the disc permitted a complete rotation to be determined, and the many responses during that rotation to be related to the corresponding filters on the disc. A sample record is shown in Fig. 8.

The flash produced by squirting a suspension of Noctilucae lasted about 3–4 sec, and during that time it changed greatly in intensity, rising quickly to a maximum, and then decaying. In order to follow changes in absolute intensity, identical filters, termed reference filters, were placed between each of the other spectral filters. The reference filters were Ilford blue-green 603 or Ilford green 604. The value for the measured response of each of the spectral filters was then altered, relative to the responses of the two contiguous reference filters.

Values for relative spectral energy were calculated from the photographic records. The method is described in detail in other papers (Nicol, 1957*b*, *c*, 1958*b*).

A curve for relative spectral emission is shown in Fig. 9. The light is blue: emission extends from about 420–580 mμ, with a maximum at 470 mμ. The curve is unimodal, and resembles that of luminous extracts of the dinoflagellate *Gonyaulax polyedra* (Hastings & Sweeney, 1957). Several other pelagic animals emit blue light of somewhat similar spectral composition (Kampa & Boden, 1957; Nicol, 1958*c*). It may be that a curve of this kind is fairly representative of the luminescence of many marine organisms. Ctenophores, with green light, are obvious exceptions.

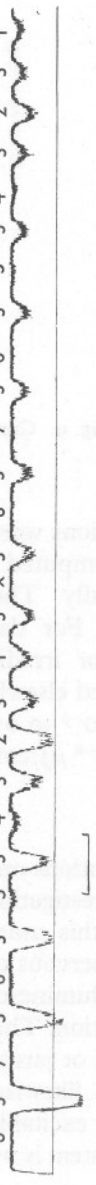

Fig. 8. Spectral analysis of the light of *Noctiluca*. Photographic strip showing deflexions corresponding to passage of spectral filters during a luminescent flash. Time below, 100 msec. Disc I, 1 revolution/sec. Ilford filters as follows: 1, 601; 2, 602; 3, 603; 4, 604; 5, 605; 6, 606; 7, 607; 8, 608; × double space as marker.

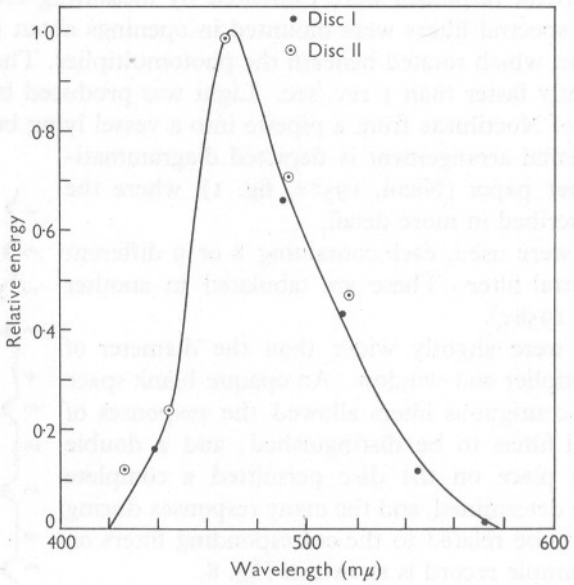

Fig. 9. Curve showing relative spectral composition of the light of *Noctiluca*.

INTENSITY OF FLASH

Estimations were made of the intensity of light in a flash of *Noctiluca*. These were computed from oscilloscope records of flashes of a single cell, excited electrically. The whole system was calibrated against a substandard light source. For daily use, a photometric standard consisting of a stilbene phosphor irradiated by ^{60}Co was used. Calibration and calculations are described elsewhere (Nicol, 1958*a*). Radiant flux in a single flash varied from $0{\cdot}03 \times 10^{-6}$ to $0{\cdot}16 \times 10^{-6}$ $\mu J/cm^2$ receptor surface at 1 cm. Mean flux was $0{\cdot}1 \times 10^{-6}$ $\mu J/cm^2$ receptor surface at 1 cm (23° C).

DISCUSSION

Observations on *Noctiluca* by E. B. Harvey (1917), and by myself in the present investigation, have revealed many points of similarity between the flashing of this unicellular organism, and of metazoans where luminescence is under nervous control.

The luminescence of *Noctiluca* is intracellular, and is evoked by external stimulation. The natural stimulus is mechanical, *Noctiluca* flashing when it is agitated or jarred. But flashing is also produced by electrical stimulation and there is likewise evidence that the photocytes of some higher animals are directly excitable by electrical pulses, e.g. those of polynoids when the nervous system is put out of action by anaesthesia (Nicol, 1957*a*). The luminescent

systems of these animals can thus be added to the list of effectors which are directly excitable by electrical stimuli, viz. muscle, exocrine glands, flagella, and electrical tissue.

The flash of *Noctiluca* is very brief, usually about 100 msec following mechanical stimulation, but showing considerable variation. Some comparable data for the intracellular flashes of other animals, recorded from point sources of photogenic tissue, are assembled in Table 1. Of equal brevity are the flashes of *Gonyaulax* and of single scales of polynoids; in contrast is the prolonged glow of *Pyrosoma*, 7 sec or more in duration. The brief latency (about 10 msec) is comparable to that found in luminescent flashes of some metazoans, e.g. untreated and anaesthetized scales of polynoids, where the response is normally under nervous control.

TABLE 1. DURATION OF INTRACELLULAR FLASHES OF SOME MARINE ANIMALS

(Recordings from point sources.)

Animal	Duration	Temp. ° C	Reference
Gonyaulax polyedra	130 msec	—	Hastings & Sweeney, 1957
Noctiluca miliaris	22–95 msec	17	Original
Aequorea forskalea	0·2–0·4 sec	14–16	Davenport & Nicol, 1955
Renilla köllikeri	0·25–1 sec	17–20	Nicol, 1955
Beroë ovata	0·16 sec	20–21	Nicol, 1958*c*
Mnemiopsis leidyi	0·290 sec	21–23·5	Chang, 1954
Acholoë astericola	63–103 msec	18–20	Nicol, 1953
Pyrosoma atlanticum	7 sec	25	Nicol, 1958*c*

Under repetitive electrical stimulation, the flashes of *Noctiluca* show summation, fusion and facilitation, as do those of various higher forms, e.g. hydromedusae, sea pens, ctenophores and polynoids (Nicol, 1953; Chang, 1954; Davenport & Nicol, 1955). There has been some question whether the facilitatory process takes place within the photogenic cell, or in the nervous system, or whether it operates at the neurophotocyte boundary. The observations on *Noctiluca* show that facilitation can occur within the confines of a single photogenic cell. It has also been demonstrated to occur in anaesthetized elytra of polynoids, when the nerve-fibres are non-operative; in this instance, also, one must postulate a facilitatory process within the photocyte (Nicol, 1957*a*). Still to be resolved is the intracellular level at which facilitation operates, whether it involves the initial stages of excitation, or some later stages of the biochemical reactions producing the light.

The emission spectrum of Noctiluca light extends from about 420 to 580 mμ, with a peak at about 470 mμ. Clear oceanic water is most transparent to blue light of this composition, and it is in this region of the spectrum that the eyes of some deep-sea species are most sensitive, viz. squid and teleosts ($\lambda_{max.}$ 493 and 480 mμ, respectively) (Denton & Warren, 1957; Hubbard & St George, 1958).

The radiant flux in a flash of a *Noctiluca* ranges from $0{\cdot}03 \times 10^{-6}$ to

$0{\cdot}16 \times 10^{-6}$ μJ/cm^2 receptor surface at 1 cm. On the assumption that the cell emits uniformly in all directions, the total energy irradiated from a *Noctiluca* is $0{\cdot}38 \times 10^{-6}$ to $2{\cdot}01 \times 10^{-6}$ $\mu J/4\pi$ sterads. Values for radiant flux are available for two other protozoans, viz. the radiolarians *Cytocladus* and *Aulosphaera* which emit $0{\cdot}6 \times 10^{-5}$ to $5{\cdot}3 \times 10^{-5}$ μW/cm^2 receptor surface at 1 cm (Nicol, 1958*c*). Nichols (1924) has estimated the brightness of individual flashes of dinoflagellates at 0·116 mlam. When allowance is made for the blue composition of dinoflagellate light, this brightness estimate is equivalent, approximately, to a radiant flux of $0{\cdot}354 \times 10^{-5}$ μW/cm^2 receptor surface at 1 cm distance. Since the individual flashes of dinoflagellates are only some 0·1 sec in duration, equivalent flux in Nichols's estimates, averaged over 1 sec, is of the order of $0{\cdot}15 \times 10^{-6}$ μJ/cm^2 receptor surface at 1 cm distance. This shows reasonably good agreement with the present estimates of radiant flux of *Noctiluca*.

I am indebted to Dr M. Parke for undertaking the culture of *Noctiluca*, and to Mr E. I. Butler for technical assistance. Mr G. N. Harding of the U.K. Atomic Energy Authority supplied the ^{60}Co-stilbene phosphor, for which I am grateful. Part of the apparatus used in this research was purchased with grants from the Royal Society.

SUMMARY

The luminescent flashes of *Noctiluca miliaris* have been recorded by means of a blue-sensitive photomultiplier. Following mechanical stimulation, a cell gives a brief flash, lasting up to 90 msec. Repeated stimulation quickly leads to fatigue of photogeny; rest allows recovery. With electrical stimulation there is a flash for each pulse. With repetitive electrical stimulation, there is summation, then fusion of flashes, depending on the frequency. Some cells gave clear evidence of facilitation. Increasing the current produced brighter flashes. Illumination was without effect on the photogenic response.

The relative spectral composition of the light was determined by means of glass and gelatine filters. Emission extends from about 420 to 580 mμ, with a maximum at about 470 mμ. Radiant flux in a flash from a single cell ranges from $0{\cdot}03 \times 10^{-6}$ to $0{\cdot}16 \times 10^{-6}$ μJ/cm^2 receptor surface at 1 cm distance (23° C).

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OBSERVATIONS ON THE LUMINESCENCE OF *PENNATULA PHOSPHOREA*, WITH A NOTE ON THE LUMINESCENCE OF *VIRGULARIA MIRABILIS*

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(Text-figs. 1–8)

Pennatula phosphorea Linn. is a well-known luminescent animal, which was studied by that pioneer investigator, Panceri (1871, 1872*a*, *b*). He found that the animal luminesces when excited, and that the light emanates from the zooids. From the region stimulated luminous waves proceed, with measurable velocity, to the extremities of the animal. Since waves can be initiated in either direction, up or down the colony, it follows that the transmission system is non-polarized. Recent studies on other species of pennatulids have shown that luminescence is under control of a nerve net (Nicol, 1955*a*, *b*, *c*; Davenport & Nicol, 1956). Harvey's book on *Bioluminescence* (1952) gives a review of pertinent literature, plus a bibliography.

In the present study, the luminescent responses of *P. phosphorea* have been analysed by means of photoelectric recording, with special attention to the flashes of individual zooids. Spectral emission has been determined, and estimates made of the intensity of the luminescence of *P. phosphorea* and *Virgularia mirabilis*.

MATERIAL AND METHODS

Specimens of *Pennatula phosphorea* Linn. and *Virgularia mirabilis* O. F. Müll. were obtained in the otter trawl 15 miles south of Penmarch light, position 47° 32′–35′ N., 4° 11′–12′ W., depth 90 m. These were examined in the ship's laboratory at sea (R. V. 'Sarsia') or brought back to the Plymouth Laboratory.

Luminescence was recorded with photomultiplier tubes, E.M.I. types nos. 6685 and 6095B, connected to double-beam C.R.O.'s containing DC amplifiers. Oscilloscope deflexions were photographed on moving paper or stationary film. Spectral emission and radiant fluxes were determined with photomultiplier type no. 6685, the spectral sensitivity of which is given elsewhere (Nicol 1958*a*, fig. 2A). For the former measurements spectral filters were used, incorporated in a disc (no. II) and described in table 1 of another paper (Nicol 1958*c*). The methods of calculation are described in earlier papers (Nicol 1958*a*, *b*).

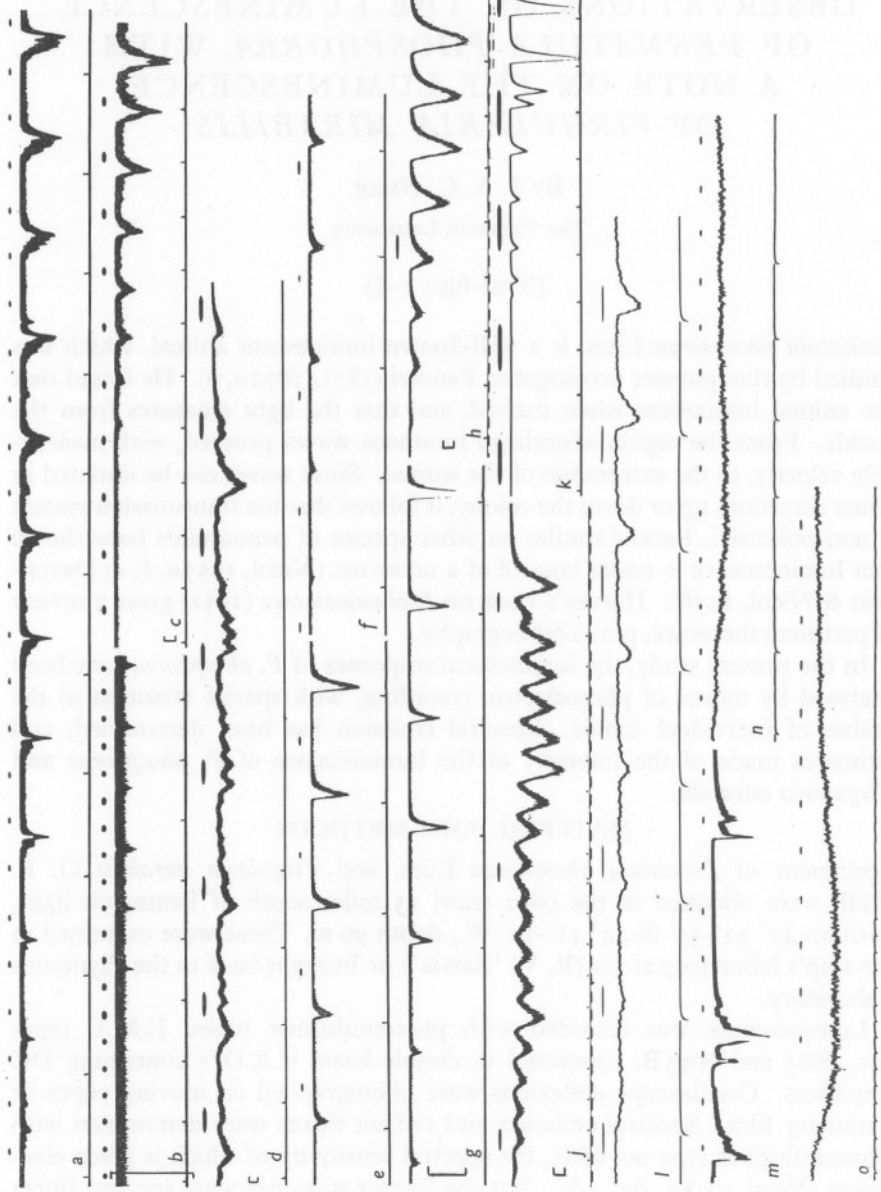

Fig. 1

Electrical stimuli were condenser shocks or square wave pulses, applied through Ag or Pt electrodes.

The observations which follow pertain to the autozooids of *Pennatula phosphorea*, unless indicated to the contrary.

Temperatures at which observations were made ranged from 18° to 20·8° C.

OBSERVATIONS

Both *Pennatula* and *Virgularia* are elongated sea pens, having a feather-like shape. There is a basal stalk or peduncle, from which arises the distal rachis. The latter has a central shaft, forming a support for a series of leaves on either side. The leaves of the rachis bear numerous autozooids, whereas the back of the shaft is covered with siphonozooids. *Virgularia* is long and whip-like compared with *Pennatula*.

When disturbed, *Pennatula* contracts; when left quiet, it takes in water and gradually swells. Observations were made on rested specimens, that had not been disturbed for an hour or more.

Light is emitted by the zooids (both autozooids and siphonozooids) and when the animal is excited, luminescent waves run over the length of the rachis. With persistent and repeated stimulation, the whole rachidial surface becomes aglow with a scintillating and shifting pattern of luminous points. The response is quickly fatigued, and time is required for recovery.

ELECTRICAL STIMULATION

Under repetitive electrical stimulation *Pennatula* responds with luminous waves which run over the surface of the colony from the region of the electrodes (Fig. 1*a*). Usually a response appears after the first shock, sometimes after the second or third shock. At slow frequencies (intervals > 1 sec), there

Legend to Fig. 1

Fig. 1. Oscilloscope recordings of the luminous flashes of sea pens. Time scale above each record, 1/sec; downward deflexion of middle trace represents luminous response; pips on lower line, if any, are electrical stimuli. Photographs (positives) made on moving paper. (*a*) *Pennatula phosphorea*. Recording of transmitted waves from autozooids of whole animal. Burst of 12 shocks at 1/2 sec. Temp. 18·5° C. (*b*, *c*, *d*) *Pennatula*. Responses of siphonozooids in the intact animal to various rates of stimulation (1/2 sec, 1/sec, 90/min, respectively). *d* is latter part of a longer record, beginning with the 13th pulse, and shows much flickering and after-discharge. Relative amplification given by height of vertical lines. Temp. 20° C. (*e*, *f*) Flashes of an isolated autozooid of *Pennatula*, showing fatigue. The autozooid was stimulated with burst of 10 shocks (1/sec), 2 min interval between bursts. *e*, 2nd burst; *f*, 7th burst. Last 5 shocks only shown. Temp. 20·8° C. (*g*, *h*, *j*) Responses of an isolated autozooid of *Pennatula* to electrical stimulation at various frequencies. *g*, burst at 1/sec, last 7 pulses of 14; *h*, 4/sec, last 8 pulses of 12; *j*, 9/sec, last 20 pulses of 24. Relative amplification shown by vertical lines. Temp. 20·8° C. (*k*) Isolated autozooid of *Pennatula*. Burst of pulses at 132/min. Note double flashes. Temp. 20° C. (*l*) Localized responses of siphonozooids of *Pennatula*. Burst of shocks at 72/min. Temp. 20° C. (*m*) *Virgularia mirabilis*. Transmitted waves elicited by mechanical stimulation. Temp. 17° C. (*n*, *o*) *Virgularia*. Bursts of pulses at 36/min and 3/sec. Low band pass filter. Recording from a stretch about 5 cm long. Temp. 19° C.

is 1 flash/shock, and successive flashes increase progressively in intensity (Fig. 1*a*). The response pattern is often rather irregular when stimulus intervals are long (Fig. 2).

At slow frequencies, each response has time to return to base-line, thus excluding summation, or the build-up of flash intensity by one response being superposed on its predecessor. Despite the absence of summation, there is still an increment of flash intensity in consecutive responses, an increment which can be ascribed to facilitation (Fig. 1*a*) (Pantin, 1952). The same patterns of responses are shown by other sea pens, e.g. *Renilla* and *Leioptilus* (Nicol, 1955*a*, *b*; Davenport & Nicol, 1956).

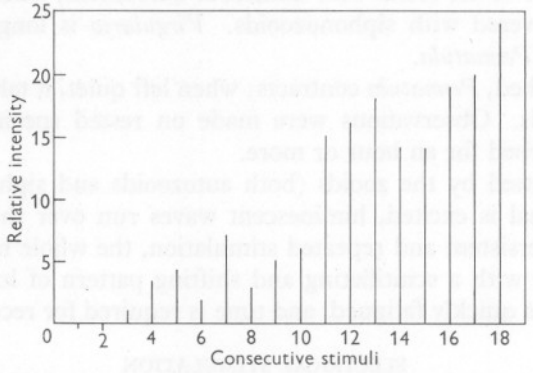

Fig. 2. Histogram showing increase in height of successive flashes of autozooids (*Pennatula*). Recording from whole animal stimulated with a burst of shocks at 48/min. Temp. 18·2° C.

Facilitation lasts at least 1 min. An animal was stimulated with bursts of shocks (frequency 1-2/sec), the several bursts being separated by intervals of 30 sec or 1 min. The responses in the second series were brighter than those in the first, and those in the third series brighter still. The enhancing or facilitatory effect is carried over from one period to the next, despite the long intervening intervals of quiescence.

After a burst of impulses, there is often a certain amount of after-discharge, in which several luminous waves continue to arise after stimulation has ceased (cf. Fig. 1*d*). The luminous waves in a bout of post-stimulatory flashing gradually decrease in frequency and amplitude.

The latency after electrical stimulation was measured as follows. An animal was covered, except for a slit 1 cm wide across the body, and the electrodes were placed at this level. The animal was stimulated with a burst of shocks at 1/sec, and responses were recorded at maximal amplification. The mean latent period, in 8 responses, was 0·25 sec; variations in measurements were $\pm$0·02 sec, and were random.

When recordings were made from a slit lying some distance from the elec-

trodes, it was found that the latency of the flash increased markedly during a long burst of pulses. Some actual examples are as follows:—

Burst of 15 shocks at 40/min. Latency increased from 0·76 to 1·54 sec, i.e. an increment of 2 times.

Burst of 18 shocks at 4/sec. Latency increased from 1·2 to 3·2 sec, i.e. an increment of 2·7 times

These recordings were made from a 1 cm aperture on the rachis. Since the electrodes were some distance away, the latencies include conduction time to the region from which the flashes were recorded.

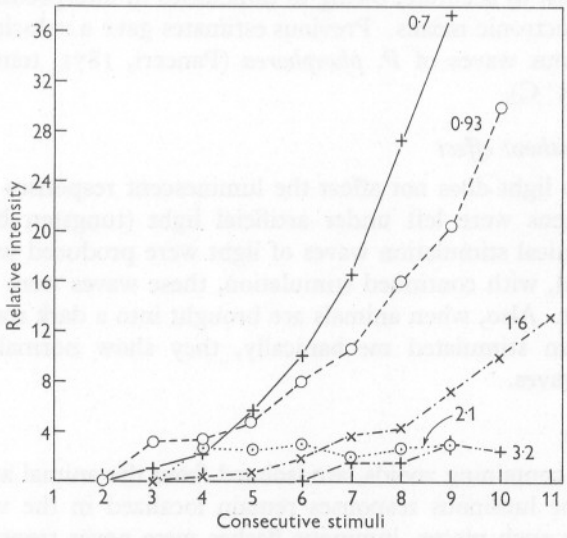

Fig. 3. Facilitation in siphonozooids of *Pennatula*. Curves showing how the amplitude of consecutive responses increases, and the effect of different frequencies of stimulation. Figures on the curves give the interval between stimuli. Recording of responses of siphonozooids of an intact animal. Temp. 20° C.

Responses of siphonozooids

Luminescent responses of the siphonozooids are similar to those of autozooids in the intact animal. Repetitive stimulation evokes luminescent waves that are propagated along the back of the rachidial stem. These increase progressively in intensity, and show the same pattern of facilitation as do the autozooids (Fig. 1*b–d*). The rate of facilitatory increment becomes greater as the frequency is raised (Fig. 3). Following prolonged stimulation there is much after-discharge (Fig. 1*d*).

Temporal characteristics of flash

Recordings were made from a slit, 8 mm wide, extending across a sea pen (*Pennatula*). The animal was stimulated electrically. Total duration of

response was 0·7 sec; rise to maximum occupied 0·2 sec; time to ½ maximum was 0·14 sec; decay from maximum was 0·5 sec. (18·4 °C). Even in this small field, of course, many autozooids were contributing to the flash.

Conduction velocity

I made some measurements of conduction velocity, by recording from two slits at a known distance. One or two photomultipliers were used, the latter arrangement being more satisfactory. Average conduction speed was 6·4 ± 1·4 cm/sec (18°–20° C). A visual estimation of conduction speed is probably at least as accurate, owing to difficulties in interpreting the records obtained by electronic means. Previous estimates gave a velocity of 5 cm/sec for the luminous waves of *P. phosphorea* (Panceri, 1871, temp. ?; Moore, 1926, temp. 15° C).

Illumination without effect

Exposure to light does not affect the luminescent responses of *Pennatula*. Three specimens were left under artificial light (tungsten bulb) for ½ h. Under mechanical stimulation waves of light were produced which ran over the animal and, with continued stimulation, these waves were succeeded by flickering light. Also, when animals are brought into a dark room from daylight, and then stimulated mechanically, they show normal, transmitted luminescent waves.

Local responses

When pieces, containing zooids, are isolated from the animal and stimulated electrically, the luminous responses remain localized in the vicinity of the electrodes. In such pieces, luminous flashes were never transmitted, either from autozooid to autozooid, or along a strip of siphonozooids. Preparations which behaved in this way were isolated under $MgCl_2$-anaesthesia, washed in sea water, and allowed long periods for recovery. It would seem that transmission in that part of the nervous system concerned with the luminous response becomes disorganized in an isolated piece of tissue.

Autozooids

When a pinna is cut off and electrodes are placed on one of the autozooids, only the autozooid immediately under the electrodes responds. No transmission of luminescence is visible in such isolated pieces. The following observations were made on excised autozooids of *Pennatula*.

With repetitive electrical stimulation an autozooid flashes each time it receives a shock, and consecutive flashes increase progressively in intensity (Figs. 1*e*, 4, 5). This is facilitatory increment. Occasionally an autozooid flashes twice in response to one shock (Fig. 1*k*). At fast rates of stimulation, the responses run into each other, and fusion is nearly complete at a frequency

of 10/sec. Continued stimulation leads to fatigue, and the intensities of the flashes decrease. This effect is well seen when an autozooid is stimulated at regular intervals with identical bursts of shocks. In the later series the flashes gradually diminish (Fig. 1*e*, *f*).

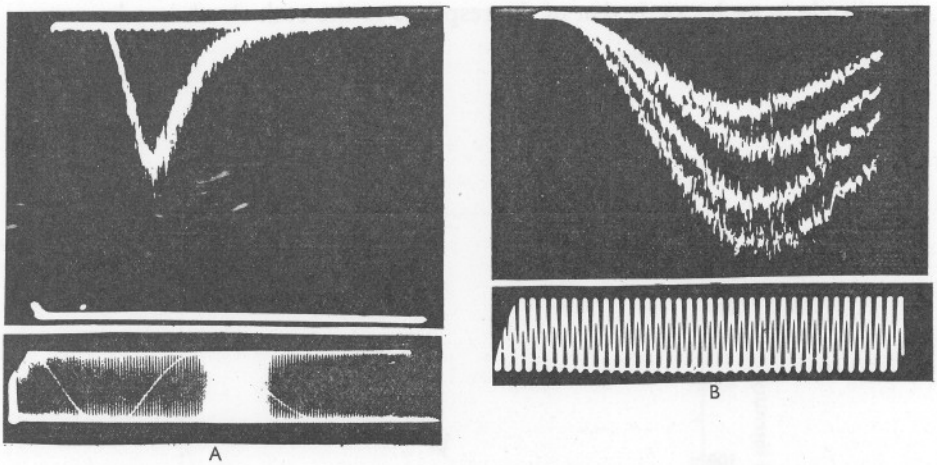

Fig. 4. Responses of an isolated autozooid of *Pennatula* to a single shock (A), and a burst at 2/sec (B). Sweeps. Time scale, 50~. Note facilitation in B. Temp. 20° C.

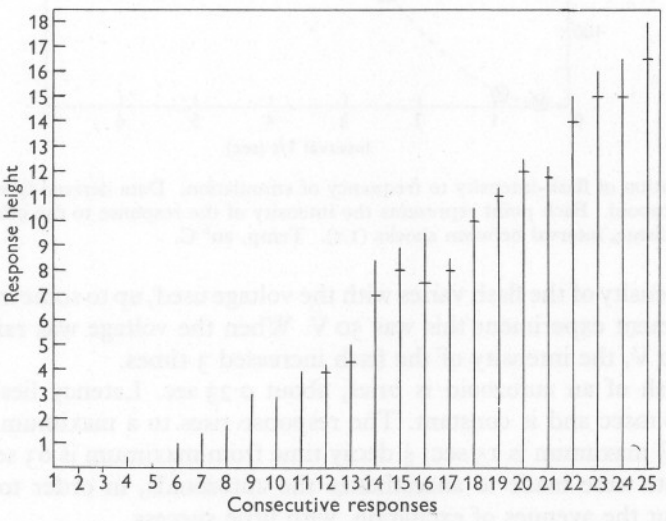

Fig. 5. Histogram showing changes in flash intensity of an isolated autozooid of *Pennatula* under repetitive electrical stimulation. Bursts of 25 shocks at 39/min. The cross-marks on the vertical lines represent response-height less residual luminescence obtaining at the start of the response. Temp. 20° C.

Facilitatory increment becomes more pronounced as the frequency is raised (Figs. 1*h–k*, 6). At very short intervals (around 0·1 sec) the process is reversed, the responses become irregular, and amplitudes are smaller than at longer intervals. The following measurements, as an illustration, refer to the responses of an autozooid stimulated with bursts of electrical shocks. The amplitude in each case is that of the response to the 10th shock in a burst:

Interval between stimuli	Amplitude (relative)
0·106 sec	14·27
0·200	42·7
0·371	20
0·970	5

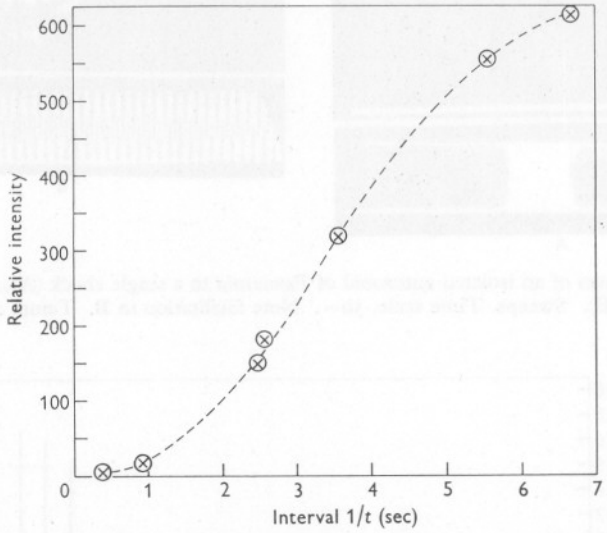

Fig. 6. Relation of flash-intensity to frequency of stimulation. Data derived from flashes of a single autozooid. Each point represents the intensity of the response to the 9th shock in a series. Abscissae, interval between shocks ($1/t$). Temp. 20° C.

The intensity of the flash varies with the voltage used, up to some maximum. In the present experiment this was 50 V. When the voltage was raised from 20 V to 50 V, the intensity of the flash increased 3 times.

The flash of an autozooid is brief, about 0·23 sec. Latency lies between 20 and 30 msec and is constant. The response rises to a maximum in about 39 msec; $\frac{1}{2}$ maximum is 15 sec; $\frac{1}{2}$ decay time from maximum is 63 sec.

Attempts were made to anaesthetize the autozooids, in order to find out more about the avenues of excitation, with little success.

Autozooids were placed in the following drugs for 3–4 h: cocaine, 0·1%; procaine hydrochloride, 0·5%; MS 222 (Sandoz), 0·1%; novocaine, 0·5%; chloretone, 0·1%; isosmotic $MgCl_2$: sea water, 1·1. There were very weak

responses in autozooids poisoned with cocaine and chloretone, none in the others. To a burst of shocks, the autozooid in cocaine gave a series of flashes, 1/stimulus; the first was brightest, and succeeding ones fell off in amplitude. Responses in chloretone were too weak to resolve satisfactorily. All these materials depress excitability too much to yield much information about the luminescent responses.

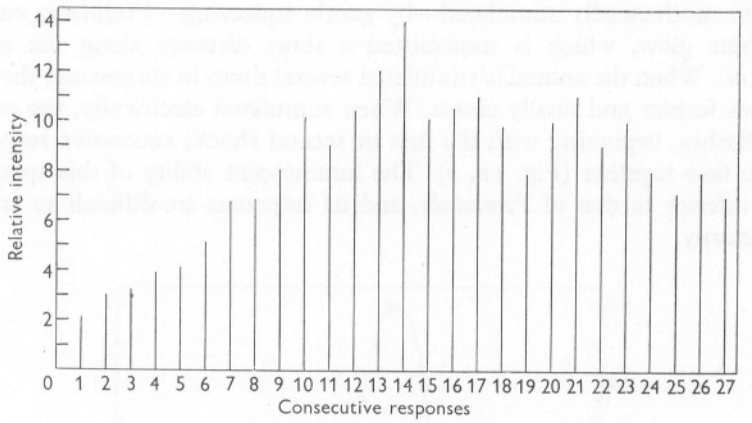

Fig. 7. Change in amplitude of consecutive flashes of siphonozooids (*Pennatula*). Localized responses from an isolated preparation of siphonozooids. Bursts of 27 shocks at 72/min. Ordinates, relative intensity; abscissae, consecutive responses. Temp. 20° C.

Siphonozooids

Isolated preparations of siphonozooids were made by cutting strips from the back of the rachidial stem. Under electrical stimulation luminescent responses are localized to the immediate vicinity of the electrodes. Each shock brings out a flash, the first response is relatively bright and prolonged, slowly reaching maximum; later flashes tend to be briefer, and to increase progressively in amplitude (Fig. 7). The increase in flash intensity occurs at slow rates of stimulation, and suggests that facilitation is operative in these instances (Fig. 1*l*). In a prolonged burst fatigue sets in, and later flashes decrease in amplitude.

Latency, in localized responses of siphonozooids, is about 50 msec. In the first flash of a series, total duration was > 1 sec; time to maximum was 0·22 sec. The 14th flash of a series had a duration of 0·43 sec; rise to maximum occupied 0·078 sec (20 °C). There was no obvious increase in latency of consecutive responses. When high rates of stimulation were used, individual flashes could still be resolved at intervals of 0·1 sec.

LUMINESCENT RESPONSES OF *VIRGULARIA MIRABILIS*

Earlier workers were of the opinion that *Virgularia* is non-phosphorescent (Hickson, 1916, p. 154). *V. mirabilis*, however, is luminescent, but the light is very transitory, and the animal's photogenic ability is easily fatigued. In these respects it resembles *Stylatula elongata*, belonging to the same family (Virgulariidae) (Davenport & Nicol, 1956).

When mechanically stimulated—by gentle squeezing—*Virgularia* emits a faint blue glow, which is transmitted a short distance along the zooids (Fig. 1*m*). When the animal is stimulated several times in succession, the light becomes feebler and finally ceases. When stimulated electrically, the animal emits flashes, beginning with the first or second shock; successive responses tend to fuse together (Fig. 1*n*, *o*). The luminescent ability of this species is much inferior to that of *Pennatula*, and its responses are difficult to analyse satisfactorily.

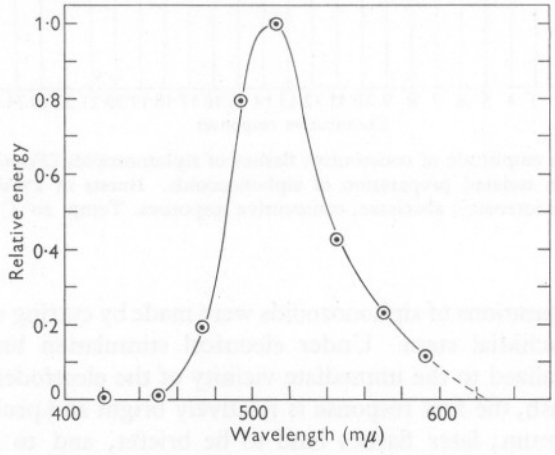

Fig. 8. Relative spectral emission of *Pennatula phosphorea*.

RELATIVE SPECTRAL EMISSION AND RADIANT FLUX

Spectral emission in *Pennatula phosphorea* extends from about 450 to 620 mμ. Maximal emission occurs at about 510 mμ (Fig. 8). The light is blue-green in colour.

Using the relative spectral emission curve shown in Fig. 8, estimates have been made of the intensity of light emitted by *Pennatula* and *Virgularia*. The light of *Virgularia* appears blue to the eye, and it is assumed that its spectral composition resembles that of *Pennatula*. Any difference is unlikely to be sufficient to introduce much error into the estimates of radiant flux.

Pennatula phosphorea. During electrical stimulation, the separate flashes

increase progressively in intensity, owing to facilitation (p. 554). Flashes, recorded from the whole animal, last 0·4–0·7 sec (Fig. 1*a*). Radiant flux, in a series of 12 flashes, increased from $0{\cdot}84 \times 10^{-6}$ to $6{\cdot}96 \times 10^{-6}$ μJ/cm^2 receptor surface at 1 cm distance (18·5° C.)

Measurements were made of the intensity of light in flashes of isolated autozooids following electrical stimulation. Radiant flux in a single flash varied from $0{\cdot}096 \times 10^{-9}$ to $62{\cdot}80 \times 10^{-9}$ μJ/cm^2 receptor surface at 1 cm distance (temp. 20·8° C). The first value refers to the smallest measurable response in a series, the second to a maximal facilitated response.

Virgularia mirabilis. The luminescent response of *Virgularia*, evoked by mechanical stimulation, lasts about $1\frac{1}{2}$ sec. Estimated radiant flux, at 1 cm distance, is $1{\cdot}4 \times 10^{-4}$ to 12×10^{-4} μW/cm^2 receptor surface.

DISCUSSION

When *Pennatula* is stimulated waves of light appear which are propagated over the surface of the rachis. The luminescent response is followed by contraction of the animal and expulsion of water. The transmission system responsible for propagation of the luminescent response is presumably nervous; direct proof of this would be best afforded by electric recording. Propagation takes place in any direction (*Pennatula* and other sea pens), indicating that a non-polarized system is involved. This system could be a neural network possessing two-way synapses, i.e. interneural junctions capable of transmitting with equal facility in either direction. The luminescent response is propagated uniformly and without decrement; that part of the neural network involved, therefore, would appear to partake of the nature of a through-conduction system (cf. Pantin, 1950).

Horridge (1957) has investigated the retractile responses of alcyonarian, zoanthid and madreporarian polyps. In most groups there is extensive co-ordination over the colony, and in astraeid corals and *Tubipora* the polyps are linked by a through-conducting system. There appears to be little or no co-ordination of the retractile responses of the polyps of the sea pansy *Renilla*, according to Parker (1919). Peristaltic waves of contraction have been noted in this animal, but these are transmitted at much slower velocities than the wave of luminescence (Parker, 1920). Sea pens possibly possess several transmitting systems, each of which is concerned with regulating a particular kind of response, and to test this, or alternative ideas, an analytical study of the various responses of *Renilla* would be well worth while.

One of the most noteworthy features of the luminescence of sea pens is the progressive increase in the intensity of consecutive responses, as revealed by photoelectric recordings. This increment, termed facilitation, is revealed in localized recording from the intact animal, and in the responses of a single isolated zooid. Now, it is an interesting fact that when a piece of tissue,

containing several zooids, is removed from *Pennatula* and is stimulated electrically, only the zooid immediately under the electrodes responds, and no transmission of excitation occurs. Therefore, one may argue, the nerve net is inexcitable in a severed fragment, and the photocytes are responding directly to electrical stimulation. When recordings are made of the flashes of isolated autozooids, it is found that these records show a pattern similar to those recorded from the intact animal. Latency is short, presumably because no transmission time is involved, and facilitation is evident.

In a previous paper dealing with luminescence in *Renilla* (Nicol, 1955*b*), evidence was presented that facilitation in that animal involved recruitment of photogenic loci with continued stimulation. Two obvious possibilities relating to facilitation in an isolated autozooid of *Pennatula* are: (*a*) individual photocytes have different levels of excitability, some of them responding to a single shock, others requiring many shocks before they respond; continued stimulation, therefore, leads to recruitment of photocytes, and greater light emission; (*b*) facilitation is an intracellular process involving a progressive increase of excitation in all the photocytes with continued stimulation. The increase in flash-intensity which accompanies a rise of voltage could be explained either way. Intracellular facilitation involving a single cell has been discovered in the flashes of *Noctiluca* (Nicol, 1958*d*), which provides an analogy for a similar phenomenon in *Pennatula*.

Another feature brought out by photo-electric recording is latency. In flashes from a single autozooid the latent period remains constant. But when records of transmitted waves are taken from the intact animal, measured latency from the stimulus to incidence of light emission shows progressive lengthening during a series of pulses. Since transmission through a series of neurones is involved in the latter preparation, but not in the former, it appears that the increase of latent period takes place in the nerve net. Possibly an increase in conduction time is involved, but the records are ambiguous in this respect.

The light of *Pennatula phosphorea* is blue green in colour. Other animals with similar spectral emission are ctenophores and polynoids (Nicol, 1957, 1958*c*). Values for radiant flux, ranging up to 7×10^{-6} μJ/cm^2 receptor surface at 1 cm, are of about the same magnitude as those for flashes of a single polynoid elytrum (Nicol 1958*a*).

SUMMARY

The luminescent responses of *Pennatula phosphorea* and *Virgularia mirabilis* were investigated by means of photo-electric recording. *Pennatula* produces luminescent waves which are transmitted over the surface at 6·4 cm/sec (20° C). Facilitation is shown in responses of the whole animal and in responses of isolated autozooids and siphonozooids. Data are given for latency and flash-duration. *Virgularia* is more easily fatigued than *Pennatula*. Spectral emis-

sion of *Pennatula* extends from about 450 to 620 mμ, with a peak at 510 mμ. Values for radiant flux are:

P phosphorea, $0{\cdot}8 \times 10^{-6}$ to 7×10^{-6} μJ/cm^2 receptor surface at 1 cm; *V. mirabilis*, $1{\cdot}4 \times 10^{-4}$ to 12×10^{-4} μW/cm^2 receptor surface at 1 cm (responses of the intact animal). A flash from a single autozooid of *Pennatula* has an intensity of $0{\cdot}1 \times 10^{-9}$ to $62{\cdot}8 \times 10^{-9}$ μJ/cm^2 receptor surface at 1 cm.

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NOTES ON STARFISH ON AN ESSEX OYSTER BED

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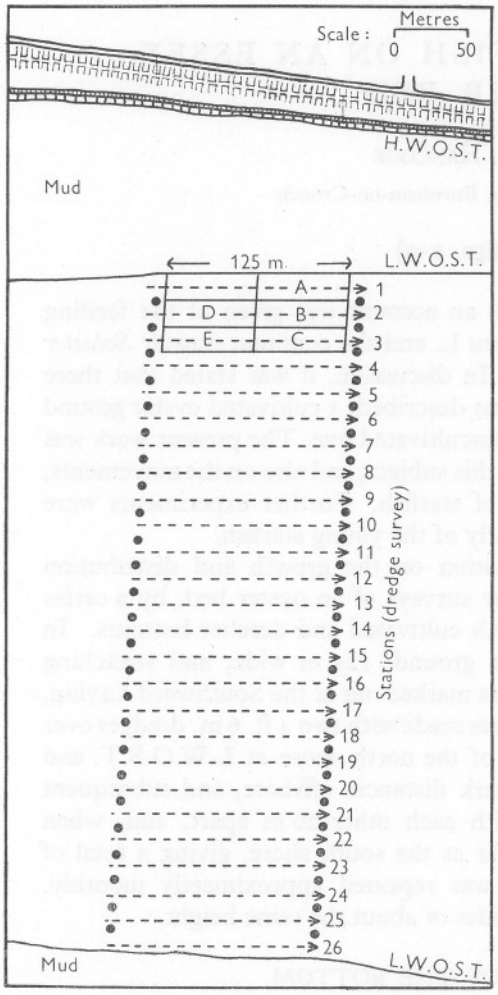
(Text-figs. 1–9)

In a previous paper (Hancock, 1955) an account was given of the feeding behaviour of the starfish *Asterias rubens* L. and the common sunstar *Solaster papposus* (L.) on Essex oyster beds. In discussion, it was stated that there was no evidence that, in the conditions described, a cultivated oyster ground provided a greater attraction than an uncultivated one. The present work was undertaken to provide information on this subject, and also on the movements, growth and ecological relationships of starfish. Further experiments were made on feeding behaviour, particularly of the young starfish.

Samples required to give information on the growth and distribution of starfish were obtained from regular surveys of an oyster bed, by a series of parallel dredge hauls covering both cultivated and derelict bottoms. In November 1954, a section of oyster ground, 125 m wide, and stretching from one bank to the other (Fig. 1), was marked out at the Southward Laying, River Crouch. The first dredge haul was made with two 4 ft. 6 in. dredges over the 125 m width, parallel to the edge of the north shore at L.W.O.S.T. and 10 m from it. Buoys were used to mark distances offshore, and subsequent dredge hauls were made parallel with each other 20 m apart, and, when time permitted, were continued as far as the south shore, giving a total of twenty-six stations. This procedure was repeated approximately monthly. The survey dates were chosen with tides of about the same height.

DESCRIPTION OF THE BOTTOM

At the Southward Laying, an area below L.W.O.S.T. is fully cultivated; most of the slipper limpets (*Crepidula*) have been removed and oysters have been relaid. Farther offshore the ground becomes semi-derelict with more *Crepidula*, and towards midstream is covered by an almost pure population of *Crepidula* (Table 1, Stations 6–11). In mid-river there is a submerged bank shallowest at Station 16 (Fig. 2) where, although little cultivation is done, tidal scour has made the bottom less muddy, and there is plenty of shell with large quantities of 'ross' or *Sabellaria*. There are some oysters, and, although *Crepidula* is present, the bottom is very much cleaner than in the deeper water over stations 6–11. The nature of the bottom at each dredge station is given in Table 1.



Results of grab survey
(Showing numbers of *Asterias* in approx. position of grab hauls)

I. Stations A E: 10 grabs per station

						2	2	4	12	0	A
						4	1	11	0	0	
D	2	2	3	2	2	1	1	3	1	3	B
	3	0	2	1	1	4	3	3	5	3	
E	2	9	1	8	3	6	7	4	9	15	C
	0	5	4	5	6	7	8	1	0	2	

II. Stations D B (repeat): 5 grabs per station

D	5	6	3	6	2	6	11	22	1	3	B

Fig. 1. Map showing part of the Southward Laying, River Crouch used for dredge surveys, recapture experiment and grab sampling. Dotted lines show positions of parallel dredge hauls 1–26 between buoys (●). Enclosed rectangles (A–E) show areas surveyed by grab sampler. Areas B and D (dredge Station 2) were also used for the recapture experiment (see text). The results of the grab survey are also shown diagrammatically.

DISTRIBUTION OF ADULT STARFISH

From the results of the surveys the distribution of *Asterias* and *Solaster* was plotted (Fig. 2). Figures for bottom animals taken in dredges should be compared with caution because a dredge is not a fully reliable sampler (Shelbourne, 1957). However, the regular appearance of concentrations of

particular animals on certain sections of the river suggests that in this instance, the dredge gave a satisfactory distribution picture.

It was shown previously (Hancock, 1955) that during 1954 the largest numbers of adult *Asterias* were taken from stations 3–6 (50-110 m below L.W.O.S.T., Fig. 2). Later, during 1955 and in 1956, the main area of abundance shifted offshore, perhaps as a result of the removal by dredging

TABLE 1. SOUTHWARD LAYING, RIVER CROUCH. NATURE OF BOTTOM SHOWN BY DREDGING ON STATIONS 1–26.

Station	Nature of bottom	
	1955	1956
1	Shell, oysters, few *Crepidula*	Shell, oysters, very few *Crepidula*
2	Shell, oysters, few *Crepidula*	Shell, oysters, very few *Crepidula*
3	Shell, oysters, *Crepidula*	Shell, oysters, very few *Crepidula*
4	Shell, *Crepidula*, some oysters	Shell, oysters, few *Crepidula*
5	Shell, *Crepidula*	Shell, *Crepidula*, oysters
6	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, oysters
7	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, muddy
8	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, muddy
9	Shell, *Crepidula*	As 1955
10	Shell, *Crepidula*	As 1955
11	Shell, *Crepidula*	As 1955
12	Shell, *Sabellaria*, *Crepidula*, some oysters	As 1955
13	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
14	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
15	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
16	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
17	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
18	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
19	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
20	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
21	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
22	Clean shell, *Sabellaria*, few oysters	As 1955
23	Shell, *Sabellaria*, some stones	As 1955
24	Shell, *Sabellaria*, stones and mud	As 1955
25	Shell, *Sabellaria*, stones and mud	As 1955
26	Hard mud and boulders, some shell	As 1955

of large numbers of *Crepidula*, close to the cultivated ground, causing the *Asterias* to seek more abundant food farther offshore. No evidence was obtained of extensive migrations, and, particularly, there was no mass movement of adult *Asterias* to the cultivated oyster ground inshore just below L.W.O.S.T. The population was maintained just offshore in association with large numbers of *Crepidula*.

Solaster, however, had quite a different distribution and there was little overlapping between the adult populations of *Asterias* and *Solaster* (Fig. 2). The largest numbers of adult *Solaster* occurred throughout the year on grounds commencing 180 m from the north shore (Station 10 onwards) and extending to the opposite shore. They were not associated with the cultivated oyster ground near the north shore, nor with the main *Crepidula* zone (Stations 6–11). *Solaster* was mainly found on the submerged bank (Fig. 1), where

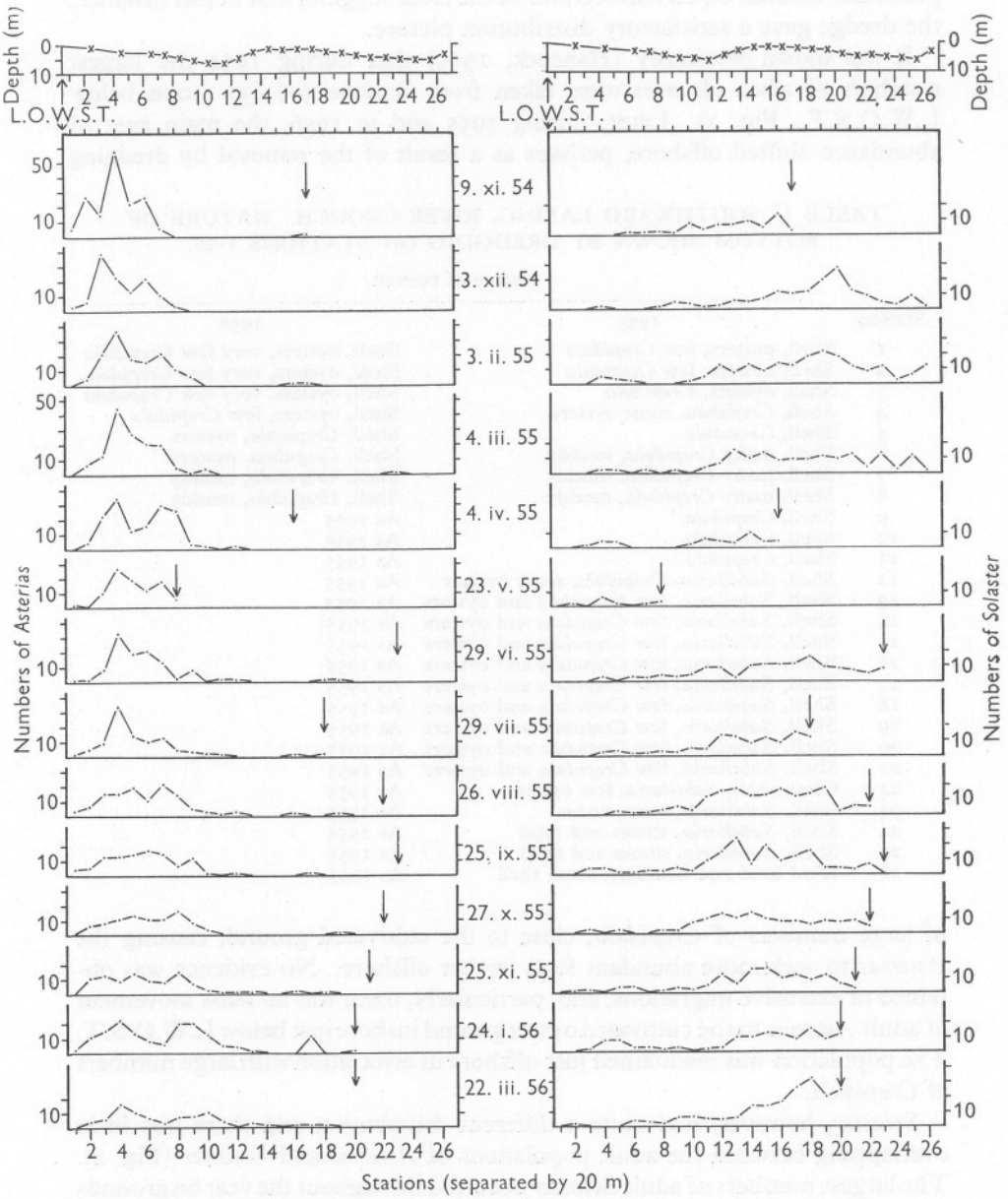


Fig. 2. Numbers of adult *Asterias* and *Solaster* taken using two 4 ft. 6 in. power dredges in parallel dredge hauls across the River Crouch at the Southward Laying 1954–56, commencing 10 m from L.W.O.S.T. on the north shore. Sections across the river showing mean depths are given. The final dredge station on each date is indicated by an arrow.

the bottom was of 'ross' (*Sabellaria*), some *Crepidula* and oysters, with *Alcyonidium*, *Sertularia*, *Dendrodoa* and some barnacles. The type of bottom at each station is shown in Table 1.

DISTRIBUTION AND SETTING OF YOUNG STARFISH

Juvenile *Asterias* were taken in 1955, for the first time, on 29 July, when they were 1–7 mm in maximum radius (Figs. 3, 5 and 6). By 'maximum radius' is meant the length of the largest arm from its tip to the centre of the mouth. The distribution of juveniles on the stations at the Southward Laying was compared at first by counting the population on fifty oyster shells taken at random from the dredge hauls on each station. On 29 July the largest numbers were taken on stations 2 and 3, with little settlement offshore (Fig. 3). Further settlement had occurred by 26 August when numbers had increased on all stations, but particularly offshore. When sampled on 25 November the juveniles had grown so much (Fig. 5) that they became easily detached from shells in the dredges, and the numbers on shells could no longer be used for comparison. On this and subsequent dates, the density of young starfish was estimated by subsampling the dredge contents, and calculating the numbers in two full dredges. These numbers could be compared more easily with the numbers of adult starfish (Fig. 2). Most juveniles continued to be found on inshore stations, with a fairly large settlement on Stations 12–20.

Juvenile *Solaster* appeared earlier in the year than *Asterias*, on 23 May 1955. This was expected, as in the laboratory *Solaster* spawned from 25 to 27 February 1954 at a mean temperature of 9° C, and on 16 March 1955 when the temperature was again 9° C. *Asterias*, however, did not spawn in 1954 until 29 May, when the temperature had reached 15° C. *Solaster* eggs spawned on 25 February 1954, kept under observation in the laboratory, were floating orange spheres 0·9 mm in diameter. By 2 March they had become gastrulae, which elongated in a day or two, and by 10 March had developed three larval arms (as figured by Gemmill, 1912, for *Solaster endeca*, and by Chadwick, 1914). Metamorphosed stages, less than 1 mm in diameter, with the first tube feet, were found attached to the bottom of the tank early in April. *Solaster* eggs were taken in the plankton from the River Crouch in 1956 for the first time on 26 March. The distribution of young *Solaster* at the Southward Laying was very similar to that of the adults, the greatest settlement being consistently about 250 m from the north shore (Fig. 3, Stations 11–14).

The numbers of *Asterias* settling in 1955 were much greater than those of *Solaster*. The greatest quantity taken during the year in two full dredges was 2724 on Station 2 on 23 September. The corresponding total for *Solaster* was 42 taken on Station 11 on 27 October 1955. In 1956, no settlement of *Asterias* was observed. Small numbers of *Solaster* settled, but they were not seen until 4 June, when they were considerably smaller than the previous year group was in June 1955.

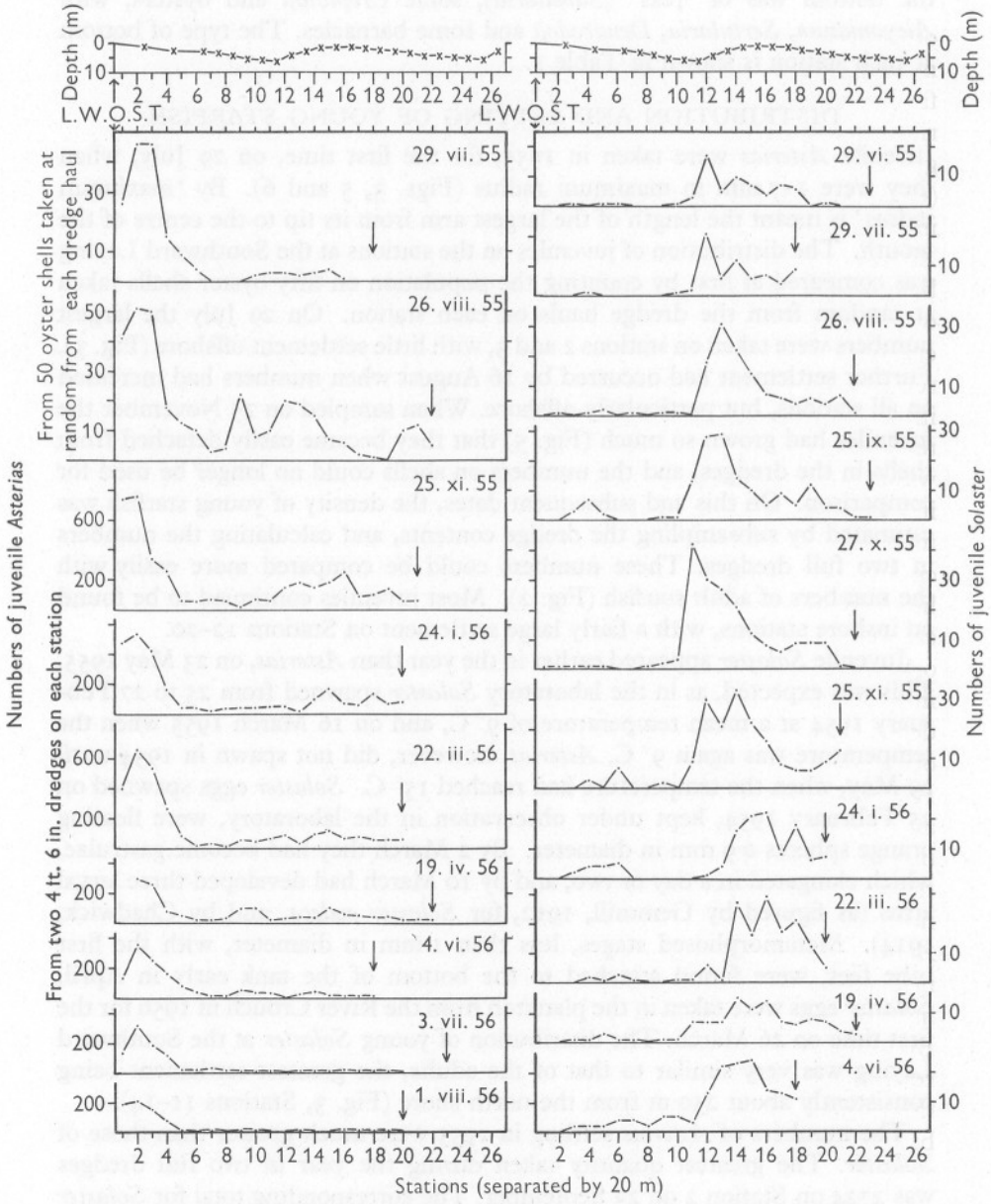


Fig. 3. Numbers of juvenile *Asterias* and *Solaster* taken using two 4 ft. 6 in. power dredges in parallel dredge hauls across the River Crouch at the Southward Laying 1955–56, commencing 10 m from L.W.O.S.T. on the north shore. On 29 July and 26 August 1955 *Asterias* were counted from only 50 shells in each dredge haul. From 25 November onwards, the total number in each dredge haul has been represented. Sections across the river showing mean depths are given. The final dredge station on each date is indicated by an arrow.

There was in 1955, therefore, considerably more overlapping of the juveniles of the two starfishes than of the adult populations. Young *Asterias* settled in maximum density inshore on cultivated oyster ground, but settling also occurred farther offshore in the *Solaster* zone. Young *Solaster* settled mainly in mid-river in the region of greatest abundance of adults, suggesting perhaps a gregariousness of settling near the parents as in certain other invertebrates (Cole & Knight-Jones, 1949, in oysters; Knight-Jones & Stevenson, 1950, in *Elminius*). Both young and adult *Solaster* have been observed devouring *Asterias*, particularly juveniles, and this, coupled with the discrete settling behaviour of *Solaster*, is believed to be responsible for the no more than slight overlapping of the two adult populations. *Asterias* is capable in a lesser capacity, of devouring young *Solaster*. Although there was such an enormous settlement of *Asterias* on the Southward Laying in 1955, the numbers taken in dredge hauls decreased steadily—from over 2700 on Station 2 on 23 September 1955 to only 44 on 15 October 1956. The distribution at the Southward Laying showed that this decrease was occurring on all stations, that is, it was not due to an inshore or offshore movement. A certain amount of migration of juveniles to neighbouring grounds might have occurred, but conditions there were no different from the Southward Laying. It is believed that the great decrease in the numbers was due to a heavy mortality caused by competition and cannibalism, resulting from a prolonged shortage of natural food and predation by *Solaster*. Galtsoff & Loosanoff (1939), in America, observed that an abundant set of *Asterias forbesi* Desor, greatly decreased within 1 month after settling, and suggested that cannibalism, observed frequently between young starfish in the laboratory, was responsible. It is significant that, before the settlement of young *Asterias* in 1955, shells and oysters at the Southward Laying were densely covered by barnacles, but by the end of August 1955 it was impossible to find a live barnacle there. Until the end of 1956, although barnacle settlement was elsewhere normal, the Southward Laying was still free. It is believed that the juvenile *Asterias* devoured the barnacles, giving them no chance to grow to recognizable size. The absence of freshly settled stages of *Asterias* in 1956 may have been a direct consequence of the lack of young barnacles required as food. By mid-1956, the distribution of the young of the two species of starfish resembled that of the adult populations (Figs. 2, 3). It is interesting to note that following the reduction of the numbers of *Asterias* to a normal level, barnacles reappeared in large numbers on the Southward Laying in 1957.

POPULATION DENSITY

Two methods were employed to estimate the density of young *Asterias* on the Southward Laying. These had been used previously with some success for determining the population density of *Urosalpinx* (Hancock, in press), and

comprised (*a*) marking and recapture experiments, and (*b*) a survey using a $\frac{1}{10}$ m² van Veen grab. Loosanoff (1937, 1953) described the marking of starfishes from the Atlantic coast of America with Nile Blue Sulphate, and Vernon (1937) used Neutral Red. Feder (1955) used both these methods with success on Pacific coast starfishes, and found that plastic disc tags attached by stainless steel were useful, but very liable to cause injury or loss of the tagged arms. No doubt the proportion surviving uninjured would be useful in migration or growth studies, but the method would be less reliable for recapture data.

Employing method (*a*), an area of oyster ground 20 m wide was marked out with buoys, its inner edge being parallel to, and 20 m below, the shore at L.W.O.S.T. on the Southward Laying (Fig. 1, area D–B). Dredge hauls were made on this area on 23 September 1955, parallel to the shore, and 1000 young *Asterias* were marked and returned, to be searched for by subsequent dredging. Marking was done by diluting a stock solution of Nile Blue Sulphate about ten times with sea water. This was sufficient to dye a large number of *Asterias* immersed in it in 5–10 min. The normal reddish brown of the aboral surface became darker and bluish-green in colour. The blue coloration showed up most clearly on the parts normally white, such as the surface of spines, and the oral surface. The blue stain of Nile Blue Sulphate was retained by marked starfish until at least 10 months after marking. A series of young and old dyed *Asterias* were retained in tanks in the laboratory for several months with no significant mortality.

Young *Asterias* were capable of quite rapid movement and for this reason only an hour or two was allowed for mixing with the normal population before redredging. Dredging, marking and redredging was continued on 12 and 14 October. The first group marked on 23 September totalled 1000, and on 12 October a second group of 1450 and a final group of 2165 were dyed making a total of 4615. Bailey's (1951) modification of the 'Lincoln Index' was applied to the numbers recaptured on each date. This is: $\check{x}=a(n+1)/(r+1)$, where $\check{x}$ is the total population in the marked area, a is the number of individuals marked, n is the size of a random sample containing r marked individuals. The total number of recaptured starfish was 365, compared with 16,903 unmarked. From calculations based on marking of the three groups (Table 2), the average figure for young *Asterias* per m² over the total area of 2500 m² used for recaptures was found to be 131. Uneven distribution of marked starfish over the area may account for the large variation between 28 and 296 per m² shown in Table 2.

The sorting of several thousand small starfish from the contents of a dredge is tedious and lengthy, and it was felt that a grab survey might be more accurate and would take less time. Grabbing could not be done until a month later, on 10 November, so that the results cannot be compared strictly with those from the recapture experiment described above. An area of oyster ground below L.W.O.S.T. was divided up with buoys to include the area used in the

recapture experiment (Fig. 1). Ten grab hauls ($\frac{1}{10}$ m^2) were made at random in each subarea (Fig. 1, A–E), so that their total represents the density per square metre for each station. The results showed great variation between single grab samples, from 0–15 on one station (Fig. 1, C). The bottom deposits were found to be variable, and the absence of *Asterias* could usually be related to clay or mud with no shells. A maximum of 59 per m^2 was found on Station C, with an average of 37 per m^2 for the whole area. Station D had 18, and Station B, 27 starfish per m^2, giving an average of 23 for the area D–B used in the recapture experiment.

The mid-level area D–B (Fig. 1) used for the recapture experiment was re-examined by a further 10 grab hauls intended to confirm the original results (Fig. 1). This time, however a total of 65 starfish per m^2 was obtained, compared with the previous average of 23 per m^2. The variation from 1 to 22 in individual grab hauls (Fig. 1) again emphasizes the patchiness of *Asterias*, and shows that a much larger number of grab hauls would be required to give more significant results.

TABLE 2. RECAPTURES OF MARKED *ASTERIAS* FROM DREDGE HAULS OVER STATION 2 (D–B)

(Each haul with two 4 ft. 6 in. dredges.)

Date of marking	Total number marked (a)	Date of recatpure	Number of re-captures (r)	Number un-marked ($n-r$)	Calculated total in the area (2500 m^2) $\frac{a(n+1)}{(r+1)}$	Average per m^2	Average (per m^2) for group
23 Sept. 55	1000	23 Sept. 55	7	2717	340,625	136	167
23 Sept. 55	1000	26 Sept. 55	3	2481	621,250	249	
23 Sept. 55	1000	12 Oct. 55	6	1997	286,286	115	
12 Oct. 55, (x)	2450	12 Oct. 55	8	1718	470,128	188	166
12 Oct. 55, (x)	2450	12 Oct. 55	1	290	357,700	143	
12 Oct. 55, (y)	4615	14 Oct. 55	30	636	99,297	40	95
12 Oct. 55, (y)	4615	14 Oct. 55	126	1770	68,934	28	
12 Oct. 55, (y)	4615	14 Oct. 55	10	1754	740,498	296	
12 Oct. 55, (y)	4615	14 Oct. 55	33	1511	209,711	84	
12 Oct. 55, (y)	4615	14 Oct. 55	141	2029	70,558	28	

Final average per 2500 m^2 for all recaptures = 326,499.

Average per m^2 for all recaptures = 131.

(x), (y): separate batches marked on the same day.

The figure of 37 per m^2, representing the average of the two series of grab hauls on Stations D–B, differs substantially from that of 131 obtained from recapture data from the same area, but it must be remembered that grab sampling was delayed for one month. Dredge survey results (Fig. 3) indicated that the density of young *Asterias* over the whole Southward Laying area was decreasing during this period; on 25 November 1955, for example, less than 800 were obtained per haul with two dredges on Station 2 (Fig. 1, over D–B) compared with the usual catch of nearly 2000 before the recapture

experiment. The largest number obtained in two 4 ft. 6 in. wide dredges dragged over 125 m on the same area was 2724 on 23 September 1955 on Station 2, which, when related to the area covered by the dredges, represents only 8 per m^2, and demonstrates the low efficiency of dredges for catching small starfish.

It is evident that, by either method, the estimation of density of a large population with such irregular distribution, even over a small area, can be based with confidence only on intensive sampling.

FEEDING

LABORATORY EXPERIMENTS

It was demonstrated in laboratory experiments (Hancock, 1955) that, although *Asterias* occasionally ate spat and adult oysters, the greater part of its food was composed of animals in competition with the oyster. The smaller sizes of *Asterias* ate large numbers of barnacles, with occasional spat of oysters and *Crepidula*. The larger ones occasionally ate oysters and oyster spat, but almost always exhibited a preference for mussels, and, in the absence of these, for *Crepidula*, and sometimes even for *Urosalpinx*.

To assess the effects of the very large number of juvenile *Asterias* which settled on the cultivated part of the oyster ground at the Southward Laying during 1955, further studies were made of the feeding behaviour of young starfish. These experiments also provided valuable information on growth.

Experiment 1

Ten *Asterias* of maximum radius 1–8 mm, were confined with an unlimited supply of barnacles, mainly *Elminius modestus* and *Balanus* spp. From 6 to 15 August 1955, 954 barnacles were devoured, representing an average of 10·6 barnacles per *Asterias* per day. The maximum feeding rate was 15·2 barnacles per day.

Experiment 2

From 9–15 August 1955, ten *Asterias* of maximum radius 1–8 mm were confined with shells bearing oyster spat, *Crepidula* spat and barnacles. During the first 3 days barnacles were eaten from all the shells, but no oyster spat, which were on the same shells, were taken. Towards the end of the experiment some oyster spat were taken, but nearly all of the barnacles had been destroyed. A total of 582 barnacles and 11 oyster spat (6 of 2 mm, 4 of 3 mm, and 1 of 7 mm average diameter), but no *Crepidula* spat, were eaten in 6 days. The *Asterias* finally measured 3·7–10·9 mm.

Experiment 3

Thirty *Asterias*, 12–13 mm max. radius, were isolated with *Crepidula* spat. In 7 days, 10–17 September 1955, only 5 *Crepidula* (7–9 mm in length) were eaten. When ten of these *Asterias* were transferred to a tank containing mussel spat, these were attacked immediately and the feeding rate greatly increased. The remaining 20 *Asterias* were retained with *Crepidula* spat, but the feeding rate continued to be low. From

10 September to 19 November 1955, only 26 *Crepidula* spat (4–13 mm in length) were eaten. The *Asterias* finally measured 8–12 mm. Only fourteen of the *Asterias* remained on 19 November 1955, the others having been the victims of cannibalism.

Experiment 4

Twenty *Asterias*, 12–13 mm, were isolated with oyster spat. Between 10 September and 2 October 1955, only 6 spat (4–8 mm diameter) were eaten. When barnacles were added on 12 October, the feeding rate increased, and, although 2566 barnacles were devoured between 12 October and 31 December 1955, no further oyster spat were taken. This experiment showed a maximum feeding rate of 5 barnacles per *Asterias* per day. The measurements of the *Asterias* were as follows:

Date (1955)	Maximum radius (mm)	Food
10 Sept.	12–13	—
12 Oct.	9–12	Oyster spat
4 Nov.	9–14	Barnacles
31 Dec.	9–19	Barnacles

Experiment 5

17 September 1955. Ten *Asterias* from Expt. 3 (12–13 mm) were confined with many mussel spat. Initially the feeding rate was high, but, as the size range of the mussel spat increased through growth, they gradually became too large for small starfish to open, and, by the beginning of December, when the mussels were all about 20 mm in length, feeding virtually ceased. When the mussels were replaced with barnacles, however, a high feeding rate was resumed.

Date (1955)	Size range of mussels (mm)	Number eaten by 10 *Asterias*	Number per *Asterias* per day
17–30 Sept.	3–10	165	1·3
1–31 Oct.	2–15	269	0·9
1–30 Nov.	3–24	84	0·3
1–7 Dec.	20–23	3	0·04
7–31 Dec.	Barnacles	480 barnacles	2 barnacles

The measurements of the starfish were as follows:

Date (1955)	Maximum radius (mm)	Food
10–17 Sept.	12–13	*Crepidula* spat
17 Sept.–12 Oct.	10–17	*Mytilus* spat
12 Oct.–14 Nov.	15–24	*Mytilus* spat
14 Nov.–31 Dec.	16–29	*Mytilus* spat and barnacles

Experiment 6

Eleven *Asterias* (all of maximum radius 20 mm) were offered equal numbers of *Crepidula* and oyster spat. Between 1 January and 29 March 1956, 32 oyster spat and 42 *Crepidula* spat were eaten. By the end of March the range of maximum radius length had decreased from 20 mm to 8–16 mm. Oyster spat eaten had a maximum diameter range of 8–25 mm and *Crepidula* 5–22 mm. The growth of these starfish is discussed below.

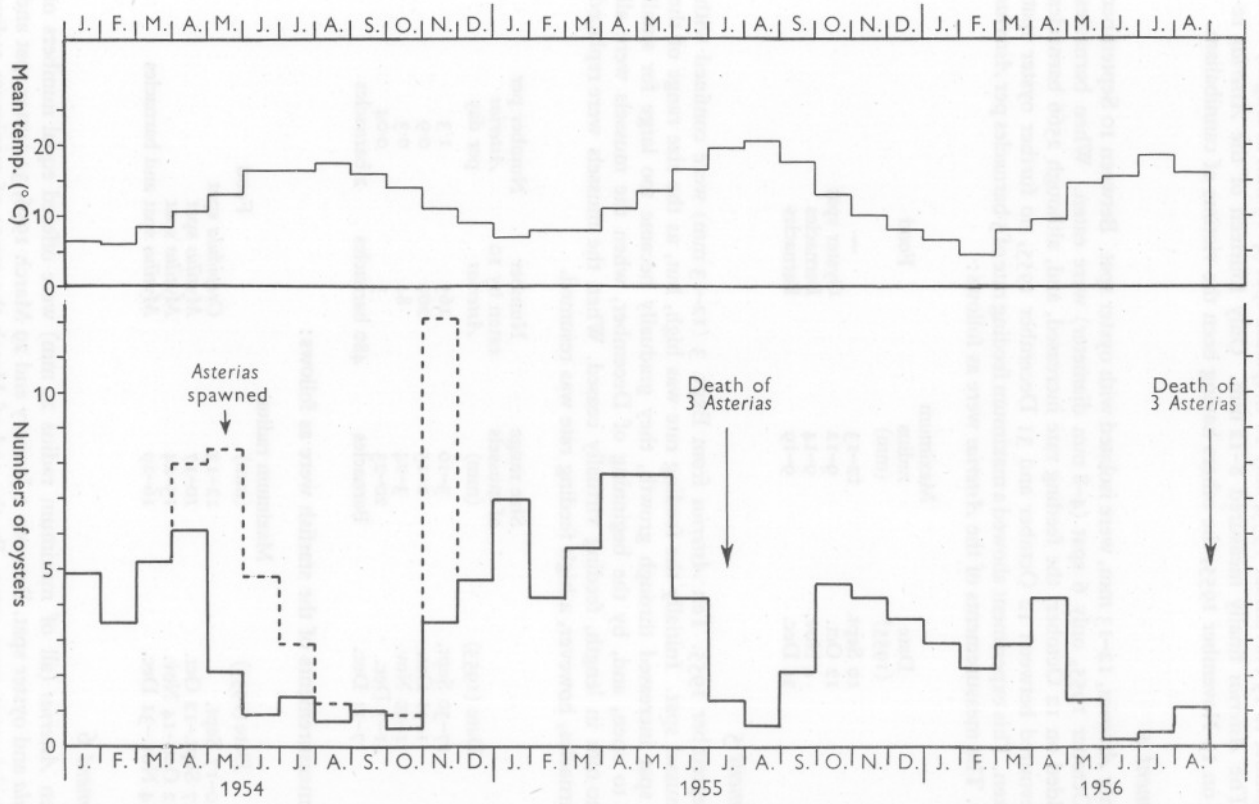


Fig. 4. Average numbers of adult oysters eaten per week by four large *Asterias* during each month from January 1954 to August 1956. From April to November 1954, *Crepidula* were offered as an alternative, and the numbers eaten in addition to oysters have been shown by a broken line. Mean monthly temperatures are also given.

Experiment 7

Five *Asterias* (maximum radius 20–30 mm) were confined with roughly equal quantities of barnacles and mussel spat. Between 26 September and 22 October 1956, 665 barnacles and 293 mussels were eaten; between 23 October and 19 November a further 262 barnacles and 636 mussels. Mussel spat occur infrequently on the Southward Laying. This experiment may provide an instance of starfish attacking, at first, familiar food, and then turning their attention to an unfamiliar alternative, which they evidently liked. Alternatively, food habits may change with growth.

Experiment 8

On 10 September 1955 a medium-sized *Solaster* (31 mm maximum radius) was confined with 20 *Asterias* (14–15 mm) and no other food. The *Solaster* needed from 10 September to 12 November 1955 to devour all the *Asterias*. During this time the size measurements of the starved *Asterias* decreased.

Experiment 9

On 10 September 1955 two small *Solaster* (maximum radius, 10–11 mm) were isolated with 20 *Asterias* (10–11 mm) and no other food. When this experiment was ended on 19 November, 12 *Asterias*. remained, though greatly decreased in size, and one *Solaster* had been eaten by the *Asterias*. The size-range of the starved *Asterias* decreased as follows: 10 September, 10–11 mm; 12 October, 8–11 mm; 14 November, 6–10 mm.

Experiment 10

The experiment described previously (Hancock, 1955, Expt. 1, p. 317), in which four large adult *Asterias* (maximum radius 140 mm) were fed on adult oysters, was continued to try to demonstrate changes in feeding rate at different times of the year. The results are shown in Fig. 4. They are slightly complicated by the addition of a number of *Crepidula* on 21 April 1954, and their removal on 13 November 1954. The numbers of *Crepidula* eaten are shown in Fig. 4, and can be seen to exceed the numbers of oysters eaten by the *Asterias*, even though the latter had been conditioned to feeding on oysters for several months. Spawning of the *Asterias* took place in the laboratory during May, and feeding reached a maximum in April–May of each year, but the rate dropped soon after spawning and reached a minimum in August during the period of highest water temperatures. Steady feeding took place throughout the winter, with a slight drop in feeding rate each February, usually corresponding with the lowest monthly average of mean daily temperatures. The optimum feeding temperature appears to be between 10 and 13° C. and occurs in April–May; above this temperature the feeding rate declines. It must be remembered, however, that the lowered feeding rate after April–May may have been associated with post-spawning effects.

Galtsoff & Loosanoff (1939) kept starfish (*Asterias forbesi*) in tanks in the United States, and found that during the pre-spawning period, from the end of May until July, at temperatures from 11·0 to 14·5° C., the majority were indifferent to food. Soon after the completion of spawning starfish became exceedingly voracious, and continued to be so until the onset of cold weather. With the vernal rise of temperature, starfish became more and more activated but ceased eating with the approach of the breeding period.

FIELD OBSERVATIONS

Throughout the surveys of the Southward Laying, records were kept of observations of feeding by *Asterias* and *Solaster*. *Asterias* was only occasionally taken when feeding, but the food of *Solaster*, which can ingest most food without pre-digesting it, was more easily recorded. *Asterias* was observed on four occasions devouring an oyster, and sixteen times eating *Crepidula*. The records of the food of *Solaster* were: *Asterias* 64, *Crepidula* 9, *Alcyonidium* 15, *Gibbula* 11, and the anemone *Diadumene* 7. The *Solaster* which were feeding on *Asterias* varied in size from 13 to 85 mm maximum radius, and it was not until late September 1955 that the incidence of feeding on *Asterias* became frequent, increasing to a maximum in March 1956. Before September *Solaster* was observed feeding mainly on other animals, this change no doubt being associated with the settlement of young *Asterias* on the offshore part of the Southward Laying inhabited by *Solaster*. Two *Solaster* (62 and 66 mm maximum radius) were found eating smaller ones of the same species. One *Solaster* of only 14 mm maximum radius was found to have enveloped a *Gibbula* of 10 mm shell diameter. Feeding on *Alcyonidium* was mostly confined to the summer months when this bryozoan was in the active phase. These results agree with the observations of Fulton (1895), who found arms of *Asterias* protruding from the mouths of many specimens of *Solaster* dredged on oyster beds in the Firth of Forth.

Adult *Asterias* taken in dredge hauls in the River Swale, Kent, in December 1956, were observed to be feeding both on adult mussels and *Crepidula* which existed together there in abundance.

PRACTICAL CONSIDERATIONS

The laboratory feeding experiments showed that young *Asterias* ate large numbers of barnacles and young mussels, on which they maintained a steady growth. Oyster spat and *Crepidula* spat were much less acceptable, and such a diet alone was inadequate for growth, with actual reduction in size often resulting. Subsequent growth of the prey under these conditions made it less liable to attack by *Asterias*. Smith (1940) found that the rate of growth of *A. vulgaris* in eastern Canada varied with the kind and abundance of food. Mussels provided a much more favourable food for growth than oysters.

The spatfall of oysters at the Southward Laying is rarely intense, and *Urosalpinx* regularly destroys nearly all those present (Hancock, 1954), so that as juveniles the starfish would normally not be a serious problem there. In fact some benefit must have resulted from the activities of the *Asterias* in keeping down the barnacles, which are the most important competitors of settling oysters for space and food (Waugh & Ansell, 1956). A study of the seasonal feeding rate of adult *Asterias* showed that the best time to inspect for damage to highly cultivated oyster grounds is in the spring of the year before

the starfish spawn. There has been no fresh evidence that *Asterias* is a serious pest of oysters under the conditions obtaining in Essex rivers, and both in the laboratory and in nature the starfish have continued to feed preferentially on competitors of the oyster.

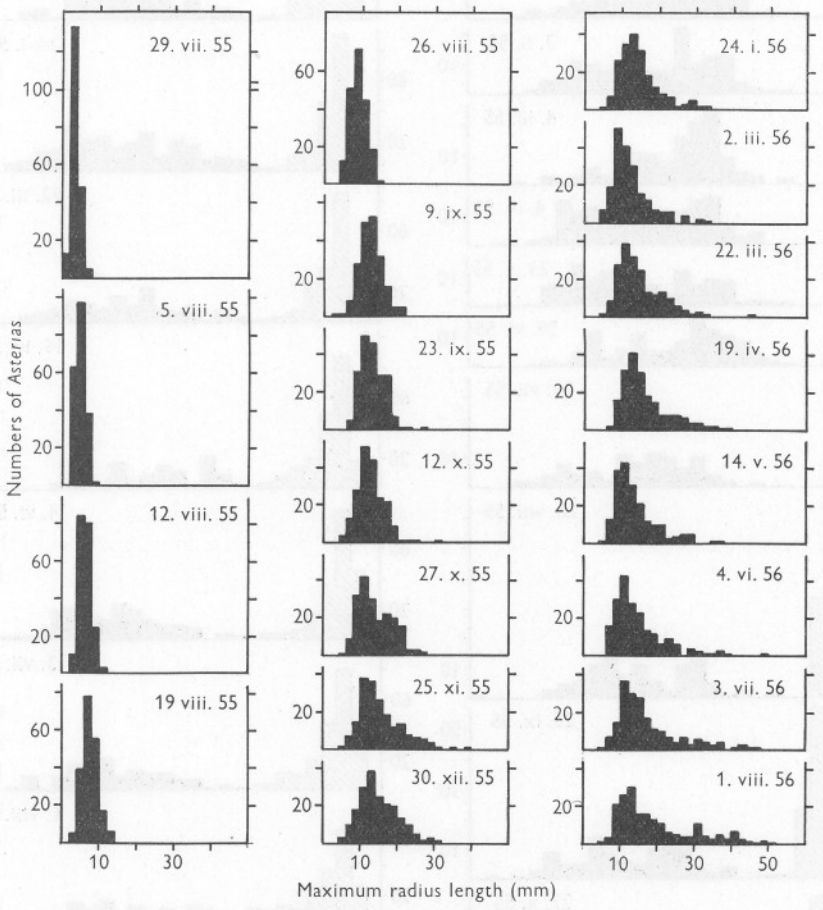


Fig. 5. Histograms showing the size distribution of young *Asterias* collected in dredge surveys from the Southward Laying 1955–56. Each sample was composed of 200 individuals. The radius lengths have been grouped at 2 mm intervals.

GROWTH

The study of population histograms does not give a clear indication of growth under natural conditions unless (1) settlement of any year group takes place over a restricted period, and (2) a large number of the form being studied settle in a particular year, so that the progress of this year group can be traced

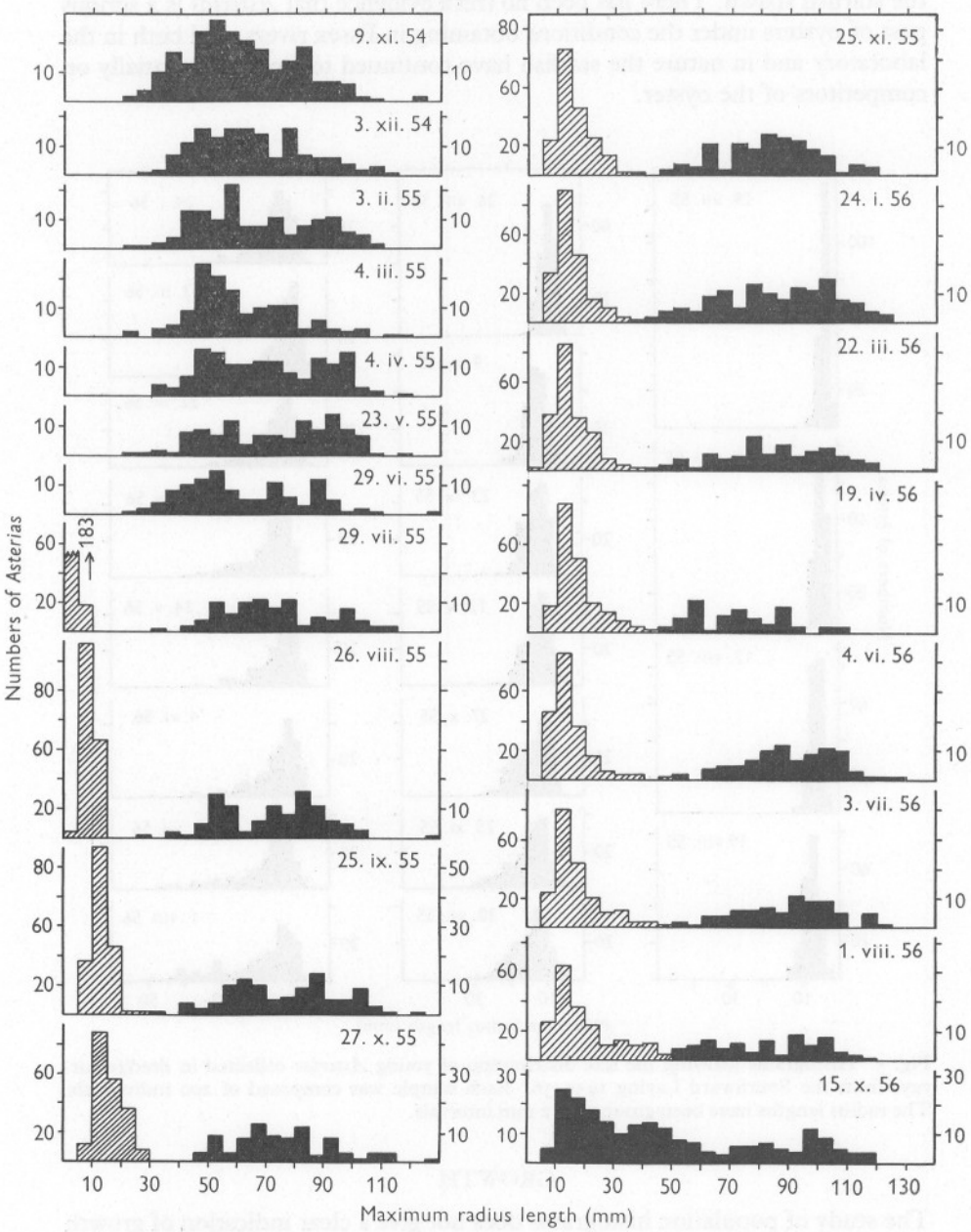


Fig. 6. Histograms showing the size distribution of young (shaded) and adult *Asterias* (blackened) collected in dredge surveys from the Southward Laying, 1954–56. Samples of 200 juveniles were measured, but all adult *Asterias* taken in the dredge surveys are shown. On 15 October 1956 all of both juveniles and adults taken were measured. The radius lengths have been grouped at 5 mm intervals, using different ordinate scales for adult and young starfish.

in consecutive histograms. It was fortunate that heavy settlements of both *Asterias* and *Solaster* occurred in 1955.

Histograms have been plotted at intervals of 2 mm for measurements of the maximum radius of arm to show the growth within the 1955 year group (Figs. 5, 7) and at 5 mm intervals to show the relationship of the year groups and their progress along the histograms (Figs. 6, 8). The *Asterias* population was sampled in two ways. First, the resident population was sampled,

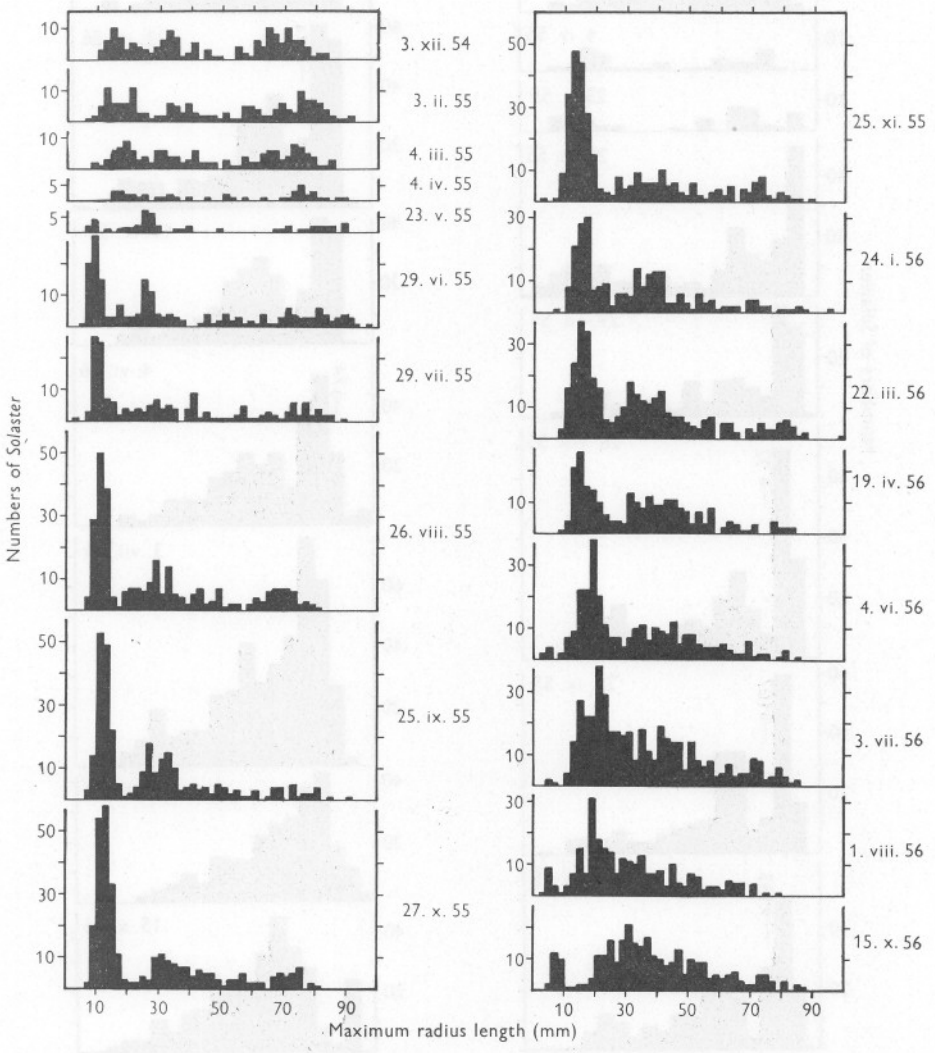


Fig. 7. Histograms showing the size distribution of *Solaster* collected in dredge surveys from the Southward Laying 1954–56. The radius lengths have been grouped at 2 mm intervals.

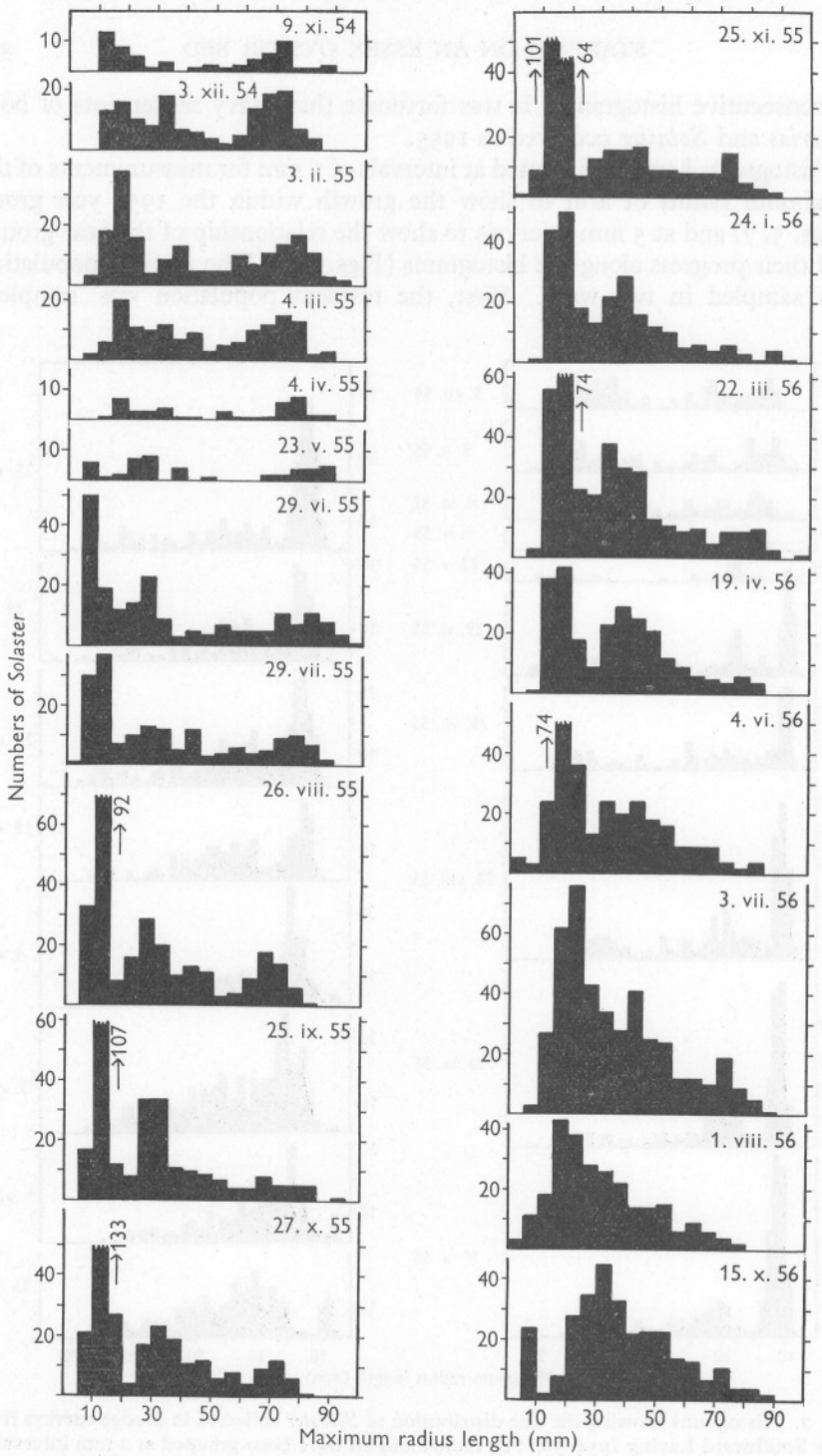


Fig. 8. Histograms showing the size distribution of *Solaster* collected in dredge surveys from the Southward Laying 1954–56. The radius lengths have been grouped at 5 mm intervals.

beginning on 9 November 1954, by measuring all *Asterias* collected in two dredge hauls over the stations examined on a particular date (Fig. 2). The settlement of 1955 0-group individuals was first noted on 29 July 1955, when the juveniles had a size range of 1–7 mm and could readily be distinguished from the older year groups in the population. Measurement of all of the enormous quantity of juveniles collected was impracticable, so that although the remainder of the population was measured as before, only a randomly selected sample of 0-group individuals from Station 2 was measured.

TABLE 3. GROWTH OF JUVENILE *ASTERIAS* AND *SOLASTER* AT SOUTHWARD LAYING, RIVER CROUCH

	Asterias			*Solaster*		
Date of collection	No. in sample	Mean length of sample (mm)	Standard error of mean	No. in sample	Mean length of sample (mm)	Standard error of mean
29. vi. 55	—	—	—	69	8·5	0·21
29. vii. 55	200	2·9	0·08	71	10·2	0·29
5. viii. 55	200	4·3	0·10	—	—	—
12. viii. 55	200	5·7	0·11	—	—	—
19. viii. 55	200	7·0	0·14	—	—	—
26. viii. 55	200	8·6	0·15	127	10·7	0·16
9. ix. 55	200	12·1	0·22	—	—	—
23. ix. 55	210	12·2	0·23	—	—	—
25. ix. 55	—	—	—	149	11·8	0·19
12. x. 55	200	12·1	0·27	—	—	—
27. x. 55	200	15·4	0·33	184	12·3	0·18
25. xi. 55	210	15·0	0·40	189	13·9	0·24
30. xii. 55	200	14·4	0·36	—	—	—
24. i. 56	246	14·2	0·34	114	15·8	0·33
2. iii. 56	241	11·8	0·32	—	—	—
22. iii. 56	473	14·3	0·26	160	15·8	0·28
19. iv. 56	278	15·9	0·38	105	16·6	0·40
14. v. 56	253	13·2	0·35	—	—	—
4. vi. 56	275	13·8	0·39	149	18·2	0·35
3. vii. 56	215	16·6	0·57	—	—	—
1. viii. 56	216	19·2	0·72	—	—	—

This sample was used to determine the standard error of the mean (Table 3). The measurements of only the first 200 individuals in each sample, however, were used for the comparative histograms (Figs. 5, 6). For this reason, in Fig. 6, the 0-group is shown on a different scale from that of the main population and is distinctly shaded. In fact, the 0-group *Asterias* represented a far larger proportion of the population than shown, and some idea of their density can be obtained by reference to Fig. 3. This method of subsampling was continued until 15 October 1956, when this year group had become so reduced that all the *Asterias* taken in the dredges could be measured. The numbers of young *Solaster* were never so great that they could not all be measured with the remainder of the population.

The mean size of each sample of 1955 0-group *Asterias* and *Solaster* (Table 3) has been plotted in fig. 9. *Solaster* showed a regular growth rate except between 24 January and 22 March 1956. The average growth between

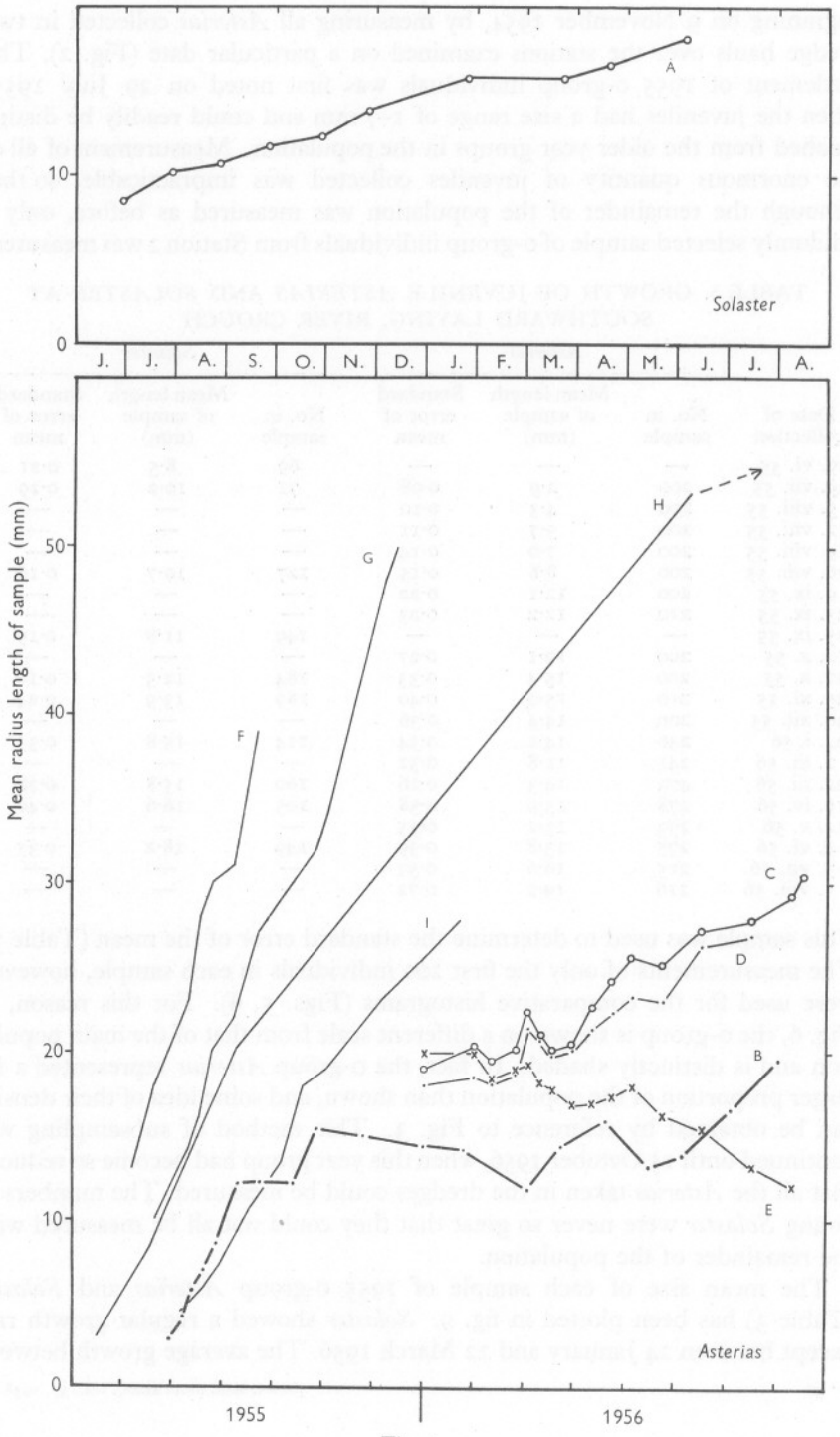

A
Solaster
J. J. A. S. O. N. D. J. F. M. A. M. J. J. A.
Mean radius length of sample (mm)
0
10
20
30
40
50
F
G
H
I
C
D
B
E
Asterias
1955
1956

Fig. 9

29 June 1955 and 4 June 1956 has been calculated as 0·028 mm per day, with a maximum rate of 0·056 mm per day between 27 October and 25 November 1955.

A 1956 settlement of *Solaster* was first observed on 4 June, but the juveniles were less abundant than in 1955, and on 15 October 1956 their mean size was only 6·8 mm, compared with 12·3 mm for the 1955 0-group on 27 October 1955. This may have been due to a later settlement in 1956, or to the negligible crop of *Asterias* in 1956, whose young form the main food of *Solaster*. It is possible to trace the progression of the 1954 0-group *Solaster* from November 1954. A comparison of the year groups on 3 February 1955 and 24 January 1956 (Fig. 8), shows the first two modes in a similar position, indicating that in 1954 and 1955 similar conditions of growth and settlement prevailed. On 4 June, when the 1956 settlement was first observed, the 1955 set of *Solaster*, at just over 1 year old, had a mean size of 18·1 mm while the 1954 set averaged about 40 mm. From Fig. 8, it appears that in October the modes of the first few year groups are separated by regular intervals of about 20 mm; they occurred at about 10, 30–35, 50, and 70–75 mm respectively. Subsequent year groups were not clearly defined.

To state precisely the growth pattern of *Asterias* on the Southward Laying is more difficult. Newly settled juveniles were first detected in 1955 on 29 July at a mean radius of 2·9 mm. Regular rapid growth, averaging 0·22 mm per day, was recorded until 9 September (mean radius 12·1 mm), but then a check occurred. Mean size increased again between 12 and 27 October, but then decreased sharply until 2 March 1956. Reference to Fig. 5 shows that the decrease in mean size resulted from two processes; first, the range of size was increased by the slight growth of a small proportion of larger individuals, and, secondly, the mean size decreased. This is less surprising than may at first appear, in view of the shrinkage in radius length of starving *Asterias* noted in a previous section (see also Vevers, 1949). It is known that very small food organisms, e.g. barnacles, are necessary for the normal feeding and growth of young starfish. It is believed that the shortage of natural food was responsible for the enormous decline in numbers of young *Asterias* (Fig. 3) and for the reduction in the mean sizes of samples by actual shrinkage of individuals.

Growth of part of the juvenile population continued steadily from 2 March

Legend to Fig. 9

Fig. 9. Graphs showing the growth of young *Asterias* and *Solaster*. A: mean radius lengths of samples of young *Solaster* from the Southward Laying. B: mean radius lengths of samples of young *Asterias* from the Southward Laying (see Table 3). C–E: mean radius lengths of young *Asterias* kept well fed (C, D) and starved (E) in the laboratory (see Table 4). The results of other workers are given for comparison, showing the correct calendar months for their readings. F, G: radius lengths of two typical well-fed individuals of *Asterias*, B8 and B9, kept in the laboratory by Vevers (1949). H: average radius of the arms of an *Asterias* kept in the laboratory by Bull (1934). I: mean radius lengths of samples of *Asterias* from Millport measured by Barnes & Powell (1951).

to 19 April 1956, while the mode still remained at 10–15 mm (Fig. 5). Then, after another setback in mean size, growth of juveniles continued to give the bimodal size-distribution shown for 15 October 1956 in Fig. 6. The first mode, at 10–15 mm, lies in exactly the same position as it was a year previously on 27 October 1955. Unless one knew that 1956 settlement of *Asterias* had failed, the bimodal year group shown on the October 1956 histogram might be attributed to two normal year groups, instead of to the effect of abnormal growth conditions.

Bull (1934) showed that in three *Asterias* kept in the laboratory, first spawning occurred simultaneously when two were 5 years old and the third was 6 years old. Their average size was 114 mm. It seems unlikely therefore that the checks in growth observed during the first 2 years of the present observations were associated with spawning. Galtsoff & Loosanoff (1939), however, found that in America young *Asterias forbesi* which grew rapidly were sexually mature by the end of the first year, whereas small, slowly growing animals did not mature until 2 years of age.

TABLE 4. GROWTH OF WELL-FED AND STARVED JUVENILE *ASTERIAS* IN THE LABORATORY

(12 *Asterias* in each group.)

	Starved *Asterias*		Well fed *Asterias*			
Date of measurement	Mean size of group	Range	Mean size of group	Range	Mean size of group	Range
1. i. 56	20	20	19	19	18	18
1. ii. 56	20	18–22	20·3	18–26	18·5	17–20
11. ii. 56	18·3	16–21	19·5	17–25	18·2	17–20
25. ii. 56	19·0	16–22	20·2	18–25	18·8	17–23
3. iii. 56	19·3	16–21	22·4	20–25	21·5	20–24
10. iii. 56	18·2	16–20	21·0	19–24	20·8	17–23
17. iii. 56	17·8	15–19	20·1	18–24	19·8	17–22
29. iii. 56	16·8	14–19	20·4	19–22	20·2	17–23
11. iv. 56	17·0	14–19	22·7	21–24*	21·4	15–25
23. iv. 56	17·4	16–19*	24·3	22–26	22·3	19–26
5. v. 56	18·0	17–20	25·7	23–27*	23·3	18–27
23. v. 56	16·2	15–18	25·2	23–28	23·0	20–28
16. vi. 56	15·5	13–18	27·3	25–29	26·3	21–32*
16. vii. 56	13·2	11–15	27·8	23–31	26·9	21–33**
10. viii. 56	12·0	11–14	29·3	24–33	—	—
17. viii. 56	—	—	30·5	28–33	—	—

* 1 *Asterias* died.

Experiments were set up to compare the growth of regularly fed and starved starfish. On 1 January 1956, a group of twelve 20 mm *Asterias* was confined with oyster and *Crepidula* spat; from previous experience, one would regard these as having virtually starved. Separate groups of twelve 19 mm and twelve 18 mm *Asterias* were confined with an excess of live barnacles. The starfish were measured regularly, along a selected radius, until July–August 1956, when the original 20 mm group had reached 11–14 mm, the 19 mm

group 28–33 mm, and the 18 mm. group 21–33 mm (Table 4). The mean sizes of each group on the dates of measurement are shown in Fig. 9, and it is interesting to note that decreases in mean size were recorded, even for regularly fed *Asterias*, in February, March and May 1956. A sharp decrease, followed by an increase in size, was recorded in February among both the starved 20 mm *Asterias* in the laboratory and the natural population at the Southward Laying; this corresponded with the minimum water temperatures recorded in the winter of 1955–56. The May decrease in mean size of well-fed laboratory individuals was evident in the Southward Laying population, and was also shown to a certain extent by a slightly accelerated decrease in the size of starved laboratory specimens. The author is indebted to Mr S. J. Holt of F.A.O., Rome, who, from an analysis of the growth data obtained from these experiments, was able to demonstrate the general consistency between observations from the field and the laboratory. He concluded that the concurrent rearing of two groups of animals, one fed at a predetermined level and one starved, is a useful method of studying growth parameters and their relation to environmental influences. The details of this analysis will be presented in a separate paper. In the natural population it appears therefore that the gradual decrease in mean size was due to starvation, and the final increase in mean size (14 May–1 August 1956) can be related to maximum summer settlement of barnacles in the presence of greatly depleted numbers of juvenile *Asterias*.

Bull (1934) reared three specimens of *Asterias* from newly settled young to sexual maturity in laboratory tanks at Cullercoats. He recorded the average radius, from the tip of the arm to the centre of the disc, of five arms, and obtained regular growth curves. The three starfish average 42 mm in the June after settling and 114 mm at the time of first spawning. Vevers (1949) followed the growth of individual *Asterias* in the laboratory and Barnes & Powell (1951) recorded a similar and quite rapid growth rate of young *Asterias* on a barnacle-covered raft at Millport. Graphs prepared from some of their figures are included in Fig. 9 for comparison with the present observations. The growth rate shown by the Southward Laying juveniles during the period soon after their settlement, and from June to August 1956, after reduction in numbers by competition had allowed the survivors to grow normally, was very similar to earlier records. Smith (1940) found that where high population densities of *Asterias vulgaris* Verrill occurred in eastern Canada, the size of individuals tended to be smaller. The growth of well fed individuals in our laboratory approached that found by Bull (1934) and Vevers (1949), but these also had been undersized for their age when transferred to laboratory tanks on 1 January 1956. Orton & Fraser (1930) examined a population of *Asterias* on a buoy near Liverpool: Vevers (1949) converted their measurements of diameter to radius sizes, and concluded that the Mersey population had grown considerably more slowly than the individuals in his laboratory experiments.

The use of Nile Blue Sulphate for marking starfish in the field suggested an application for studying growth increments. Five *Asterias* from each group used to study growth in the laboratory were dyed with Nile Blue Sulphate. Their growth during the period 11 February–17 August 1956 was not significantly different from that of undyed starfish, indicating that dyeing did not interfere with their normal growth processes. Eventually white undyed tips were produced on the dyed radii, but the relationship between the undyed and total increments was somewhat variable. The following typical examples showed that up to half the total increment was undyed, suggesting, not very conclusively, that intercalary and terminal growth take place in equal proportions:

Original radius length (mm)	Total increment (mm)	Undyed increment (mm)
19	12	6
19	12	3
19	10	5
18	7	3
18	6	3

It is interesting to note that the stomach pouches of *Solaster*, which had eaten dyed *Asterias*, became coloured blue, giving a useful confirmation of their feeding behaviour.

SUMMARY

Observations on the distribution of adult starfish (*Asterias rubens* L. and *Solaster papposus* (L.)) on an oyster laying in the River Crouch have revealed no marked changes in their numbers or position throughout a period of nearly two years. Slight movement of *Asterias* was recorded, not inshore on to cultivated oyster ground but offshore to more derelict ground infested by slipper limpets (*Crepidula fornicata* Say). This offshore movement may have resulted from the clearing by dredging of large quantities of slipper limpets from the inshore region, necessitating a wider search for food by *Asterias*.

Young *Asterias* settled in 1955 in maximum density inshore on cultivated oyster ground, but some settlement also occurred farther offshore in the area inhabited by *Solaster*. Young *Solaster* settled mainly in mid-river in the region of greatest abundance of adults. Both young and adult *Solaster* have been observed devouring *Asterias*, particularly juveniles, while on a lesser scale *Asterias* may eat young *Solaster*. These facts, coupled with the discrete settling behaviour of *Solaster* are believed to be responsible for the very slight overlapping of the two adult populations.

The very dense population of *Asterias* which settled in 1955 on this oyster ground in the River Crouch has decreased steadily due to the combined effects of prolonged shortage of food, cannibalism and predation by *Solaster*. The dense population of barnacles formerly present on this ground has disappeared and none were seen in 1956. There was no settlement of *Asterias* in that year.

Young *Solaster* showed a steady growth rate, but *Asterias* remained stunted until great reduction of the population allowed normal growth to be resumed. Feeding experiments showed that young *Asterias* grew well on barnacles and young mussels, which they ate readily, but young oysters and *Crepidula* were less acceptable and inadequate for normal growth.

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GROWTH OF OYSTERS (*OSTREA EDULIS* L.)

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(Text-figs. 1–11)

Although the biology of the oyster *Ostrea edulis* has been well studied, its growth has received little attention. Orton (1928) worked on the populations in the Rivers Fal and Blackwater, but his conclusions have not been supported by Havinga (1928) or Korringa (1955), while America studies on *Crassostrea virginica* have given further evidence of the need for new investigations.

As the Conway breeding experiments necessitate the maintenance of a small oysterage at Tal-y-foel, Anglesey, stocked with oysters of known age and homogeneous origin, a good opportunity was available for studying the growth of marked or isolated oysters. This paper records some observations on the seasonal and annual patterns and on the effect of tidal exposure.

CONDITIONS AND EXPERIMENTAL METHODS

The position of the oysterage is shown in Fig. 1. The beach above mid-tide level is of steeply sloping shingle; but below this level the slope is much more gradual and the beach varies from mud with varying proportions of sand to small shingle bound together by mud and sand. Near Tal-y-foel pier there is a small, exploited, mussel bed; while the oyster grounds are occasionally picked over for periwinkles. The lower part of the shore, where the oysters are kept, is protected from rough weather by a sand bank, Traeth Gwyllt, separating the Tal-y-foel inlet from the main channel. A tidal current of 1–2 knots flows parallel with the shore, associated with a tidal range of about 17 ft. at springs and 10 ft. at neaps.

Salinity samples were taken only at low water springs—the time of lowest salinity—as, when the tide is up, the local drainage water from small streams has less influence. Most of the samples (Fig. 2) were of a salinity of 31‰ or more; lower records were scattered roughly at random throughout the year, and were probably associated with recent heavy rain which, as consecutive samples show, has no lasting effect.

Water temperature was recorded by a thermograph for 17 months. From these records it was found that the mean monthly water temperature could be estimated from the mean monthly air temperature at Valley, 13 miles to the north-west, as published in the Monthly Weather Report of the Meteorological Office (Fig. 3). The regression calculated from this data allows the

mean water temperature at the oysterage to be estimated with an error of less than 0·5° C. For consistency, all the mean temperatures quoted in this paper are calculated from the Valley air temperatures using the curve shown in Fig. 3.

Observations on the position of low-water mark on a graduated staff showed that there was a close correlation between the level to which a given tide fell at Tal-y-foel and the level to which the same tide fell in Holyhead Docks (Fig. 4). As a tidal recorder was in continuous use at Holyhead, it was possible to calculate the number of times to which the tide fell to certain levels at Tal-y-foel in a given period. The amount of exposure to the air of

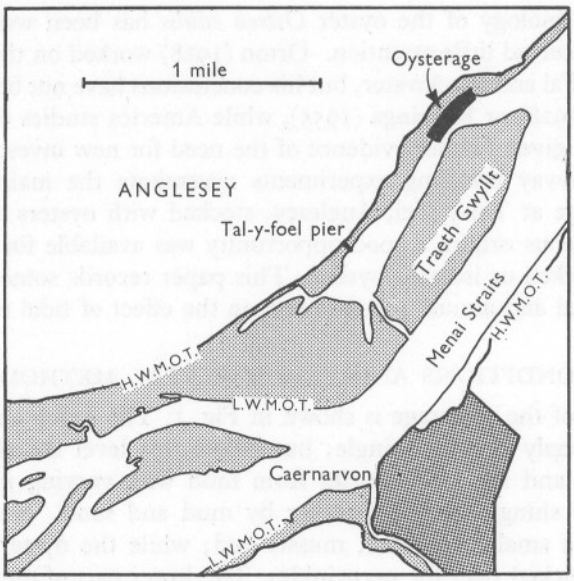

Fig. 1. Map showing the position of the oysterage. The sand banks, exposed at low tide, are lightly stippled.

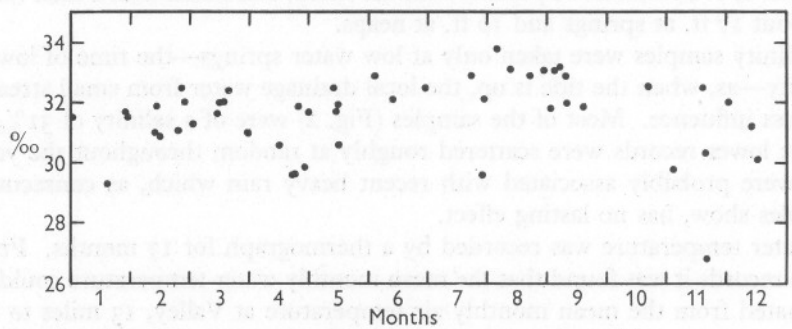

Fig. 2. Salinity of the water at low water of spring tides at the oysterage. The data covers the period December 1951–November 1953.

various levels on the shore by tides of different heights was determined by setting up a continuously recording tide gauge for a period on the pier at Tal-y-foel, the instrument being calibrated in terms of levels at the oysterage. From these values, combined with the data on the frequency to which the tide fell to different levels, a tidal exposure curve for that part of the shore used for the oyster experiments has been calculated (Fig. 5).

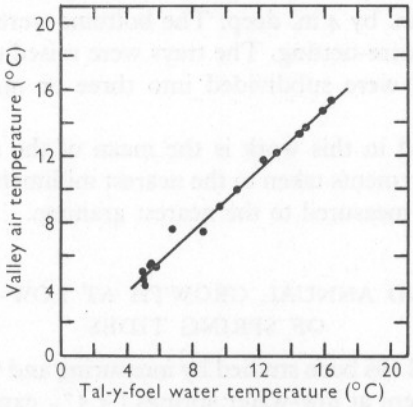

Fig. 3. The relation between the mean monthly air temperature at Valley, Anglesey, and the mean monthly water temperature at Tal-y-foel. The line drawn is the regression giving the best estimate of the water temperature from the air temperature.

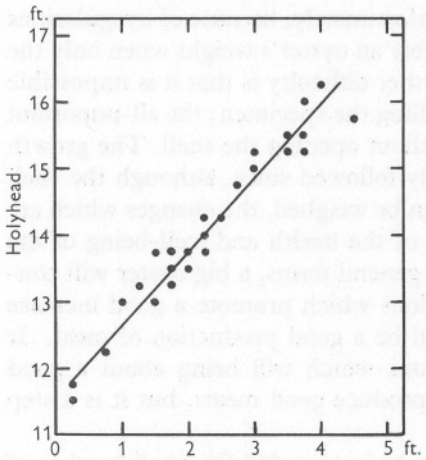

Fig. 4

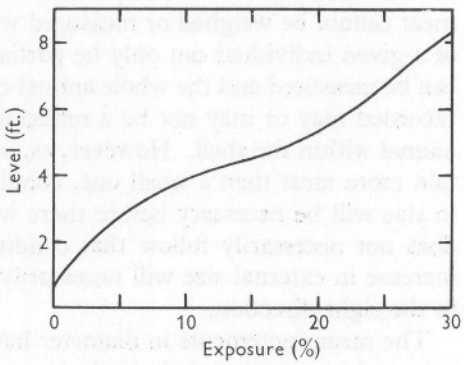

Fig. 5

Fig. 4. The relation between the height of low-water springs at Holyhead and Tal-y-foel. The line drawn is the regression giving the best estimate of the height of tide at Tal-y-foel.

Fig. 5. The percentage of the time for which the lower levels of the shore at Tal-y-foel are exposed.

The general treatment of spat and older oysters in trays was that described and illustrated by Cole (1938). The oysters are first brought to the oysterage when 1–2 months old, attached to earthenware tiles coated with a lime mortar. The tiles are wired together in bundles of ten and stood on racks at low-water mark. When the spat are about 12 months old they are stripped off the tiles and kept in wooden trays with wire tops and bottoms.

The trays in which most of the growth observations were made measure 5 ft. 4 in. by 3 ft. 0 in. by 4 in. deep. The bottoms were of $\frac{1}{2}$ in. woven wire and the top of $\frac{1}{2}$ in. wire-netting. The trays were raised on posts about 18 in. above the mud and were subdivided into three or nine compartments as required.

The diameter used in this work is the mean of the antero-posterior and dorsi-ventral measurements taken to the nearest millimetre below. The weight, when recorded, was measured to the nearest gramme.

SEASONAL AND ANNUAL GROWTH AT LOW-WATER MARK OF SPRING TIDES

Growth at Tal-y-foel has been studied by measuring and weighing at intervals, samples of oysters kept at low-water springs ($< 5\%$ exposure). In some experiments the growth of marked individuals has been followed, and in others the mean increase in size or weight of groups has been recorded. While weight is a more useful parameter of growth than a linear measurement, it is not the easiest to measure in the field. Unfortunately, because of irregularities in shape, it is impossible to estimate reliably an oyster's weight when only the mean diameter has been recorded. A further difficulty is that it is impossible to determine size satisfactorily without killing the specimen; the all-important meat cannot be weighed or measured without opening the shell. The growth of a given individual can only be partially followed since, although the shell can be measured and the whole animal can be weighed, the changes which are recorded may or may not be a reflexion of the health and well-being of the animal within the shell. However, as, in general terms, a big oyster will contain more meat than a small one, conditions which promote a good increase in size will be necessary before there will be a good production of meat. It does not necessarily follow that conditions which will bring about a good increase in external size will necessarily produce good meats, but it is a step in the right direction.

The mean increments in diameter have been recorded for small batches of oysters for various periods in the years 1945, 1952, 1953, and 1956 (Fig. 6). So as to give a satisfactory standard of comparison between periods of unequal length, the recorded increment for each period has been converted to the mean increment in 30 days. In general there was little or no growth between the beginning of November and the end of March, and, in fact, the diameter

and weight usually decreased slightly in this period, due to the abrasion of the shell by winter storms. This happened both to oysters laid on the ground and to those in trays, as the following example, which gives the mean weight and mean length of two samples of 200 18-month old oysters, shows:

	In trays		Laid on ground	
	Weight (g)	Length (mm)	Weight (g)	Length (mm)
29. xi. 44	10·8	46·9	10·9	46·6
14. iii. 45	10·3	45·9	10·2	45·3
Decrease	0·5	1·0	0·7	1·3

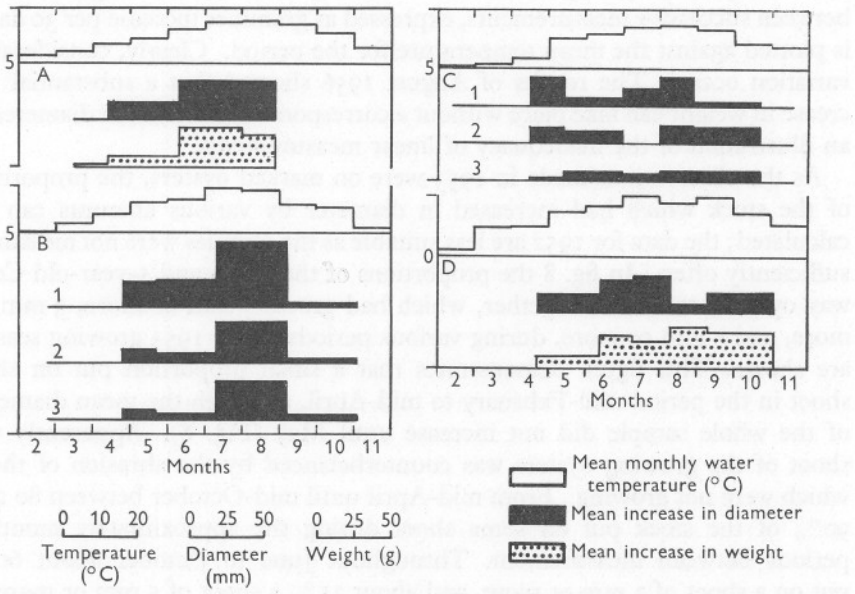

Fig. 6. Seasonal growth at Tal-y-foel. The increment, either mean diameter or mean weight, in the various periods has been calculated as the mean for 30 days. The base-line for all graphs is 0 except for three of the water temperatures where it is 5°. Vertical scales given at bottom left. A. 1945. Growth in mean diameter and weight of 1½-year-old oysters. B. 1952. Growth in mean diameter only of: (1) 1½-year-old oysters; (2) 2½-year-old oysters; (3) 3½-year-old oysters. C. 1953. Growth in mean diameter only of: (1) 2½-year-old oysters; (2) 3½-year-old oysters; (3) 4½-year-old oysters. D. 1956. Growth in mean diameter and weight of 1½-year-old oysters.

In none of three years when observation began in the winter months was growth in mean diameter found in the April samples, although there was a slight increase in weight in 1954. In the samples taken in May growth was general—the mean temperature had risen to about 12° C. Growth continued, the rate varying in different years, until October or early November. In September 1952 the temperature dropped rather sharply to 12·7° C, and little subsequent growth occurred. In 1953 and 1956 when temperatures were

higher, with means of 15·8° and 16·0° C in September, and 12·0° and 11·9° C in October respectively, growth continued into October. These results suggest that the beginning and end of a season's growth, both in diameter and total weight, is controlled by temperature. Once the critical limits, about 10°–12° C are passed, other factors, of which food is probably the most important, determines the growth rate. Andreu & Arté (1956) showed that the growth of young oysters in the Ria de Vigo was more closely related to the abundance of small diatoms than to the temperature which was sufficiently high for growth to continue throughout the year. The relationship between water temperature and growth is shown in Fig. 7, where the weight increase between successive measurements, expressed as grammes increase per 30 days, is plotted against the mean temperature for the period. Clearly, considerable variation occurs. The results of August 1956 showed that a substantial increase in weight can take place without a corresponding increase in diameter—an illustration of the inadequacy of linear measurements.

As the observations made in 1953 were on marked oysters, the proportion of the stock which had increased in diameter by various amounts can be calculated; the data for 1952 are less suitable as the samples were not measured sufficiently often. In fig. 8 the proportions of the 3-, 4- and 5-year-old Conway oysters, combined together, which had grown 1 mm or more, 3 mm or more, and 5 mm or more, during various periods in the 1953 growing season are shown. This figure demonstrates that a small proportion put on shell shoot in the period mid-February to mid-April, although the mean diameter of the whole sample did not increase until May (Fig. 6). Apparently the shoot of the growing oysters was counterbalanced by the abrasion of those which were not growing. From mid-April until mid-October between 80 and 90% of the stock put on some shoot during the approximately monthly periods between measurement. Throughout June to October about 60% put on a shoot of 3 mm or more, and about 35% a shoot of 5 mm or more in each period of about a month. The variations from period to period are largely due to differences in the intervals between measurements.

These results differ in some respects from those obtained by Orton (1928) from a study of growth in the Rivers Fal and Blackwater in the years 1926 and 1927. Orton found that growth was confined to temperatures above about 10° C, but believed that, both in the river Fal and the River Blackwater, there were two growing periods, one in the spring and one in the autumn, while in the summer months, June, July and August, there was no increase in diameter. In the Menai Straits, however, the proportion of oysters showing an increase in diameter (Fig. 7) rises during the spring and is maintained at an approximately constant level throughout the summer and drops again in the autumn; there was no period in the summer when growth in diameter did not occur.

Orton suggested that the cessation of growth in the summer was due to the

energies of the Fal and Blackwater oysters being taken up by spawning activity, but, according to Korringa (1955), oysters are able to continue growing at a normal rate during the spawning period, provided that feeding conditions are satisfactory. An oyster which was weighed in water daily by Havinga (1928) spawned and brooded its larvae during the period of observation.

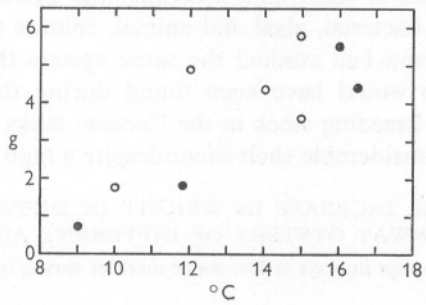

Fig. 7. The relation between mean water temperature and increment in weight in 1½-year-old Conway oysters for various periods in 1945 (solid circles) and 1956 (open circles).

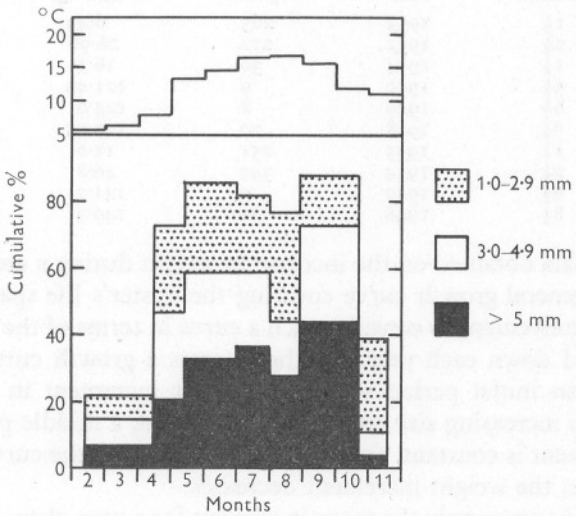

Fig. 8. The percentage of oysters showing shell shoots of varying size in different periods of 1953. The shell shoot has been taken as the maximum increase in either breadth or length.

Growth was retarded for 13 days but stopped only for 4 days. As both the Blackwater and the Fal produce large fat oysters, it is difficult to believe that food is inadequate for simultaneous growth and spawning. Orton, examining at weekly intervals, samples of oysters for the presence or absence of a shoot of new shell growth, decided that few had any shoot in the summer months and concluded that they were not growing. In my experience, the new shoot at

the beginning of the year is readily seen, because, during the winter months, the shell becomes uniformly coloured, and the edge abraded, so that when growth starts the new clean white or transparent shell is very readily visible. In the summer, however, two factors disguise the new shoot: the more rapid growth of shell causes the new shoot to harden much more quickly so that less new flexible shell is seen, and, secondly, the increased growth of encrusting organisms, bacterial, algal and animal, colours the shell uniformly. I suggest that if Orton had studied the same oysters throughout the year, considerable growth would have been found during the summer months. The oysters kept as breeding stock in the Conway tanks during the summer months produce a considerable shell shoot despite a high rate of spawning.

TABLE 1. ANNUAL INCREASE IN WEIGHT IN DIFFERENT YEARS OF CONWAY OYSTERS OF DIFFERENT AGES

The oysters were kept in trays at low water mark of spring tides at Tal-y-foel.

Year of observation	Age at beginning of growing season (Years)	Year class	No. of oysters	Initial mean weight (g)	Increment (g)
1955	$1\frac{1}{2}$	1953	265	6·43	17·19
1955	$2\frac{1}{2}$	1952	272	26·96	17·24
1956	$1\frac{1}{2}$	1954	30	16·7	25·3
1956	$5\frac{1}{2}$	1950	9	121·42	19·80
1956	$6\frac{1}{2}$	1949	8	124·0	8·0
1956	$7\frac{1}{2}$	1948	20	129·05	13·65
1957	$1\frac{1}{2}$	1955	251	12·6	25·50
1957	$2\frac{1}{2}$	1954	342	46·8	22·92
1957	$6\frac{1}{2}$	1950	9	141·2	23·5
1957	$8\frac{1}{2}$	1948	20	140·3	20·3

From the data obtained on the increase in weight during a season's growth (Table 1), a general growth curve covering the oyster's life span can be suggested. It is convenient to consider such a curve in terms of the actual weight increment laid down each year. In these terms a growth curve is made of three parts: an initial period when the weight increment in a given time increases with increasing size and age of the animal, a middle part where the weight increment is constant, and a third part where, as the curve approaches the asymptote, the weight increment decreases.

To determine accurately the mean increment for a year-class, it is necessary to work with very large samples since any year-class is made up of fast, average and slow growing oysters, a point demonstrated by some data obtained in 1957. At the beginning of the growing season random samples of two year classes, 1955 and 1954, of Conway oysters were collected and the oysters, after being assigned to 4 g weight-groups, were planted in separate tray compartments. At the end of the growing season the mean weight increment per oyster was obtained for each group. Fig. 9, plotted from this data, shows that the larger oysters of a year class have bigger increments than the smaller ones.

Since the oysters were of the same age, differences in initial size must have resulted from more rapid growth which was clearly continued into the experimental period. After several years growth these differences result in a considerable range of weights among any 1-year-group. For example, at the end of 1957, a sample of twenty $8\frac{1}{2}$-year-old oysters, which had been kept continuously in a cage, had individual weights varying from 91 to 235 g.

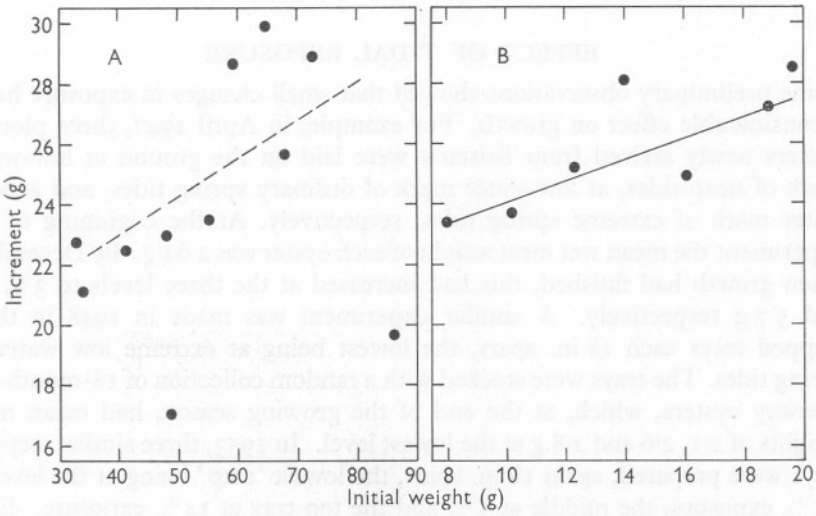

Fig. 9. The weight increment in samples of oysters of different initial weight but the same age during the 1957 growing season. (A) Oysters $3\frac{1}{2}$ years old at the beginning of the growing season. Trend line fitted by eye. (B) Oysters $2\frac{1}{2}$ years old at the beginning of the growing season. The line drawn is the regression giving the best estimate of the increment.

If these differences in growth rate are due, at least in part, to genetic factors, they provide a basis for selective breeding work. The existence of such differences does, however, show that a reliable average growth rate can only be obtained from very large samples.

During the first growing season after settlement, the spat, which weighed around 1–2 g at the beginning, increased in mean weight by 5–15 g, according to the year, so that at the end of this season (when $1\frac{1}{2}$ years old) the mean weight varied from 6 to 16 g. In 1955 and 1957 there was an approximately equal weight increment in each year among oysters in their second and third growing seasons. The increment was larger than that occurring in younger oysters. This conclusion was confirmed (see below) during a study of growth at different levels on the shore. It is clear, therefore, that the change from an increasing size of weight increment with age to a constant increment irrespective of age occurs at about $1\frac{1}{2}$ year old—at the end of the growing season following that in which settlement occurs.

The age at which the size of the increment begins to decline has not been determined because of the scarcity of older oysters of known age. The data for 1956 suggested that a decrease might have started in oysters of $5\frac{1}{2}$–$7\frac{1}{2}$ years old, but this was contradicted by the 1957 data when oysters of $6\frac{1}{2}$ and $8\frac{1}{2}$ years old increased by approximately the same amount as those $1\frac{1}{2}$ and $2\frac{1}{2}$ years old. It may be reasonable to assume that in any 1 year oysters from $1\frac{1}{2}$ years old to at least 5 or 6 years old increase in weight by equal amounts.

EFFECT OF TIDAL EXPOSURE

Some preliminary observations showed that small changes in exposure had a a considerable effect on growth. For example, in April 1947, three plots of oysters newly arrived from Brittany were laid on the ground at low-water mark of neap tides, at low-water mark of ordinary spring tides, and at low-water mark of extreme spring tides, respectively. At the beginning of the experiment the mean wet meat weight of each oyster was 2·62 g. By December, when growth had finished, this had increased at the three levels to 3·6, 4·0 and 5·7 g respectively. A similar experiment was made in 1948 in three stepped trays each 18 in. apart, the lowest being at extreme low water of spring tides. The trays were stocked with a random collection of 18-month-old Conway oysters, which, at the end of the growing season, had mean meat weights of 2·1, 2·6 and 2·8 g at the lowest level. In 1953, three similar stepped trays were prepared, again 18 in. apart, the lowest 'step' being at the level of 1·5% exposure, the middle at 5% and the top tray at 14% exposure. Each tray was stocked with fifteen individually marked Conway oysters, half of them being 2-year-old and the rest 3-year-old; their mean diameters were recorded at intervals. The results, shown in the table below, show little difference between the 1·5% and the 5% exposure level, but at the 14% exposure level growth was much reduced:

	1949 year-group			1950 year-group		
Exposure	1·5%	5%	14%	1·5%	5%	14%
Diameter—March (mm)	70	67	66	62	63	67
Diameter—November (mm)	83	78	73	81	83	74
Increase (mm)	13	11	7	19	20	7

The data, when plotted, suggest that growth would have stopped at about 25–30% exposure. The amounts of growth made during different parts of the season varied similarly at all levels.

In 1955 a more detailed investigation was made. Six identical trays were erected individually 1 ft. above the level of the mud at positions on the shore ranging from 1 to 23% exposure. A further two trays were erected on much longer posts in order to compare the growth of oysters at the same tidal level but at different distances above the mud. Each tray was stocked with 100 1-year-old and 100 2-year-old Conway oysters; the two age-groups were

kept separate. The diameters and weights of all oysters were recorded in April and October.

The results showed (Fig. 10) that growth was sensitively related to the percentage exposure to the air. Although the point of no growth was not quite reached, extrapolation suggests that it lay at the tidal level of about

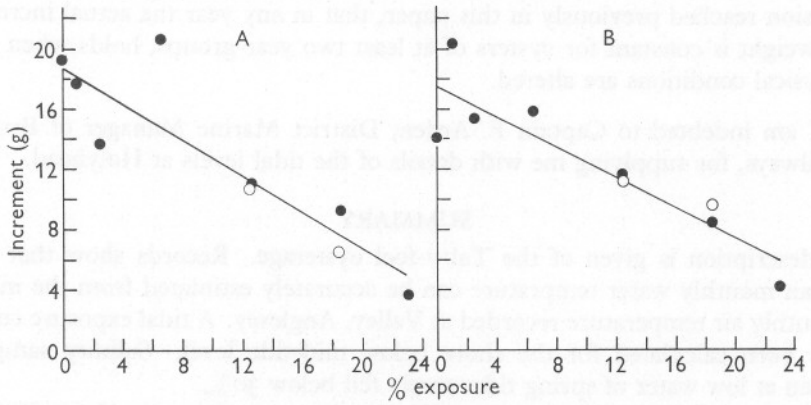

Fig. 10. The weight increment in 1955 of samples of 100 oysters exposed at different levels on the shore. Solid circles—trays standing about 18 in. above the mud. Open circles—trays standing about 4 ft. above the mud. (A) $2\frac{1}{2}$-year-old oysters. (B) $1\frac{1}{2}$-year-old oysters.

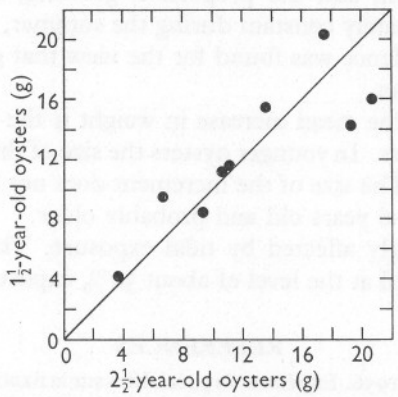

Fig. 11. A comparison of the weight increase of oysters of two age-groups, both exposed at different levels on the shore. The line drawn is that of equal increment for each age-group.

30% exposure, which agrees with the estimate from the 1953 experiment. If it is a simple relationship between growth and exposure, the data suggests that about three-quarters of the feeding activity is devoted to basal metabolism and the elaboration of reproductive products, while about one quarter is devoted to growth.

The ratio of the shell weight to the meat weight was found to be approximately the same in samples examined from the different trays. During the experimental period of 6 months no observable systematic tendency towards the development of relatively heavier shells was discernable at any level.

It is noteworthy that at each level the mean increase in weight was the same for both the 2- and 3-year-old oysters (Fig. 11). Apparently the conclusion reached previously in this paper, that in any year the actual increase in weight is constant for oysters of at least two year-groups, holds when the physical conditions are altered.

I am indebted to Captain F. Arden, District Marine Manager of British Railways, for supplying me with details of the tidal levels at Holyhead.

SUMMARY

A description is given of the Tal-y-foel oysterage. Records show that the mean monthly water temprature can be accurately estimated from the mean monthly air temperature recorded at Valley, Anglesey. A tidal exposure curve has been calculated for the shore below mid-tide level. Salinity samples taken at low water of spring tides rarely fell below 30‰.

The growth of oysters, determined by length measurements and by weighing, was confined to the period April to October inclusive, that is when the water temperature was above 10–12° C.

The rate of growth, and the proportion growing, increased during the spring, was approximately constant during the summer, and declined during the autumn. No evidence was found for the view that growth is confined to the spring and autumn.

In any given year the mean increase in weight is the same for $1\frac{1}{2}$-year-old and $2\frac{1}{2}$-year-old oysters. In younger oysters the size of the increment increases with increasing age. The size of the increment does not begin to decline until oysters are at least 5–6 years old and probably older.

Growth was strongly affected by tidal exposure. The amount of growth decreases steadily until at the level of about 30% exposure no growth occurs.

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OBSERVATIONS ON THE INCREASE IN SIZE AT MOULTING IN THE LOBSTER (*HOMARUS VULGARIS* M.-EDW.)

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(Text-fig. 1)

A knowledge of growth rates is a pre-requisite in estimating the effect of fishing upon the available stocks. In Crustacea, where there is no known means of establishing accurately the age of the individual, the importance of measuring the growth rate is increased whilst its determination is made more difficult. In *Homarus vulgaris* some experiments were undertaken by Dannevig (1936), and Wilder (1953) gives considerable data for the American lobster. Results suggest that the growth increment is not uniform in all latitudes. Experiments to augment the limited data available for *H. vulgaris* and to establish the increase in size at moulting in local lobster stocks were therefore undertaken by the Marine Laboratory of the Scottish Home Department at Aberdeen. A statement of some preliminary results was given in *Report on the Fisheries of Scotland* (Lucas, 1957, p. 58).

MATERIAL AND METHODS

The present investigations were carried out off the south-east Scottish coast. The area is characterized by an intensive creel fishery and heavy fishing mortality (Thomas, 1955*a*). A high level of returns could therefore be expected. Off the Berwickshire coast the onset of the main moulting season for lobsters occurs in about the middle of May. During the period 7–13 May, 1956, a total of 1012 lobsters were purchased from local fishermen, and, having been marked to give an indication of their size, were released on to the fishing grounds. Punch markings on the telson and tail fan were coded so as to indicate the existing minimum carapace length of the lobster, in 1 mm groups, measured from the back of the eye socket to the posterior end of the carapace.

Over the period September 1956 to April 1957 altogether 111 marked lobsters were returned which had moulted in the intervening period. The carapace length of the recovered lobsters together with a note of the initial length, as shown by the code markings, and the sex were recorded.

The present series of experiments has been limited to the narrow size range around the minimum legal landing length, because this is the most important class from the standpoint of population dynamics. Restriction of the size

range also renders the experiment more profitable since the smaller lobsters are more likely to have moulted before recapture. It also facilitates a system of coding into small groups, in this instance 1 mm.

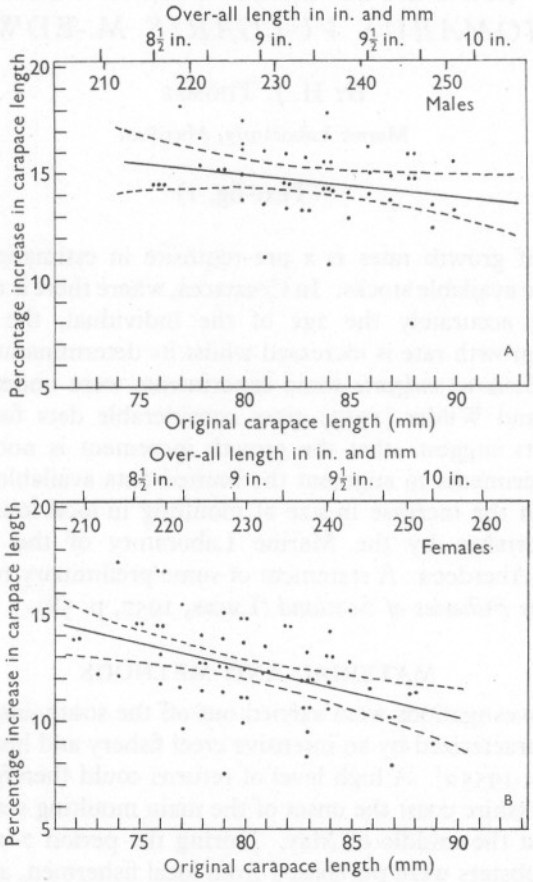

Fig. 1. (A) The percentage increase in the carapace length of male lobsters at moulting. (B) The percentage increase in the carapace length of female lobsters at moulting. The 95 % confidence limits are shown by broken lines.

The timing of the liberations, immediately prior to the main moulting season, was also chosen so that the greatest numbers of marked lobsters would have moulted before being recaptured. However, the possibility of a different increase in size at moult occurring in lobsters moulting other than at the peak season cannot be excluded.

RESULTS

The percentage increase in carapace length at moulting based on a sample of 49 male lobsters is shown in Fig. 1*a*. At carapace length 80·9 mm, equivalent to an over-all length of 9 in. (230 mm) which is the minimum legal landing size, it is about 15%. Smaller lobsters have a somewhat higher increment whilst larger individuals gain less. In terms of weight the increase of a 9-inch lobster at moulting is roughly 55%.

The comparable moult increments for a sample of 62 female lobsters is shown in Fig. 1*b*. The percentage increase at the moult is materially less than in the male lobsters, whilst the decrease in the moult increment with increasing size is more marked. At carapace length 79·6 mm, equivalent to an over-all length of 9 in., the growth at moulting is about 12·75%. In terms of weight the minimum legal-sized female lobster increases roughly 41%.

Statistical analysis shows that the moult increments of male and female lobsters, of legal landing size, differ significantly ($P < 0{\cdot}001$). The levels of moult increments are broadly comparable with those found by Dannevig (1936) for *H. vulgaris* and by Wilder (1953) for the American lobster, although in the latter a lower increment in females does not seem to have been observed. This, however, may well be because most of Wilder's observations were made on smaller lobsters. The difference in growth between the sexes is probably associated with maturity which would explain the more rapid fall-off in moult increment with increasing size of the females as opposed to that in the males. In the present experiments no specimens were returned showing abnormally high growth rates or physical characteristics suggesting that they had moulted twice during the period of liberty.

DISCUSSION

Simpson (1958) found that in North Wales lobsters had a moult increment which is lower than that found off Berwickshire. A striking fact is that out of only 41 returns in the North Wales experiments, 3 lobsters had moulted twice within a period of about 7 months. None of the 111 returns from the Berwickshire coast had moulted twice, although the average size of lobsters marked was lower. It would seem reasonable that the higher average moulting frequency should be accompanied by a lower increase in size at each moult.

The present experiments give a measure of the increase in size at the moult. From the population standpoint the important measure is the *annual* growth rate. It is difficult to envisage any marking experiments which would alone give a true measure of the annual growth rate. Nevertheless, this can be derived from the results of marking experiments in conjunction with data on the frequency of moulting. Unfortunately, knowledge of the moulting frequency in the various length groups is not precise. In certain areas a proportion of 9-in. lobsters cast twice annually (Thomas, 1958). The inci-

dence of such moulting probably varies with sea temperature. Off Berwickshire it would seem probable that few 9-in. lobsters moult twice annually. Male lobsters of between 10 and 11 in. moult only once a year. Female lobsters of this size fall into two classes—those which do not mature but moult annually; those which mature, spawn and have an inter-moult period which is normally 2 years. The normal moulting frequency of the female, however, may be upset at about maturity so that the last inter-moult period prior to maturity is reduced or the interval between moulting and spawning is less than normal. Such irregularities seem in general to be associated with an abnormally small moult increment in the second moult or a fecundity below average. In view of the inadequate knowledge of the incidence of such occurrences, it is preferable to concentrate primarily on the male lobster in using growth rates for calculation of mortality rates.

It has been noted that the female lobster approaching maturity has a lower moult increment than the male, although in smaller lobsters the rates may be similar. This will have some bearing on the sex ratio of the stock. The lower growth rate will increase the proportion of females to males in the sizes immediately above the level at which the growth rates diverge. There will also be an accompanying decrease in the proportion of females to males amongst larger lobsters. The effect is similar to and precedes that arising on account of the difference in over-all growth rates which is associated with the increased inter-moult period in the spawning female (Thomas, 1955*b*).

SUMMARY

The percentage increase in carapace length at moulting of male lobsters off the south-east Scottish coast is about 15% and for females 12·75%.

The rate of moulting increase in carapace length falls off with increasing size in both male and female lobsters of above 8 in. over-all length, but the decrease is more pronounced in the female.

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THE OCCURRENCE OF GALLIUM IN MARINE ORGANISMS

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Little is known about the occurrence of gallium in the biosphere. The first recorded instance of its detection in a living organism is due to Cornec (1919), who detected the element in *Laminaria* sp. Vinogradov (1935) suspected its presence in an undetermined gorgonian, but his statement that Zvinden had detected it in human tissue appears to be an erroneous citation (Hutchinson, 1943). Bertrand (1941) detected the element in oysters, and, after chemical concentration, in human urine.

Noddack & Noddack (1940) have determined gallium spectrographically in nine marine organisms. They found concentrations (expressed as parts per million on the dry weight) ranging from 0·1 p.p.m. in *Squalus acanthias* to 0·7 p.p.m. in the body walls of *Asterias rubens* and *Bryssopsis lyrifera*. The average amount recorded (0·4 p.p.m.) corresponds to a concentration factor over sea water of 16,000 (assuming the gallium concentration of 0·025 μg/l. in sea water, found by Burton, Culkin & Riley, 1958). The element has also been detected in *Lycopodium flabelliforme* (0·1 p.p.m.) and *Mitchella repens* (0·1–0·2 p.p.m.) (Hutchinson & Wollack, 1943); in ambergris (Ishiguro, Koga & Matsuo, 1952); in the outer layers of some seeds and fruits, and in several species of beetles (Bergman, Borovik & Borovik-Romanova, 1943; Borovik & Borovik-Romanova, 1944, 1949). From these investigations the concentration of gallium in living organisms appears to be about $n \times 10^{-5}\%$.

The biological role of gallium has been the subject of several investigations. Steinberg (1938, 1939*a*, *b*; 1941) has found that trace amounts of gallium are necessary for the growth of *Aspergillus niger* and *Lemna minor* in sterile medium. More recent investigations by Bertrand (1954) are, however, at variance with these conclusions. G. A. Riley (1943) has reported that in nutrient deficient culture the growth of the marine diatom, *Nitzschia closterium**, is stimulated by gallium, but that this effect disappeared when nitrate and phosphate were present. No definite conclusions can be drawn from this study since no control experiments were made omitting gallium alone. Hewitt & Bolle-Jones (1952) have found no evidence that gallium is an essential micronutrient for the growth of tomato, lettuce or sugar beet. Bardet, Levaditi, Tchakirian & Vaisman (1931) have studied the distribution of gallium in the organs of rabbits given gallium tartrate in their diet.

* i.e., *Phaeodactylum tricornutum*.

In a review article on the biogeochemistry of aluminium and some other elements of Groups III*a* and III*b* of the Periodic Table, Hutchinson (1943) has pointed out that in many of its properties (gallous and gallic salts, complex cyanides) gallium shows a greater resemblance to iron than to aluminium. He concluded that it might play a part in metabolism similar to iron, but on a restricted scale. Gallium deficiencies are only likely to occur rarely, since few silicate rocks or soils contain less than 5 p.p.m. of the element.

Specific spectrophotometric methods for the determination of gallium in silicates and other minerals have been developed recently (Onishi & Sandell, 1955; Culkin & Riley, 1958). These procedures have sensitivities sufficiently high to allow the estimation of less than 0·1 p.p.m. of gallium using samples weighing less than 5 g. Using a modification of these methods, a study has been made of the distribution of the element in several marine organisms, derived mainly from the Irish Sea and the shores of the Isle of Man. In several of the samples the concentrations of iron, copper and aluminium have also been determined for comparison.

METHODS

Determination of gallium in marine organisms and shells

Reagents

(1) 7·5 N nitric acid.
(2) Perchloric acid, 60 % (w/w).
(3) Titanous chloride solution, 15 % (w/v).
(4) Di-*iso*-propyl ether. Freshly distilled from sodium hydroxide.
(5) Hydrochloric acid (6·5 N) containing 1 % titanous chloride. Concentrated hydrochloric acid (S.G. 1·16, 325 ml.) was mixed with 33 ml. of 15 % titanous chloride solution and diluted to 500 ml.
(6) Rhodamine B solution. A solution was prepared containing 0·5 g of Rhodamine B in 100 ml. of water. The solution was filtered before use.
(7) Carbon tetrachloride-chlorobenzene solvent. Carbon tetrachloride (125 ml.) was diluted to 500 ml. with chlorobenzene.
(8) Standard gallium solution (5 μg/ml.) was prepared by dissolving 0·0438 g of caesium gallium sulphate in water and diluting to 1 l.

Solution of samples of shells (carbonates)

The weighed sample (5–10 g) was placed in a 250 ml. conical flask and 50 ml. of 7·5 N nitric acid was gradually added. After effervescence had ceased, the flask was heated gently on a hot-plate for 30 min, and the nitric acid was then evaporated. The residue was twice evaporated to dryness with 5–10 ml. of hydrochloric acid, to remove the nitrate, and dissolved in 50 ml. of 6·5 N hydrochloric acid containing 1 % of titanous chloride.

Solution of samples of marine organisms

The weighed sample (up to 5 g, dried at 110° C) was placed in a 250 ml. conical flask, and 25 ml. of 7·5 N nitric acid was added. The flask was closed with a small funnel and its contents were allowed to digest in the cold until all foaming had

ceased. The nitric acid was then removed by cautious evaporation on the hot plate. Repeated evaporations with 15 ml. portions of concentrated nitric acid were then carried out until all carbonaceous material was removed. The white or pale yellow residue was treated with 2 ml. of 60% (w/w) perchloric acid and fumed to dryness. It was fumed to dryness again after addition of 2 ml. of concentrated sulphuric acid, and dissolved in 50 ml. of 6·5 N hydrochloric acid containing 1% of titanous chloride.

Extraction of gallium

The solution of the sample was transferred to a 250 ml. separating funnel, and, if it was not violet in colour, an excess of 15% titanous chloride was added. Two extractions with 30 ml. portions of di-*iso*-propyl ether were carried out and the combined extracts were evaporated in a beaker on the water bath.

Photometric determination of gallium

The residue in the beaker was dissolved by warming to 70–80° with 5 ml. of 6·5 N hydrochloric acid containing 1% titanous chloride. The cold solution was transferred to a 50 ml. separating funnel containing 8 ml. of chlorobenzene-carbon tetrachloride solvent. The beaker was rinsed with a further 1 ml. of 6·5 N hydrochloric acid and the washings added to the funnel. Rhodamine B solution (0·5 ml.) was added and the separating funnel was shaken mechanically for 10 min. After the two phases had separated, the organic phase was run through a plug of glass wool into a 10 ml. calibrated flask containing 1 ml. of ethyl alcohol. The aqueous phase was washed with a further 1 ml. of the solvent and the washings added to the calibrated flask, which was then filled to the mark with the solvent. The optical density of the solution was measured at 562 mμ in a 1 cm cell. The reagent blank was determined in the same manner but omitting the sample. The method was calibrated using 1, 2, 4, 6, 8 and 10 μg of gallium. It was found that 5 μg of gallium gave an optical density of 0·565 at 562 mμ in a 1 cm cell. Recoveries of gallium added to biological samples averaged 98%.

Determination of sulphated ash, iron, aluminium and copper

The dried (110° C) sample (1 g) was weighed into a 25 ml. platinum crucible and allowed to stand for a few hours with *ca.* 5 ml. of concentrated nitric acid and 2 ml. of perchloric acid. The crucible was then carefully heated on a water bath until the nitric acid had evaporated. The evaporation with concentrated nitric acid was repeated until all organic matter had been destroyed. The perchloric acid was then fumed off under an infra-red heater, 2 ml. of concentrated sulphuric acid was added and the heating was continued until no further fumes were evolved. The contents of the crucible were treated with 2 g of powdered ammonium carbonate and heated at 450° C. in a muffle furnace for 30 min. The crucible was allowed to cool in the desiccator and weighed.

The sulphated ash was treated with 2 ml. of concentrated hydrochloric acid and 15 ml. of water and heated on the water bath; the resultant solution was filtered into a 250 ml. graduated flask. The residue (if any) in the crucible was washed well with hot water and the washings added to the graduated flask. The solution was diluted to volume and used for the spectrophotometric estimation of iron and aluminium as described by Riley (1958), and for copper as described by Riley and Sinhaseni (1958).

OBSERVATIONS

The composition of marine organisms

Gallium, aluminium, iron and copper have been determined in a number of marine plants and animals which were obtained mainly from the Irish Sea off Port Erin and Port St Mary. Unless otherwise stated the analyses were carried out on the whole organism, which had been washed thoroughly with distilled water and dried at 110° C. In addition, the distribution of gallium and copper in certain organs of *Buccinum undatum* L., *Chlamys opercularis* (L.), *Porania pulvillus* (Müll.) and *Pecten maximus* (L.) has been studied. Specimens of *Pecten maximus* were analysed directly after removal from their habitat and also after being allowed to purge themselves in clean sea water for 7 days. The results of the analyses are shown in Tables 1–6.

TABLE 1. OCCURRENCE OF GALLIUM, ALUMINIUM, IRON AND COPPER IN MARINE ALGAE

Organism	Ash (%)	Ga (μg/g)	Cu (μg/g)	Al (μg/g)	Fe (μg/g)	Ga/Al × 10⁴	Ga/Fe × 10⁴	Ga in ash (μg/g)
CHLOROPHYCEAE								
Codiaceae								
Codium sp.	56·2	0·16	85·5	1336	470	1·2	3·4	0·3
Halimeda gracilis	123	0·05	22·5	143	342	3·5	1·5	0·04
PHAEOPHYCEAE								
Fucaceae								
Ascophyllum nodosum	22·1	0·06	6·2	83·4	61·4	7·2	9·8	0·3
Fucus serratus	30·6	0·03	5·6	101	153·7	3·0	2·0	0·1
F. spiralis	9·2	0·01	15·0	34·4	33·9	2·9	3·0	0·1
F. vesiculosus	24·8	0·03	18·0	51·4	36·4	5·8	8·2	0·1
Pelvetia canaliculata	24·2	0·10	17·9	372	120·8	2·7	8·2	0·4
Laminariaceae								
Laminaria digitata	37·5	0·07	6·2	101	40·9	7·0	17	0·2
RHODOPHYCEAE								
Corallinaceae								
Corallina officinalis	114	0·56	44·7	4420	4680	1·3	1·2	0·5
Lithothamnion sp.	113	0·53	15·7	3570	3420	1·5	1·5	0·5
Lithophyllum sp.	121	0·23	18·1	243	374	1·0	0·6	0·2
Gigartinaceae								
Gigartina stellata	16·7	0·02	32·8	94·8	102	2·1	2·0	0·1
Rhodomelaceae								
Polysiphonia lanosa	24·9	0·19	41	478	493	4·0	2·6	0·8
Rhodymeniaceae								
Rhodymenia palmata	117	0·04	24·4	175	252	2·3	1·6	0·03

The range of gallium concentrations found for the various whole organisms was 0·01–0·96 p.p.m., which is in good agreement with the data for nine marine animals, published by Noddack & Noddack (1940) (0·1–0·7 p.p.m.). Hutchinson (1943) has deduced from the Noddacks' results that gallium is concentrated biologically from sea water to a greater extent than aluminium. This conclusion must be reconsidered in the light of more recent determinations of both aluminium and gallium in sea water. Greenhalgh & Riley (unpublished work) have found aluminium concentrations of *ca.* 10 μg/l. in the

TABLE 2. OCCURRENCE OF GALLIUM, ALUMINIUM, IRON AND COPPER IN MARINE ANIMALS

Organism	Ash (%)	Ga (μg/g)	Cu (μg/g)	Al (μg/g)	Fe (μg/g)	Ga/Al × 10^4	Ga/Fe × 10^4	Ga in ash (μg/g)
PROTOZOA								
Foraminifera								
Ramulina sp.	116	0·18	111	973	1148	1·9	1·6	0·2
PORIFERA								
Halichondria panicea	88·7	0·93	59·5	3700	4040	2·5	2·3	1·1
COELENTERATA								
Alcyonium digitatum	69·0	0·05	61·5	435	438	1·2	1·1	0·1
CRUSTACEA								
Cirripedia								
Balanus balanoides	120	0·07	28·7	240	146	2·9	4·8	0·05
Decapoda								
Cancer pagurus	79·0	0·03	35·0	166	157	1·8	1·9	0·04
Corystes cassivelaunus	71·6	0·36	—	1041	1045	3·5	3·4	0·5
MOLLUSCA (Shells only)								
Lamellibranchia								
Mytilus edulis	—	0·010	2·1	38	41	2·6	2·4	0·01
Pecten maximus	—	0·008	6·0	81	118	1·0	0·7	0·01
Chlamys opercularis	—	0·069	3·8	174	239	4·0	2·8	0·07
Gastropoda								
Buccinum undatum	—	0·036	1·6	76	85	4·7	4·2	0·04
Littorina littorea	—	0·011	5·2	32	45	3·4	2·4	0·01
Gibbula umbilicalis	—	0·014	7·9	48	51	2·9	2·7	0·01
MOLLUSCA (Soft parts)								
Lamellibranchia								
Mytilus edulis	15·8	0·16	53·7	465	325	3·4	4·9	1·0
Pecten maximus				See Table VI.				
Chlamys opercularis	15·7	0·05	37·1	186	1093	2·7	0·5	0·3
Gastropoda								
Buccinum undatum	8·8	0·007	53·5	198	86	0·35	0·8	0·08
Littorina littorea	12·9	0·06	50·2	198	171	3·0	3·5	0·5
L. littoralis	9·0	0·05	102	238	229	2·1	2·2	0·5
Patella vulgata	17·7	0·04	—	346	1415	1·2	0·3	0·2
ECHINODERMATA								
Asteroidea								
Asterias rubens	49·2	0·10	34·7	159	332	6·3	3·0	0·2
Henricia sanguinolenta	70·5	0·05	20·4	652	925	0·8	0·5	0·1
Luidia ciliaris	42·6	0·03	59·0	152	149	2·0	2·0	0·1
Marthasterias glacialis	64·5	0·02	37·7	142	186	1·4	1·1	0·03
Porania pulvillus	65·2	0·11	90·0	365	457	3·0	2·4	0·2
Stichastrella rosea	88·5	0·10	35·0	263	271	3·8	3·7	0·1
Echinoidea								
Echinus esculentus	111	0·03	76·0	597	597	5·0	5·0	0·03
Spatangus purpureus								
Whole organism − gut	122	0·35	36·9	1830	1700	1·9	2·1	0·3
Gut + contents	124	3·7	31·6	16,480	14,800	2·2	2·5	3·0
Ophiuroidea								
Ophiocomina nigra	105	0·09	29·5	894	1600	1·0	0·6	0·1

TABLE 3. DISTRIBUTION OF GALLIUM, ALUMINIUM, IRON AND COPPER IN *CHLAMYS OPERCULARIS*

Organ	Ash (%)	Ga (μg/g)	Cu (μg/g)	Al (μg/g)	Fe (μg/g)	Ga/Al × 10^4	Ga/Fe × 10^4	Ga in ash (μg/g)
Shell	—	0·07	3·8	174	239	4·0	2·9	0·07
Muscle	6·5	0·06	47·9	773	52·8	0·8	1·1	1·0
Gonad	10·4	0·06	—	—	—	—	—	0·6
Mantle and viscera	21·6	0·55	1150	3420	2720	1·6	2·0	2·5

TABLE 4. DISTRIBUTION OF GALLIUM AND COPPER IN *BUCCINUM UNDATUM*

	Mantle	Operculum	Digestive gland	Digestive tract	Mucous gland	Foot	Female ducts	Male ducts
Sulphated ash (%)	5·0	3·7	4·1	5·7	20·4	4·1	3·3	5·9
Ga (μg/g)	<0·01	<0·01	0·014	<0·01	<0·01	<0·01	<0·01	—
Cu (μg/g)	33·4	25·7	80·4	29·2	26·9	2·5	13·7	28·8
Ga in ash (μg/g)	<0·2	<0·3	0·28	<0·2	<0·05	<0·25	<0·3	—

	Renal organ	Female gonads	Ctenidium	Heart
Sulphated ash (%)	10·0	2·1	10·9	5·4
Ga (μg/g)	—	—	—	—
Cu (μg/g)	30·0	27·7	50·3	87·0
Ga in ash (μg/g)	—	—	—	—

TABLE 5. DISTRIBUTION OF GALLIUM IN *PORANIA PULVILLUS*

	Skin	Digestive gland	Stomach + oral region	Skin from aboral region
Sulphated ash (%)	—	11·3	95	60·4
Ga (μg/g)	0·5	0·02	0·20	0·09
Ga in ash (μg/g)	—	0·18	0·21	0·15

TABLE 6. DISTRIBUTION OF GALLIUM, ALUMINIUM, IRON AND COPPER IN *PECTEN MAXIMUS*

Unpurged	Full gonad	Spent gonad	Striped muscle	Unstriped muscle	Mantle	Digestive gland	Gonad + gut	Mantle + gut + digestive gland
Sulphated ash (%)	10·7	3·2	6·0	4·7	13·3	7·2	12·6	13·9
Ga (μg/g)	<0·01	0·009	<0·01	<0·01	<0·01	0·79	0·29	0·30
Al (μg/g)	—	—	86·6	—	161	454	833	842
Fe μg/g)	—	—	167	—	189	841	1552	766
Cu (μg/g)	—	25·2	4·0	—	—	153	—	50·8
Ga in ash (μg/g)	<0·1	0·28	<0·2	<0·2	<0·1	11·0	2·3	2·2

Purged	Gills	Male gonad	Female gonad	Striped muscle	Gut + digestive gland	Mantle
Sulphated ash (%)	25·0	3·0	10·2	12·7	10·9	9·4
Ga (μg/g)	0·14	0·034	<0·01	<0·01	0·011	0·01
Cu (μg/g)	6·3	11·3	26·6	7·5	70·9	10·2
Ga in ash (μg/g)	0·56	1·1	<0·1	<0·1	1·0	<0·1

Irish Sea and English Channel; Monaghan, Simons & Taggert (1953) have detected similar amounts in the Atlantic Ocean and in the waters of the Gulf of Mexico. These amounts are approximately two orders of magnitude less than earlier work had indicated (cf. Richards, 1957). Assuming an aluminium content of 10 μg/l. and a gallium content of 0·025 μg/l. (Burton, Culkin & Riley, 1958), the Ga:Al ratio in sea water is 25×10^{-4}. The average Ga:Al ratio in the lithosphere is *ca.* 2×10^{-4}, which shows that sea water is enriched approximately tenfold in gallium relative to aluminium compared with the lithosphere.

The average value of the Ga:Al ratio for the marine organisms examined in this paper was $2–3 \times 10^{-4}$, which is very similar to the average ratio for the lithosphere (*ca.* 2×10^{-4}). Since the majority of the specimens examined were either bottom-living or from shallow water it seems very probable that most of their aluminium and gallium was derived from the bottom muds rather than from the sea water itself. The actual range found for the Ga:Al ratio is small ($1–7 \times 10^{-4}$). This suggests that there is no significant biological separation of gallium from aluminium in the specimens examined, if allowance is made for variations in the Ga and Al contents of the muds in the various localities in which they lived.

The iron content of the organisms is generally similar to their aluminium content, but the Ga:Fe ratio shows rather greater variations than the Ga:Al ratio. The variation in the iron concentration is probably related to its role as an essential trace element in biological systems.

There is apparently no relationship between species and their contents of gallium, iron, aluminium or copper. The low concentrations of these elements found in the calcareous shells of molluscs suggests that the mechanism by which the calcium of sea water is converted into calcium carbonate is quite selective for calcium. The gallium contents of the shells are similar to those of carbonate rocks (Culkin & Riley, unpublished). All four elements are concentrated in the digestive glands and viscera of the molluscs, but it seems probable that the gallium, aluminium and iron contents of these organisms are associated with ingested detritus. This is confirmed by the low concentrations of these elements present in the gut and digestive glands of *Pecten maximus* specimens, which had been allowed to purge themselves in filtered sea water for 7 days. The copper contents of the purged and unpurged specimens were similar, and it is probable that the copper in them is mainly adsorbed on to the mucous surfaces.

The authors thank Mr D. J. Slinn for supplying, identifying and dissecting the marine organisms.

SUMMARY

A spectrophotometric method has been developed for the determination of submicrogram amounts of gallium in biological materials. Using this procedure a study has been made of the occurrence of gallium in a number of marine plants and animals (dried at 110° C). Data are also presented for the concentrations of iron, aluminium and copper in the same samples.

The gallium content of the samples ranged from *ca.* 0·01 to 0·96 p.p.m. The Ga:Al ratio varied from $1–7 \times 10^{-4}$ (average $2–3 \times 10^{-4}$), which compares well with the average Ga:Al ratio of the lithosphere, and contrasts with the ratio of 25×10^{-4} for sea water. It seems likely that the organisms examined derived their gallium, aluminium and iron from the bottom muds rather than from the sea water. There is no evidence of selective uptake of gallium in preference to aluminium. Iron and aluminium were generally present in roughly equal amounts.

The distribution of gallium in the various organs of *Pecten maximus*, *Buccinum undatum*, *Chlamys opercularis* and *Porania pulvillus*, has been investigated. Most of the tissues of these molluscs contain less than 0·07 p.p.m. of gallium, but the viscera and digestive organs contain higher concentrations, presumably contained in ingested inorganic material. The average gallium content of carbonate shells is 0·02 p.p.m.

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THE POLYCHAETE *MAGELONA ALLENI* N.SP. AND A RE-ASSESSMENT OF *MAGELONA CINCTA* EHLERS

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(Text-figs. 1–3)

Three species of the polychaete genus *Magelona* are known from the neighbourhood of Plymouth. One is the widely distributed *M. papillicornis* F. Müller, described first from the coast of Brazil (Müller, 1858) and subsequently frequently recorded for northern European coasts and the Mediterranean. Near Plymouth this species occurs in clean sand in the lower tidal region and offshore, as in Whitsand Bay. Of the other two species, one from clean sand near low water at Mill Bay, Salcombe, awaits description. The third has been known for many years but until now has not been recognized as an undescribed species. It was formerly abundant in the Rame Mud (a deposit of black sandy mud); thus Mare (1942, p. 542, as *M. cincta* Ehlers—a provisional identification by me) on 12 July 1939 found 120 per m^2, associated with large numbers of other polychaetes, lamellibranchs, etc. The locality was close to Ford's station No. 93 (Ford, 1923, chart facing p. 167, and p. 218 where the position is given as Rame Head, E. $\frac{1}{2}$ N. Tregantle, N. $\frac{1}{2}$ E.). At this station on 20 February 1923 Ford had four specimens (recorded as *M. papillicornis*) from $\frac{1}{5}$ m^2. On 11 August 1922 at station No. 53 close by (Rame Head, E., $1\frac{1}{2}$ miles) he obtained thirteen specimens of the same species from $\frac{3}{10}$ m^2, the substratum being black mud. Ford records *papillicornis* from other offshore mud or muddy-sand stations over a fairly wide area inside and outside Plymouth Sound, but in less abundance. It is certain that some of these records, especially those detailed above, are of the species taken by Mare and provisionally identified as *cincta*. In 1939 Ford showed me his collections from the Rame Mud and the *Magelona* worms in them were banded with red pigment as is *cincta*, a character which serves to separate them from *papillicornis* which has no such pigmentation. Much more recently Holme (1953) has had this red-banded species in smaller numbers at several stations some miles south of the Sound and to the eastward of the Eddystone, in sandy and muddy sand grounds, sometimes with *papillicornis* whose range the red-banded species overlaps. During the first part of 1958 many attempts have been made to find a locality where these worms can again be obtained in large numbers. Unfortunately the Rame Mud locality is a dumping ground for rubbish and seems to have changed in character of recent years. Search in

the area has yielded only two short anterior portions one of which, narcotized in 7% magnesium chloride in tap water and fixed in hot Bouin's Fluid before preservation in alcohol, forms the basis of the drawings in Fig. 1 C–E. This specimen shows very little contraction from life. The remainder of the material used in the following description of the species was fixed in 1939, either by Mare (formalin) or by myself (alcohol after narcotization).

Magelona alleni n.sp.

Adult specimens in a moderate state of expansion about 40 mm long by 1 to 1·5 mm wide anteriorly (but see p. 625) tapering gradually to the anus; a constriction at the ninth setiger. First nine setigers bristle-bearing, the following setigers with hooded hooks only. Total number of setigers about 70. Prostomium (Fig. 1, C) eyeless, spatulate, wider than long especially in contraction (Fig. 1, A) and with two elongate low dorsal ridges broadened posteriorly, on either side low raised areas. The anterior border of the prostomium is almost straight transversely, short and without horns. The proboscis when everted is globular, ridged. On each side of the mouth, ventral to the postero-lateral corners of the prostomium, there arises a long tentacle,* transversely wrinkled and bearing for much of its length distally a large number of densely crowded papillae, elongate and slightly capitate. When a tentacle has been broken off the postero-lateral border of the prostomium bends inwards ventrally, so reducing the apparent width of the prostomium viewed dorsally (Fig. 1, C, right side). First eight setigers with relatively strong dorsal and ventral winged bristles (Fig. 1, H) springing in bundles of often eight to sixteen bristles from the bases of pointed lamellae (Fig. 1, C, D and F). Some bristles are double-winged; in many, as in the one drawn, the narrow secondary wing is absent. The dorsal lamellae are flattened antero-posteriorly, the ventral lamellae dorso-ventrally, the planes of flattening thus being at right angles to one another. These first eight pairs of parapodia are situated at the anterior borders of the segments. The ninth parapodia and bristles are similar in structure but are smaller and shorter and the segment bearing them is very short with ill-defined limits: it is also much narrower than those in front and behind, producing a marked constriction of the body at this region (Fig. 1, D, E). The reduction in girth of this ninth setiger is largely responsible for the displacement of the noto- and neuropodia, especially the latter, towards the mid-dorsal and mid-ventral lines respectively.

The parapodia of the tenth and all succeeding setigers are situated near the middle of the segment to which they belong. They bear only hooded hooks, each with one main tooth surmounted by two smaller teeth (Fig. 1, I–K). There are about twelve hooks in two facing groups in each noto- and neuropodium (Fig. 1, G), except posteriorly where the numbers are less. The rows of hooks reach to within short distances of the mid-dorsal and mid-ventral lines. Between the dorsal and ventral rows of hooks of each parapodium there is a large leaf-like dorsal lamella and a much smaller ventral lamella, both lamellae flattened antero-posteriorly. Ventrally and medianly to the ventral rows of hooks there is a very small protuberance, or rudimentary ventral cirrus. Except for the incompletely developed parapodia at the extreme posterior end all the parapodia from the tenth onwards are closely similar. The body ends in a clearly defined pygidium with the anus between two short stumpy cirri (Fig. 1, B).

On both dorsal and ventral surfaces of the body there are in the anterior region a pair of longitudinal grooves. At the region of the ninth setiger these grooves merge

* Other writers variously term these organs tentacles, palps, etc. My own choice of term should not be considered an expression of opinion about their homology.

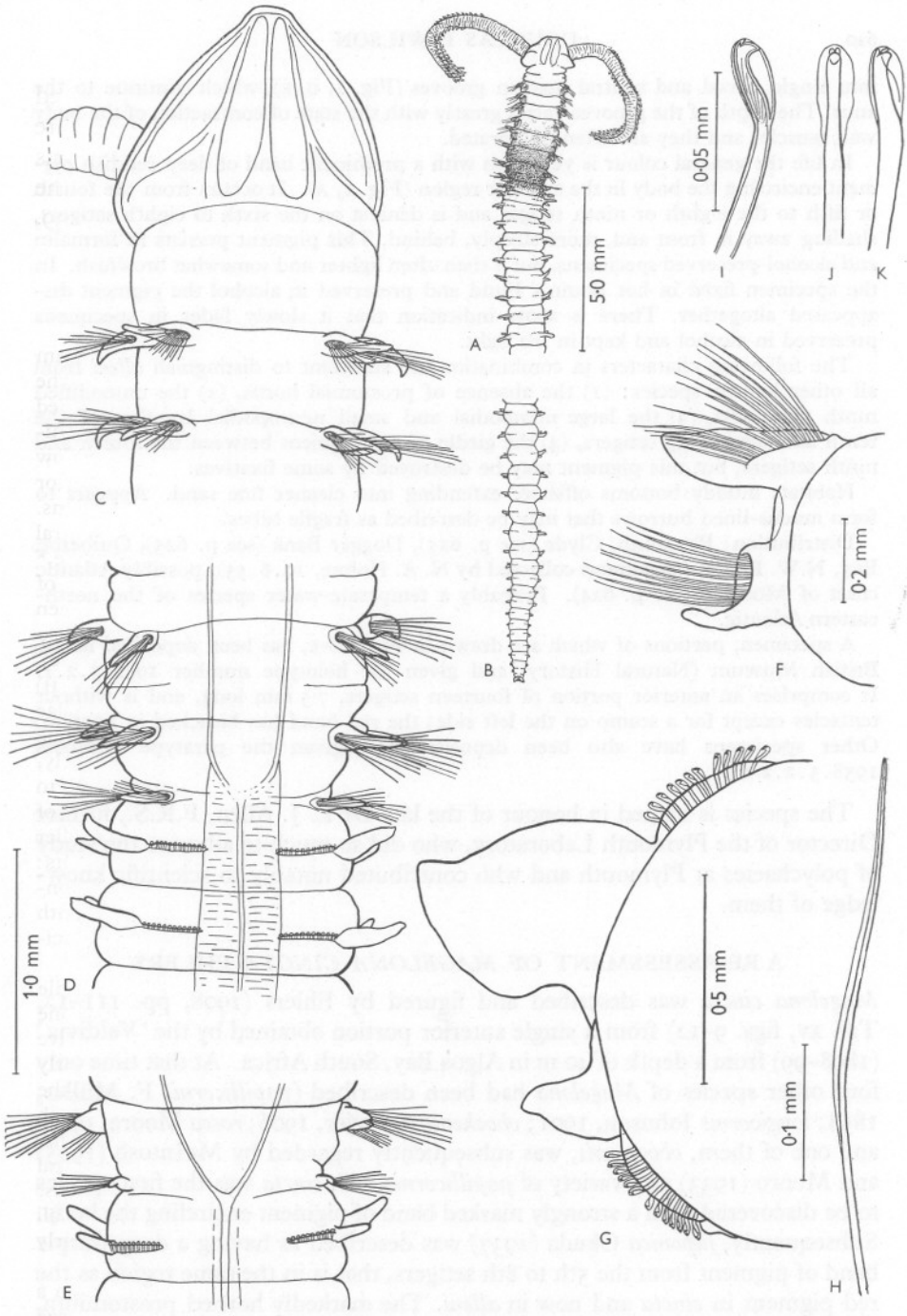

Fig. 1. *Magelona alleni* n.sp. A, dorsal view of the anterior portion of a partially contracted specimen showing band of reddish pigment. B, dorsal view of the posterior portion of another specimen. C, dorsal view of the head and first two setigers of a third specimen fixed with little or no contraction. D, dorsal view of the 7th–11th setigers of the same specimen. E, ventral view of the 8th–10th setigers of the same specimen. F, view from in front of 5th parapodium from a fourth specimen. G, 31st parapodium of the fourth specimen. H, winged bristle. I, hooded hook in side view. J, another hook in front view. K, a third hook in oblique front view.

into single dorsal and ventral median grooves (Fig. 1, D, E), which continue to the anus. The depth of the grooves varies greatly with the state of contraction of the body wall muscles and they are often obliterated.

In life the general colour is yellowish with a prominent band of deep reddish pigment encircling the body in the anterior region (Fig. 1, A). It occurs from the fourth or fifth to the eighth or ninth setiger and is densest on the sixth to eighth setigers, shading away in front and, more steeply, behind. This pigment persists in formalin and alcohol-preserved specimens, but is then often lighter and somewhat brownish. In the specimen fixed in hot Bouin's Fluid and preserved in alcohol the pigment disappeared altogether. There is some indication that it slowly fades in specimens preserved in alcohol and kept in the light.

The following characters in combination are sufficient to distinguish *alleni* from all other known species: (1) the absence of prostomial horns, (2) the unmodified ninth parapodia, (3) the large notopodial and small neuropodial lamellae of the tenth and succeeding setigers, (4) the girdle of red pigment between the fourth and ninth setigers, but this pigment may be destroyed by some fixatives.

Habitat: muddy bottoms offshore extending into cleaner fine sand. Appears to form mucus-lined burrows that may be described as fragile tubes.

Distribution: Plymouth, Clyde (see p. 625), Dogger Bank (see p. 625), Quiberon Bay, N.W. France (specimens collected by N. A. Holme, 19.6.55), possibly Atlantic coast of Morocco (see p. 624). Probably a temperate-water species of the north-eastern Atlantic.

A specimen, portions of which are drawn in Fig. 1C–E, has been deposited in the British Museum (Natural History) and given the holotype number 1958.5.2.1. It comprises an anterior portion of fourteen setigers, 7·5 mm long, and is without tentacles except for a stump on the left side; the red band has bleached in fixation. Other specimens have also been deposited and given the paratype numbers 1958.5.2.2/10.

The species is named in honour of the late Dr E. J. Allen, F.R.S., former Director of the Plymouth Laboratory, who did so much to advance the study of polychaetes at Plymouth and who contributed notably to scientific knowledge of them.

A RE-ASSESSMENT OF *MAGELONA CINCTA* EHLERS

Magelona cincta was described and figured by Ehlers (1908, pp. 111–12, Taf. XV, figs. 9–12) from a single anterior portion obtained by the 'Valdivia' (1898–99) from a depth of 40 m in Algoa Bay, South Africa. At that time only four other species of *Magelona* had been described (*papillicornis* F. Müller, 1858; *longicornis* Johnson, 1901; *obockensis* Gravier, 1906; *rosea* Moore, 1907) and one of them, *obockensis*, was subsequently regarded by McIntosh (1925) and Monro (1933) as a variety of *papillicornis*. *M. cincta* was the first species to be discovered with a strongly marked band of pigment encircling the body. Subsequently, *japonica* Okuda (1937) was described as having a deep purple band of pigment from the 5th to 8th setigers, that is in the same region as the red pigment in *cincta* and now in *alleni*. The markedly horned prostomium, parapodial structure and other features clearly separate *japonica* from *alleni* and from *cincta*. Ehlers's figures, especially the coloured one, bear a strong

resemblance to *alleni*, but his drawings and description are not entirely satisfactory (Wesenberg-Lund, 1949, p. 330, is in agreement) and lack proper figures of the parapodia. I could never satisfy myself that our species was in fact *cincta*; neither could I be quite sure on the basis of Ehlers's work that it was anything more than a variety.

Day (1957) has recorded *M. cincta* from South Africa. He has kindly sent me three of his specimens; one of them a short anterior end of about seventeen setigers from a depth of 15 m in Mossel Bay some 200 miles west of Algoa Bay, the type locality. The other two specimens, each of about forty setigers, came from intertidal sandy mud on Inhaca Island, Delagoa Bay, some 800 miles along the coast north-eastwards of Algoa Bay. These specimens are undoubtedly the same species and I am in agreement with Day's identification

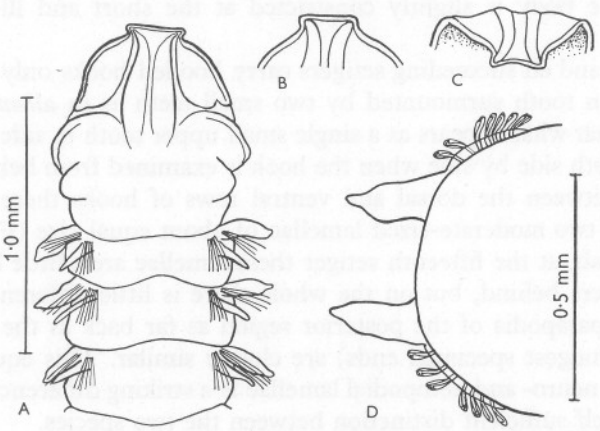

Fig. 2. *Magelona cincta* Ehlers. A, dorsal view of the head and first three setigers of a specimen from Mossel Bay, South Africa. The anterior third of the prostomium is bent upwards a little, giving a slightly foreshortened view of this end. The bristles are more numerous than drawn. B and C, anterior extremities of two specimens from Delagoa Bay, South Africa, both in dorsal view but C has the tip bent over backwards, revealing the ventral surface. D, 39th parapodium.

with *cincta*. They agree closely with Ehlers's description and figures, except that in all three the anterior extremity of the prostomium has at each side of the almost straight front edge much more pronounced corners—almost horns (Fig. 2 A–C)—than Ehlers indicates in his drawings. We are entitled to conclude that Day's specimens are true *cincta* and that they can be used to add to and amend the original description of the species by Ehlers. This will now be done so far as is necessary to define *cincta* more precisely and to distinguish it clearly from *alleni*.

The prostomium of *cincta* is in preserved specimens (Fig. 2A) about as long as broad, terminating anteriorly in a straight edge with pronounced corners, or very short horns. Two medianly placed low ridges extend anteriorly into the corners and are separated by shallow troughs from slightly convex areas

on either side. There are no eyes. One specimen retains one tentacle; it is at least twice as long as that indicated by Ehlers. The tentacle bears long and densely crowded papillae on one face for most of its length; the distal portion is slender, tapering gradually almost to a point and has evidently been fixed in a state of extension.

The anterior setigers all bear winged bristles only, unmodified on the ninth setiger. The bristles are relatively less robust than are those of *alleni*, a feature immediately obvious when similar-sized specimens of the two species are placed side by side. The parapodial lamellae of the first three or four setigers (Fig. 2A) are larger than those of succeeding setigers and they are quite small on the ninth. The neuropodial lamellae are larger than the notopodial. A band of brownish red (in alcohol) pigment encircles the body from the 5th to 8th setigers. The body is slightly constricted at the short and ill-defined 9th setiger.

The 10th and all succeeding setigers carry hooded hooks only. Each hook has one main tooth surmounted by two small teeth as in *alleni*. Ehlers did not notice that what appears as a single small upper tooth in side view is seen to be two teeth side by side when the hook is examined from behind or from in front. Between the dorsal and ventral rows of hooks there are in each parapodium two moderate-sized lamellae of about equal size (Fig. 2D). On the 10th to about the fifteenth setiger these lamellae are a little broader than on the setigers behind, but on the whole there is little difference anywhere and all the parapodia of the posterior region as far back as the 40th setiger (where the longest specimen ends) are closely similar. This equality in size between the neuro- and notopodial lamellae is a striking difference from *alleni* and is in itself sufficient distinction between the two species.

The two specimens from Delagoa Bay, each of about forty setigers and incomplete posteriorly, are both about 15 mm long and about 0·7 mm wide. Day informs me that his most westerly specimens, three in number, are from False Bay and were living in green mud at a depth of 43 fathoms.

The type specimen

Since the foregoing was written I have received on loan from the Zoologisches Museum, Berlin, to whose authorities and Dr G. Hartwich in particular I should like to express my gratitude, the type specimen described and figured by Ehlers (1908). It enables me to confirm that Day's specimens are definitely *cincta*. The type specimen is a fragment from a somewhat larger worm than those sent by Day but is very much smaller than full-grown *alleni*. Ehlers's specimen, as he recorded, is about 16 mm long by 1 mm wide and consists of a head and nineteen setigers. The right tentacle is missing; part of the left one is present and is clearly broken short. The specimen shows every indication of having been partially flattened. This has resulted in the extruded proboscis, which in *Magelona* worms normally forms a ventral bulbous

protrusion, being compressed and forced to extend forwards almost to reach the anterior end of the prostomium, as seen in Ehlers's figures (taf. XV, figs. 9, 10*a*) and in my Fig. 3A drawn with the aid of a camera lucida. The prostomium has been so flattened on top that the dorsal ridges, clearly visible in Day's specimens, can only just be distinguished. Ehlers's artist, when drawing his fig. 10*a* (but not his fig. 9) misinterpreted the structural relations

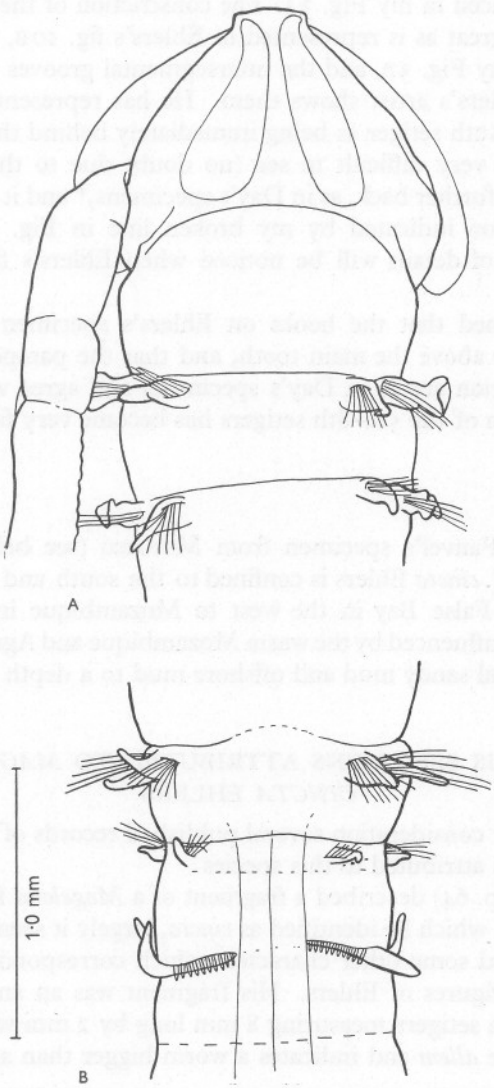

Fig. 3. The type specimen of *Magelona cincta* Ehlers in dorsal view. The bristles are more numerous than drawn. A, head and first two setigers. B, 8th–10th setigers.

between the postero-lateral corners of the extruded proboscis and the overlying prostomium, for he makes the proboscis tissue merge with the lateral walls of the body. The text shows that Ehlers himself was not clear in his own mind concerning the morphology of these parts. The artist has also 'smoothed out' the forwardly projecting anterior tip of the prostomium with its marked corners, which whilst not quite as prominent as in Day's specimens (no doubt due to the flattening) are none the less present, and have been carefully traced in my Fig. 3A. The constriction of the trunk at the 9th setiger is not as great as is represented in Ehlers's fig. 10B, which should be compared with my Fig. 3B, and the intersegmental grooves are by no means as distinct as Ehlers's artist shows them. He has represented the posterior boundary of the 10th setiger as being immediately behind the parapodia, but this boundary is very difficult to see (no doubt due to the flattening). It undoubtedly lies further back, as in Day's specimens,* and it can just be made out in the position indicated by my broken line in Fig. 3B. Some other reinterpretations of details will be noticed when Ehlers's figures and mine are compared.

I have confirmed that the hooks on Ehlers's specimen bear two small teeth side by side above the main tooth, and that the parapodial lamellae of the posterior region are as in Day's specimens and agree with my Fig. 2D. The pigmentation of the 5th–8th setigers has become very faint but is still to be seen.

Distribution

If we except Fauvel's specimen from Morocco (see below), the known distribution of *M. cincta* Ehlers is confined to the south and south-east coast of Africa, from False Bay in the west to Mozambique in the north-east, a length of coast influenced by the warm Mozambique and Agulhas Current. It occurs in intertidal sandy mud and offshore mud to a depth of at least 43 fm.

VARIOUS SPECIMENS ATTRIBUTED TO *MAGELONA CINCTA* EHLERS

There remain for consideration several published records of *M. cincta* Ehlers and of specimens attributed to this species.

Fauvel (1936, p. 64) described a fragment of a *Magelona* from the Atlantic coast of Morocco which he identified as *cincta*, largely it seems on the basis of the coloration and some other characters which corresponded well with the description and figures of Ehlers. His fragment was an anterior portion of head and thirteen setigers measuring 8 mm long by 2 mm wide, a dimension which fits mature *alleni* and indicates a worm bigger than any known *cincta*.

* In some specimens of *cincta* a transverse groove exists at parapodial level, depending on the state of contraction.

The prostomium was without horns, and 'les pieds portent une grande lamelle dorsale et une plus petite ventrale, et sont dépourvus de cirre'. This description almost perfectly describes the posterior parapodia of *alleni*. Fauvel's specimen may well be *alleni*, it cannot be *cincta*.

Clark & Milne (1955) found below tidal levels off the Island of Cumbrae in the Firth of Clyde some red-banded *Magelona* worms and, following a conversation with me, recorded them as *cincta*. Recently I have had an opportunity of examining several of their specimens and find that they are *alleni*.

From the British Museum (Natural History), through the kind offices of Mr N. Tebble, I have received on loan all their specimens attributed to *Magelona cincta*. They include one specimen (Reg. No. 1955.4.1.96) from the Morrumbene Estuary, Portuguese East Africa, which is indeed *M. cincta* Ehlers. It is of similar dimensions to those from Delagoa Bay (p. 622). A number of specimens (Reg. No. 1954.1.1.85/88) from the Dogger Bank, North Sea, are definitely *alleni*. Some further specimens (Reg. No. 1954.1.1.90/95) from Plymouth (collected originally by Mr N. A. Holme) are also *alleni*. It is interesting that several of these latter, all anterior ends, are fragments of larger worms than any in my own collection. One of them, comprising the head and seventeen setigers measures approx. 13 mm long by 2·5 mm where it is widest at the 6th–7th setigers; it was fixed in a state of contraction.

SUMMARY

A *Magelona*, common at Plymouth and previously provisionally identified as *M. cincta* Ehlers, is described as a new species and given the specific name of *alleni*.

M. cincta Ehlers is partially re-described from South African specimens and from the type specimen.

M. alleni n.sp differs from *M. cincta* Ehlers in several details including the shape of the prostomium and unmistakably in the structure of the parapodia of the posterior region. In *alleni* the notopodial lamellae are very much larger than the neuropodial while in *cincta* they are almost equal in size.

M. alleni occurs in the Firth of Clyde, on the Dogger Bank and in Quiberon Bay, N.W. France. A *Magelona* from the Atlantic coast of Morocco, described in the literature as *cincta*, is not *cincta* and is likely to be *alleni*. A wide distribution in the north-eastern Atlantic is indicated for this new species.

M. cincta Ehlers is known only from the southern and south-eastern coasts of Africa influenced by the warm Mozambique and Agulhas Current.

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ON SOME POGONOPHORA FROM THE NORTH-EAST ATLANTIC, INCLUDING TWO NEW SPECIES

By EVE C. SOUTHWARD and A. J. SOUTHWARD

The Plymouth Laboratory

(Text-figs. 1–3)

In the course of dredging for the rich epifauna of the continental slope near 48° 30′ N., 10° W. (Southward & Southward, 1958*b*) in May 1957, several hauls were made by chance on a muddy bottom at 500–700 fm. depth. At the time, these hauls were examined only cursorily after sieving, and the contents immediately preserved. One of the hauls contained several damaged siliceous sponges, and a recent careful examination disclosed a number of pogonophore tubes entangled among the threads and spicules of the sponges.

TABLE 1. RECORDS OF POGONOPHORA FROM THE CONTINENTAL SLOPE

Date	Position	Depth (fm.)	Bottom deposit	Species of *Siboglinum* found
4. v. 57	48° 28′ N., 10° 04′ W.	700	Mud containing a little sand and foraminiferan shells	*S. atlanticum*, *S. inermis*, *S. ekmani*
	48° 32′ N., 10° 10′ W.	670–720	Mud and a few stones	*S. atlanticum* (tubes only)
	48° 31′ N., 10° 11′ W.	520–680	Mud and some gravel	*S. atlanticum* (tube only)
17. v. 58	47° 56′ N., 7° 57′ W.	340–350	Mud containing sand and foraminiferan shells	*S. ekmani*
	47° 50′ N., 7° 57′ W.	300–450	Mud containing sand and foraminiferan shells	*S. inermis*
	47° 50′ N., 8° 08′ W.	670–710	Mud and cretaceous rocks	*S. atlanticum*

Nearly forty tubes, of three types, were found in this haul, most of them containing the animal in a good state of preservation (Southward & Southward, 1958*a*). Further searches among our collections have brought to light some empty tubes taken in two other hauls on the same cruise of R.V. 'Sarsia'. Once it was known that Pogonophora were present on the continental slope further dredging was arranged, and to date (June 1958) these interesting animals have been taken alive at three more stations (Table 1).

Although three species have been obtained, all belong to the genus *Siboglinum* Caullery. This was the first genus of the group to be described, and *S. weberi* remained for a long time the only known representative (Caullery, 1914, 1944). Later the Class name Pogonophora was suggested

(Johansson, 1937) for *Lamellisabella zachsi* Uschakov. *Siboglinum* was assigned to this group by Ivanov, who erected a new phylum of the Deuterostomia, Phylum Brachiata A. Ivanov, for the group (Ivanov, 1951, 1955). Investigations in the Pacific and Arctic oceans have revealed many new genera and species of pogonophores, while recently a species of *Siboglinum* has been discovered in deep water in the Skagerak (Jägersten, 1956; Ivanov, 1957; Kirkegaard, 1958). The Pogonophora are thus becoming well known, and their occurrence in the Atlantic Ocean proper is not unexpected.

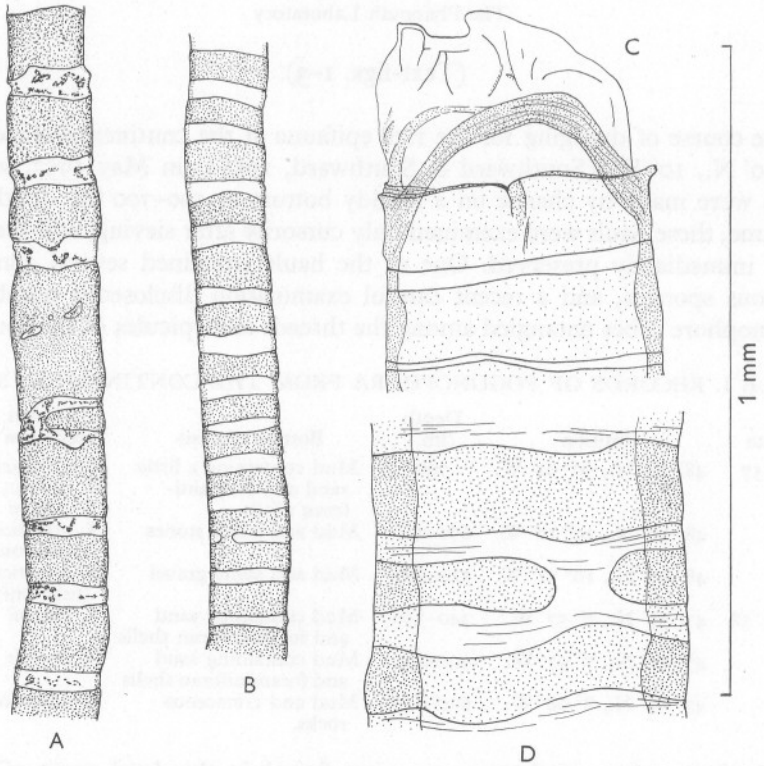

Fig. 1. Appearance of tubes: A, *Siboglinum inermis*; B, *S. ekmani*; C, anterior end of tube of *S. atlanticum*; D, middle of tube of *S. atlanticum*.

Of the three species included in this work, one is the Scandinavian species *S. ekmani*. The other two appear to be new, even though seven species of *Siboglinum* have already been described (Ivanov, 1957), omitting *S. weberi* which appears to include more than one species. The two new species are described first below, followed by some notes on our specimens of *S. ekmani*. Later we hope to deal with the biology of these animals, and to describe further species taken in only 80–90 fm. off the west coast of Ireland.

Siboglinum atlanticum sp.nov.

From twenty tubes of this species we obtained parts of fourteen animals. The two longest tubes were 40 and 32 cm long; most of the shorter ones were obviously incomplete. The diameter of each tube was about 0·42 mm near the anterior end, increasing to about 0·5 mm in the middle. The general colour was pale brownish grey, and the walls were ringed as shown in Fig. 1 D.

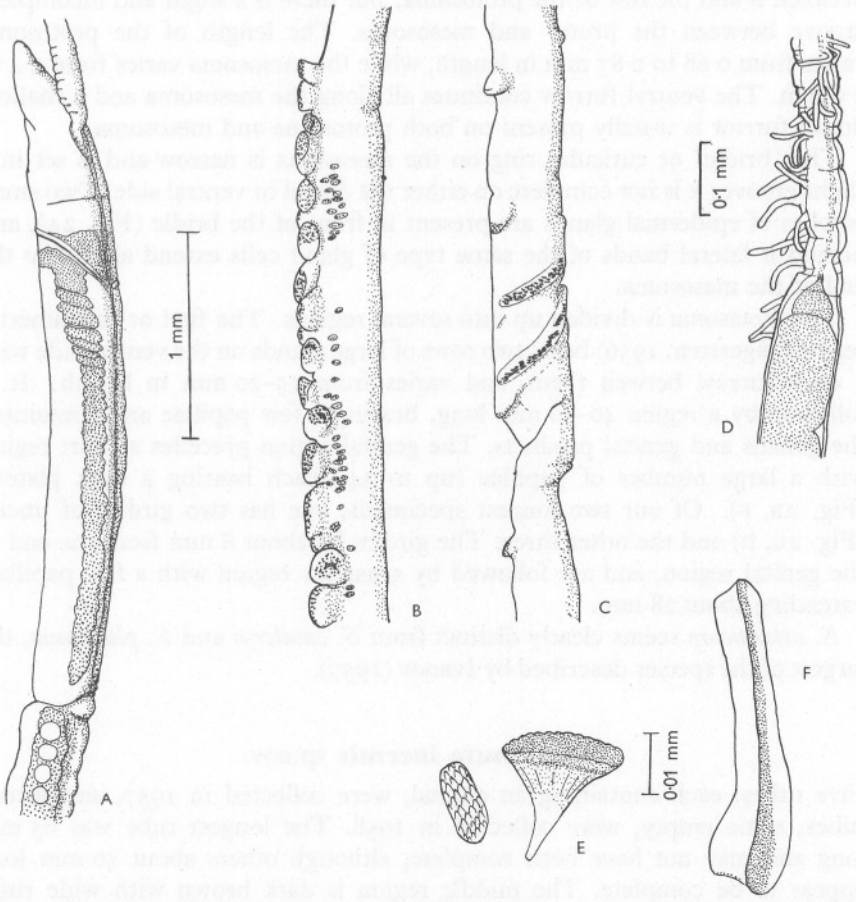

Fig. 2. *Siboglinum atlanticum*: A, anterior end, lateral view; B, part of region with papillae, lateral view; C, girdle region, lateral view; D, part of tentacle; E, uncini, surface and side view; F, platelet from one of the papillae, side view.

The anterior end is paler and in most cases is sealed by an extension of the tube lining (Fig. 1 C). Seven to 10 cm below this end is a brown mark, not more than 1 cm long, which may indicate the surface of the mud.

The two longest animals are both about 13 cm long, excluding the tentacle,

which may reach 2 cm in length. The other specimens are anterior ends up to 4 cm long. The tentacle is usually coiled up in preserved material; it bears two rows of pinnules set close together and in many specimens it is distended with blood for all or parts of its length (Fig. 2D). The blood is bright red in living specimens and brown when preserved. The tentacle rises from a furrow on the ventral side (Fig. 2A), and its junction with the body is narrow. The dorsal lobe is small and pointed, with no perceptible groove between it and the rest of the protosoma, but there is a slight and incomplete groove between the proto- and mesosoma. The length of the protosoma varies from 0·68 to 0·87 mm in length, while the mesosoma varies from 2·4 to 2·9 mm. The ventral furrow continues all along the mesosoma and a shallow dorsal furrow is usually present on both protosoma and mesosoma.

The 'bridle' or cuticular ring on the mesosoma is narrow and is set in a slight groove; it is not complete on either the dorsal or ventral side. Two small patches of epidermal glands are present in front of the bridle (Fig. 2A), and behind it lateral bands of the same type of gland cells extend almost to the end of the mesosoma.

The metasoma is divided up into several regions. The first or 'metameric' region (Jägersten, 1956) bears two rows of large glands on the ventral side with a deep furrow betwen them, and varies from 15–20 mm in length. It is followed by a region 40–50 mm long, bearing a few papillae and containing the gonads and genital products. The genital region precedes a short region with a large number of papillae (up to 34,) each bearing a dark platelet (Fig. 2B, F). Of our two longest specimens, one has two girdles of uncini (Fig. 2C, D) and the other three. The girdles lie about 8 mm from the end of the genital region, and are followed by a narrow region with a few papillae, extending about 28 mm.

S. atlanticum seems clearly distinct from *S. caulleryi* and *S. plumosum*, the largest of the species described by Ivanov (1957).

Siboglinum inermis sp.nov.

Five tubes, each containing an animal, were collected in 1957, and fifteen tubes, some empty, were collected in 1958. The longest tube was 65 mm long and may not have been complete, although others about 50 mm long appear to be complete. The middle region is dark brown with wide rings (Fig. 1A). These rings are almost opaque, and it is difficult to see the animal inside. Both ends of the complete tubes are colourless. The diameter of the tube ranges from 0·13 to 0·18 mm. The complete animal varies from 13·5 to 25 mm long, with a tentacle up to 3 mm long. The tentacle, in preserved and living specimens, is entirely without pinnules, and the specific name refers to this. The anterior part of the body varies from 0·70 to 0·96 mm in length, of which the protosoma forms 1/5 to 1/4 (Fig. 3A). The narrow bridle is com-

plete ventrally, but broken dorsally; a faint longitudinal groove runs along the ventral side of the mesosoma (Fig. 3A, B). It is difficult to distinguish epidermal glands on the mesosoma, but there seem to be at least two small patches just behind the bridle. The metasoma is short compared with that of *S. ekmani*; in one complete female it is 14 mm long, of which 5 mm carries metameric glands, 3 mm contains ovaries, 2 mm has a few papillae (without platelets), which are followed by the girdles and about 4 mm with a few papillae. Of

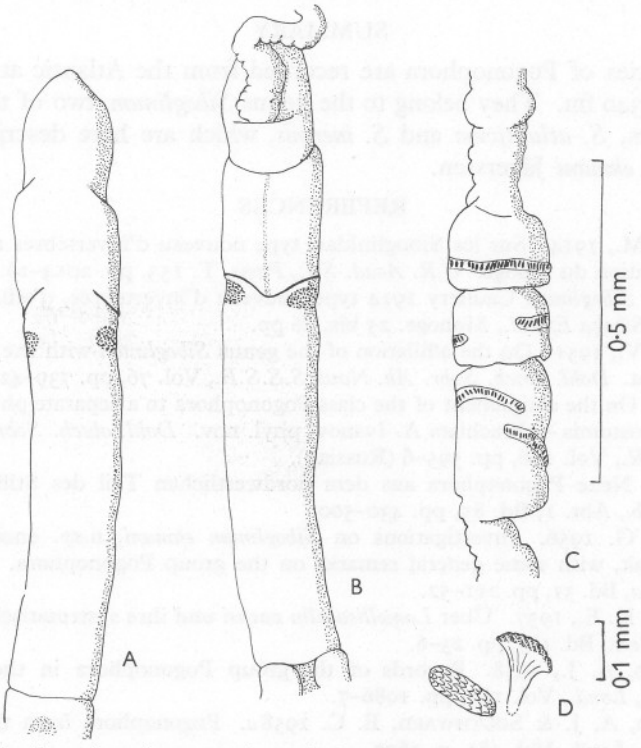

Fig. 3. *Siboglinum inermis*: A, anterior end, dorsal view; B, anterior end, ventral view; C, girdle region; D, uncini, surface and side view.

six specimens with complete girdle regions, two have three girdles and four have two. Each girdle is made up of a single row of uncini (Fig. 3C, D).

This species differs from *S. ekmani* in the type of tube, the diameter, the proportions of the body and in having a tentacle without pinnules.

Siboglinum ekmani Jägersten

The specimens described by Jägersten (1956) were incomplete, but our specimens agree with his description in the form (Fig. 1B) and size of the tube, in the proportions of the body and in having two rows of pinnules on the

tentacle. In our specimens the length of the longest tube was 10·5 cm, and the complete animal would appear to be about 30 mm long. The 'endobody' noted by Jägersten must have been produced by damage or preservation, since our specimens have a girdle region similar to *S. inermis*, except for the arrangement of the girdles. Each is composed of one row of uncini; the first and second are less than 0·2 mm apart, while the third is at least 1·5 mm behind the second. In one specimen there is a further 10 mm of body behind the girdles.

SUMMARY

Three species of Pogonophora are recorded from the Atlantic at depths of 710 up to 340 fm. They belong to the genus *Siboglinum*, two of them being new species, *S. atlanticum* and *S. inermis*, which are here described. The third is *S. ekmani* Jägersten.

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ON THE OCCURRENCE AND BEHAVIOUR OF TWO LITTLE-KNOWN BARNACLES, *HEXELASMA HIRSUTUM* AND *VERRUCA RECTA*, FROM THE CONTINENTAL SLOPE

By A. J. and Eve C. Southward
with an appendix by L. H. N. Cooper
The Plymouth Laboratory

(Plate I and Text-figs. 1–5)

The fauna of the continental shelf and slope between Ireland and Spain has been described by Le Danois (1948), but very little faunistic work has been carried out in the area recently. Since R.V. 'Sarsia' was brought into service at Plymouth there have been several opportunities of investigating that part of the slope lying to the south-west of the British Isles. It has been found that, in addition to beds of coral, quite extensive exposures of rocks, stones and gravel occur between 200 and 1000 fathoms. There is a rich epifauna in this area and barnacles are one of the dominant groups.

Only two species of barnacles are abundant. Both of them have been found, either as live specimens or dead shells, at many of the stations investigated. They are *Hexelasma hirsutum* (Hoek) and *Verruca recta* Aurivillius. We will first describe these species and their associated fauna, and then discuss their behaviour, as observed in the laboratory.

We are indebted to Dr L. H. N. Cooper for advice in this work, and to Dr J. P. Harding for facilities at the British Museum (Natural History). Thanks are due to Captain C. A. Hoodless and the crew of R.V. 'Sarsia', for their patience during many days of fruitless dredging, and to Dr D. Atkins, whose request for dredging on the slope led to the discovery of the barnacles.

Hexelasma hirsutum (Hoek)

Balanus sp. undescribed, Jeffreys, 1878.
B. hirsutus Hoek, 1883.
B. hirsutus Hoek, Gruvel, 1920.

Hexelasma hirsutum was first described by Hoek from material collected by H.M.S. 'Triton' in the Faroë–Shetland Channel, Station 10, 1882. The two specimens are now in the British Museum. Hoek assigned the species to the genus *Balanus*, and it was not until other related species were found that their

TABLE 1

Collection	Station	Depth	No. of specimens	Substratum	Author, or present location of material
		Hexelasma hirsutum			
'Porcupine'	48° 31′ N., 10° 03′ W.	690 fm	1	Shell of living brachiopod	Jeffreys, 1878 (as *Balanus* sp.)
'Triton'	59° 40′ N., 7° 21′ W.	516 fm.	2	*Cidaris* spine	Hoek, 1883 (as *B. hirsutus*)
Monaco	38° 31′ N., 26° 49′ W.	845 m	2	—	Gruvel, 1920 (as *B. hirsutus*)
Monaco	Azores area	—	3	Telegraph cable	Gruvel, 1920 (as *B. hirsutus*)
'Monarch'	48° 04′ N., 9° 23′ W.	1000 fm.	24	Telegraph cable	Specimens in British Museum
'Monarch'	48° 02′ N., 9° 25′ W.	930 fm.	6	Telegraph cable	
'Monarch'	48° 02′ N., 9° 27′ W.	900 fm.	10	Telegraph cable	
'Marie-Louise Mackay'	51° 23′ N., 11° 32′ W.	210 fm.	3	Telegraph cable	Specimens in authors' possession
'Sarsia' 1956/4	48° 33′ N., 10° 05′ W.	570–770 fm.	>60 and old shells	Rocks, gravel, dead coral, living brachiopod	
'Sarsia' 1956/8	47° 30′ N., 7° 20′ W.	870–970 fm.	Old shells only	—	
'Sarsia' 1957/1	48° 34′ N., 10° 0′ W.	570–700 fm.	>90 and old shells	Rocks, gravel, antler	
'Sarsia' 1957/1	48° 33′ N., 10° 01′ W.	580–680 fm.	Old shells only	—	
'Sarsia' 1957/1	48° 31′ N., 10° 11′ W.	520–680 fm.	Old shells only	—	
		Verruca recta			
Monaco	Azores area (8)	861–1385 m	10	Stones, rocks, coal and dead coral	Aurivillius, 1898; Gruvel, 1920
'Talisman'	Azores area (1)	960–990 m	1	Coral	Gruvel, 1902
'Travailleur'	—	2018 m	1	Coral	Gruvel, 1902
Monaco	28° 04′ N., 16° 49′ W.	1340–1530 m	1	—	Gruvel, 1920
'Sarsia' 1956/4	48° 33′ N., 10° 05′ W.	570–770 fm.	13	Stones, dead coral, shell fragments	Specimens in authors' possession
'Sarsia' 1956/8	47° 30′ N., 7° 28′ W.	550–600 fm.	1	Coral	
'Sarsia' 1956/8	47° 38′ N., 7° 28′ W.	710–750 fm.	8	Small stones, coral, clinker	
'Sarsia' 1956/8	47° 30′ N., 7° 20′ W.	870–970 fm.	2	Coal, coral	
'Sarsia' 1957/1	48° 42′ N., 9° 48′ W.	180–200 fm.	1	Shell	
'Sarsia' 1957/1	48° 33′ N., 10° 01′ W.	580–680 fm.	Old shells only	Stones, coral	
'Sarsia' 1957/1	48° 34′ N., 10° 00′ W.	570–700 fm.	12	Stones, coral	

affinity with the Chthamalidae was recognized, and the new genus *Hexelasma* erected (Hoek, 1913). Table 1 shows the older and the more recent records of *H. hirsutum*. Jeffreys's record is almost certainly this species, even though the specimen was not described (Jeffreys, 1878, p. 414). Its occurrence at the 'Porcupine' station on the shell of a living brachiopod (*Hispanirhynchia cornea* (Davidson), recorded by Jeffreys as *Rhynchonella sicula* Seguenza) has been repeated in one of the 'Sarsia' hauls; a living specimen of the same brachiopod was taken with a live *H. hirsutum* on one valve and a live *Verruca recta* on the other valve.

The known range of *Hexelasma hirsutum* is from the Faroë–Shetland ridge to the Azores. A related species, *H. americanum* Pilsbry, found on the western side of the Atlantic, appears to differ in external features and in the shape of the tergum (Pilsbry, 1916).

Description

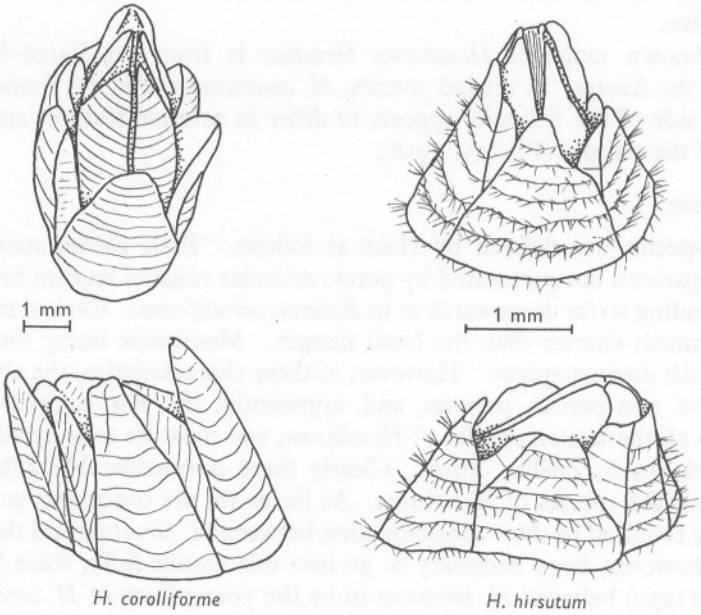
The species was defined by Hoek as follows: 'Basis membranous; radii absent; parietes not permeated by pores; articular ridge of tergum broad, but not extending so far downwards as in *Balanus corolliformis*. Carinal margin of tergum much shorter than the basal margin. Membrane lining the growth ridges with distinct spines.' However, of these characteristics, the absence of radii, the non-porous parietes, and, apparently, the non-calcareous basis apply to all the known species of *Hexelasma*, and must be considered generic (cf. Hoek, 1913; Pilsbry, 1916). Clearly there is considerable difficulty in separating the species of *Hexelasma*. As far as we are concerned at present, it is only required to show the distinction between *H. hirsutum* and the others. It has, however, been necessary to go into this matter fully, since Nilsson–Cantell (1930) believed *H. hirsutum* to be the young form of *H. corolliforme*. We have therefore re-examined the type specimens of *B. corolliformis* and *B. hirsutus* in the British Museum, as well as Nilsson–Cantell's specimens of *H. corolliforme* in the 'Discovery' collection.

H. hirsutum can be distinguished from other species by its markedly conical or tent-like shape (Pl. 1, fig. 1). Even on restricted substrata, such as sea-urchin spines and branches of coral, the diameter of the orifice is much smaller than the maximum diameter of the specimen (usually less than half). In normal uncrowded specimens from stones the diameter of the orifice is about two-fifths to one-third of that of the base, and the compartments do not diverge from one another. In these characters this species differs strongly from *H. corolliforme*. We have examined small specimens of both species (down to 1 to 2 mm in diameter in *H. hirsutum*) and find the shape still distinctive (Text-fig. 1).

The difference in shell form is clearly demonstrated by the rostral compartment, which is triangular in *H. hirsutum* and elongate in *H. corolliforme* (Text-fig. 2). The rostra of both old and young *H. hirsutum* have an index

(height/width) of 0·8–0·9, while the type and other specimens of *H. corolliforme* have an index of 1·2–3·1. The other main character distinguishing *H. hirsutum* from *H. corolliforme* and most other species is the shape of the tergum.

	Length carinal margin/ length of basal margin	Length articular ridge/ length of basal spur
H. hirsutum	1/1·4	1/1·5
H. corolliforme	1/1·1–1·2	1/1·1–1·2



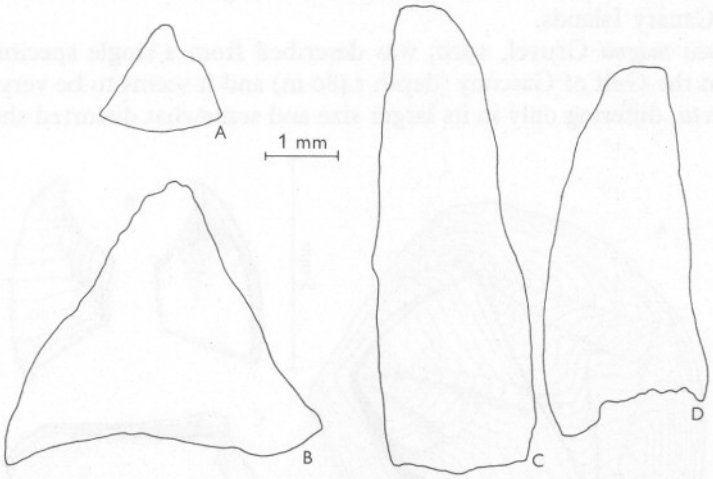
Text-fig. 1. Small specimens of *Hexelasma corolliforme* and *H. hirsutum*. Above, oblique view from rostral aspect; below, side views with rostra adjacent.

These measurements show that, in *H. hirsutum*, as reported by Hoek, the tergum is more elongate from apex to spur and the articular ridge is relatively shorter (Text-fig. 3).

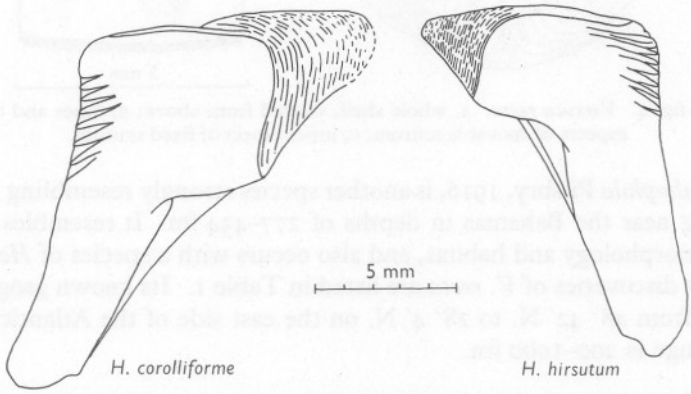
There appear to be few other differences between the species of *Hexelasma*, and we have not been able to find any differences between the mouthparts of *H. hirsutum* and *H. corolliforme*.

All our specimens are conical in shape and fully hirsute all over (Pl. I, figs. 1–5). The edges of the compartments are reflexed under the basis for 1–2 mm or less depending on size. On removal from the substratum a distinct 'scar' can be seen. This is possibly the same as the thin calcareous basis reported by Pilsbry (1916) for another species of the genus. Only the remains of the reflexed edges of the compartments show strong effervescence with acetic acid. The vaguer white patches in the middle of the scar partly

disappear in acid and may be weakly calcified. The scar shows distinct growth rings, and must therefore be formed by the reflexed margins of the compartments rather than by the basal membrane. It cannot be regarded as a true calcified basis such as is found in species of *Balanus*.



Text-fig. 2. Outline drawings of rostra of *Hexelasma hirsutum* (A and B), and *H. corolliforme* (C and D).



Text-fig. 3. Terga of large specimens of *Hexelasma*, inner side, showing articular ridge.

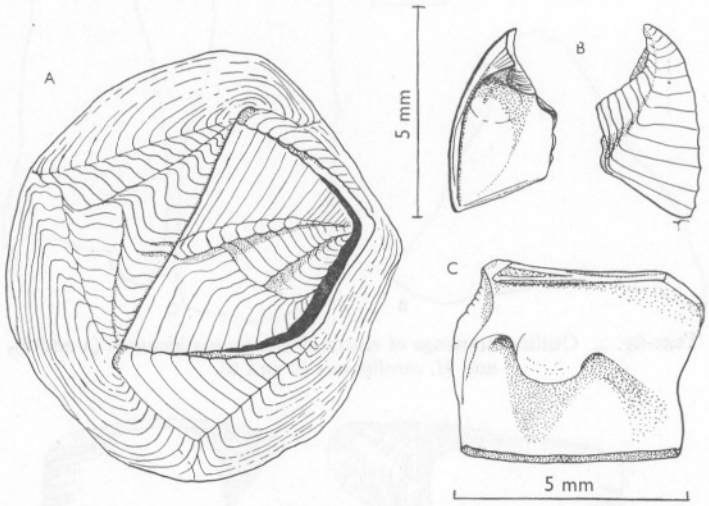
Verruca recta Aurivillius

Verruca recta Aurivillius, 1898.
V. linearis Gruvel, 1902.
V. recta Aurivillius, Gruvel, 1920.

This species was first described by Aurivillius (1898), who found it among material from the Azores region (see Table 1). It was next encountered by

Gruvel (1902) in another collection from the Azores. He named it *V. linearis*, believing his specimens to be specifically distinct from those of Aurivillius. However, when he examined the Monaco collections he decided that his earlier specimens were, after all, *V. recta* (1920). By this time specimens had been collected at further stations in the Azores regions and also at one station off the Canary Islands.

Verruca magna Gruvel, 1920, was described from a single specimen collected in the Gulf of Gascony (depth 1480 m) and it seems to be very similar to *V. recta*, differing only in its larger size and somewhat distorted shell.



Text-fig. 4. *Verruca recta*. A, whole shell, viewed from above; B, inner and outer aspects of movable scutum; C, inner aspect of fixed scutum.

V. coraliophila Pilsbry, 1916, is another species strongly resembling *V. recta*, occurring near the Bahamas in depths of 277–434 fm. It resembles *V. recta* in both morphology and habitat, and also occurs with a species of *Hexelasma*.

Recent discoveries of *V. recta* are listed in Table 1. Its known geographical range is from 48° 42′ N. to 28° 4′ N. on the east side of the Atlantic, and its depth range is 200–1000 fm.

Description

The external characters of *V. recta* were described by Aurivillius (1898) and Gruvel (1902, 1920); we will here describe certain variations in these features and also some of the internal features.

The appearance of the whole animal is shown in Text-fig. 4A; the operculum is formed of either the right of left tergum and scutum, and we have about equal numbers of specimens of each type. The movable scutum (Text-fig. 4B) has two large articular ridges and a third very narrow ridge,

which is not visible from above in about half our specimens. The basal edges of the fixed plates are reflexed inwards as in *V. coraliophila* (Pilsbry, 1916), and there is a tongue-shaped adductor ridge protruding from the inner side of the fixed scutum (Text-fig. 4c). Neither of these characters was noted by Aurivillius or Gruvel; they indicate that *V. recta* belongs to the same subgroup of the genus as *V. coraliophila*, and that the two species may be synonymous.

The mouthparts are of the usual *Verruca* type, with no distinctive characters. The proportions of the rami of the first three pairs of cirri are of more help. The first cirrus has equal rami; the second has an anterior ramus about two-thirds the length of the posterior; in the third cirrus the anterior ramus is about four-fifths the length of the posterior. The caudal appendages are shorter than in other species of *Verruca*, being only one-fourteenth of the length of the sixth cirrus, and about three-quarters the length of its protopodite. In a large specimen each appendage had only seven segments. Pilsbry (1916) has recorded measurements of the cirri and caudal appendages for several species of *Verruca*, though not for *V. coraliophila*. Of these species the one with the most nearly corresponding measurements is *V. halotheca* Pilsbry, a Pacific species belonging to the same subgroup of the genus, and one which also resembles *V. recta* in both external features and habitat.

HABITAT AND ASSOCIATED FAUNA

The depths at which *Hexelasma hirsutum* and *Verruca recta* have been found, and the nature of the substrata on which they occur, are included in Table 1. Both species have been found on the same variety of substrata, including igneous and sedimentary rocks and living or dead shells of other animals, though only *Hexelasma* has been recorded from telegraph cables. Presumably they will settle on almost any exposed solid object if other conditions are favourable.

The two species differ somewhat in depth range. *Verruca* was found from just under 200 fm. to about 1000 fm., although most abundant at the 500–700 fm. level. It appears to be the more widespread, occurring alive at more of the 'Sarsia' stations than *Hexelasma*. The latter, with one exception, has been found only between 500 and 1000 fm. The exception is material from a cable, and it seems possible that the cable was hauled up from deeper water than that beneath the ship. *Hexelasma* is very abundant in the vicinity of the original 'Porcupine' station. The sea bed in this region of the continental slope is not particularly steep, but is very irregular. The echo-sounder records show the multiple criss-crossing bottom traces characteristic of submarine valleys, and it seems possible that the steep sides of these valleys may offer a very favourable habitat.

At the 500–700 fm. level, where both *Hexelasma* and *Verruca* are abundant,

there is a characteristic associated fauna. Sponges, probably *Hymedesmia* sp., cover some of the rocks and sometimes the barnacles themselves. Attached to the rocks and stones, among the barnacles, are several species of solitary corals; two or three as yet unidentified species of serpulid worms; and the holothurian *Psolus squamatus* Koren. Mobile animals found in the same dredge hauls included the polychaetes *Eunice pennata* (O. F. Müller) and *E. oerstedii* Stimpson, the decapod *Munida tenuimana* Sars*; the echinoderms *Ophiacantha* sp., *Ophiactis* sp., and *Stereocidaris ingolfiana* Mortensen; and the brachiopods† *Hispanirhynchia cornea* (Davidson) and *Dallina septigera* (Lovèn).

At one of the deeper stations (47° 30′ N., 70° 20′ W., 870–970 fm.) at which *Verruca* was found in the living condition, the fauna was rather different. Living and dead branches of the coral *Anisopsammia rostrata* (Pourtales) were abundant. Also present were *Munida microphthalma* A. Milne-Edwards*; the echinoderms *Ophiacantha* sp., *Ophiactis* sp., *Korethraster hispidus* Wyv. Thomson and *Hypsechinus* sp.; and the brachiopod *Platidia* sp.

At the shallower station (48° 42′ N., 9° 48′ W., 180–200 fm.) at which only *Verruca* was obtained, the fauna was characteristic of the coral region of Le Danois (1948), with *Lophohelia*, *Dendrophyllia*, and *Caryophyllia*, as well as several decapods and eunicid worms.

BEHAVIOUR

Some notes on the behaviour of *Hexelasma hirsutum* were made on the material collected in 1956. Regular beating of the cirri, such as occurs in most other species of barnacles, was never seen; it was found that water movement was necessary to induce extension of the cirri, which were fully protruded from the shell only within a restricted range of temperatures (Southward, 1956). These findings have been partly confirmed and partly amended by experiments on the 1957 material, as described below.

Water currents

The influence of water movement was studied at several temperatures (Table 2). Full extension of the cirri was induced only by water currents in excess of 1 cm/sec. Raising the velocity from 1 to approx. 5 cm/sec. caused a sharp increase in the number of barnacles with their cirri extended. Above 5 cm/sec up to the highest speed obtained in the apparatus (30 cm/sec) there was little or no increase in the number reacting, and in some experiments there were signs that very fast currents had an inhibiting effect.

Sensitivity to water movement was very strong. Extension of the cirri

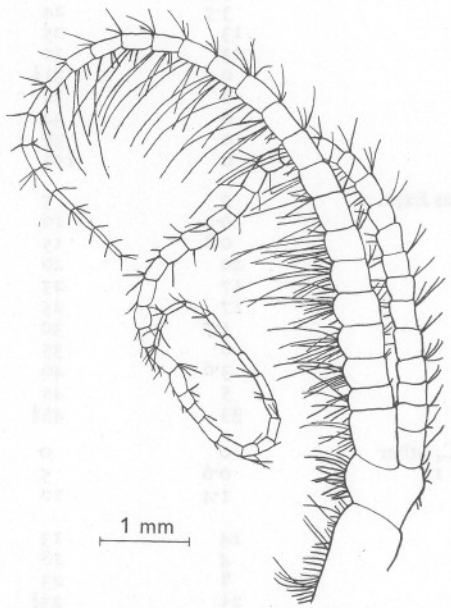
* Identified by Dr R. B. Pike. † Identified by Dr D. Atkins.

TABLE 2. EFFECT OF WATER MOVEMENT ON THE BEHAVIOUR OF *HEXELASMA HIRSUTUM*

	(Water speed cm/sec)	Min from start	No. with cirri extended, out of 47
Expt. 1. In constant temp. room at 5° C; overnight without water movement. Light for Expt. 48 W.	0	0	0
	0·8	10	0
	2·2	12	1
	2·2	17	2
	3·5	18	2
	3·5	23	5
	3·5	24	6
	13	25	6
	13	31	8
	0	31½	2
	0	32	3
	0	34	1
	0	38	3
	0	158	0
Expt. 2. Conditions as Expt. 1	0	5	0
	0·4	10	0
	0·8	15	0
	20	20	3
	17	23	8
	17	25	7
	1·7	30	2
	6	35	7
	3·6	40	5
	5	45	7
	33	45½	8
Expt. 3. Temp. 7° C, other conditions as Expt. 1	0	0	0
	0·6	5	(1 intermittent)
	1·4	10	(2 intermittent, (3 'pumping')
	14	13	9
	4	18	7
	8	23	14
	25	23¼	10
	0	23½	6
	0	24	3
	0	26	1
	0	31	0
Expt 4. Four hours without water movement; temp. 8° C; other conditions as Expt. 1	0	0	(1 intermittent)
	0·4	5	(1 intermittent)
	0·6	10	(1 intermittent)
	1·3	15	1
	3·3	20	3
	17	25	7
Expt. 5. Overnight without water movement at 4° C then temp. reduced to 0·3° C in 2 h using current of 17 cm/sec to circulate water over cooling vessels of ice and salt	0·8	5	(2 intermittent)
	1·2	10	(3 intermittent)
	11	15	4
	17	20	6
	25	25	7
Expt. 6. Specimens kept at 10° C for 2 days, then brought into room with diffuse daylight, temp. 15·6° C.	0	5	(5 intermittent)
	0·7	10	6
	7	15	9
	10	20	6

occurred within a few seconds of starting the paddle wheel that generated the current, and most of the specimens withdrew their cirri a few seconds after the paddle wheel stopped, although one or two remained extended for 5 min or so after prolonged periods of current stimulation. Slowing down the velocity of the current from over 10 cm/sec to less than 5 cm/sec caused an immediate reduction in the number extended; an immediate increase could be obtained by speeding up the current again (Table 2, expts. 2 and 3).

Some of this sensitivity to water currents may lie in the peculiar 3rd cirri



Text-fig. 5. Third cirrus of preserved specimen of *Hexelasma hirsutum*, 9 mm diameter.

of *Hexelasma*. The rami are usually of unequal length, as in most Chthamalidae, with a ratio varying from 1·4:1 down to almost 1:1 (the latter in older specimens). The longer ramus is very flexible, and thinner than the short ramus (Text-fig. 5). When the cirri are extended in a water current (Pl. 1, figs. 2, 3) the long ramus streams out and contrasts with the rest of the cirral net which is held stiffly in the current. The flexible ramus is insensitive to touching that causes bending of some of the other rami, and does not therefore appear to be part of a captorial apparatus. Possibly the long rami function as direction indicators, allowing the cirral net to be swung into the best position for capturing particles carried by the current (Pl. I, figs. 4, 5).

In contrast to *Hexelasma*, *Verruca* may extend its cirri in still water. Nevertheless, some experiments showed that water currents of 5–25 cm/sec would stimulate closed specimens of *Verruca* to full extension. Specimens of

the holothurian *Psolus squamatus*, which were present on stones with the barnacles, were also observed. Extension of the tentacles was stimulated by water movement, though the extension was very much slower than cirral extension in the barnacles.

Temperature

Experiments on the effect of temperature on extension of the cirri of *Hexelasma* are reported in Table 3. Up to one-third of the specimens under observation would extend their cirri between 7° and 12° C. Outside this

TABLE 3. EFFECT OF TEMPERATURE ON THE BEHAVIOUR OF *HEXELASMA HIRSUTUM*

(Water current approx. 7–25 cm/sec.)

Temperature (° C)	Number of specimens out of 47 showing extension of cirri
−0·4	(10 intermittent)
0	(5 intermittent)
0·1	7
0·3	7
0·8	7
1·6	8
5·0	8
7·0	10–14
8·0	7
9·0	8–13
11·3	8
12·1	8–11
15·6	9
16·5	(5 intermittent)
18·0	8
19·8	3
20·5	(4 intermittent)
22·2	(2 intermittent)
24·0	(1 intermittent)
24·5	50 % coma
26·5	100 % coma

optimum range some extension was observed between 0° and 20° C. Some activity, but not full extension, was shown up to 24·5° C., at which temperature more than 50% succumbed to heat coma. *Verruca* also showed heat coma at this temperature. The range of temperatures over which *Hexelasma* would extend the cirri is greater than that reported previously for the 1956 material. The latter showed extension only between 3° and 8° C.

Both the 1956 and 1957 collections of *Hexelasma* were first examined 5–6 days after capture, but during this period they were treated differently. The 1956 material was brought back on the deck of R.V. 'Sarsia' under a flow of sea water from the deck supply; the specimens must have been subjected to great temperature variation during the voyage and may have suffered damage. The 1957 material was transferred immediately on capture to a

refrigerator at 5–7° C and brought back to the laboratory constant temperature room which was also at 5–7° C. Since the sea temperature at the depth the specimens came from was about 7–9° C (see Table 4), there would be much less chance of shock or damage.

Orientation of Hexelasma

The sensitivity of *Hexelasma* to water movement suggested that it might settle or grow in a position with the cirral net facing the prevailing water current in the habitat, as do many other barnacles (Crisp & Stubbings, 1957). Since the stones were very irregular, and as their original orientation on the sea bed was not known, the possibility of orientation to a current was tested by measuring the correspondence of the carino-rostral axes of barnacles on stones bearing groups of five or more. Of fifty-six barnacles measured in this way, the approximate angles subtended between them and a selected reference specimen (usually the largest in the group) were, in percentages:

0° C	45° C	90° C	135° C	180° C
48	30	9	6	7

That is, on average, three out of four specimens in each group faced the same way, or at an angle that allowed them to swing the cirral net, which easily traverses an arc of 90° (Pl. I, figs. 4, 5), to face the same way. It is not known, of course, whether all groups tested faced the same way, but it is a reasonable assumption that they did. The specimens facing away from the direction of the majority were mostly on large or irregular stones and may have been orientated to minor reverse eddies.

DISCUSSION

Barnacle communities of shallow water areas are best developed on wave-beaten rocky coasts or in estuaries with strong tidal currents, and it is a general rule that most species need water movement in their habitat to succeed in competition with other sessile organisms. This rule seems to apply to the deep-water species described here; their behaviour and orientation strongly suggest that they receive considerable water movement in their natural habitat.

These barnacles, and many other common animals in the same habitat, are sessile, and need hard substrata to grow on. Hard substrata are more likely to be exposed where water movement prevents the accumulation of fine particles. At the stations where the barnacles were most abundant the rocks and stones were partially embedded in a muddy bottom, as shown by the absence of a black deposit of manganese oxide present on the exposed parts (see Peach, 1912). Similar partly embedded rocks have been dredged elsewhere, and their position in the deposit, as deduced from the blackening, has been held as evidence that they were once buried in the deposit and more

recently exposed by water currents that carried away the fine particles (Peach, 1912).

Biologically and geologically, therefore, there is strong evidence for the existence of water currents where the barnacles occur. The velocity of the currents, judging from the behaviour of the barnacles, must be at least 1–5 cm/sec (0·9–4·3 km/day); such a current would be able to remove particles of fine sand (0·02–0·2 mm diameter) as well as the finer particles of silt and clay.

SUMMARY

Hexelasma hirsutum (Hoek) and *Verruca recta* Aurivillius are common at many stations on the continental slope to the south-west of the British Isles, the former at depths of 500–1000 fm., the latter from 200 to 1000 fm. Certain external and internal features of these species are described and their systematic status redefined. Their behaviour in the laboratory suggests that they are accustomed to considerable water movement in their natural habitat, and the significance of this inference is discussed.

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APPENDIX

Environmental conditions on the slope

By L. H. N. Cooper

In Table 4 an attempt is made to assess the hydrographic conditions under which the larger barnacle, *Hexelasma hirsutum*, was living. It will be seen that temperatures ranged from 4·2° to 9·4° C., salinities were between 35·1 and 35·5‰, and the water was well oxygenated. These temperatures agree with the range of temperatures over which *Hexelasma* showed most activity.

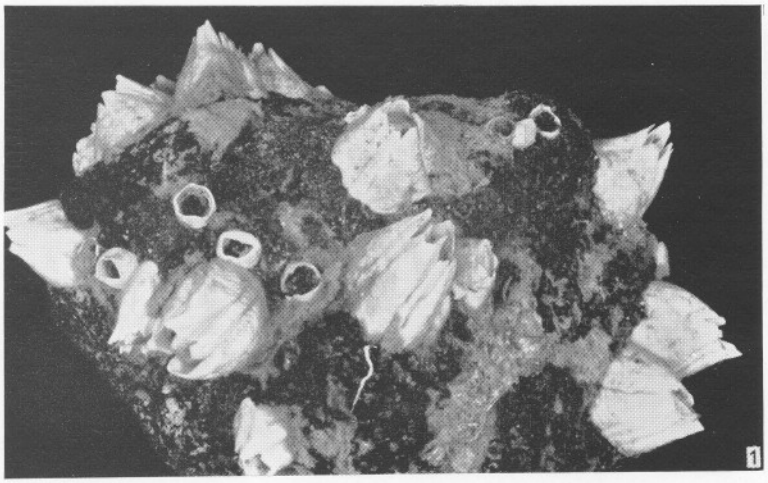
TABLE 4. HYDROGRAPHIC CONDITIONS AT STATIONS ADJACENT TO THOSE AT WHICH LIVING *HEXELASMA HIRSUTUM* WERE TAKEN

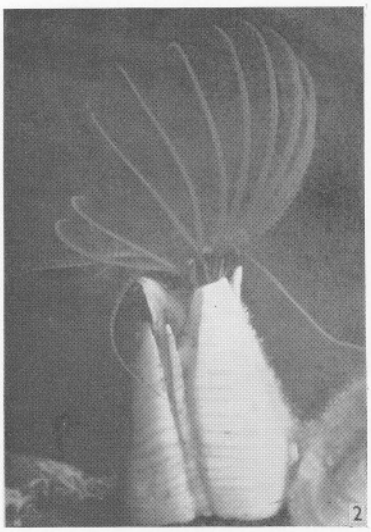
Dredge station	Depth (fm.)	Temp. (° C)	Salinity (‰)	Oxygen (ml./l.)	Silicate (μg-atom/l.)
48° 31′ N., 10° 03′ W.	690	6·9–7·7	35·4	4·5	13
59° 40′ N., 7° 21′ W.	516	8·4	35·3	—	— *
38° 31′ N., 26° 49′ W.	845	7·9–8·7	35·3	—	— †
48° 04′ N., 9° 23′ W.	1000	4·2	35·0	5·0	20
48° 02′ N., 9° 25′ W.	930	4·5	35·1	5·1	15
48° 02′ N., 9° 27′ W.	900	4·6	35·1	5·2	15
48° 33′ N., 10° 05′ W.	570–770	6·5–9·4	35·3–·5	4·1– ·8	12–14
48° 34′ N., 10° 00′ W.	570–700	6·7–9·4	35·3–·5	4·2–5·8	11–14

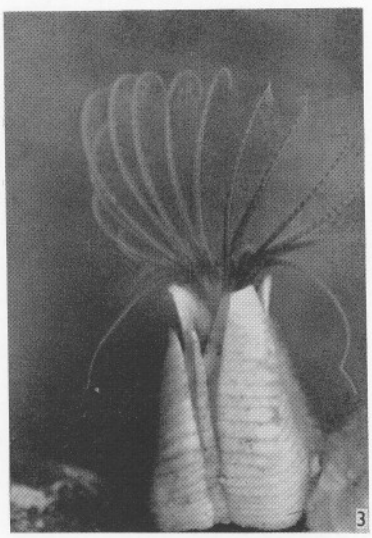
* From Tait (1957). † From International Council (1944, p. 126); the remainder from unpublished data, L. H. N. Cooper.

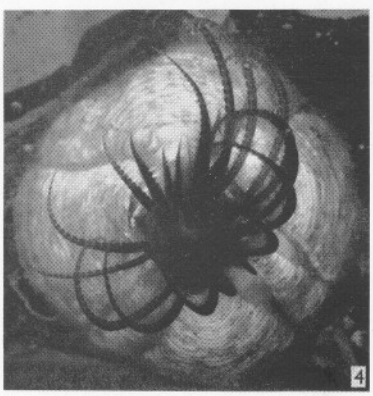
It is probably coincidental, but water at all stations would have contained a proportion of 'Gibraltar Water' formed by mixing of warm, deep, saline water from the Mediterranean basin with deeper North Atlantic Central water. The occurrence of *Hexelasma* at the Azores suggests that the barnacle is not in need of materials which may be carried by cascading water from the continental shelf.

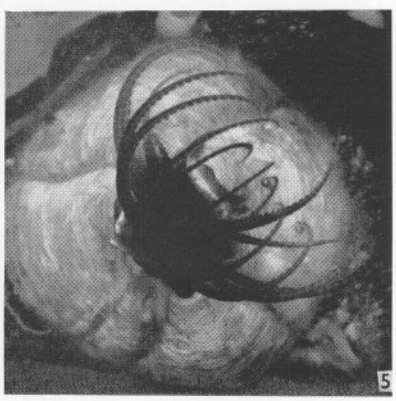
To the physical oceanographer the inference that the habitat of these deep-water barnacles is one of considerable water movement is of much importance. Such water movements could be oscillating surges resulting from internal waves or steady currents running along the slope, and it would be helpful if the barnacles themselves could be orientated. Dried specimens of *Hexelasma* were sent to Dr R. S. M. Nairn of Newcastle, in the hope that they might have measurable magnetic orientation, when the direction of the water current could be assumed to be the same as the carino-rostral axis (i.e. the direction which the cirral net faces). However, no deflexion of the magnetometer needle was observed. Sometimes iron objects discarded from ships are dredged up: if such an object is found in future, with barnacles growing on it, the residual magnetism may provide a measure of the direction of water movement *in situ*.











(*Facing p.* 646)

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EXPLANATION OF PLATE I

Fig. 1. Group of *Hexelasma hirsutum* on a piece of rock, which also bears one live and several dead specimens of *Verruca recta*, as well as patches of sponge and a serpulid tube. $\times \frac{1}{2}$.
Fig. 2. *Hexelasma* viewed from the carinal aspect, showing cirral net turned to face water current coming from the left. Note long rami of 3rd cirri streaming in current. $\times 1\frac{1}{2}$.
Fig. 3. The same specimen as fig. 2 just after water current was stopped.
Figs. 4, 5. View of larger *Hexelasma* from above showing rotation of cirral net. Current from left. In this specimen the 3rd cirri have almost equal rami. Approx. natural size.

Figs. 2–5 taken at 5° C in constant temperature room, with specimens subjected to water current of 5–20 cm/sec in apparatus described by Southward (1957). Approx. 2:1 on negative (Pan F); electronic flash tube $\frac{1}{2}$–1 ft. away, 100–300 J; Elmar 50 mm lens at f18.

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THE BREEDING SEASON OF SOME LITTORAL ASCIDIANS IN SCOTTISH WATERS

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(Text-fig. 1)

In previous papers (Millar, 1952; 1954*a*; 1954*b*) I have dealt with the reproductive cycle of several ascidians in Scottish waters, and in the present account observations are extended to other species.

The course of breeding was studied in the following species. Family Polyclinidae: *Sidnyum turbinatum* Savigny, *Aplidium nordmanni* (Milne Edwards), *A. punctum* (Giard), *A. pallidum* (Verrill) and *Polyclinum aurantium* Milne Edwards. Family Didemnidae: *Didemnum candidum* Savigny and *Lissoclinum argyllense* Millar. Family Clavelinidae: *Clavelina lepadiformis* (Müller).

Material was collected at intervals, mostly of 1–2 months, throughout the years 1952 and 1953, from the lower part of the shore of the island of Luing, Argyll. At the collecting station Luing and a neighbouring island converge to form a narrow sheltered channel much of which dries at low water of spring tides, and in this area ascidians of several species are abundant.

Breeding condition of each sample was measured by the percentage of specimens having embryos or larvae in the zooids (Families Polyclinidae and Clavelinidae) or in the common test (Family Didemnidae).

Fig. 1 (C–H, J, K) shows the course of breeding in the eight species just studied. Comparable results for other species previously investigated (Millar, 1952; 1954*a*; 1954*b*) are also shown graphically (A, B, I, L). All results are plotted on the same time base, although they refer to different years, this procedure being justified, first by the need to get a general picture of breeding, and second by the relatively small year-to-year variations.

A relationship between sea temperature, breeding and geographical distribution in marine animals has been widely recognized, particularly by Appellöf (1912), Orton (1920), Runnström (1927, 1929, 1936), and Hutchins (1947). Orton noted that temperature apparently controls the breeding season in many marine animals, and Runnström found experimentally that embryonic development of species occupying the high, middle and low latitudes of the boreal region was possible only at the temperatures prevailing in the corresponding geographical ranges.

The ascidian species of which the breeding period in Scottish waters is now known fall into three geographical groups, as follows: (1) boreo-arctic

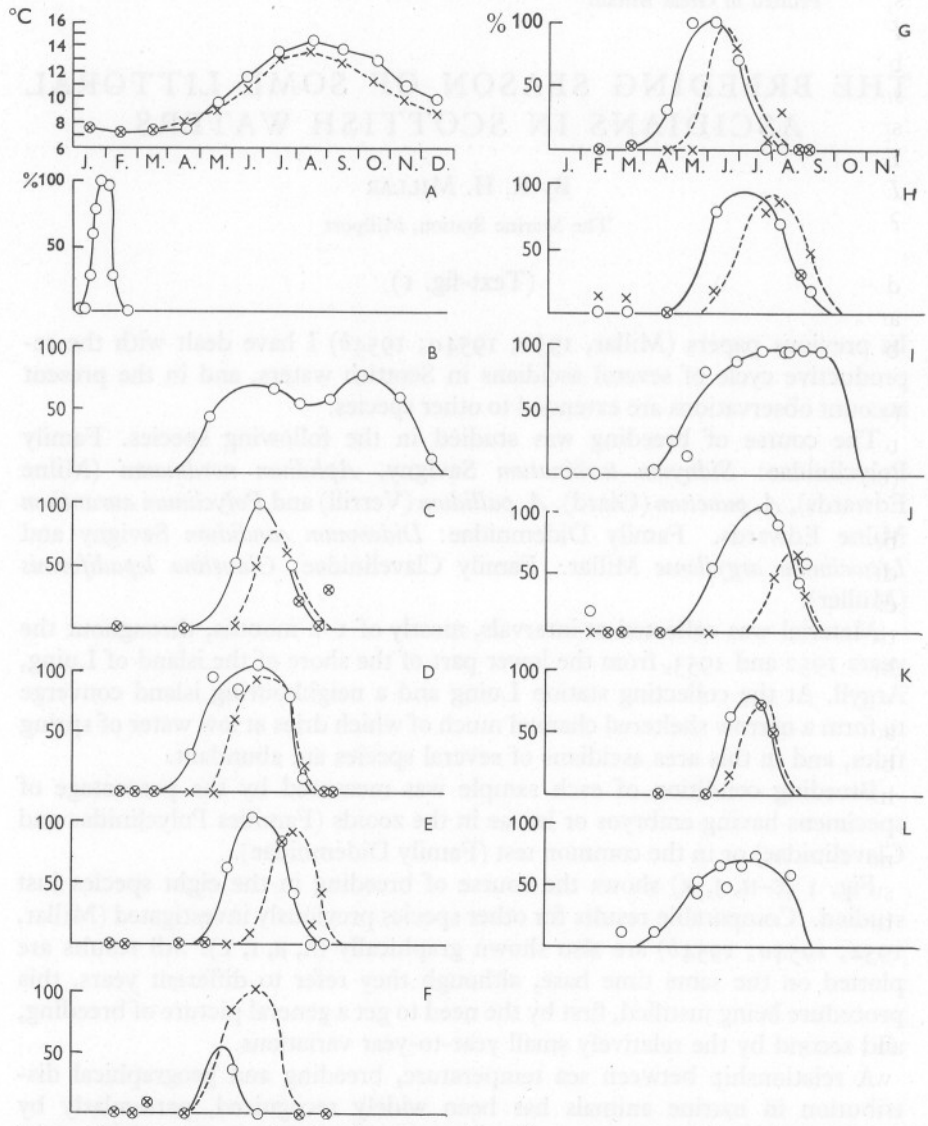

Fig. 1. Smoothed curves showing the course of breeding as represented by the percentage of each sample with developing embryos (○—○) and with larvae (×---×) in the colonial species (C–L). In *Pelonaia corrugata* (A) the curve shows the percentage of each sample in the process of spawning, as indicated by the condition of the gonad. In *Dendrodoa grossularia* (B) the curve shows the percentage of each sample with developing embryos or larvae. At the top left corner of the figure is shown the monthly mean sea surface temperature at Millport for the year 1952 (×---×) and 1953 (○—○). A, *Pelonaia corrugata;* B, *Dendrodoa grossularia;* C, *Aplidium pallidum;* D, *Sidnyum turbinatum;* E, *Aplidium nordmanni;* F, *A. punctum;* G, *Polyclinum aurantium;* H, *Didemnum candidum;* I, *Diplosoma listerianum;* J, *Lissoclinum argyllense;* K, *Clavelina lepadiformis;* L, *Botryllus schlosseri.*

species centred in arctic and extending southwards into boreal waters, e.g. *Pelonaia corrugata* Forbes and Goodsir; (2) boreo-arctic species centred in boreal and extending northwards into arctic waters, e.g. *Dendrodoa grossularia* (van Beneden) and ? *Aplidium pallidum* (Verrill); (3) true boreal species, including *Sidnyum turbinatum* Savigny, *Aplidium nordmanni* (Milne Edwards), *A. punctum* (Giard), *Polyclinum aurantium* Milne Edwards, *Didemnum candidum* Savigny, *Diplosoma listerianum* (Milne Edwards) and ? *Lissoclinum argyllense* Millar.

The question mark before *Aplidium pallidium* indicates that its centre of distribution is uncertain, and the one before *Lissoclinum argyllense* that records are still very scarce. The remaining six of the eight species newly studied are boreal.

It is evident from Fig. 1 that the breeding periods are of three kinds: (1) short and restricted to the winter (A), (2) long, and extending from spring to late autumn (B), (3) short or moderately long, and restricted to the summer (C–L).

These three groups of species, defined by the time and extent of the breeding season, are the same groups as those defined earlier by geographical distribution. It appears, therefore, that in the species studied the time and extent of the breeding period is related to the centre of geographical distribution of the species. Water temperature is the factor most likely to control the breeding period.

North boreo-arctic species are in British waters near their southern limit, and the short breeding period of *Pelonaia corrugata* suggests that the southern boundary of species in this group may be fixed by winter temperatures too high for breeding farther south.

Boreal, and especially south boreal, species are in British waters near their northern limit and the short breeding period of several boreal ascidians suggests that the northern boundary is probably fixed by summer temperatures too low for breeding, farther north.

SUMMARY

The breeding season is given of a number of ascidian species on the Scottish west coast.

The species can be divided into north boreo-arctic, south boreo-arctic, and boreal species, and each of these groups has a characteristic duration and time of breeding season.

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THE BREEDING OF THE SCALLOP, *PECTEN MAXIMUS* (L.), IN MANX WATERS

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(Plates I and II and Text-figs. 1–5)

MATERIAL AND METHODS

An important fishery for the scallop, *Pecten maximus* (L.), is carried on during the winter months round the Isle of Man. A knowledge of the breeding of this lamellibranch would be useful should legislation become necessary with regard to the fishery.

Regular samples of scallops were dredged, whenever possible, at roughly weekly or fortnightly intervals throughout the period October 1950–October 1952, from a depth of 13–16 fm. off Bradda Head and Bay Fine, near Port Erin. Approximately 8000 scallops of all ages up to 13 years were examined, though very few young ones were caught. Scallops were aged by means of the growth-rings on the shell, of which one is laid down each spring (Mason, 1957).

The gonad of every scallop was examined macroscopically and classified as regards degree of development (see p. 656). *Pecten maximus* is a hermaphrodite, the gonad consisting of separate male and female parts.

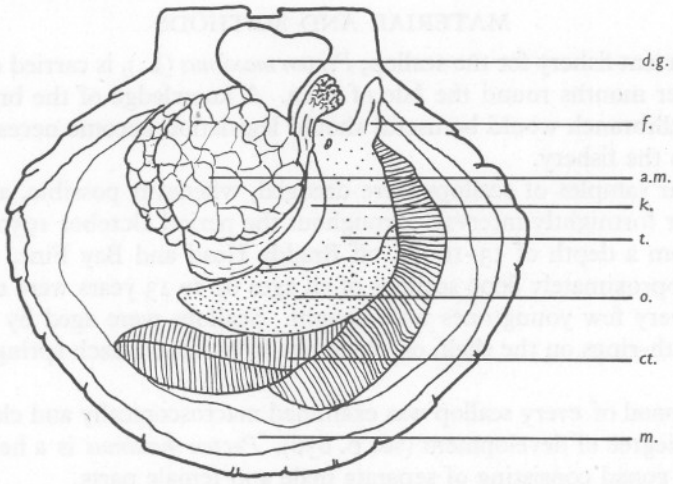
Several gonads in each stage of development were examined histologically by means of transverse sections, and serial sections were prepared of the whole of some small gonads. The material was always taken so as to include both ovarian and spermatic tissue. Three fixatives were used, Bouin, Heidenhain's Susa, and Zenker, of which Bouin proved the most satisfactory.

There is always some loss of reproductive cells from the cut surface of the gonad, and so all pieces to be fixed were cut large enough to allow for this loss. Penetration of the fixative was facilitated by making needle-holes in the material, which was then placed in the fixative and left for several days. The material was then cut into halves, each half containing both ovary and testis, and replaced in the fixative. This second cutting involved no loss of reproductive cells. After dehydration with ethyl and *n*-butyl alcohols, clearing in cedarwood oil and embedding in paraffin wax, sections were cut parallel to the newly-cut face. Sections were cut between 5 and 8 μ thick, and stained with Ehrlich's acid haematoxylin and eosin.

Fixation always resulted in a slight contraction of the gonad, and so did handling.

THE STRUCTURE OF THE GONAD

The mature gonad of *Pecten maximus* was described, but not in detail, by Dakin (1909). The single gonad is posterior and ventral to the rudimentary foot, forming a tongue-shaped mass attached to the adductor muscle (Text-fig. 1). The proximal part is white and forms the testis; the ovary is orange-red and lies distal to the testis. A loop of the alimentary canal passes through the gonad, penetrating into the ovary. This loop cannot be seen in the mature gonad unless, as occasionally happens, it passes close to the free, ventral edge of the ovary.



Text-fig. 1. The gonad of *Pecten maximus in situ*, seen from the right side. *a.m.*, adductor muscle; *ct.*, ctenidium; *d.g.*, digestive gland; *f.*, foot; *k.*, kidney; *m.*, mantle; *o.*, ovary; *t.*, testis.

The boundary between testis and ovary is usually quite sharp, though irregular, but sometimes islets of tissue of one kind occur within the tissue of the other kind. This irregularity in the distribution of the spermatic and ovarian tissue occasionally reaches a state in which the gonad is almost exclusively either male or female. I found two gonads composed entirely of female tissue.

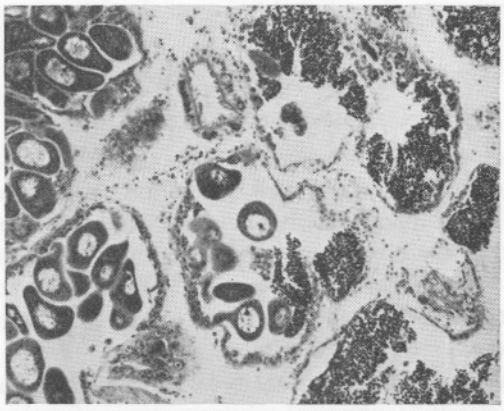
The gonad is made up of many branched, ciliated tubules or ducts, which bear many sacs, the alveoli or follicles. The ducts are round in cross-section, 70 μ or more in diameter. The lumen may be as small as 20–25 μ, and is lined with ciliated epithelium. In serial sections the ducts may be traced and are seen to join and rejoin. They eventually join one of the two main ducts, one on each side, which are much wider, up to 1000 μ in section, and open dorsally, one into each kidney.

The sexual products arise by proliferation of the germinal cells which line the follicle walls. The follicle wall is usually less than 1 μ thick. A few scat-

tered nuclei, 4–7 μ long, which are elongated and sometimes spindle-shaped, may be seen in the follicle wall, though they may be difficult to find in a full gonad.

The follicles become filled with sexual products, and those near the surface of the gonad appear to the naked eye as small, rounded, red or white bodies; the full follicles range in size from 300 to 700 μ.

In each follicle all the contents are normally of one sex, though in one gonad follicles were found containing both male and female elements, spermatozoa, spermatocytes and large oocytes being found side by side (Text-fig. 2).



Text-fig. 2. Transverse section of an abnormal gonad, showing ambisexual follicles. × 100.

The male follicle usually contains a few early stages of spermatogenesis near the follicle wall, but the lumen is filled with spermatozoa. Each spermatozoon has a minute conical head, about 1·4 μ, which stains intensely in haematoxylin, and a tail about 50 μ long. The spermatozoa are arranged radially from the centre of the follicle, or from the point where the follicle opens into the ciliated duct, with their tails pointing towards the centre or towards the duct. The female follicle contains a few young oocytes attached to the wall, while the lumen is full of large oocytes. The large oocytes appear polygonal in sections, and are packed tightly in the follicles; their greatest diameter in sections is about 80–90 μ. The large oval, or spherical, vesicular nucleus has a diameter roughly two-thirds that of the cell. A delicate network of chromatin fibres extends through the nucleus, and one conspicuous acentrally-placed nucleolus is present. The nucleus is surrounded by granular cytoplasm, which often contains bodies which stain purple in haematoxylin. The whole cell is surrounded by a membrane some 1·5 μ thick, which is not stained by either haematoxylin or eosin, but which stains blue in Azan.

Little connective tissue is present between the follicles of the full gonad, although some is present round the loop of the alimentary canal and the ducts, and sometimes near the outer wall of the gonad. The connective tissue

consists mainly of a network of fibres in which are seen various nuclei, spindle-shaped, oval and spherical, whose functional relationships are not known. Among the fibres are a few vacuolated cells. Also present are some small cells, 6–7 μ in diameter, each with a nucleus 2 μ in diameter, surrounded by a clear cytoplasm which stains pink in eosin; similar cells are seen in the lumina of the thick-walled blood vessels which are sometimes seen in sections of the gonad. Also between the follicles are transverse muscle fibres.

The outer wall of the gonad consists of two layers, an outer epithelial and an inner muscular layer. The muscles of the wall, together with the transverse muscles, probably assist the ciliated lining of the ducts in ejecting the genital products.

THE BREEDING OF THE SCALLOP

THE BREEDING CYCLE

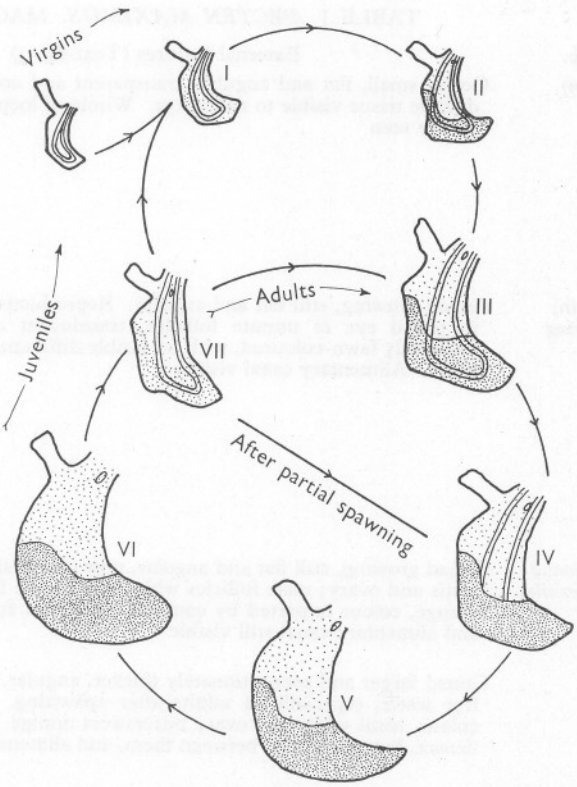
In Manx waters, scallops first spawn in the autumn following the deposition of the second growth-ring on the shell, when most of them are just 2 years old (Mason, 1957). In the following year they have one main spawning, in autumn, and thereafter they have two main spawnings each year, one in spring and one in autumn. In this paper scallops which have never spawned are called virgins, between the first and second spawnings they are called juveniles, and after the second spawning adults.

In order to determine the breeding cycle, gonads from the regular samples of scallops were classified into eight arbitrary stages of maturity, stages 0–VII, which are described in Table 1, the colour nomenclature being that of Ridgway (1912). The external features of the various gonad stages are shown in Text-fig. 3, and their microscopic structure in Text-fig. 4 and Pls. I and II.

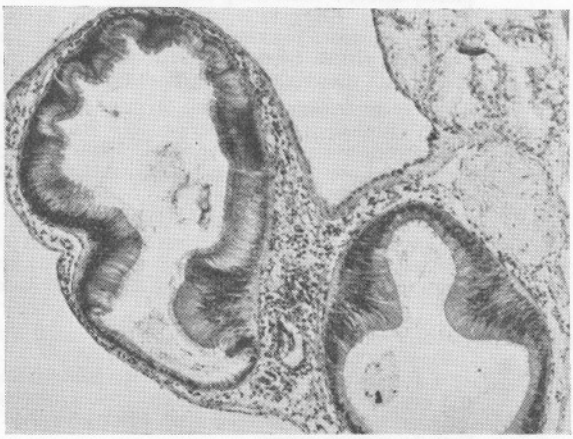
Tang (1941) and Gibson (1956), who made similar studies of scallops, used a classification of only five stages, but their material consisted largely of commercial samples of adult scallops, and no account was taken of the differences between virgins, juveniles and adults. The classification shown in Table 1 assigns three stages (0, I and II) to young scallops, virgins and juveniles, which were not, therefore, represented in the material studied by Tang and Gibson. The 'spawning' stage of Tang and Gibson was not used in the present study, since the duration of the act of spawning was found to be so short as to make it most unlikely that many scallops in the spawning condition would be observed in nature.

The virgin scallop

Table 2 shows the monthly percentages of gonads of virgin scallops in each stage of maturity during the first 2 years or so of the scallop's life. So few young scallops were caught that data for corresponding months in the period considered (e.g. March 1951 and March 1952) were combined, and all the scallops were treated as if they were spawned in the same year.



Text-fig. 3. Macroscopic changes in the gonad of *Pecten maximus*.



Text-fig. 4. Transverse section of stage 0 gonad, 2–3 months old (December). × 100.

TABLE 1. *PECTEN MAXIMUS*. MACROSCOPIC AND

Gonad stage	External features (Text-fig. 3)
0. *Immature (virgin)*	Gonad small, flat and angular, transparent and colourless. No reproductive tissue visible to naked eye. Whole of loop of alimentary canal clearly seen
I. *Developing (virgin) or spent-recovering (juvenile)*	Gonad growing, still flat and angular. Reproductive tissue now visible to naked eye as minute follicles, translucent and sparse. Gonad uniformly fawn-coloured, with no visible differentiation into testis and ovary. Alimentary canal visible
II. *Differentiated gonad (virgin and juvenile)*	Gonad growing, still flat and angular, now obviously differentiated into testis and ovary; male follicles white and female fawn or light salmon orange, colour imparted by contents. Follicles still small and sparse, and alimentary canal still visible
III. *Recovering*	Gonad larger and proportionately thicker, angular. Flabby, containing free water, especially in adults after spawning. Assuming brighter colour, testis white and ovary bittersweet orange. Follicles larger and denser, but still spaces between them, and alimentary canal still visible
IV. *Filling*	Gonad still larger and thicker (thickness about $\frac{1}{3}$ width); still somewhat flabby, containing a little free water. Outline less angular, but not completely smooth. Colouring brighter due to denser colouring of follicles, testis white, ovary bittersweet orange or grenadine pink. Follicles larger and closer together, the latter especially in ovary. Alimentary canal still visible between follicles in testis, but not in ovary, but its outline still discernible owing to thinness of gonad
V. *Half-full*	Gonad again larger and thicker, firmer, and containing very little free water. Rounded, with tapering tip. Brighter, testis creamy-white, ovary grenadine pink or grenadine. Follicles larger, becoming packed together. Loop of alimentary canal invisible, but still causes wall of gonad to bulge
VI. *Full*	Gonad is now at its largest, thickest (thickness about $\frac{1}{2}$ width) and firmest, containing no free water. Rounded to tip. Bright, with follicles highly coloured and closely packed; testis cream coloured, ovary usually grenadine. Loop of alimentary canal indiscernible
VII. *Spent and partially spent*	Spawning may be partial or complete. Gonad dull, angular, thin and collapsed; flabby, containing much free water *Spent gonad* fawn-coloured and loses visible differentiation into testis and ovary after spawning for first time. Older scallops usually retain differentiation, testis yellowish-brown, ovary dull orange pink. Follicles appear empty *Partially spent gonad* always retains differentiation; testis yellowish white, ovary dull, bittersweet orange or orange chrome. Follicles appear hollow, with a coloured ring round periphery indicating retention of some genital products

MICROSCOPIC CHANGES IN THE GONAD

Histological details (Text-fig. 4; Pls. I and II)

Youngest scallops caught (2–3 months old) showed beginning of development, which then continues. Gonad at first almost completely occupied by loop of alimentary canal, but later connective tissue develops. Narrow tubules, bearing primary germ cells on walls, ramify and give rise to follicles and ciliated ducts, rounded in section. Primary germ cells irregular, 8–14 μ, with oval, vesicular nucleus and scattered chromatin, lightly stained in haematoxylin. Follicular cells also present. Primary germ cells give rise to gonia, each with a spherical, vesicular nucleus, 3·5–7 μ; chromatin scattered, but stains more densely than primary germ cell; well-defined nucleolus; usually a little cytoplasm. Formation of gametocytes, shown by synapsis, occurs first in distal (female) part of gonad (synapsis shows as clumping together of chromatin into an irregular, densely-staining mass). Gonad increases in size with formation of follicles and connective tissue. (Text-fig. 4; Pl. I A)

Developing (*virgin*). Follicles growing. Synapsis now occurs in proximal (male) part of gonad. Male follicles lined by several layers of spermatogonia, and lumina filled with synaptic and post-synaptic spermatocytes, with occasionally a few spermatids. Spermatocyte has a little cytoplasm, and appears polygonal in sections; nucleus roughly spherical 2·5–3·5 μ, unevenly distributed chromatin, fairly densely stained, no visible nucleolus. Spermatid 2 μ, spherical nucleus, chromatin evenly or somewhat unevenly distributed. Female follicles have oogonia and synaptic oocytes near walls, and young oocytes up to 30 μ, growing rapidly, in lumina. Young oocytes have somewhat fibrillar cytoplasm; nucleus spherical, vesicular, with a delicate chromatin network and spherical nucleolus. Spaces in female follicles. Much connective tissue between follicles. (Pl. I B, C)

Spent-recovering (*juvenile*) is similar, but has larger spaces in follicles. Before recovery becomes obvious to naked eye many gonia are produced from residual gonia and primary germ cells, and synapsis occurs as above

Spermatozoa appear at centre of male follicles; many synaptic and post-synaptic spermatocytes and some spermatids; several layers of spermatogonia near walls. A few oogonia and synaptic oocytes on wall of female follicles; many half-grown (30–60 μ) oocytes, appearing stalked, with granular cytoplasm, and a few young oocytes. Less connective tissue, but still continuous between follicles. (Pl. I D)

Male follicles contain more spermatozoa, not yet closely packed, arranged radially; still many spermatogonia and spermatocytes near walls, and some spermatids. Few oogonia and synaptic oocytes in female follicles, and lumina almost filled with growing oocytes, mostly half-grown, a few larger and smaller. Few spaces left in follicles, rather more in adults (in which stage III is the first recognizable stage of recovery after spawning) than in virgins and juveniles. Connective tissue still present, but disappearing. Main genital ducts becoming flattened. (Pl. I E)

Spermatogonia still form a continuous layer on walls of male follicles, and inside them a band of spermatocytes and a few spermatids; lumina contain many spermatozoa arranged radially. Few oogonia and synaptic oocytes in female follicle; fewer young oocytes; lumen contains more half-grown and a few almost fully grown (60–80 μ) oocytes. Little connective tissue except round alimentary canal and ducts. Main ducts larger and more flattened. (Pl. I F, G)

A few spermatogonia and spermatocytes remain near walls of male follicles, lumina full of spermatozoa which are becoming closely packed. Walls of female follicle lined with a few young and half-grown oocytes; lumina filled with almost fully grown oocytes, each with germinal vesicle still intact; very few oogonia and synaptic oocytes, indicating that production of oocytes has now almost ceased. Very little connective tissue

Follicles maximum size. Male follicles packed with spermatozoa, still arranged radially; few scattered spermatogonia and spermatocytes persist near walls. Female follicles packed with fully-grown (80–90 μ) polygonal or pear-shaped oocytes, whose germinal vesicles show signs of breaking down; very few scattered oogonia and young oocytes persist near walls. No connective tissue except round alimentary canal and ducts. Main ducts flattened. (Pl. II H, J)

Follicles smaller and collapsed, containing large spaces. Main ducts wide. Some connective tissue visible

Spent gonad after spawning for first time contains a few residual primary germ cells, spermatogonia and spermatocytes on walls of male follicles, but few or no spermatozoa; female follicles have a few primary germ cells, oogonia and young oocytes on walls. Older scallops retain more spermatocytes and a few spermatozoa, and more young and some half-grown oocytes. (Pl. II N)

Partially spent gonad retains more genital products. Many residual spermatocytes and spermatozoa, and half-grown and almost fully grown oocytes. (Pl. II M)

TABLE 2. MONTHLY PERCENTAGES OF VIRGIN SCALLOPS AT EACH STAGE OF MATURITY DURING THE FIRST 2–2½ YEARS OF LIFE

[Owing to the small numbers caught, data for scallops caught in corresponding months of the period of the investigation (e.g. March, 1951 and March, 1952) are combined, and all the scallops are treated as if they were spawned in the same year.]

Month	Gonad stages: o	I	II	III	IV	V	VI	VII	No. of gonads
Apr.	—	—	—	—	—	—	—	—	—
May	—	—	—	—	—	—	—	—	—
June	—	—	—	—	—	—	—	—	—
July	—	—	—	—	—	—	—	—	—
Aug.	—	—	—	—	—	—	—	—	—
Sept.	—	—	—	—	—	—	—	—	—
Oct.	100·0	—	—	—	—	—	—	—	2*
Nov.	—	—	—	—	—	—	—	—	—
Dec.	100·0	—	—	—	—	—	—	—	1
Jan.	100·0	—	—	—	—	—	—	—	2
Feb.	100·0	—	—	—	—	—	—	—	12
Mar.	100·0	—	—	—	—	—	—	—	17
Apr.	100·0	—	—	—	—	—	—	—	3†
May	100·0	—	—	—	—	—	—	—	9†
June	100·0	—	—	—	—	—	—	—	5
July	100·0	—	—	—	—	—	—	—	2
Aug.	100·0	—	—	—	—	—	—	—	5
Sept.	100·0	—	—	—	—	—	—	—	6
Oct.	100·0	—	—	—	—	—	—	—	12
Nov.	100·0	—	—	—	—	—	—	—	23
Dec.	100·0	—	—	—	—	—	—	—	18
Jan.	100·0	—	—	—	—	—	—	—	15
Feb.	97·7	1·2	1·2	—	—	—	—	—	85
Mar.	92·3	5·5	2·2	—	—	—	—	—	91
Apr.	40·2	27·8	8·2	12·4	11·3	—	—	—	97‡
May	22·7	14·7	28·0	20·0	10·7	4·0	—	—	75‡
June	10·2	28·6	16·3	10·2	16·3	6·1	12·2	—	49
July	—	17·4	21·7	17·4	30·4	8·7	4·3	—	23
Aug.	—	8·3	13·9	8·3	8·3	5·6	5·6	50·0	36
Sept.	—	—	—	8·1	13·5	5·4	9·5	63·5	37

* Millport scallops. † 1st growth ring. ‡ 2nd growth ring.

EXPLANATION OF PLATES I AND II

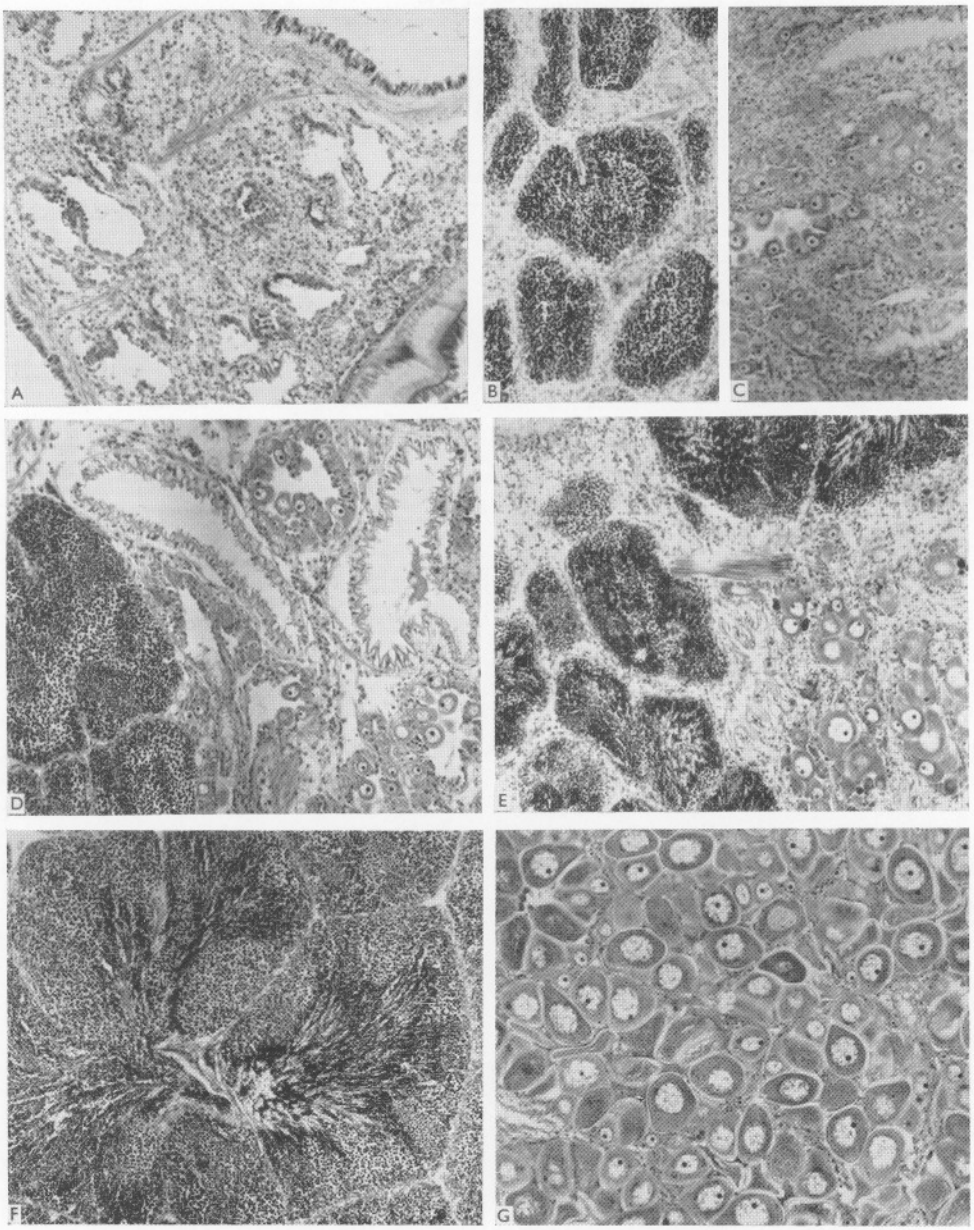
Pecten maximus. Photomicrographs of transverse sections through gonads in the various stages of maturity.

PLATE I

A. Stage o gonad, at time of deposition of second growth ring (April). Gonia showing as thickenings on edge of follicles. × 96.
B. Stage I testis. × 96.
C. Stage I ovary (cells with enlarged nuclei are young oocytes). × 96.
D. Stage II testis and ovary. × 96.
E. Stage III testis and ovary (spermatozoa have appeared in the former). × 96.
F. Stage IV testis. × 96.
G. Stage IV ovary. × 96.

PLATE II

H. Stage VI testis. × 93.
J. Stage VI ovary, showing fully-grown oocytes. × 93.
K. Running testis, showing sperm in genital ducts. × 93.
L. Running ovary, showing mature ova. × 93.
M. Stage VII testis and ovary (partially spent). × 93.
N. Stage VII testis and ovary (spent). × 93.



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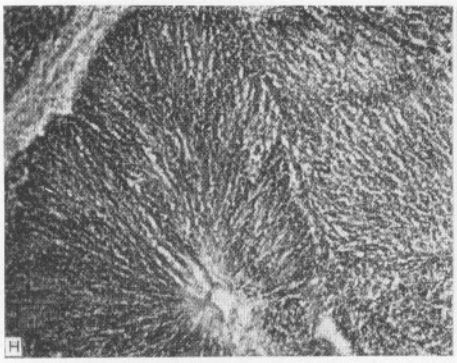
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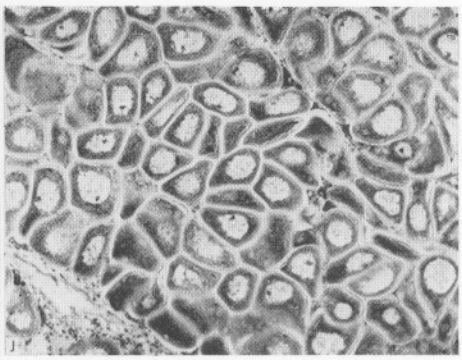
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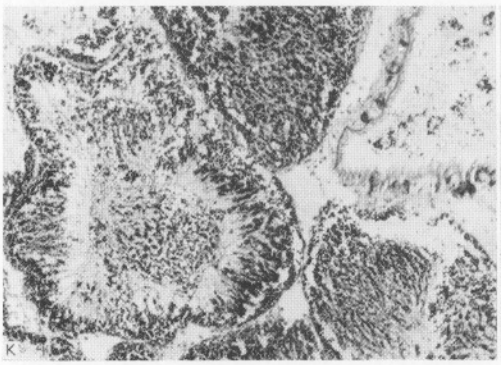
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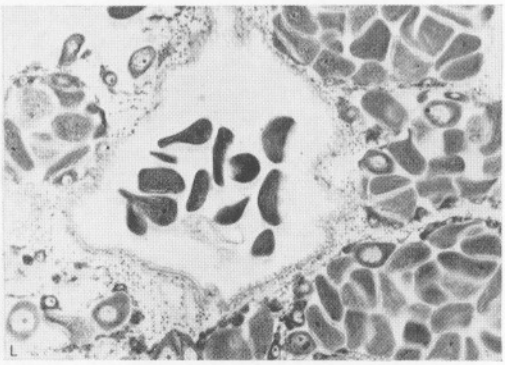
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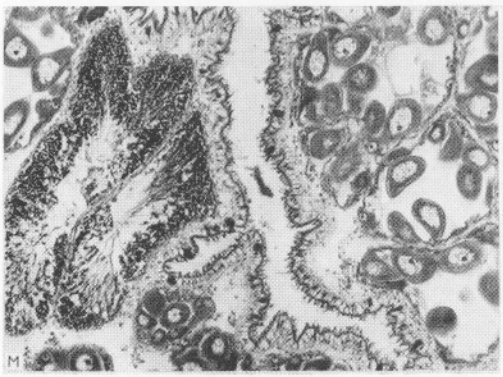
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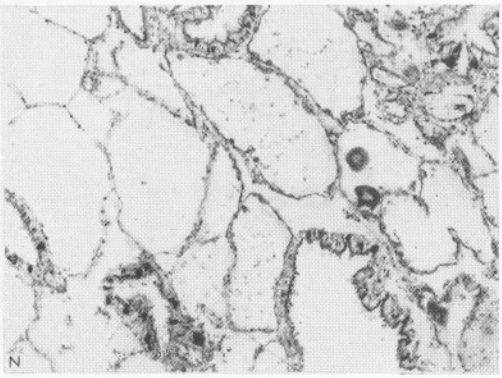
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All scallops with no growth-rings and almost all with one ring possessed stage 0 (immature) gonads, and the first sign of development obvious to the naked eye appeared in the late winter or early spring about the time of deposition of the second growth-ring, although development of tubules and germ cells had been going on continuously since a very early age (Table 1). Development continued throughout the spring and summer, through stages I to VI, and culminated in the act of spawning in the August or September after the deposition of the second growth-ring. Spawning was complete in most individuals, and involved the complete loss of differentiation into testis and ovary. The macroscopic and histological details of the various stages of gonad development are given in full in Table 1.

The juvenile scallop

The breeding cycle of the juvenile scallop begins with those scallops which have just spawned for the first time in August or September. Since the juveniles themselves spawn in the following August or September, the period of the investigation, October 1950–October 1952, almost covers two complete breeding cycles.

The gonads began to show signs of recovery externally in October or November (Table 3), although production of gonia had occurred before this. Since most gonads had spawned completely and lost their differentiation into testis and ovary, it was possible to distinguish stages I (spent-recovering) and II (differentiated), which cannot be distinguished in adult gonads owing to their retention of more genital products, and, therefore, of their differentiation. Recovery continued throughout the winter, stages III and IV predominating from January to March. The third growth-ring was laid down on the shell in the spring. Stage V gonads were commonest in April and May, and by June or July most juvenile scallops had full (stage VI) gonads. The main spawning occurred in the second half of August in 1951 and between 5 and 11 September in 1952 (Table 3B), and most scallops of this age took part. Spawning was almost complete in most individuals, but more sexual products were retained than in the first (virgin) spawning, and the gonads usually retained their differentiation. In addition, some juvenile scallops released a very small proportion of their gametes between 9 and 17 July 1952 (Table 3B).

The adult scallop

The principal spawning of adult scallops, like that of juveniles, was found to occur in August or September, so that two annual breeding cycles are again almost covered by the period October 1950–October 1952. At the beginning of each cycle were found mostly spent and a few partially spent gonads resulting from the spawning of juvenile and adult scallops (Table 4). Recovery soon began, and, owing to the larger numbers of reproductive cells

TABLE 3. PERCENTAGE OF JUVENILE SCALLOPS AT EACH STAGE OF MATURITY

(A) MONTHLY PERCENTAGE

(All samples in each month combined.)

Month	October 1950–September 1951 Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
Oct.	—	—	—	—	—	—	100·0	6
Nov.	25·0	8·3	16·7	8·3	—	—	41·7	12
Dec.	—	25·0	—	50·0	—	—	25·0	4
Jan.	17·6	19·6	5·9	33·3	7·8	—	15·7	51
Feb.	17·0	5·4	19·7	39·5	4·8	—	13·6	147
Mar.	11·9	6·8	13·7	36·3	15·9	7·9	7·9	278
Apr.	2·3	4·7	7·0	30·2	14·0	41·9	—	43
May	—	0·8	2·5	27·5	34·2	27·9	7·1	120
June	—	—	—	0·8	27·7	68·1	3·4	177
July	—	—	—	—	10·3	88·5	1·3	39
Aug.	—	—	—	—	21·2	51·5	27·3	33
Sept.	—	—	12·3	36·3	0·9	12·3	38·2	106

Month	September 1951–October 1952 Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
Sept.	—	—	16·7	22·2	—	—	61·1	18
Oct.	—	14·3	21·4	14·3	—	—	50·0	14
Nov.	2·3	4·5	25·0	13·6	2·3	—	52·3	44
Dec.	—	—	—	37·5	—	—	62·5	8
Jan.	2·4	11·9	19·0	33·3	13·1	1·2	19·0	42
Feb.	6·0	1·2	20·2	46·4	16·7	7·1	2·4	84
Mar.	—	—	11·1	50·0	22·2	16·7	—	18
Apr.	1·1	1·4	2·8	37·9	43·3	13·2	0·3	178
May	—	—	1·3	10·2	51·6	36·8	—	152
June	—	—	—	1·4	56·4	40·0	2·1	70
July	—	—	—	6·7	15·6	62·2	15·6	90
Aug.	—	—	—	6·8	12·8	65·5	14·9	74
Sept.	—	—	—	4·1	8·2	58·2	29·6	49
Oct.	—	—	34·4	37·5	—	9·4	18·8	32

(B) SPAWNING MONTHS

(Samples arranged to show dates between which spawning occurred.)

1951	Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
15, 18 Aug.	—	—	—	—	25·0	75·0	—	4
31 Aug.	—	—	—	—	20·7	48·3	31·0	29
5–12 Sept.	—	—	—	12·0	—	38·0	50·0	25
21, 28 Sept.	—	—	16·0	43·8	1·2	4·3	34·6	81

1952	Gonad stages I	II	III	IV	V	VI	VII	No. of gonads
9 July	—	—	—	—	26·3	73·7	—	38
17 July	—	—	—	9·1	—	45·5	45·5	11
21, 29 July	—	—	—	12·2	9·8	56·1	22·0	41
5 Sept.	—	—	—	5·7	11·4	72·9	10·0	35
11 Sept.	—	—	—	—	—	21·4	78·6	14

TABLE 4. PERCENTAGE OF ADULT SCALLOPS AT EACH STAGE OF MATURITY

(A) MONTHLY PERCENTAGE

(All samples in each month combined)

Month	October 1950–September 1951 Gonad stages III	IV	V	VI	VII	No. of gonads	Month	August 1951–October 1952 Gonad stages III	IV	V	VI	VII	No. of gonads
							Aug.	—	—	12·4	27·0	60·6	113
							Sept.	9·4	30·2	4·0	13·9	42·5	260
Oct.	31·3	34·3	—	—	34·3	67	Oct.	23·0	63·1	3·4	4·9	5·5	293
Nov.	26·3	62·5	6·9	—	4·4	160	Nov.	9·2	53·9	31·4	4·5	1·0	191
Dec.	8·5	74·5	17·0	—	—	47	Dec.	1·8	33·5	40·4	22·0	2·3	109
Jan.	1·2	36·8	54·0	8·0	—	201	Jan.	1·0	15·1	55·4	28·3	0·2	288
Feb.	2·0	14·3	59·2	24·5	—	98	Feb.	—	3·7	49·8	45·7	0·8	246
Mar.	0·3	4·4	32·9	62·2	0·1	343	Mar.	—	1·5	17·6	79·9	1·0	259
Apr.	0·4	2·0	6·5	90·4	0·6	245	Apr.	—	21·0	7·1	59·3	12·5	554
May	—	10·1	4·1	39·0	46·9	318	May	—	5·1	79·6	15·2	0·2	445
June	—	2·9	76·9	10·8	9·4	346	June	—	0·2	52·6	46·5	0·7	227
July	—	—	10·0	85·7	4·3	70	July	—	5·2	10·0	76·2	8·6	296
Aug.	—	0·7	23·4	25·2	50·7	141	Aug.	—	7·1	10·7	71·1	11·1	140
Sept.	5·9	25·8	5·9	14·1	48·3	145	Sept.	—	—	6·8	52·1	41·1	96
							Oct.	43·5	42·7	—	2·4	11·3	62

(B) SPAWNING MONTHS

(Samples arranged to show dates between which spawning occurred)

1951	Gonad stages III	IV	V	VI	VII	No. of gonads	1952	Gonad stages III	IV	V	VI	VII	No. of gonads
4 May	—	—	3·3	93·3	3·3	60	1–12 Apr.	—	0·3	6·6	92·5	0·5	286
11 May	—	5·2	3·4	29·3	62·1	116	15, 17 Apr.	—	—	3·6	41·6	54·8	83
18 May	—	18·3	4·9	23·9	52·8	142	25 Apr.	—	62·4	9·4	15·9	12·2	185
17, 24 July	—	—	10·0	85·7	4·3	70	9 July	—	—	13·2	86·8	—	148
15, 18 Aug.	—	1·8	45·5	34·5	18·2	55	17–29 July	—	10·5	6·8	65·5	17·2	148
23, 31 Aug.	—	—	9·3	19·2	71·5	86	5 Sept.	—	—	11·0	83·1	5·9	59
							11 Sept.	—	—	—	2·7	97·3	37

retained by juveniles and adults after spawning, the first recognizable stage in recovery was stage III (recovering). Recovery continued throughout the winter months, stages III and IV predominating in October and November, and stages IV and V in December. Half-full (stage V) gonads were abundant in the late winter, and by March or April most adult scallops had full (stage VI) gonads. The latter, however, still had considerable numbers of spermatocytes and growing oocytes in the follicles, so that, although a mass-spawning occurred in the spring, it was only partial. In 1951 this spawning occurred between 4 and 11 May, and in 1952 between 12 and 15 April (Table 4B). The spring spawning was followed at once by recovery, and, since only a proportion of the gonad contents had been shed, the resulting partially spent gonad resembled somewhat the stage III gonad, so that the first recognizable stage of recovery was stage IV. Recovery continued throughout the summer, through stages IV and V, so that by July most adult scallops again had full (stage VI) gonads, this time with few spermatocytes and growing oocytes. These then took part in another mass-spawning, which resulted, in most individuals, in the production of almost completely spent gonads. This spawning occurred at approximately the same time as that of the juveniles, i.e. late in August (actually between the 18th and 23rd in the adults) in 1951 and between 5 and 11 September in 1952 (Table 4B). In addition, between 9 and 17 July 1952, again at the same time as the juveniles, a few adult scallops spawned slightly, and recovered quickly to take part in the main September spawning. In 1951, a sample taken on 15 August showed that a similar slight spawning had occurred in a few scallops between 24 July and 15 August, again before the main spawning.

The majority of adult scallops, then, spawn together twice during each annual breeding cycle, partially in April or May ('spring' spawning), and more completely in late August or September ('autumn' spawning). There is also a minor 'summer' spawning in July or early August. Virgin and juvenile scallops differ from adults in having only one major spawning, in autumn, though juveniles show some evidence of a minor summer spawning. The autumn spawning is therefore by far the most important in terms of numbers of gametes released.

SPAWNING

The spawning of *Pecten maximus* was observed on several occasions in the laboratory. The genital products are passed out through the two main ducts, through the kidneys, and into the mantle cavity, whence they are emitted in a cloud through the exhalant opening of the shell. No violent flapping of the shell valves occurs, but they may open and close gently at intervals of 1 or 2 min. The eggs settle and form an orange layer on the bottom of the container, while the sperm become dispersed in the water and make it cloudy.

Both kidneys become filled with either eggs or sperm. Dakin (1909) stated that the smaller left genital duct, which leads into the left kidney, serves only the left-hand side of the testis in the neighbourhood of its opening. In my observations, however, both eggs and sperm were found to pass out through either kidney. Eggs and sperm are not shed at the same time, but usually within a few hours of one another, sometimes the eggs and sometimes the sperm being shed first. This was found to be true in *Pecten maximus* by Dakin (1909) and in *Chlamys opercularis* by Fullarton (1890). In about 4% of cases one or other of the two parts of the gonad remained unspawned.

On the only occasion on which the act of spawning was observed from the beginning, the ovary spawned in 45 min., and was followed at once by the testis, which became spent in 2 h. On several occasions both parts of the gonad spawned overnight.

The running gonad has a patchy appearance, having dull areas which have shed all their ripe products, and bright areas which still contain them.

Sections of a running testis (Plate II K) show follicles in varying stages of spending; most follicles are partly empty, having spaces in their centres, but, while these spaces contain many free spermatozoa, some spermatozoa are still arranged radially, as in the full gonad, with their tails pointing inwards. The ducts are wide, and their lumina contain spermatozoa. The duct walls contain a secretion which stains purple in haematoxylin, which is thought to facilitate passage of the genital products.

Sections of a running ovary (Pl. II L) show that some follicles are in a spent condition, and contain the remains of oocytes, while others are still full, and in some of these are seen ova which have undergone or are undergoing maturation. In these ova, the germinal vesicle has broken down, the cytoplasm is evenly distributed, and a spindle with chromosomes can sometimes be seen. The ovum is still polygonal, and possesses a conspicuous membrane. Other follicles have shed a few ova, and have a few loose in their lumina. The ducts are wider and contain mature ova, and a purple-staining secretion is sometimes present in their walls.

It was found that ripe oocytes, cut from the full gonad and placed in sea water, quickly become spherical, lose the germinal vesicle, and can then be readily fertilized artificially. Eggs passed naturally from the gonad into the surrounding water behave similarly. These facts suggest that contact with sea water might cause the onset of maturation. It is possible that the eggs are often passed out of the ovary before maturation, since, in an ovary which has commenced to spawn, many fully-grown oocytes still retain their germinal vesicles, and also that contact with sea water in the mantle cavity results in the dissolution of the nuclear membrane. The genital ducts in the running gonad are so wide that water from the mantle cavity and kidneys might conceivably pass along them to the follicles, and cause the onset of maturation

in some oocytes before they leave the follicle. Coe (1933) found such a state of affairs in *Teredo*, with sea water causing the initiation of maturation.

Tang (1941) stated that *Pecten* off Port Erin began to spawn in numbers when the water temperature reached 10° C, but this is contradicted by the present study. Of the six spawnings which occurred in 1951 and 1952 it was possible in five cases to state, to within a few days, when spawning had occurred (the exception was the small summer spawning of 1951, when insufficient samples could be taken). Spawning was not caused by the attainment of a definite temperature, but occurred at several temperatures between 7·2 and 13·7° C, viz. spring 1951—7·2° C, autumn 1951—13·7° C, spring 1952—8·1° C, summer 1952—12·7° C, autumn 1952—13·5° C.

FERTILIZATION

Fertilization is external, and, at the times of the mass spawnings, there are relatively high concentrations of genital products in the sea, greatly increasing the chances of successful fertilization.

In the laboratory, artificial fertilization of eggs cut from the gonad was readily carried out. In nature, where each individual sheds its two types of genital products separately into the sea, cross-fertilization must be the general rule. Experimentally, however, cross- and self-fertilization were obtained with equal facility. On one occasion a rough count showed that about 80% fertilization was obtained, though usually the percentage was much lower than this. Better results were obtained using ripe gametes which had been shed normally by the scallop.

Normally only mature eggs from a full gonad are capable of being fertilized. However, sperm from stage IV, V and VI gonads, as well as residual sperm from partially spent gonads, are capable of fertilizing them.

LARVAE AND SPAT

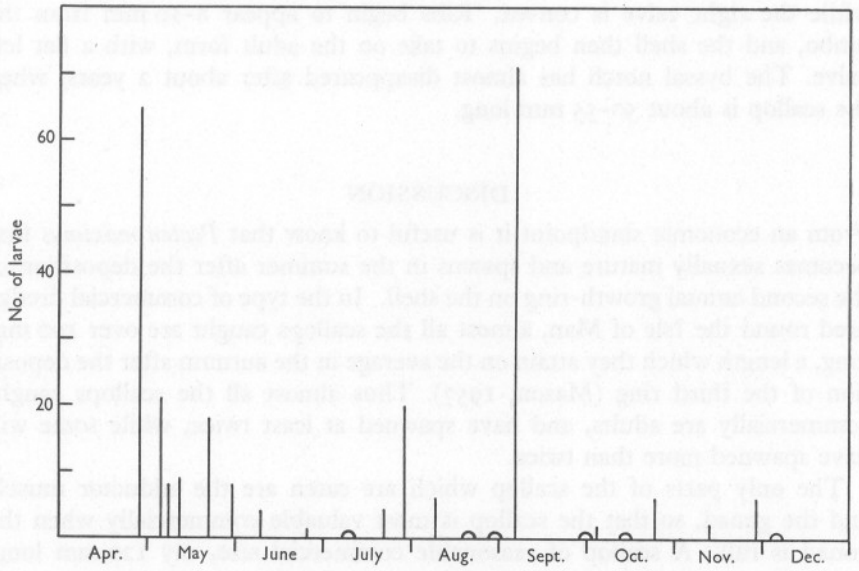
No description of the larva of *P. maximus* as such was found in the literature. Rees (1950) figured and described various pectinid larvae, but was unable to allocate the larvae to particular species.

Plankton samples were taken off Bay Fine, just below the surface, using a fine townet, 129 meshes to the inch, at intervals of 1–2 weeks during the period 28 April–24 December 1952. Dr Rees very kindly examined any pectinid larvae present, together with the prodissoconchs of recently settled spat, and as a result he was able to identify his pectinid E as the larva of *P. maximus* (Rees, 1954).

Text-fig. 5 shows the numbers of larvae in the samples. There are three main peaks, two large ones on 28 April and 5 September, and a smaller one on 29 July. The first large peak would probably be composed of larvae arising from the spring spawning, the small peak of larvae from the small

summer partial spawning, and the second large peak of larvae from the autumn spawning. Since the mass spawning of scallops in the population studied did not occur until between 5 and 11 September, the larvae found on 5 September probably originated from the spawn of a different group of scallops in the vicinity, which had spawned somewhat earlier.

The large numbers of larvae in the plankton haul of 28 April show that the spring spawning resulted in the successful production of larvae. When spawning was recorded, between 12 and 15 April, the temperature was 8·1° C, indicating that a temperature of 10° C is not minimal for the production of larvae, as was thought by Tang (1941).



Text-fig. 5. Numbers of larvae in plankton samples, April-December 1952. Blank hauls are indicated by semicircles.

The sampling was not adequate to show the exact times and compositions of the peaks in Text-fig. 5, this being especially so in the September peak, when there was a gap of 25 days after the sample of 5 September. The September peak would be expected to be much higher than the April peak, owing to the much greater amount of spawn shed in the autumn than in the spring spawning (see above, p. 664).

Elmhirst (1945) stated that the larvae of *P. maximus* settle on *Laminaria saccharina*, while Hertling (1934) found a few young specimens attached to a drifting trunk off Heligoland. On only one occasion, however, did I find the spat of *Pecten maximus*, namely on 29 August 1952, when two specimens, 3·0 and 3·5 mm long respectively, were found on *Desmarestia* on the Bradda

bed. These presumably arose from the small summer spawning. In addition, Mr T. B. Bagenal kindly sent me a few young specimens which he found attached to *Laminaria saccharina* at Millport. My inability to find more young *Pecten maximus* was surprising in view of the large numbers of newly settled *Chlamys opercularis* which I found attached to *Laminaria saccharina*.

The two recently settled individuals of 3·0 and 3·5 mm found off Port Erin were easily recognized, since the shape of the young shell can be deduced from the concentric striae on the adult shell (Mason, 1957). The shell was transparent and almost colourless, with a conspicuous byssal notch, and both shell valves were convex. Larger specimens, some 5–25 mm long, possess a left valve which is concave except for a small convex area near the umbo, while the right valve is convex. Ribs begin to appear 8–10 mm from the umbo, and the shell then begins to take on the adult form, with a flat left valve. The byssal notch has almost disappeared after about 2 years, when the scallop is about 50–55 mm long.

DISCUSSION

From an economic standpoint it is useful to know that *Pecten maximus* first becomes sexually mature and spawns in the summer after the deposition of the second annual growth-ring on the shell. In the type of commercial dredge used round the Isle of Man, almost all the scallops caught are over 100 mm long, a length which they attain on the average in the autumn after the deposition of the third ring (Mason, 1957). Thus almost all the scallops caught commercially are adults, and have spawned at least twice, while some will have spawned more than twice.

The only parts of the scallop which are eaten are the adductor muscle and the gonad, so that the scallop is most valuable commercially when the gonad is full. A scallop of reasonable commercial size, say 120 mm long, with a full gonad, yields on the average approximately 32 g of edible material, of which the muscle accounts for 24 g and the gonad for 8 g. Thus scallops are in the prime of condition in the months immediately prior to spawning, namely March–April and July–August, but they are not normally caught in the summer months owing to the difficulty of keeping them in good condition in hot weather during transport to London, the main market.

The occurrence of two main spawnings yearly among adult scallops has not been noted by previous workers in Manx waters, though recently, since the present work was completed, Gibson (1956) has noted it in *P. maximus* in Irish waters.

With the occurrence of two main spawnings can be correlated the fact that two types of first year's growth can be recognized on the shell, according to the length of time available for growth before the first winter cessation (Mason, 1957). Autumn-spawned scallops are greatly in the majority owing

to the much greater amount of spawn released then as compared with the spring spawning.

In the system of classification used by Coe (1945), *P. maximus* is a 'functional hermaphrodite', in which both types of sexual cells are produced at the same time, but are not usually discharged together. Coe (1945) stated that in the genus *Pecten* there is a strong tendency towards protandry, that in the young gonad spermatogenesis may be in progress long before the ova have begun the deposition of yolk, and that some or all of the sperm is discharged before the eggs are fully ripe. Pelseneer (1935) said that hermaphrodite molluscs in general are protandrous, the sperm being ripe before the eggs, so that self-fertilizing hermaphrodites are rare and cross-fertilization is the general rule. Dalmon (1938) went so far as to say that *P. maximus* is so distinctly protandrous as to render self-fertilization impossible. The results of the present study contradict Dalmon's statement and support one made by Coe (1945) that, experimentally, self-fertilization in fully-ripe functional hermaphrodites seems to take place as readily as cross-fertilization.

The present study has shown that, in the virgin gonad of *P. maximus*, there is an early tendency, not towards protandry, but towards protogyny, in that oocytes are first produced before spermatocytes (Table 1). Later, however, this tendency is reversed, and spermatogenesis so far outstrips oogenesis that the male follicles contain some spermatozoa while the female follicles still contain only half-grown oocytes. Similarly, after spawning, spermatogenesis occurs more rapidly than oogenesis, and many sperm are present long before the oocytes are fully grown. These sperm from the earlier gonad stages are physiologically ripe and capable of fertilizing ripe eggs which, however, occur only in the full (stage VI) gonad. The sperm are stored in the testis until the gonad is full, and the products of the two sexes are discharged separately, but within a few hours of each other, often some weeks after the full stage is reached. The products of either sex may be shed first, so that some individuals are functionally protandrous and others are functionally protogynous.

A retention of morphologically ripe gametes in the gonad for considerable periods of the year was also found in *Venus mercenaria* by Loosanoff (1937). *Pecten maximus* also resembles *Venus mercenaria* in that there is no resting period in the gonad after spawning, and that gametogenesis occurs over most of the year, even in the autumn and winter months when the temperature is falling. Loosanoff considered these phenomena as unusual among lamellibranchs.

This paper is based on parts of a thesis[1] presented to the University of Liverpool in 1953 for the degree of Ph.D. The work was carried out at the Marine Biological Station, Port Erin, while I held a Herdman Studentship

[1] Investigations on the scallop [*Pecten maximus* (L.)] in Manx waters, 1953.

and University Research Fellowship. I wish to thank the Director, Mr J. S. Colman, for suggesting the work, for his valuable criticisms and guidance, and for reading the manuscript. Mr A. B. Bowers and Mr A. D. MacIntyre also read the manuscript and made helpful suggestions. My thanks are due to Dr H. A. Cole of the Ministry of Agriculture, Fisheries and Food, for his help in the interpretation of sections. I am grateful to Prof. R. J. Pumphrey, F.R.S., for the use of photographic apparatus in the Department of Zoology, University of Liverpool, and to Mr R. A. Fleming and Mr Irvine for assistance in the preparation of photomicrographs. The help given by the scientific staff, students and technical staff of the Marine Biological Station, Port Erin, is gratefully acknowledged. Lastly, I wish to thank the masters and crews of the R.V. 'William Herdman' and the M.B.'s 'Cypris' and 'Runa'.

SUMMARY

Pecten maximus is a functional hermaphrodite, whose gonad consists of separate male and female parts. Its breeding cycle in Manx waters was determined by examination of the macroscopic and microscopic changes in the gonad. The virgin scallops spawn in the autumn after the deposition of the second growth ring on the shell. In the next year, as juveniles, they have one main mass spawning, in autumn, and a very small, partial one earlier in the summer. In all subsequent years, as adults, they have two mass spawnings, a partial one in spring and a more complete one in autumn, while a much smaller, partial one occurs in the summer. Gametogenesis occurs throughout the year, and there is no resting period after spawning.

P. maximus shows an early tendency to protogyny in the development of the virgin gonad, but this is soon reversed, and a tendency to protandry appears, which is also apparent in the recovery after spawning, so that ripe sperm are present long before fully-grown oocytes. These ripe sperm are retained until the gonad is full, and the two parts of the gonad spawn separately within a short time of each other, the whole act of spawning taking a few hours. The products of either sex may be shed first. While cross-fertilization must be the rule in nature, experimentally both cross- and self-fertilization of mature eggs, which had lost their germinal vesicles, were obtained easily.

Spawning does not take place at a definite temperature.

The numbers of larvae in plankton hauls show three peaks, two large and one small, corresponding to the two main and one small spawnings. No reason can be advanced for my inability to find more than a few recently settled individuals.

Almost all scallops caught commercially have spawned at least twice. Scallops are most valuable commercially when their gonads are full prior to spawning.

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A METHOD FOR THE MEASUREMENT OF VITAMIN B_{12} CONCENTRATION IN SEA WATER

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(Text-fig. 1)

The vitamin B_{12} concentration in sea water is so very low that only the most sensitive microbiological assay techniques are likely to be capable of measuring it, but the salt concentration is so high as to be inhibitory to most of the organisms conventionally used for the microbiological assay of the vitamin. Nevertheless, the consideration that vitamin B_{12} concentration may have an influence on the amounts and types of life present in sea areas has persuaded several investigators to attempt its measurement.

The methods so far employed have each their own advantages and disadvantages (Droop, 1954, 1955; Lewin, 1954; Sweeney, 1954; Cowey, 1956; Adair & Vishniac, 1958). The method to be described here offers advantages in sensitivity, permitting direct measurement of the vitamin in small quantities of oceanic waters after further dilution; samples to be measured pass through comparatively few different containers and thus there is less risk of their accumulating adventitious vitamin; simple and easily cleaned apparatus is used, and much less bench-work is involved than when methods other than dilution are used for lowering the salt concentration.

I am deeply indebted to Dr L. R. Fisher and Dr S. K. Kon who introduced me to the subject of vitamins in the sea and their possible significance, and to Dr J. E. Ford for his advice on microbiological techniques.

Thanks are also due to Dr G. I. M. Ross, then at the Vincent Square Laboratories, Westminster Hospital, who provided the culture of *Euglena gracilis* strain *z* with details of the growth medium before their publication; and to Dr R. Johnston of the Scottish Home Department Marine Laboratory, Aberdeen, for providing sea-water samples.

MATERIAL AND METHODS

Principle

The organism used is the freshwater flagellate *Euglena gracilis* strain *z*, grown in the medium of Hutner, Bach & Ross (1956). Carsted (cited by

* Grant-aided by the Development Fund.

Hutner, Bach & Ross, 1956) found that this organism shows a growth response not only to cyanocobalamin (the form of vitamin B_{12} active for man and other higher animals), but also to two of its analogues, pseudovitamin B_{12} and Factor A. In this it resembles *Monochrysis lutheri* (Droop, 1955) but differs from some other marine algae (Droop, 1957). In his 1957 paper, Droop mentions that in the sea the analogues of vitamin B_{12} may have an importance equal to that of the vitamin.

The assay is carried out in a manner rather different from that described by Hutner *et al.* (1956); instead of measuring the growth of the *Euglena* population turbidimetrically, the chlorophyll from the cells is extracted and measured colorimetrically by the procedure of Heinrich & Lahann (1952). Various chlorophyll-measuring techniques resembling this procedure have of course long been familiar to marine biologists, who use them to obtain estimates of the phytoplankton standing crop in the sea (e.g. Harvey, 1934; Atkins & Parke, 1951).

Chlorophyll production was found to be proportional to the amount of vitamin B_{12} supplied to the *Euglena* population during its growth; which provides an exceptionally sensitive index of the vitamin concentration.

The sea-water sample has to be diluted with distilled water before use in order to reduce its salt concentration to a level which will not interfere with the growth of *Euglena*.

Several different dilutions of the sea-water sample, and at least two flasks of each dilution, are assayed together. Other flasks containing known amounts of vitamin B_{12} are necessary in each assay to provide the calibration.

Cleaning of glassware

Careful cleaning of the glassware for use in the assay is essential, as otherwise it might contribute significant amounts of vitamin B_{12}; perhaps even more than would be contained in the sample itself. The extent to which the glassware can be freed of vitamin B_{12} may well be the factor which imposes a practical limit on the accuracy and sensitivity of the assay.

Conical flasks of 50 and 100 ml. capacities are used. Before being brought into use for sea-water assays, flasks are filled with an approximately 10% (w/v) solution of sodium hydroxide and then steamed. They are then washed in turn with distilled water, dilute hydrochloric acid and several changes of distilled water.

With flasks used for sea-water assays and no other purpose, it has been found sufficient to wash them in a dilute detergent (Lissapol; I.C.I.) followed by distilled water acidulated with hydrochloric acid; then to fill them with distilled water and autoclave them, repeating this two or three times. The clean flasks are left in a drying oven until they are needed.

Preparation of medium

The medium recommended and described by Hutner *et al.* (1956) is prepared in solution at five times single strength, and stored in Polythene bottles at $-20°$ C.

Preparation of sea water

In the procedure to be described the assay is set up with four graded dilutions of the sample, each in triplicate. For such an assay 10 ml. of sea water are sufficient. Amounts for assays to be done with greater replication to provide higher precision can readily be calculated.

While awaiting assay, the sea water is stored cold with approximately 1% of the preservative of Hutner & Bjerknes (1948) (1 part by volume *o*-fluorotoluene, 1 part dichloroethane, 2 parts *n*-butyl chloride).

10 ml. of the sea water are placed in a 100 ml. conical flask, together with 0·5 ml. citrate-phosphate buffer of pH 4·6 (McIlvaine, 1921*) and 0·5 ml. of a freshly prepared 0·001% solution of NaCN. 60–80 ml. of glass-distilled water are then added, and the flasks heated in the autoclave in flowing steam for 15 min. This treatment eliminates any volatile preservative present; and any vitamin B_{12} not originally in the free cyano form is converted into it (Ford, 1952; Coates & Ford, 1955). In the free cyano form, the vitamin is relatively stable, and nutritionally available to the assay organism.

After the steaming, the flask is cooled and the contents made up to 100 ml. with distilled water, which represents a 1 in 10 dilution of the original sea water.

This degree of dilution has been found to be usually suitable for bringing samples within the sensitivity range of the assay. A lesser degree of dilution should if possible be avoided as higher salt concentrations interfere increasingly with the growth of *Euglena* (Hutner *et al.*, 1956).

Layout of assay.

This prepared sea water is now distributed into twelve flasks as follows:

2 ml., 4 ml., 8 ml., and 16 ml. portions respectively into each of three flasks

To each of these flasks are then added 4 ml. of the five-times strength medium and, where necessary, distilled water to make up the volume to 20 ml.

Parallel series of flasks are prepared containing graded amounts of cyanocobalamin within the concentration range of 0·025–0·20 $\mu\mu$g/ml. For this standard range a solution containing 0·25 $\mu\mu$g cyanocobalamin/ml. distilled

* McIlvaine's buffer is described in laboratory handbooks, e.g. Vogel, 1939.

water is prepared by serial dilutions with distilled water from a stock solution containing 5 μg cyanocobalamin/ml. 25% aqueous ethyl alcohol, and is distributed as follows:

2 ml., 4 ml., 8 ml. and 16 ml. portions respectively into each of three flasks

Medium and distilled water are then added as to the test extracts.

At least one other flask is made up to contain medium and water only, with no added vitamin B_{12}. This flask provides the experimental blank in the subsequent colorimetric measurement.

The flasks are closed with tight-fitting metal caps,* or are plugged with non-absorbent cotton-wool and covered with greaseproof paper caps. They are then autoclaved at 10 lb. pressure for 10 min.

Preparation of inoculum

For the *Euglena* inoculum 4–7-day-old cultures are used, grown at room temperature under approximately 200 f.c. illumination in 10 ml. portions of single-strength medium containing 80 $\mu\mu$g cyanocobalamin/ml. Such cultures contain about 10^4 cells/cu.mm.

Before use, the inoculum culture is washed so as to reduce carry-over of vitamin B_{12}, and to remove the inhibitory factor present in the culture liquors (Kristensen, 1955; cf. Ford, Gregory & Holdsworth, 1955).

This washing is performed by centrifuging down the cells and decanting the growth medium. The cells are re-suspended in sterile single-strength medium containing no vitamin B_{12}, and are again centrifuged and the medium is discarded. This procedure is repeated and the cells are finally suspended in 10 ml. of the single-strength medium containing no vitamin B_{12}.

The washing procedure is carried out under aseptic conditions to minimize risk of contamination of the *Euglena* culture.

Inoculation and Incubation.

The assay flasks, cooled to room temperature after the autoclaving, are each inoculated with one drop of the washed *Euglena* suspension. During this inoculation care must again be taken to prevent contamination by air-borne organisms.

The flasks are then incubated for about 10–12 days under 180 f.c. illumination and at approximately 28° C.

During the period of incubation the flasks are daily given a brief shaking to break any clumping of the *Euglena* cells. They are put back in random rearrangement.

* Moncrieff Ltd. of Perth supply flasks suitable for use with 'Oxoid' caps.

Reading of assay.

After incubation, the contents of each flask are poured into a centrifuge tube, the *Euglena* cells centrifuged down, and the medium decanted; 3 ml. acetone are added to each tube and the cells stirred up. Chlorophyll leaves the cells and goes into solution. The cell debris is again centrifuged down and is extracted with a further 1 ml. acetone; this extract is added to the first. The volume is finally made up to 4 ml. just before the colorimetric measurement to compensate for any evaporation of the acetone.

The chlorophyll extract from the *Euglena* grown in one of the flasks containing no added vitamin B_{12} is used as the blank in the measurement. The intensity of the colour of each chlorophyll extract is read against this blank. In this laboratory a Beckman DU spectrophotometer with 1 cm Corex cells is used, the optical density reading, log I_0/I at 432 mμ, being taken.

Calculation of results

The optical density readings deriving from the standard series of cultures grown with known amounts of cyanocobalamin are used to construct a calibration curve (Fig. 1). The concentration of cyanocobalamin corresponding to the optical density readings obtained from each of the dilutions of the sea-water sample is then read from the curve, and an average value for the cyanocobalamin concentration in the sea water is calculated.

Internal standards

The extent of agreement between results calculated from the optical density measurements at different sample dilutions gives an indication of their validity. It can be further checked by the use of an 'internal standard'. If an internal standard is to be employed, the procedure for setting up the assay is modified as follows: before the final dilution step in the preparation of the sea-water sample, two equal portions are taken and to one is added a known amount of cyanocobalamin. Both portions are then made up to the same volume with distilled water to provide the solutions for two series of assay flasks. A comparison of these two series makes possible the calculation of the vitamin B_{12} concentration originally present in the sea water without reference to the 'external' (cyanocobalamin in distilled water) standard.

Agreement between the values calculated by means of such an internal standard and those obtained with reference to the external standard provides good evidence for the validity of the result.

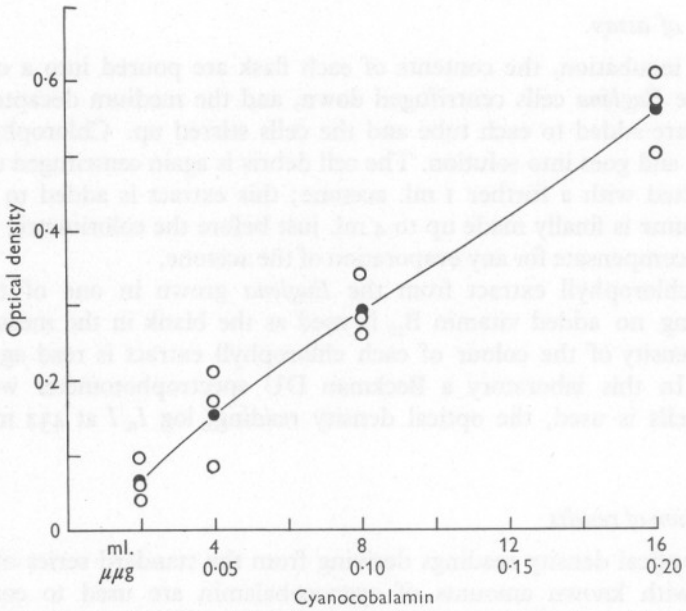

Fig. 1. Standard curve for assay of vitamin B_{12} by *Euglena gracilis* strain *z*. Standard cyanocobalamin 0·25 μμg/ml.; incubation for 12 days in this instance. ○ ○, values for individual flasks; ● ●, mean values. A smooth curve is drawn through the mean optical density values at the different levels of vitamin concentration. Slope and shape of the curve vary slightly from assay to assay. The horizontal ml. units refer to standard solution per flask, and the μμg units to cyanocobalamin per ml. The vertical units represent optical density of chlorophyll extract at 432 mμ.

TESTS OF THE *EUGLENA* ASSAY METHOD

Comparison with a previous method

Two 4 l. samples of surface sea water, collected 7 March 1956 at 58° 40′ N., 6° 10′ W. were supplied for assay by Dr R. Johnston of the Scottish Home Department Marine Laboratory, Aberdeen.

TABLE 1. COMPARISON OF METHODS OF MEASURING VITAMIN B_{12} IN SEA WATER

(Two surface samples taken 7 March 1956 at 58° 40′ N., 6° 10′ W.)

	Assay method			
	Dilution; *E. gracilis z* Vitamin B_{12} in mμg/l.		Phenol passage; *Lb. leichmannii* Vitamin B_{12} in mμg/l.	
Sample	By external standard	By internal standard	By external standard	By internal standard
A	2·0	1·6	1·7	1·5
B	1·5	1·4	1·0	1·0

10 ml. portions of each were assayed as described; 3500 ml. portions of each were subjected to the techique used by Cowey (1956) of phenol passage and subsequent assay with *Lactobacillus leichmannii*. The results (Table 1) show that agreement between the results from the different methods was reasonably close. The accompanying paper (Daisley & Fisher, 1958) lists six more examples of sea water assayed by both the *Euglena* method and the method of Cowey (1956), as well as results for thirty-five other samples assayed by the *Euglena* method alone.

Variation between repeated assays of samples during storage

Three samples of sea water, also supplied by Dr Johnston, were stored for 9 months and assayed four times at intervals during that period. Each assay was carried out with the same degree of replication as that described in this paper, and results were calculated with reference to external standards. The results (Table 2) give no indication of a fall in the vitamin B_{12} concentration

TABLE 2. VARIATION BETWEEN REPEATED ASSAYS OF SAMPLES OF SEA WATER DURING STORAGE

(The figures refer to vitamin B_{12} concentrations as measured with *Euglena gracilis* strain *z*)

Sample collected:	Time	7 Mar. 1957	13 Mar. 1957	15 Mar. 1957
	Place	57° 02′ N. 1° 45′ W.	58° 30′ N. 0° 30′ E.	59° 25′ N. 4° 00′ E.
	Depth	10 m	10 m	10 m
		Vitamin B_{12} in mμg/l.		
Assay batch	25 Apr. 1957	1·6	1·4	0·9
	21 May 1957	1·2	1·4	0·8
	7 Aug. 1957	1·9	1·8	1·2
	9 Dec. 1957	1·4	1·1	1·0

during storage; they do, however, show some variation between results from different assay batches. The degree of variation is greater than is customarily obtained with other methods discussed by Coates & Ford (1955), but this may result from the higher sensitivity of the *Euglena* assay, which will make it more susceptible to the effects of adventitious vitamin B_{12} and to slight variations in the experimental procedure.

The precision of the assay method is, however, adequate for showing any considerable variation in vitamin B_{12} concentration between different samples, such as the several-fold differences between the concentrations in coastal and oceanic waters or between summer and winter water (Cowey, 1956), or water from different depths (Daisley & Fisher, 1958).

DISCUSSION

It is probable that assays with other chlorophyll- (or other pigment-) producing organisms, such as those mentioned by Droop (1954), could be increased in sensitivity by the procedure described: starting with a washed

depleted inoculum, growing a large volume of the organism, and then extracting its pigment into a small volume of solvent and measuring the colour intensity obtained.

If there were available a range of organisms each responsive specifically to a different member of the vitamin B_{12} family of compounds, it would be possible to make separate estimates of the concentrations of each such compound present in the sea; but it is an interesting fact that those organisms so far investigated which need members of the vitamin B_{12} family all respond to cyanocobalamin itself, in addition to any other analogue which they may utilize (see the lists given by Coates & Ford, 1955; Droop, 1957).

Some degree of differentiation would, however, be possible by comparison of results obtained with a cyanocobalamin-specific organism and an organism responding to several of the analogues, as was done by Cowey (1956) following the work of Ford (1953).

Not all the vitamin B_{12} which, in assay procedures such as that described in this paper, is made available to the assay organism is necessarily in a free and nutritionally active form in the original sea water. Some or even all may be bound in cells or cell fragments, or be combined with other substances. To differentiate between 'free' and 'bound' vitamin B_{12} in sea water, more complex procedures would have to be applied, as was found necessary with milk samples (Gregory, 1954); and if some proportion of the vitamin B_{12} in the sea was found to be in 'bound' forms, there would remain the problem that these might be differently available to different marine organisms.

Further work on these various aspects discussed is continuing.

Results obtained with the *Euglena* assay method with samples taken to study the vertical distribution of vitamin B_{12} in the sea are presented in a companion article (Daisley & Fisher, 1958).

SUMMARY

A sensitive method for the measurement of vitamin B_{12} concentration in sea water is described.

Small volumes, e.g. 10 ml., of sea water are diluted with distilled water and a microbiological assay using the fresh-water flagellate *Euglena gracilis* strain *z* is carried out. The diluted sea-water samples are enriched with a growth medium, washed inocula of the *Euglena* are added, and these cultures are grown for up to 2 weeks under constant conditions of temperature and illumination. The chlorophyll is then extracted from the cultures into small volumes of solvent and the optical densities measured. These optical density readings are related to the concentrations of vitamin B_{12} available to the *Euglena* populations during their growth.

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VERTICAL DISTRIBUTION OF VITAMIN B_{12} IN THE SEA

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A considerable seasonal variation in the vitamin B_{12} concentration in oceanic surface water has been demonstrated by Cowey (1956).

The present investigation was undertaken to examine any variation with depth.

The samples were taken in the Bay of Biscay during cruises of the R.V. 'Sarsia' in May and June 1956 and May 1957. Stations sampled were:

Station A:	47° 30′ N., 7° 18′ W.
Station C:	46° 30′ N., 8° 00′ W.
Station 15:	48° 25′ N., 9° 57′ W.
Station 16:	48° 24′ N., 10° 00′ W.
Station 17:	48° 24′ N., 9° 53′ W.
Station 19:	47° 47′ N., 9° 18′ W.

The water was collected in a Nansen Pettersson bottle and in Nansen reversing bottles, then filtered through Whatman No. 3 filter-paper, preserved and assayed by the *Euglena* method as already described (Daisley, 1958). The 1956 samples were assayed twice each and the mean values are given in Table 1; the 1957 samples were assayed once only.

In addition, some of the 1956 samples, which were larger (but consequently fewer) than the 1957 samples, were also assayed by the Cowey (1956) procedure as a check on the accuracy of the *Euglena* method.

The results are given in Table 1. For the depth calculations and oxygen measurements we are indebted to Dr L. H. N. Cooper and Mr F. A. J. Armstrong of the Plymouth Marine Laboratory. They calculated the oxygen saturation values by reference to the tables of Truesdale, Downing & Lowden (1955).

The 1956 results indicated an inverse relationship between the vitamin B_{12} concentration and the oxygen concentration, suggesting that perhaps the vitamin was being synthesized in association with respiratory activity by organisms in these waters. The more detailed 1957 survey showed, however, that although the vitamin B_{12} concentration is in general highest at intermediate depths (*ca.* 200–2000 m) and the oxygen concentration reaches its minimum values within this region, the inverse relationship between them is not a close one.

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TABLE 1. VERTICAL DISTRIBUTION OF VITAMIN B_{12} IN THE SEA

Date station and sounding	Depth (to nearest 10 m) (m)	Oxygen concentration (ml./l.)	Oxygen saturation (%)	Vitamin B_{12}: Daisley's method (*E. gracilis z*) (mμg/l.)	Vitamin B_{12}: Cowey's method (*Lb. leichmannii*) (mμg/l.)
28 May 1956	100	5·74	97·4	0·8	0·7
C	500	4·92	81·9	2·1	—
4710 m	880	4·20	68·8	2·2	—
	990	4·40	71·3	4·6	4·2
	2110	5·51	77·1	3·0	—
29 May 1956	0	—	—	0·6	—
C					
4710 m					
20 June 1956	20	6·44	113·4	0·6	0·4
A					
1260 m					
22 June 1956	4040	4·82	65·0	0·5	0·5
C					
4710 m					
23 June 1956	600	—	—	2·5	1·7
A	1190	4·52	71·1	1·1	1·5
1260 m					
5 May 1957	220	5·76	97·0	0·3	—
15	310	5·61	94·3	1·9	—
590 m	400	5·31	88·8	1·9	—
	490	5·15	85·8	1·9	—
	580	4·93	81·5	1·7	—
5 May 1957	1270	4·93	74·9	1·0	—
16	1360	5·03	75·2	2·6	—
2620 m	1450	5·20	76·9	5·0	—
	1540	5·31	78·1	5·0	—
	1630	5·09	—	2·0	—
5 May 1957	400	5·41	90·6	1·5	—
17	490	5·05	83·9	1·7	—
2100 m	590	4·82	78·6	3·8	—
	690	4·83	78·7	3·5	—
	790	4·81	78·0	2·8	—
	860	4·48	72·7	2·4	—
	950	4·55	72·9	2·3	—
	1050	4·61	73·4	1·6	—
	1140	4·72	74·2	1·0	—
	1240	4·90	75·3	1·6	—
6 May 1957	0	—	—	0·3	—
19	190	5·72	96·5	2·0	—
3900 m	370	5·22	87·1	4·0	—
	560	4·82	80·1	1·6	—
	770	4·47	—	0·2	—
	970	4·26	68·5	1·5	—
	1170	4·61	71·4	3·9	—
	1560	5·77	82·4	1·6	—
	1980	5·74	80·3	1·0	—
	2980	5·44	74·3	0·8	—
	3580	5·38	72·7	0·4	—
	3600	5·26	71·1		

Dr Cooper intends to publish later other hydrographic data relating to this sampling programme; these other data do not, however, display any correlations with the pattern of vitamin B_{12} distribution.

No samples, even those from the greatest depths, were entirely lacking in vitamin B_{12}; the possibility must be considered, however, that the small amounts of vitamin B_{12} recorded in the deepest samples may derive from adsorptive contamination of the bottles as they passed down through the vitamin-rich regions. A means of avoiding any such possible source of experimental error will be sought.

When this present work was completed, we found a recent report of a survey of vitamin B_{12} concentration in the sea near Japan; here also a considerable variation with depth had been found, but no samples were from below 1200 m (Kashiwada, Kakimoto, Morita, Kanazawa & Kawagoe, 1957).

No conclusion can as yet be drawn regarding the cause of the variation in vitamin B_{12} concentration; possible contributory factors may be water movements, bacterial activity, consumption of the vitamin by the inhabitants of the illuminated zone and sinking of such organisms and their disintegration at lower levels.

We are grateful to the Director and staff of the Marine Biological Association for facilities and advice and especially to Dr L. H. N. Cooper and Mr F. A. J. Armstrong for their help in the collection of samples and for the provision of hydrographic data.

SUMMARY

Sea-water samples were taken from various depths in the Bay of Biscay in May and June of 1956 and 1957.

Low vitamin B_{12} concentrations were found in the upper illuminated zone and in the greatest depths (mean value for seven samples, 0·57 mμg/l.; standard deviation 0·19 mμg/l.), whereas at intermediate depths (190–2110 metres) the values were generally higher, up to 5·0 mμg/l. in two instances (mean value for 34 samples, 2·26 mμg/l.; standard deviation 1·22 mμg/l.).

Evidently there exists a considerable variation with depth of the vitamin B_{12} concentration in the sea region sampled at this season. It remains for further research to show what causes this vertical variation to exist, and what influence, if any, it has on life in these waters.

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SUBLITTORAL ALGAL POPULATION IN PORT ERIN BAY, ISLE OF MAN

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(Text-fig. 1)

In recent years much information has accumulated on the composition and distribution of algal populations in the Isle of Man, with increased knowledge of their ecological relationships (Knight & Parke, 1931, 1950; Jones, 1948; Lodge, 1948, 1954; Burrows & Lodge, 1949, 1951; Southward, 1953). This, however, has mostly come from studies made in the intertidal region, and even here many problems remain for which, at present, no satisfactory explanation can be found. The mostdifficult of these, perhaps, relates to the appearance of algal species for a limited period of the year only: it is not known where and in what form their life-histories are continued for the rest of the year. The littoral and sublittoral regions are known to have many species in common. This means that the differences between the regions, as environments for the growth of algae, can be bridged by the plasticity of the species concerned. It seemed likely, therefore, that a detailed study of the sublittoral algal populations might help towards an understanding of the ecology of both regions and also of the interactions between them.

Attempts have been made by several workers using diving equipment to find the exact distribution of sublittoral algae (Kitching, Macan & Gilson, 1934; Bursa & Wojtusiak, 1939, 1948; Waern, 1952; Forster, 1955, 1958; Aleem, 1956), but the scope of such work is limited at present. Walker (1947) made surveys of sublittoral algae around the coast of Scotland using a specially designed view-box for inspection of the sea floor and a calibrated spring grab for collecting samples from fixed points, and was able to make quantitative estimates of the distribution of the larger brown algae over a wide area.

In August 1955 a survey of the sublittoral algae of Port Erin Bay was begun using a combination of the techniques mentioned above. The bay is approximately half a mile square and partially bounded on the seaward end by a broken breakwater. On the north and south the sides are rocky, while most of the floor of the bay is sandy. From the beach at the eastern end to the breakwater and open sea on the west, the bay shelves gradually to a depth of 12 m. The deepest part lies in the angle formed by the breakwater and the south shore and reaches a depth of 14 m. The limit of the sublittoral

rock surface was determined in 1956 by echo-sounding. The limit was taken as the point at which the steeply sloping side of the bay turned abruptly to the horizontal. As far as possible this was checked by direct observation but, at the time this work was carried out, the water was not very clear. Tidal currents enter the bay on the north side and swing round towards the south, but little is known about water movement on the floor of the bay. The area was sampled by means of a spring grab of the type used by Walker (1947). It took algae from a square of side 75 cm and was used much in the same way that an ecologist on land uses a quadrat as a sampling unit. The grab was worked from the motor-boat 'Cypris' and, for each sample taken, the boat position was determined by taking sextant readings on to accurately charted points on the shore. Depths were measured with a lead line, and, so that it would be possible to relate all depths to a fixed tide level, simultaneous readings were made on a tide-staff on the harbour wall for all periods over which samples were taken in the bay. Through an analysis of the samples it was hoped to work out the over-all distribution of the algae. The action of the grab was watched through the very calm clear water, and observations on its action on different types of substrate were also made by a diver using an aqualung. On a number of occasions the diver completed clearance of squares incompletely cleared by the grab. In this way it was found that the grab did not always give a complete clearance of the sample squares and undoubtedly a good deal was missed, but the method had the advantage that, for the algae collected, the exact positions in which they were growing were determined.

Because of the extremely favourable weather conditions in 1955, the survey proved to be much easier than had been anticipated. The water was so calm and clear that the major beds could easily be seen through a glass-bottomed bucket and their limits were plotted from a rowing boat with the help of a sextant. The survey was repeated in August 1956 using the same general methods, and 125 samples were taken on each occasion.

DISTRIBUTION OF THE SUBLITTORAL ALGAE

It was found that there were two distinct algal vegetation regions in the sublittoral, associated with the two main types of substrate, continuous rock surface and sand. The bay floor consists mainly of sand overlaid by stones and boulders of varying sizes; in places these lie close together in large groups, in other places they are widely scattered and often partially buried in the sand. No doubt much movement of stones and boulders occurs on the sea bed at some seasons of the year, but many boulders brought up by dredge and grab appeared to have been buried for some time and supported growths of algae only on one surface. Certain large groups of boulders are conspicuous at all times of the year as a result of the weed they carry. An

analysis of the composition of the vegetation associated with the two regions is given in Table 1. Only those species, the identification of which is certain, have been included. Herbarium specimens of the algae collected during the survey have been deposited in the herbarium of the Botany Department of Liverpool University. The names used are those in Parke's check-list (1953), with later corrections (Parke, 1956, 1957).

The vegetation of the continuous rock surface

The algae attached to the rock surface form a more or less permanent population conspicuous at all times of the year. In this population *Laminaria digitata*, *L. saccharina*, *L. hyperborea* and *Saccorhiza polyschides* are the dominant plants, with many smaller algae present either on the rock surface or as epiphytes on the stipes of *Laminaria hyperborea*. Table 1 distinguishes the species found in this population. The *L. hyperborea* plants had an average age of 6 ± 2 years, as determined by counting the numbers of growth-rings at the base of the stipe (Parke, unpublished). The maximum age was 8 years. The population extended downwards to a depth of 12 m and appeared to be limited by the absence of continuous rock below this level. Forster (1955) records *L. hyperborea* as extending down to, and disappearing below, 17 m in the vicinity of Stoke Point rocks, Devon.

The vegetation of the floor of the bay

An extensive population, which was more or less loose-lying, was found on the floor of the bay and covering the greater part of its area. The dominant species were *L. saccharina*, *Saccorhiza polyschides*, *Chorda filum* and *Desmarestia aculeata*. The substrates available for attachment in this region consist of sand grains, loose pieces of shell, stones of various sizes, small boulders and other algae. Probably in the first instance most of the algae belonging to this population are attached, perhaps only to sand grains, but at the time that this survey was made, many of them showed no sign of having had an attachment. In the case of *Laminaria saccharina*, the haptera had many branches, but the ends were quite free or intertwined with other algae. Such haptera were, on the whole, smaller than those found for attached plants. Sometimes each hapteron branch was attached to a separate small pebble or piece of broken shell. Many of the smaller algae were found in tangled masses, and in some cases a definite adhesion had been formed so that the plants stuck firmly together. Notable in this respect were the adhesions made by the thalli of *Dictyota dichotoma* and *Plocamium coccineum*, both to other algae and also to stones. Once attached in this way, the fronds of *Dictyota* are able to grow forming flat expanded sheets.

Much of the loose-lying population was at a depth of 10–14 m, but it extended into shallower water. It disappeared, however, where the depth of the

TABLE 1. LIST OF ALGAE FOUND DURING THE SUBLITTORAL SURVEYS 1955 AND 1956

Species	Percentage occurrence in samples: Rock surface population 1955	Rock surface population 1956	Loose-lying population 1955	Loose-lying population 1956
Laminaria hyperborea (Gunn.) Fosl.	74	72	—	5
L. digitata (Huds.) Lamour.	24	5	4	—
L. saccharina (L.) Lamour.	32	40	96	52
Saccorhiza polyschides (Lightf.) Batt.	40	43	38	30
Chorda filum (L.) Stackh.	2	3	40	37
Desmarestia aculeata (L.) Lamour.	4	12	80	43
Sphacelaria pennata (Huds.) Lyngb.	4	10	62	34
Dictyota dichotoma (Huds.) Lamour.	4	17	60	35
Ulva lactuca L.	26	15	44	25
Phycodrys rubens (Huds.) Batt.	78	63	38	16
Rhodymenia palmata (L.) Grev.	70	60	56	14
Membranoptera altata (Huds.) Stackh.	54	63	10	7
Ceramium rubrum (Huds.) Ag.	42	25	44	16
Ptilota plumosa (Huds.) Ag.	46	33	4	7
Plocamium coccineum (Huds.) Lyngb.	20	25	72	30
Delesseria sanguinea (Huds.) Lamour.	20	7	20	10
Cryptopleura ramosa (Huds.) Kylin	18	53	28	16
Callophyllis laciniata (Huds.) Kütz.	38	17	30	26
Callocolax neglectus Schm.	4	—	2	—
Lithothamnion, etc.	36	27	14	4
Chondrus crispus (L.) Stackh.	14	3	2	6
Cladophora rupestris (L.) Kütz.	10	7	2	8
Sorocarpus micromorus (Bory) Silva	10	3	16	—
Rhodomela confervoides (Huds.) Silva	8	17	30	26
Odonthalia dentata (L.) Lyngb.	8	10	10	8
Brongniartella byssoides (Good. et Woodw.) Schm.	8	12	36	31
Polysiphonia violacea (Roth) Grev.	8	—	16	1
Hypoglossum woodwardii Kütz.	6	7	8	10
Gigartina stellata (Stackh.) Batt.	6	5	10	5
Fucus serratus L.	6	7	4	6
Lomentaria articulata (Huds.) Lyngb.	6	3	6	1
Phyllophora membranifolia (Good. et Woodw.) J. Ag.	6	3	2	—
Apoglossum ruscifolium (Turn.) J. Ag.	6	15	—	—
Gelidium latifolium (Grev.) Born. et Thor.	6	13	—	1
Polysiphonia elongata (Huds.) Harv.	6	—	30	10
P. nigrescens (Huds.) Grev.	6	—	16	6
Corallina officinalis L.	4	5	2	—
Litosiphon pusillus (Carm.) Harv.	4	—	4	10
Plumaria elegans (Bonnem.) Schm.	2	7	2	4
Pterosiphonia complanata (Clem.) Fkbg.	2	3	18	7
Antithamnion sarniense (Lyle) G. Feldm.	2	4	44	—
Chaetomorpha melagonium (Web. et Mohr) Kütz.	3	12	—	2
Fucus vesiculosus L.	2	3	—	2
Halidrys siliquosa (L.) Lyngb.	2	—	—	2
Polysiphonia urceolata (Dillw.) Grev.	2	17	—	4
Ectocarpus confervoides (Roth) Le Jol. s. lat.	2	—	4	1
Cruoria pellita (Lyngb.) Fries	2	—	—	—
Ceramium diaphanum (Lightf.) Roth	2	—	—	—
Stictyosiphon subarticulatus (Aresch.) Reinke	2	—	—	5
Chylocladia verticillata (Lightf.) Bliding	2	—	—	—
Asparagopsis armata Harv., tetrasporophyte	2	—	—	1
Enteromorpha compressa (L.) Grev.	2	—	—	—
E. clathrata (Roth) Grev.	2	—	2	—
Cystoclonium purpureum (Huds.) Batt.	—	25	12	20

TABLE 1 (*cont.*)

Species	Percentage occurrence in samples: Rock surface population 1955	Rock surface population 1956	Loose-lying population 1955	Loose-lying population 1956
Heterosiphonia plumosa (Ellis) Batt.	—	7	2	1
Cladostephus verticillatus (Lightf.) Ag.	—	3	4	1
Ahnfeltia plicata (Huds.) Fries	—	3	8	7
Alaria esculenta (L.) Grev.	—	7	—	2
Chondria dasyphylla (Woodw.) Ag.	—	5	—	—
Spermothamnion repens (Dillw.) K. Rosenv.	—	3	—	6
Chordaria flagelliformis (Müll.) Ag.	—	3	—	2
Griffithsia flosculosa (Ellis) Batt.	—	3	—	1
Calliblepharis ciliata (Huds.) Kütz.	—	3	—	—
Nitophyllum punctatum (Stackh.) Grev.	—	3	—	—
Bonnemaisonia asparagoides (Woodw.) Ag., sexual plant	—	—	18	7
Gracilaria verrucosa (Huds.) Papenf.	—	—	16	4
Sporochnus pedunculatus (Huds.) Ag.	—	—	16	1
Ceramium tenuissimum (Lyngb.) J. Ag.	—	—	14	1
Bonnemaisonia hamifera Hariot, tetrasporophyte, sexual plant	—	—	10	1
Naccaria wiggii (Turn.) Endl.	—	—	2	—
Polysiphonia nigra (Huds.) Batt.	—	—	4	—
Cutleria multifida (Sm.) Grev.	—	—	4	—
Corynospora pedicellata (Sm.) J. Ag.	—	—	2	1
Arthrocladia villosa (Huds.) Duby	—	—	2	—
Seirospora griffithsiana Harv.	—	—	2	—
Dictyopteris membranacea (Stackh.) Batt.	—	—	2	—
Polysiphonia spiralis Batten	—	—	2	—
Isthmoplea sphaerophora (Carm.) Kjellm.	—	—	2	—
Porphyra umbilicalis (L.) Kütz.	—	—	2	—
Enteromorpha linza (L.) J. Ag.	—	—	2	—
Furcellaria fastigiata (L.) Lamour.	—	—	—	4
Dumontia incrassata (Müll.) Lamour.	—	—	—	2
Spongonema tomentosum (Huds.) Kütz.	—	—	—	2
Asperococcus bullosus Lamour.	—	—	—	2
Scytosiphon lomentaria (Lyngb.) Endl.	—	—	—	1
Myrionema strangulans Grev.	—	—	—	1
Tilopteris mertensii (Sm.) Kütz.	—	—	—	1
Callithamnion tetragonum (Wither.) Ag.	—	—	—	1
Polyides caprinus (Gunn.) Papenf.	—	—	—	1
Holmsella pachyderma (Reinsch) Sturch	—	—	—	1
Chaetopteris plumosa (Lyngb.) Kütz.	—	—	—	1
Halarachnion ligulatum (Woodw.) Kütz.	—	—	—	1
Dudresnaya verticillata (With.) Le Jol.	—	—	—	1
Sphondylothamnion multifidum (Huds.) Näg.	—	—	—	1

The species underlined were found only in the loose-lying population and below 8 m.

water was less than 4 m at low tide. This fact will be referred to again later.

It has not been possible to identify with certainty all the algae found in the loose-lying population; some belong to genera in which the separation of species is at present extremely difficult, while others lack the reproductive stages necessary for identification. Of the eighty-eight species so far identified,

fifty-seven were also found growing in the permanent sublittoral population on the rock surface, many were also known to occur in the intertidal region, but eleven were found exclusively in the loose-lying population (see Table 1). The algae belonging to this last group of obligate sublittoral species occurred only in the deeper part of the bay and were not found at a depth of less than 8 m, measured at low tide. Some of the plants found in the loose-lying population, but not in the permanent, are also known to occur in the intertidal region and may have been washed down into the sublittoral, but they appeared quite healthy and many were fruiting. The question as to how far these algae, which were also found in the intertidal region, could be regarded as having developed in the loose-lying population or to have been washed into it during the summer, is not easily answered. Occasional plants of *Laminaria saccharina* showed evidence of having been torn from a rock surface, but the vast majority gave no sign of ever having been attached. It will be shown later that sand grains can give an attachment for algal reproductive bodies sufficient to allow them to segment and develop into new plants. In some cases no further attachment is necessary. In the loose-lying population there was a notable absence of many of the intertidal algae, such as *Ascophyllum nodosum*, *Pelvetia canaliculata* and *Fucus* species, except for *F. serratus* which was present in a very broad form at 4–7 m depth. *Laminaria hyperborea*, which is also often washed up on to the shore in quantity, was absent from the loose-lying population of 1955 and almost so in 1956. Probably owing to the calm weather of 1955, little material had been added from the intertidal region; but, in rougher weather, it seems likely that the latter region would add considerably to the loose-lying population. In this survey, interest centred, not so much in making a species list for the sublittoral algae as in finding out something about their ecological relationships. In April 1955, a dredge haul was taken across Port Erin Bay in a direction which would have passed right through the loose-lying population. On this occasion no algae at all were found. This might have been the result of temporarily unfavourable conditions, the water temperature being very low following two very cold winters and a very cool summer in 1954. In the months following April 1955, there was a period of very calm seas, and sediment settled giving very clear water. The more intense light and warmth of the sunshine passing through the clear water gave ideal conditions for the development of sublittoral algae and an extensive population was found here at the end of August.

The lack of disturbance of the sea bed in this particular year was well illustrated by the form of *Saccorhiza polyschides* growing in this region. On the rock surface in shallower water, the fronds were split into several fingers, but loose-lying plants from a depth of 10 m showed very little splitting of the frond.

It seemed obvious that with any disturbance of the bottom waters, much of the loose-lying population would be washed in and this was observed

towards the end of the period of the survey. On 2 September, a south-westerly wind sprang up and waves began to break on the rocks on the north side of the bay. During the following 24 h an appreciable quantity of sea-weed had been washed up beyond the tide line and trials with the grab suggested that some shifting of the central mass had taken place. Attempts to replot the positions of the weed beds, by visual means, failed because sand in the water obscured the view. An enormous quantity of sand was stirred up and its suspension noticeably altered the colour of the water. The heavier particles would settle rapidly, but finer material would continue to restrict the penetration of light to the sea bed for a considerable time. During the next 24 h the wind had again increased and small boulders and stones were washed in with attached weeds.

An analysis of the algae brought in during the first 24 h of the gale showed that it came from three sources: (1) the intertidal region, (2) the sublittoral attached population, (3) the sublittoral loose-lying population. Thus it is seen that under the very favourable conditions of 1955, an extensive, more or less loose-lying population was developed on the floor of Port Erin Bay and that this remained undisturbed through the prolonged calm weather of the summer. As soon as storms came, bringing about movement of the bottom waters, a considerable quantity of weed from this population was carried inshore, but the disturbance failed to remove all of it. At the end of November 1955, there was an appreciable quantity left, but the plants were very broken and rotting. Grab and dredge samples taken at intervals during the winter months showed that many fragments of algae were still present at the end of January. Many of these had begun to proliferate new branches, some of the latter primarily concerned with asexual reproduction, others giving vigorous vegetative growth. Examples of this will be discussed later.

Patches of large boulders give a firm substrate for sublittoral algae in several parts of the bay and these may be conspicuous at all times of the year. One such large patch occurs in the centre of the bay in such a position that a part of it may occasionally just be exposed to the air at extreme low water of spring tides. The distinction between patches of this kind and the general loose-lying population is only one of degree. The stability of any part of the population depends on the size and also on the firmness of the substrate and the degree of water movement.

Naylor (1955), working on species of *Idotea* (Isopoda), found large numbers of these animals feeding on decaying sea-weed in the deep corner of the bay in the angle formed by the south shore and the breakwater. It seems likely, bearing in mind the direction of tidal currents within the bay, that there is a general tendency for the bottom algae to be washed, perhaps very slowly, into this corner where they decay. Grab samples attempted in this position in March 1956 brought up no healthy plants, but many decaying fragments in the mesh of the grab net, and large numbers of *Idotea*.

Conditions in 1956

Unlike the summer of 1955 that of 1956 was stormy and lacking in sunshine. The same general distribution of sublittoral algae was found, but with some significant differences in the second year.

(1) The extent of the loose-lying population was distinctly less than in the previous August and its position was different. Whereas in 1955 the population extended over the major part of the sand of the bay, in 1956 a continuous cover of large algae was only found in shallower water. Elsewhere in the bay algae were present in more scattered patches. Many algae had already been washed up on to the beach and much of the tangled mass in shallow water had probably started life deeper down and been brought inshore by water movement.

(2) There was a considerable difference in the size of the plants of *Saccorhiza polyschides*. In 1955, the majority of the plants found were very large, with well-formed holdfast 'bells' and many with stipes winged and releasing zoospores. In 1956, no mature plants were found; the majority were in the sporeling stage with the bells just beginning to form as small rims on the stipe. The largest bells were little more than half the size of that of an adult plant. It is certain that adult plants, if formed, would have been lost more easily than sporelings, but it is unlikely that none at all would have remained on the floor of the bay. Since no adult plants at all were found in the samples at the end of August, it is likely that the whole population was at an earlier stage of development and this could have been the result of less favourable conditions for growth during this season.

(3) The species composition of the loose-lying population in 1956 was not identical with that of 1955, and many species showed an increase or decrease in quantity between the years. *Gracilaria verrucosa*, *Sporochnus pedunculatus* and *Antithamnion sarniense*, all present in quantity in the deeper parts of the bay in 1955, were quite rare in 1956. *Desmarestia aculeata* also showed a marked decrease in bulk, though it was present in fair quantity in 1956. On the other hand, *Brongniartella byssoides*, found as only occasional plants in 1955, had increased considerably the following year. These differences may have resulted from the deficiencies of the sampling method, but the general impression gained by those working on the survey in both years was that there was a very distinct difference in the species composition, particularly of the loose-lying populations, between the years. At present there is little information concerning the way in which environmental factors affect the individual species, but it seems likely that they do not all react in the same way, and certainly they must influence one another as they thrive or decrease, so that the composition of the population will continually be changing.

Over-wintering of species of the loose-lying population

In considering the question of how the various individual species composing the loose-lying population pass the winter months, one or two points may be noted.

(1) Some of the species do not survive. *Acrothrix gracilis* was dredged in quantity in the bay in 1950, but was not found at all in 1955. One small piece was found again in 1956.

(2) New species may appear. The source of these is at present not certain, but they may result from the practice of the local fishermen of throwing stones and boulders, caught in their nets, into the bay on the inner side of the breakwater. No information is available as to whether species could come from outside the bay as reproductive cells, or as small pieces of thallus travelling in the sea water.

(3) For those species occurring, not only in the loose-lying population, but also in the intertidal and/or in the sublittoral permanent population, e.g. *Laminaria saccharina* and *Saccorhiza polyschides*, plants for the following season could be obtained from these sources. It is interesting, however, that the four larger brown algae which form the bulk of the loose-lying population, *Laminaria saccharina*, *Saccorhiza polyschides*, *Chorda filum*, and *Desmarestia aculeata*, all have the same type of life history, involving an alternation between a large and structurally complex sporophyte and an exceedingly minute gametophyte. Samples of sand and gravel, as well as small stones collected at intervals during the winter months and kept in culture, all yielded young *Laminaria* sporophytes within a few weeks, as did also fragments of algae collected with the stones. This suggests that gametophytes are formed in such large numbers that they cover every available substrate, giving a continuous supply of plants for the loose-lying population.

Fragments of plants of many species were found in samples collected during January and February, many of them in a fruiting condition. The fragments were subjected to culture experiments and stages found in culture were searched for in the field at the same time. This procedure gave information on the way in which some of the individual species pass the winter. A few examples will be given from species for which the evidence is sufficiently complete to form a picture of the overwintering method. Much work remains to be done on these lines before anything like a complete picture can be obtained of the population as a whole.

CULTURE TECHNIQUES

In the culture experiments described below, the plants have been grown in an enriched Erdschreiber solution in glass troughs suspended in constant-temperature culture tanks. The tanks are lighted from above by lamps fixed into movable canopies and both 300 W. filament bulbs, and Atlas Daylight

fluorescent tubes are used as alternative light sources. Throughout the experiments the temperature has been maintained at 10° C, and a day length of 18 h has been used. The cultures have been aerated by bubbling air through the culture medium. The medium used has been Erdschreiber (Føyn, 1934) enriched by the addition of 'Tris' (Hydroxymethyl-amino-methane), the disodium salt of Ethylene-diamine-tetra-acetic acid, Vitamin Mix S_8, and the range of trace elements in the concentrations given in the marine medium ASP_2 of Provasoli, McLaughlin & Droop (1957). I am grateful to Dr Provasoli for sending the formula for this medium to me and allowing me to use it before it was published.

A GENERAL CULTURE EXPERIMENT

Six stones each bearing, apparently, only one or two small plants of *L. saccharina* were taken from a dredge sample from the bay in September 1956. The *Laminaria* plants were cut back to a length of about 3 cm above the short stipe, and the stones were kept in culture throughout the winter months, during which time the plants increased to a length ranging from 25 to 30 cm but did not form sporangia. By the beginning of April 1957, the following algae had appeared attached either directly to stones or to the haptera of the *Laminaria* plants: enormous numbers of *Laminaria* sporelings some of which were large enough to be identified as *L. saccharina*, sporelings of *Saccorhiza polyschides*, *Asperococcus bullosus* (unilocular sporangia), *Cladostephus verticillatus*, *Ectocarpus* sp. (plurilocular sporangia), *Ulva lactuca*, *Chaetomorpha melagonium*, *Enteromorpha clathrata*, *Rhodomela confervoides*, *Bonnemaisonia hamifera* (tetrasporophyte), and *Polysiphonia* sp.

Only diatoms appeared on control stones kept in the same culture medium under similar conditions in a second glass trough. If six small stones taken at random from the floor of the bay in this way could produce a population of this kind in culture, presumably from reproductive bodies or juvenile stages already present attached to the stones in the autumn, the source of the sublittoral population for the following year is not far to seek.

It is interesting that *Rhodomela confervoides* appeared on the stones in this culture experiment. This alga is found frequently in the intertidal region and was plentiful in the sublittoral loose-lying population during the summers of both 1955 and 1956. It was found also in dredge samples in January 1956 as unattached broken fronds which had lost all secondary branches and were so ragged in appearance as to be hardly recognizable. Arising from the denuded main axes, however, were large numbers of very short erect branches ending in dense tufts producing tetrasporangia. Almost frondless midribs of *Delesseria sanguinea* producing tetrasporic branches in enormous numbers were also found in the same dredge sample and it is possible that other red algae behave in a similar manner in the deeper waters of the bay during the winter. If algae are able to reproduce freely in this way in the sublittoral,

this region may be extremely important in acting as a source of new populations for the intertidal region also. Much more detailed work, however, would be required to establish this as an ecological principle.

INDIVIDUAL SPECIES

Laminaria saccharina

The life history of *L. saccharina* includes two distinct morphological phases, a structurally elaborate diploid plant alternating with an extremely minute gametophyte, the latter consisting of a branched filament of a few cells, sometimes reduced to a single cell (Williams, 1921; Harries, 1932). Parke (1948) reported, as a result of her investigations, that 'sporophytes of *Laminaria saccharina* can be produced in nature during all months of the year at some level of the shore,.... The gametophyte generation of the species must, therefore, be capable of reproduction during all months of the year'. In the sublittoral zone, 1–4 m below E.L.W.S.T., Parke reports cessation of sporophyte development from November to February. She suggests that this is due to low light intensity. Parke gives the region in the sublittoral zone of 6–12 m below E.L.W.S.T. as a habitat in which no development of young plants was obtained on prepared surfaces. She remarks, however, that well developed plants of *L. saccharina* have been brought up from depths down to 12 m and suggests that, since these were growing on shingle, they may have been washed down into deeper water, having started their development in shallower water.

Sporelings of *L. saccharina* have been found in samples taken from the floor of Port Erin Bay during all months of the year. There seems little doubt that sporophyte production occurred on quite a large scale at depths down to 14 m here during the winter of 1955–56. A dredge sample taken across the bay at the end of January 1956 included the following: (1) plants of *L. saccharina* with the previous year's frondage attached to new frondage. The plants had either no apparent attachment or they were attached to stones and shells. Some had obviously been torn away from a rock surface, but had new hapteron branches attached to small stones, suggesting that this latter attachment had developed while the fronds were lying on the bottom gravel; (2) very small plants attached to stones and other algae; (3) broken pieces of large plants.

Both whole fronds and also broken pieces were found with ripe sporangia. Zoospores were released and allowed to settle in sea water on glass slides in glass dishes which were kept covered in a dim light in a constant temperature room at 10° C. Later the dishes were transferred to the constant temperature culture tank at 10° C, again under a low light intensity. The zoospores germinated to give both male and female gametophytes. In the female gametophytes no branched filaments were formed. The development was similar to that described by Williams (1912) and Harries (1932) as sometimes occurring in this species. After the zoospore had settled, a germination tube

grew out and the contents of the spores passed into its swollen end which was then cut off by a wall. The swollen cell, which Harries described as the 'effective plant' functioned directly as an oogonium. Harries's work suggested that this might have been the effect of the culture conditions in which a fairly low temperature and a low light intensity were used, a high temperature and light intensity inducing a filamentous form in the gametophyte. Although no idea has yet been obtained of the exact conditions at the bottom of the bay, the temperature and light levels during the winter months would certainly have been below those used in the culture experiments. Fertilization was not observed, but since male gametophytes producing antheridia were also present on the same slides, it may actually have occurred. Since, however, young sporophytes were observed to be developing before any antheridia were seen, there is a possibility that parthenogenesis may have occurred. This has been recorded for *L. saccharina* by Schreiber (1930), though his haploid sporophytes showed an abnormal development. Since the zoospore can act directly as an oogonium and the male gametophytes are exceedingly small, a particle as small as a sand grain would be sufficient to provide attachment for the growth of the new sporophyte. Zoospores are produced in enormous numbers by the mature sporophytes so that, given suitable conditions of temperature and light intensity, and if undisturbed too greatly by water movements, there is the potentiality for the production of a large sublittoral population of *L. saccharina*. That this does, in fact, happen was shown by the presence, in samples taken at the end of March by dredge, of large numbers of sporelings of varying sizes, attached to sand grains and to small and large stones and to other algae. The range of size of frond found suggested that sporophyte production had proceeded throughout the winter. That a proportion of the sporophytes, even including some of very small size, had started to develop the previous autumn, was shown by a distinction in the fronds between narrow and broad regions of growth. A period of more active vegetative growth is reported by Parke (1948) to begin in January and the autumn and spring regions of growth can be distinguished by a marked difference in width in the frond. Since the young sporophytes were found in dredge samples, the exact depth from which they were taken could not be determined, but their presence on one or two large boulders taken in a position close to the seaward end of the breakwater suggests that they can develop at a depth approaching 14 m.

In culture the developing sporophytes were removed from the slides as soon as they had reached a size of between 0·5 and 1 cm and were large enough to handle and they were left lying loose in the culture solution. They continued to develop, and by May 1957 had reached a maximum length of 30 cm and a width of 8 cm. The total amount of frondage formed during this period was, however, greater than is indicated in this length measurement since decayed frondage was cast at the free end, while new tissue was added from

the meristem above the stipe. It is of particular interest that the haptera of these plants have developed many branches and appear in all respects similar to those found on plants in the loose-lying population suspected of having developed unattached on the floor of the bay (Fig. 1). It appears therefore that, except in the very earliest stages of the development of the sporophyte, an attachment to a substrate is not necessary for the growth of *L. saccharina*. That the free hapteron branches can become secondarily attached to a substrate is suggested by systems of the type in which each branch is attached separately to a small stone or shell.

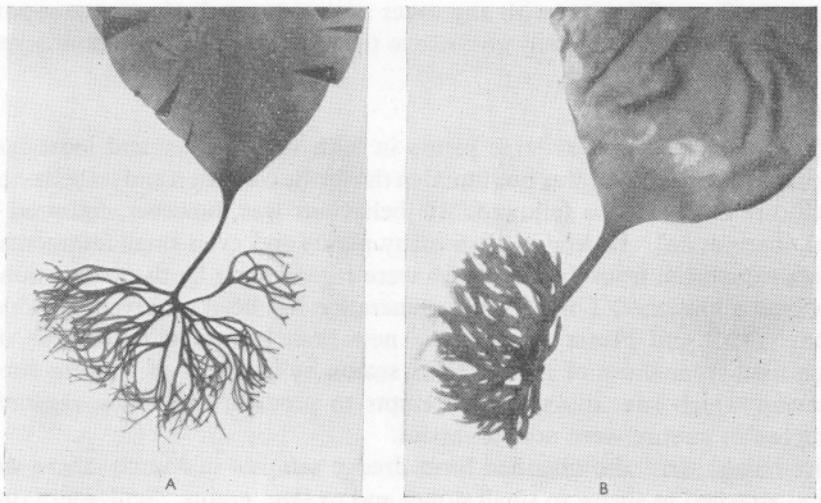

Fig. 1. Hapteron systems of *Laminaria saccharina* (L.) Lamour. A, plant from loose-lying population (from herbarium sheet) $\times \frac{2}{9}$; B, plant grown unattached in culture $\times \frac{2}{3}$. Photos J. H. Bloor.

Saccorhiza polyschides

Spence (1918) reports that for the Orkney Islands, during the winter months the fronds of *S. polyschides* are washed ashore, but that the attaching 'bells' which become very firmly attached to the substrate, remain behind. Possibly this also happens in the sublittoral permanent population in Port Erin Bay, but it was not possible to find them. Samples taken in the winter months here showed that, while the majority of the mature plants, together with the stipes carrying the reproductive frills, had disappeared, there were still many basal bells lying loose on the floor of the bay. Some of these were dredged in January 1956, dark with sporangia all over the surface of the wart-like projections. Zoospores were released from these and allowed to settle on slides which were kept in culture in the laboratory. Male gametophytes were formed as short slender branched filaments, but, as with *Laminaria saccharina*, there

was a tendency for the female gametophyte to be represented by a single cell: the first division cut off a cell which behaved as an oogonium developing directly into a new sporophyte. Fertilization was not observed. By March the sporophytes had reached a length of 3–4 cm. Sampling by dredge in Port Erin in March produced similar sporophytes in large numbers on stones and other algae. Some of the sporophytes found in the field were larger than those grown in culture, but many were at the same stage of development. Probably for *Saccorhiza polyschides* the attaching bell is of greater importance as a reproductive structure than the frill to the stipe which disappears earlier in the autumn with the blade of the plant. Such loose-lying bells, rolling round the floor of the bay with any water movement and releasing zoospores in large numbers, could easily give rise to the population for the ensuing year.

Desmarestia aculeata

D. aculeata occurred as large plants in both rock surface and loose-lying populations. This plant was not found in the fertile condition and its behaviour in culture could not be followed. Its behaviour was, however, followed by field observations. In March 1956 many plants and even small fragments of plants were taken from the bay which were regenerating by the production of new lateral branches. This type of regeneration has been observed by Söderström (1889) and Printz (1926). The new branches could readily be distinguished from those of the previous season by the tufts of delicate lateral branches which later disappear. Attempts to produce these new vegetative branches in culture were not successful.

Sporelings were also obtained from dredge samples in March: these were found attached to shells, to small stones and to sand grains. Schreiber (1932) has shown that the zoospores released by adult fronds give rise to filamentous gametophytes bearing oogonia and antheridia; and it may be assumed that these are formed on stones and shells and sand grains on the sea floor, sporelings later arising from them.

This plant therefore appears to have two distinct methods of building up its numbers for the following year, first, by regeneration from old plants and fragments of plants and, secondly, by the completion of its dimorphic life-history at the bottom of the bay.

DISCUSSION

To determine the behaviour of the sublittoral loose-lying population as a whole, one must know the behaviour of its component species and the interrelationships between them, and autecological studies will have to be made on the majority of its species. The composition of the population undoubtedly changes from time to time, both in the identity of the component species and also in their relative abundance. Changes in the conditions to which the

population is subjected will almost certainly affect different species in different ways and the species themselves will affect one another by their absence or presence and abundance. Since the sublittoral loose-lying population has many species in common with that of the sublittoral rock-surface and intertidal areas, it is likely that there are complex interactions between the three regions. A slight indication that this is so is given by the fact that some species, as for example *Rhodomela confervoides*, occurring frequently in the intertidal region, can reproduce freely in the deeper parts of the bay during the winter months. The evidence given in this paper suggests that a detailed knowledge of the requirements and behaviour of algae in the sublittoral region will help towards an understanding of the ecology, not only of this, but also of the intertidal region.

I am much indebted to the Council of the Royal Society for a grant from the Browne Research Fund towards the cost of the survey, and I wish to thank Prof. N. A. Burges for help and encouragement throughout the course of the work. The work was carried out from the Marine Biological Station in Port Erin, and I should like to thank the Director, Mr J. S. Colman and his Staff, particularly Mr A. B. Bowers and Dr J. Kain, for their help in many ways: also Mr J. Faragher and Mr L. Collister, the crew of the 'Cypris'. The spring grab was loaned by the Institute of Seaweed Research, Musselburgh, by kind permission of the Director, Dr F. N. Woodward and I should also like to thank Mr F. T. Walker for much help and advice on the use of the grab for this survey work. Dr P. S. Dixon was responsible for the echo-sounding of the bay and Mr N. Hawkins of the Liverpool Sub-Aqua Club made the dives to check the grab. The following helped with the field work either in 1955 or 1956 or in both years: Mr B. Appleby, Miss M. Beaumont, Mr J. Chubb, Mrs P. S. Dixon, Miss J. Hawkins, Mr B. Kendrick, Mr I. Prestt and Mr G. Strafford. My thanks are due to all of these people for their help.

SUMMARY

A combination of dredge, grab and diving techniques was used to make a survey of the sublittoral algae of Port Erin Bay, Isle of Man. Two distinct populations were found, one attached to the rock surface on the sides of the bay and the other more or less loose-lying on its sandy floor.

The loose-lying population is conspicuous only during the summer months, usually from July until October, and is washed up on to the beach by storms or decays on the floor of the bay.

Culture experiments combined with field observations at different times of the year have been used to determine the overwintering methods of some of the individual species of the loose-lying population. For two of the dominant species, *Laminaria saccharina* and *Saccorhiza polyschides*, both of which are

extreme dimorphic diplohaplonts, it has been shown that gametophytes are formed in extremely large numbers on all possible substrates on the floor of the bay during the winter and give a continuous supply of young sporophytes to renew the population.

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OBSERVATIONS ON LUMINESCENCE IN PELAGIC ANIMALS

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(Plate I and Text-figs. 1–19)

Luminescence is very common among marine animals, and many species possess highly developed photophores or light-emitting organs. It is probable, therefore, that luminescence plays an important part in the economy of their lives. A few determinations of the spectral composition and intensity of light emitted by marine animals are available (Coblentz & Hughes, 1926; Eymers & van Schouwenburg, 1937; Clarke & Backus, 1956; Kampa & Boden, 1957; Nicol, 1957*b*, *c*, 1958*a*, *b*). More data of this kind are desirable in order to estimate the visual efficiency of luminescence, distances at which luminescence can be perceived, the contribution it makes to general background illumination, etc. With such information it should be possible to discuss more profitably such biological problems as the role of luminescence in intraspecific signalling, sex recognition, swarming, and attraction or repulsion between species. As a contribution to this field I have measured the intensities of light emitted by some pelagic species of animals.

Most of the work to be described in this paper was carried out during cruises of R. V. 'Sarsia' and R.R.S. 'Discovery II' (Marine Biological Association of the United Kingdom and National Institute of Oceanography, respectively). Collections were made at various stations in the East Atlantic between 30° N. and 48° N. The apparatus for measuring light intensities was calibrated ashore at the Plymouth Laboratory; measurements of animal light were made at sea. In addition to the physical measurements, some histological descriptions of the light organs of several species are presented, together with miscellaneous observations on regulation of flashing in several species.

MATERIALS AND METHODS

Animals were captured in vertical and oblique hauls with a 2 m stramin net or ring trawl (R.T.), or with an Isaacs Kidd trawl (I.K.T.); and in surface hauls with a 1 m stramin net (N. 100).

Stations were as follows.

'Discovery' stations:

No. 3344. 18 Oct. 1955. 41° 16′–17½′ N., 9° 28′ W. R.T. oblique. 1000 m of wire out, estimated depth 500 m.

No. 3354. 6 Nov. 1955. 31° 12·5′ N., 15° 58′ W. to 31° 14·5′ N., 16° 01·5′ W. R.T. oblique; estimated depth 250 m.
No. 3355. 8 Nov. 1955. 30° 13′ N., 15° 58′ W. R.T. surface.
No. 3365. 18 Feb. 1956. 43° 47·2′ N., 13° 8·6′ W. R.T. oblique. 1500 m of wire out; estimated depth about 1000 m.
No. 3366. 19 Feb. 1956. 41° 11′ N., 14° 35′ W. R.T. oblique. 2000 m of wire out; estimated depth about 1300 m.
No. 3368. 21 Feb. 1956. 41° 03′ N., 14° 23′ W. R.T. oblique. 2000 m of wire out; estimated depth about 1300 m.
No. 3369. 24 Feb. 1956. 38° 39′ N., 9° 40·5′ W. N. 100 surface.
No. 3372. 28 Feb. 1956. 41° 09′ N., 14° 35′ W. R.T. oblique. 3000 m of wire out; estimated depth about 2000 m.
No. 3374. 29 Feb. 1956. 41° 11′ N., 14° 34′ W. R.T. oblique. 3000 m of wire out; estimated depth about 2000 m.
No. 3375. 2 Mar. 1956. 41° 09′ N., 14° 33′ W. R.T. oblique. 3000 m of wire out; estimated depth about 2000 m.
No. 3376. 6 Mar. 1956. 46° 59·5′ N., 7° 54·5′ W. R.T. oblique. 3000 m of wire out; estimated depth about 2000 m.

'Sarsia' stations:

No. 1, cruise 6/55. 17 June 1955. 46° 49′ N., 5° 44′ W. R.T. vertical. 280 m of wire out.
No. 5, cruise 3/57. 20 June 1957. 46° 55′ N., 5° 57′ W. I.K.T. oblique. 1800 m of wire out; estimated depth about 1200 m.
No. 6, cruise 3/57. 20 June 1957. 47° 07′ N., 6° 06′ W. R.T. vertical haul. 1829 m of wire out.
No. 8, cruise 3/57. 20/21 June 1957. 47° 00′ N., 6° 05′ W. Hand nets. Surface.
No. 10, cruise 3/57. 21 June 1957. 46° 57′ N., 6° 09′ W. I.K.T. oblique. 1800 m of wire out; estimated depth about 1200.
No. 21, cruise 3/57. 28 June 1957. 46° 47′ N., 5° 56′ W. R.T. oblique. 2742 m of wire out; estimated depth about 1800 m.
No. 23, cruise 3/57. 29 June 1957. 46° 42′ N., 6° 22′ W. I.K.T. oblique. 1800 m of wire out; estimated depth 1000 m.

The animals were examined either immediately on capture, or they were retained in cold sea water in a refrigerator for several hours. Some measurements were made of animals at room temperature (> 14° C), but it was found that animals from deep waters survived better when placed in cooled sea water. Accordingly, an arrangement was devised for delivering cooled sea water to the vessel containing the animal, and this arrangement was used for deep-sea species. The method consisted of taking sea water from the ship's system, and passing it through a lead coil lying in a refrigerator. A visual indicator was placed in the circulation to monitor flow-rate. Water temperatures were noted for each experiment, and are given in the text.

Measurements of spectral composition and intensity were made by means of a multiplier phototube (E.M.I. type no. 6685). The photomultiplier was connected to a cathode-ray oscilloscope having a d.c. amplifier. Mains supply for the photomultiplier and oscilloscope was regulated by a voltage stabilizer.

Occasionally two oscilloscopes were used, having different amplifications. Deflexions on the oscilloscope screen were photographed on moving paper. A time scale was provided by a periodically flashing light, regulated by a Palmer relay.

The spectral sensitivity of the photomultiplier (type no. 6685) had been determined by the National Physical Laboratory; a curve is given elsewhere (Nicol, 1958*a*, fig. 2A). The photomultiplier was calibrated against a substandard lamp (supplied by the National Physical Laboratory). From the data a constant, q, was calculated, such that $q/S_\lambda = \text{W/cm}^2$ of a given wavelength (λ) required to produce unit deflexion

$$q = \frac{p}{D_L} \int_{400}^{700} \mathcal{J}_\lambda S_\lambda T_\lambda \, d\lambda \ \text{W/cm}^2 \text{ receptor surface,}$$

$$= 0{\cdot}49 \times 10^{-12} \text{ W/cm}^2 \text{ receptor surface.}$$

S_λ = relative sensitivity of photomultiplier E.M.I. type no. 6685 at a given wavelength; $\mathcal{J}_\lambda$ is the spectral energy distribution of the substandard lamp; T_λ is the transmission of neutral filters used in the measurements; D_L is the deflexion occasioned by the substandard lamp on the cathode-ray oscilloscope at a given amplification; and p is a quantity for the particular experimental set-up. The method and calculations are described in more detail elsewhere (Nicol, 1958*a*).

For daily checks on the sensitivity of the apparatus at sea, a stable light source was employed, which consisted of a stilbene phosphor irradiated by ^{60}Co (supplied by the United Kingdom Atomic Energy Authority). This source had a measured output of 0·07 μlm.

Spectral sensitivity was determined by a method making use of a rotating disc containing alternating spectral and reference filters about its circumference. Spectral filters were Ilford gelatine and Chance glass. Reference filters were Ilford blue-green 603 or Ilford green 604. Two discs were used, containing the filters listed in Table 1, in order of rotation. Disc I was intended for analysing green light, Disc II for blue light. Curves for the combined effect of filter transmission (T_λ) and photomultiplier sensitivity (S_λ) are given in Text-figs. 1 and 2 ($S_\lambda T_\lambda$ plotted against λ). The luminescent flashes vary greatly in intensity, and the responses obtained with the reference filters gave periodical values for fluctuating flash intensity. First approximate results for relative spectral composition of luminescent light were corrected for wide band-width of the filters. The method is described in more detail in earlier papers (Nicol, 1957*b*, *c*).

When measuring intensity, the animal was placed at a known distance directly beneath the photomultiplier. When measuring spectral emission, the rotating disc was aligned close beneath the photocathode, so that each filter in turn passed across the face of the latter. The animal was placed as close as

possible to the disc, vertically underneath the end window of the photomultiplier (see Nicol, 1957*c*, fig. 1). The species from which luminescence was recorded are listed in Table 2.

For studying regulation of luminescence, controlled electrical stimulation was employed, either condenser shocks or square wave pulses. Electrodes were Ag, Pt, sometimes non-polarizable Ag/AgCl. Some earlier recordings were made with an R.C.A. photomultiplier, type no. 931A, with battery supply; extracts of these records have already been published (Nicol, 1955*a*). Later observations were made with E.M.I. photomultiplier, type no. 6685.

Particulars concerning chemistry and histology are given in the text.

TABLE 1. FILTERS IN ORDER OF ROTATION

Disc I	Disc II
Double space (position marker)	Double space (position marker)
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford red 608	Ilford orange 607
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford orange 607	Ilford yellow 606
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford yellow 606	Ilford yellow-green 605
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford yellow green 605	Ilford blue-green 603 + neutral density D 0·5
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford green 604 + neutral density D 0·5	Ilford blue 602 + neutral density D 0·5
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford blue 602 + neutral density D 0·5	Ilford violet 601
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
Ilford violet 601	Chance purple OV 1
Ilford blue-green 603 + neutral density D 0·5	Ilford green 604
	Chance u.v. OX 1

OBSERVATIONS AND RESULTS

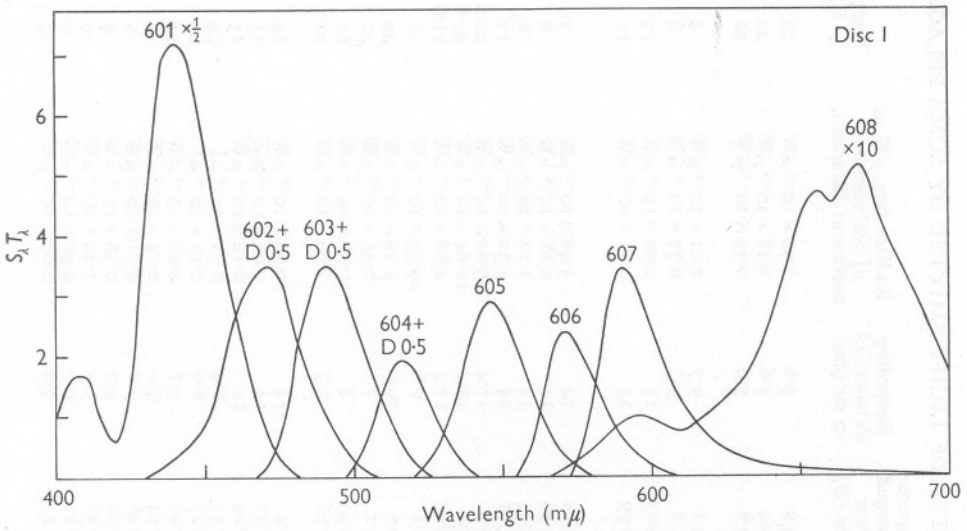
In order to calculate radiant flux, a curve for relative spectral emission is required (E_λ plotted against λ). This curve is then put on an absolute basis in terms of a quantity r, such that $E_\lambda r$ gives W/cm² of receptor surface/mμ under the experimental conditions specified.

$$r = \frac{Dq}{E_\lambda S_\lambda \mathrm{d}\lambda} \text{ W/cm}^2/\text{m}\mu,$$

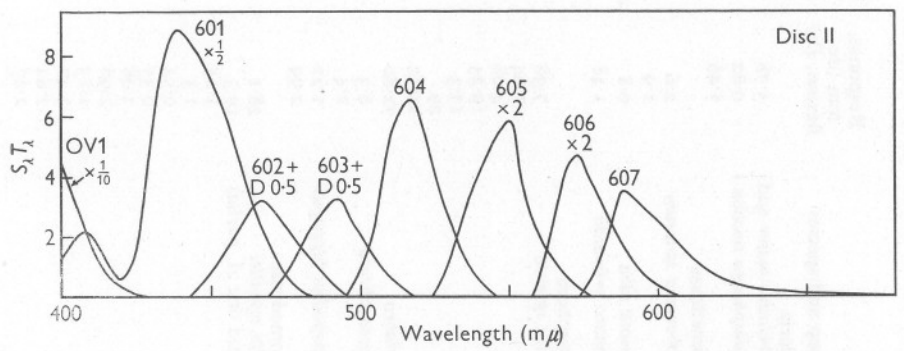
$$r = D \times \frac{0{\cdot}49 \times 10^{-12}}{E_\lambda S_\lambda \mathrm{d}\lambda} \text{ W/cm}^2/\text{m}\mu.$$

Data for various species, and calculated values of light intensities, are assembled in Table 2. Details are presented in the following sections, arranged according to zoological classification.

Radiolaria. Two specimens were examined belonging to the species *Cytocladus major* Schröder and *Aulosphaera triodon* Haeckel ('Discovery' Sta. no. 3375). Both specimens were spherical in shape and about the same diameter (some 12 mm). That they were two separate species was not apparent at the time, and the records of their luminescence were not distinguished from each other. Results for both specimens are combined.



Text-fig. 1. Curves showing the combined effect of sensitivity of the photomultiplier (S_λ) times transmission of spectral filters (T_λ) used in recording Disc I ($S_\lambda T_\lambda$ plotted against λ). Neutral filters, having a density of 0·5, were used in conjunction with Ilford spectral filters, nos. 602, 603 and 604.



Text-fig. 2. Curves showing the combined effect of sensitivity of the photomultiplier (S_λ) times transmission of spectral filters (T_λ) used in recording Disc II ($S_\lambda T_\lambda$ plotted against λ). Neutral filters, having a density of 0·5, were used in conjunction with Ilford spectral filters, nos. 602 and 603.

TABLE 2. CALCULATIONS OF THE INTENSITY OF LIGHT EMITTED BY SOME PELAGIC ANIMALS

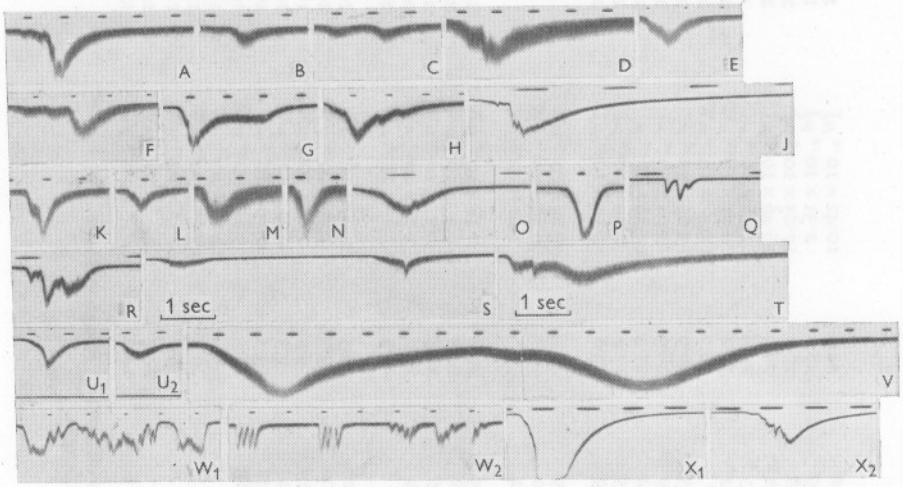
Group and species	Response, mm (deflexion, D_s)	Response duration (sec)	Response averaged over 1 sec (D)	Recording distance (L) in air (cm)	Radiant flux, μW or μJ/cm^2 receptor surface at distance L	Temp. (° C)	Size of animal
Radiolaria							
Cytocladus major and	5·78	2·7	3·9	5·6	$1{\cdot}70 \times 10^{-6}$ μW	22	1·2 cm diam.
Aulosphaera triodon	0·82	1·1	0·4	5·6	$0{\cdot}18 \times 10^{-6}$ μW	22	1·2 cm diam.
	1·45	1·7	0·8	5·6	$0{\cdot}35 \times 10^{-6}$ μW	22	1·2 cm diam.
Hydromedusae							
Colobonema sericeum	2·6	1·9	2·1	9·7	$1{\cdot}01 \times 10^{-6}$ μW	8	4 cm diam
	1·9	1·9	1·6	9·7	$0{\cdot}77 \times 10^{-6}$ μW	8	4 cm diam.
Crossota alba	0·8	*ca.* 1	0·05	13	$0{\cdot}02 \times 10^{-6}$ μW	13	2·5 cm diam.
Aeginura grimaldii	1·48	3·8	0·99	14	$0{\cdot}47 \times 10^{-6}$ μW	11	*ca.* 1·2 cm diam.
Siphonophora							
Vogtia spinosa	7·98	11·2	7·58	14	$3{\cdot}48 \times 10^{-6}$ μW	8	2 cm diam.
	1·94	1·9	1·49	14	$0{\cdot}68 \times 10^{-6}$ μW	8	2 cm diam.
	4·08	3·1	2·45	14	$1{\cdot}12 \times 10^{-6}$ μW	8	2 cm diam.
	19·35	3·8	11·61	14	$5{\cdot}32 \times 10^{-6}$ μW	12	2 cm diam.
	13·3	3·3	10·9	17·4	$5{\cdot}00 \times 10^{-6}$ μW	21·8	1 cm diam.
	29	2·9	23·2	17·4	$10{\cdot}64 \times 10^{-6}$ μW	21·8	1 cm diam.
	14·52	2·9	10·60	17·4	$4{\cdot}86 \times 10^{-6}$ μW	21·8	1 cm. diam.
V. glabra	72·80	3·5	42·2	7·8	$19{\cdot}35 \times 10^{-6}$ μW	8	2 cm diam.
Rosacea plicata	6·3	1·9	2·6	10·7	$1{\cdot}19 \times 10^{-6}$ μW	20	2.5 cm diam.
	2·4	1	1·2	7	$0{\cdot}55 \times 10^{-6}$ μW	20	2·5 cm diam.
Hippopodius hippopus	1·22	2	0·93	8	$0{\cdot}43 \times 10^{-6}$ μW	22	0·8 × 0·3 cm
	2·99	1	1·50	7·7	$0{\cdot}69 \times 10^{-6}$ μW	22	1·3 cm diam.
Scyphomedusae							
Atolla wyvillei	28·1	1·6	21·4	14	$10{\cdot}24 \times 10^{-6}$ μW	13	9 cm diam.
(and one *A. parua*)	19·3	1·4	8·27	14	$3{\cdot}96 \times 10^{-6}$ μW	13	9 cm diam.
	1·25	0·14	0·29	14	$0{\cdot}14 \times 10^{-6}$ μW	13	9 cm diam.
	1·3	0·6	0·35	8·9	$0{\cdot}17 \times 10^{-6}$ μJ	24	5 cm diam.
	0·54	0·5	0·27	8·9	$0{\cdot}13 \times 10^{-6}$ μJ	24	5 cm diam.
	0·35	1·0	0·20	5·7	$0{\cdot}10 \times 10^{-6}$ μW	24	1·2 cm diam.
	3·08	1·1	1·54	9·0	$0{\cdot}74 \times 10^{-6}$ μW	9	2·7 cm diam.
	2·96	1·9	1·48	9·0	$0{\cdot}71 \times 10^{-6}$ μW	9	2·7 cm diam.
	1·13	1·3	0·79	9·0	$0{\cdot}38 \times 10^{-6}$ μW	9	2·7 cm diam.
	3·42	1·9	2·50	9·0	$1{\cdot}20 \times 10^{-6}$ μW	9	2·7 cm diam.
	2·84	1·4	1·87	9·0	$0{\cdot}90 \times 10^{-6}$ μW	9	2·7 cm diam.
	2·27	1·9	1·25	9·0	$0{\cdot}60 \times 10^{-6}$ μW	9	2·7 cm diam.

Ctenophora							
Beroë ovata	29·3	0·8	17·6	28·4	$10{\cdot}42 \times 10^{-6}$ μJ	14	1 × 1·2 cm
	11·8	0·8	3·9	28·2	$2{\cdot}31 \times 10^{-6}$ μJ	11	1 × 1·2 cm
	70·2	0·18	28·8	26	$17{\cdot}05 \times 10^{-6}$ μJ	24·5	1 × 1·5 cm
	83·6	0·6	27·8	26·9	$16{\cdot}46 \times 10^{-6}$ μJ	24·5	1 × 1·5 cm
	6·7	0·1	2·5	24·4	$1{\cdot}48 \times 10^{-6}$ μJ	24·5	1 × 1·5 cm
	53·6*	1	16·4*	34·4	$9{\cdot}71 \times 10^{-6}$ μW	24	1 × 1·5 cm
	300*	1·6	200*	26·9	$118{\cdot}4 \times 10^{-6}$ μW	24·5	1 × 1·5 cm
	66·3	0·5	26·5	26·9	$15{\cdot}69 \times 10^{-6}$ μJ	24·5	1 × 1·5 cm
	13·8	0·7	6·9	26·9	$4{\cdot}08 \times 10^{-6}$ μJ	24·5	1 × 1·5 cm
	34·4	0·8	22·4	27·4	$13{\cdot}26 \times 10^{-6}$ μJ	24	1 × 1·5 cm
	4·6	0·3	1·5	13·8	$0{\cdot}89 \times 10^{-6}$ μJ	24	2 × 4 cm
	13·8	0·3	1·9	13·8	$1{\cdot}12 \times 10^{-6}$ μJ	24	2 × 4 cm
Crustacea							
Acanthephyra purpurea	0·9	1	0·5	9	$0{\cdot}23 \times 10^{-6}$ μW	9	—
	2·9	1·4	1·0	9	$0{\cdot}46 \times 10^{-6}$ μW	9	—
	2·4	4·7	2·2	9	$1{\cdot}01 \times 10^{-6}$ μW	9	—
Tunicata							
Pyrosoma atlanticum	2·6	4·7	2·5	10·8	$1{\cdot}18 \times 10^{-6}$ μW	14	1 × 4 cm
	10·8	2·3	4·8	20·8	$2{\cdot}3 \times 10^{-6}$ μW	24·5	1·2 × 6 cm
	5·5	1·7	3·6	20·8	$1{\cdot}7 \times 10^{-6}$ μW	24·5	1·2 × 6 cm
	8·3	11	7·9	27	$3{\cdot}7 \times 10^{-6}$ μW	20	1 × 4 cm
	35·4	17	35	28·3	17×10^{-6} μW	23	0·9–1·2 × 4·4 cm
Teleostei							
Myctophum punctatum	0·56	0·9	0·20	9·5	$0{\cdot}09 \times 10^{-6}$ μJ	16	88 mm long
	11·97	2·0	7·06	9·5	$3{\cdot}20 \times 10^{-6}$ μW	16	88 mm long
	1·03	1	0·51	9·5	$0{\cdot}23 \times 10^{-6}$ μW	16	85 mm long
	1·88	1	0·47	9·5	$0{\cdot}21 \times 10^{-6}$ μW	16	85 mm long
	1·71	0·42	0·42	9·5	$0{\cdot}19 \times 10^{-6}$ μJ	16	89 mm long
	25·65	4·23	12·83	9·5	$5{\cdot}81 \times 10^{-6}$ μW	16	89 mm long
Searsia schnakenbecki	57	2	36	9	19×10^{-6} μW	11	12·7 cm long†
	150	2·3	100	9	53×10^{-6} μW	11	12·7 cm long†
	55		37	9	20×10^{-6} μW	11	12·7 cm long†
S. koefoedi	321	3·9	245	14·7	130×10^{-6} μW	12–15	12·2 cm long†
	245	4	184	14·7	98×10^{-6} μW	12–15	12·2 cm long†

* Deflexion off screen. Rough estimate.
† Standard length.

Both radiolarians gave a luminescent glow, lasting some 1–2 sec when subjected to tactile stimulation (Text-fig. 3A, B, C). The light had a bluish colour and it illuminated the whole sphere, although it appeared brightest at the centre. Neither of these two species has hitherto been reported to be luminescent (cf. Harvey, 1952). The light of other radiolarians is blue and of low intensity (Brandt, 1885; Harvey, 1955).

Light intensity of *Cytocladus major* and *Aulosphaera triodon*, measured at a distance of 5·6 cm in air, ranged from $0{\cdot}2 \times 10^{-6}$ to $1{\cdot}7 \times 10^{-6}$ μW/cm^2



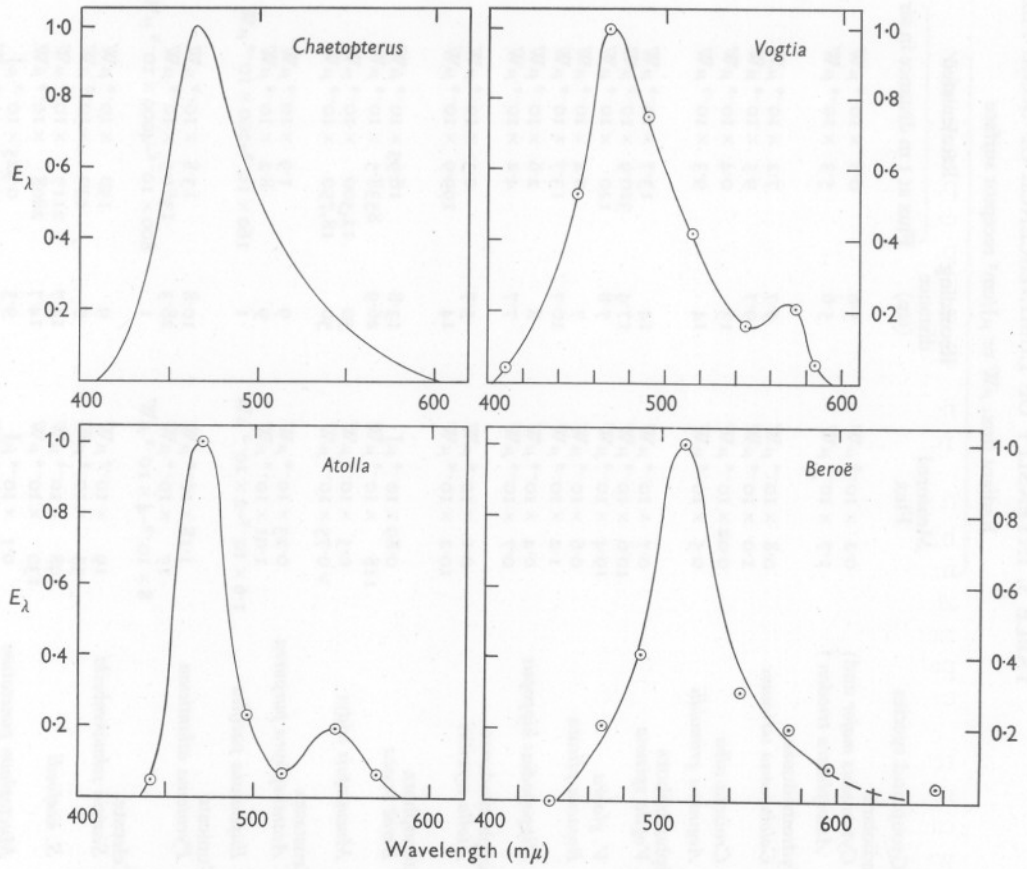
Text-fig. 3. Oscillograph records of the luminescent responses of pelagic animals. Deflexion downwards of the oscilloscope beam corresponds to the luminescent glow or flash. Periodical time scale above. A–C. Flashes of radiolarians (*Cytocladus major* and *Aulosphaera triodon*), evoked by mechanical stimulation. Water temperature, 22° C. Time scale, period 0·96 sec. D. *Aeginura grimaldii*. Glow evoked by mechanical stimulation. Temperature of sea water 11° C. Time scale, period 0·97 sec. E, F. Responses of *Colobonema sericeum* to mechanical stimulation. Time, 1/sec. Temperature of sea water 8° C. G, H. Flashing of *Vogtia spinosa* under mechanical stimulation. Time scale, period 0·98 sec. Temperatures of sea water: G, 12° C, H, 21·8° C. J. *Vogtia glabra*. Luminescence evoked by mechanical stimulation. Time scale, 1/sec. Temperature of sea water 8° C. K, L. Luminescence of *Rosacea plicata* evoked by mechanical stimulation. Time scale, period 0·96 sec. Temperature of sea water 20° C. M, N. *Hippopodius hippopus* (Forskål). Luminescent responses resulting from mechanical stimuli. Time scale, 1/sec. Water temperature about 22° C. O, P. Flashes of *Atolla wyvillei* under mechanical stimulation. Time, 1/sec. Water temperature 11° C. Q, R. Flashes of *Beroë ovata* subjected to mechanical stimulation. Time scale, period 0·96 sec. Temperature of sea water, 24° C (Q), 11° C (R). S, T. 'Puffs' of light produced by the luminous discharge of a deep-sea shrimp, *Acanthephyra purpurea*. Luminescence was provoked by tactile stimulation. Time scale, 1 sec. Temperature of sea water, 9° C. Amplification of S 0·58 times that of T. U_1, U_2. *Pyrosoma atlanticum*. Glow produced by mechanical stimulation of whole animal (6 cm long). Time, 1/sec. Water temperature, 24·5° C. V. *Pyrosoma atlanticum*. Glow following mechanical stimuli (animal 4 cm long). Time period, 0·96 sec. Temperature of sea water, 20° C. W_1, W_2. *Myctophum punctatum*. Flashing of photophores induced by mechanical stimulation of intact living fish. Time scale, 1/sec. Water temperature, 16° C. X_1, X_2. *Searsia koefoedi*. Records of the glow produced when a fish discharges a luminous secretion into sea water. Tactile stimulus. Time scale, 1/sec. Water temperature 12–15° C.

TABLE 3. INTENSITY OF LUMINESCENCE OF SOME PELAGIC ANIMALS

Group and species	Radiant flux, μW or μJ/cm^2 receptor surface: Measured Flux	Recording distance (cm)	Recalculated: Flux at 1 m distance in air	Temp. (° C)	Source
Radiolaria					
Cytocladus major and *Aulosphaera triodon*	$0{\cdot}2 \times 10^{-6}$ μW	5·6	$0{\cdot}6 \times 10^{-9}$ μW	22	Original
	$1{\cdot}7 \times 10^{-6}$ μW	5·6	$5{\cdot}3 \times 10^{-9}$ μW	22	Original
Hydromedusae					
Colobonema sericeum	$0{\cdot}8 \times 10^{-6}$ μW	9·7	$7{\cdot}2 \times 10^{-9}$ μW	8	Original
	$1{\cdot}0 \times 10^{-6}$ μW	9·7	$9{\cdot}5 \times 10^{-9}$ μW	8	Original
Crossota alba	$0{\cdot}02 \times 10^{-6}$ μW	13	$0{\cdot}4 \times 10^{-9}$ μW	13	Original
Aeginura grimaldii	$0{\cdot}5 \times 10^{-6}$ μW	14	$9{\cdot}3 \times 10^{-9}$ μW	11	Original
Siphonophora					
Vogtia spinosa	$0{\cdot}7 \times 10^{-6}$ μW	14	$13{\cdot}7 \times 10^{-9}$ μW	8	Original
	$10{\cdot}6 \times 10^{-6}$ μW	17·4	$320{\cdot}9 \times 10^{-9}$ μW	21·8	Original
V. glabra	$19{\cdot}4 \times 10^{-6}$ μW	7·8	120×10^{-9} μW	8	Original
Rosacea plicata	$0{\cdot}6 \times 10^{-6}$ μW	7	$2{\cdot}4 \times 10^{-9}$ μW	20	Original
	$1{\cdot}2 \times 10^{-6}$ μW	10·7	$13{\cdot}7 \times 10^{-9}$ μW	20	Original
Hippopodius hippopus	$0{\cdot}4 \times 10^{-6}$ μW	8	$2{\cdot}6 \times 10^{-9}$ μW	22	Original
	$0{\cdot}7 \times 10^{-6}$ μW	7·7	$4{\cdot}2 \times 10^{-9}$ μW	22	Original
Scyphomedusae					
Atolla wyvillei	$0{\cdot}1 \times 10^{-6}$ μW	5·7	$0{\cdot}3 \times 10^{-9}$ μW	24	Original
	$10{\cdot}2 \times 10^{-6}$ μW	14	$199{\cdot}9 \times 10^{-9}$ μW	13	Original
Ctenophora					
Beroë ovata	$0{\cdot}89 \times 10^{-6}$ μJ	13·8	$16{\cdot}95 \times 10^{-9}$ μW	24	Original
	118×10^{-6} μW	26·9	$8538{\cdot}5 \times 10^{-9}$ μW	24·5	Original
Mnemiopsis leidyi	$0{\cdot}5 \times 10^{-4}$ μW	50	$12{,}500 \times 10^{-9}$ μW	—	Clarke & Backus, 1956
	$>0{\cdot}75 \times 10^{-4}$ μW	50	$18{,}750 \times 10^{-9}$ μW	—	Clarke & Backus, 1956
Crustacea					
Acanthephyra purpurea	$0{\cdot}23 \times 10^{-6}$ μW	9	$1{\cdot}9 \times 10^{-9}$ μW	9	Original
	$1{\cdot}01 \times 10^{-6}$ μW	9	$8{\cdot}2 \times 10^{-9}$ μW	9	Original
Euphausia pacifica	$1{\cdot}6 \times 10^{-3}$–2×10^{-3} μW	1	160×10^{-9}–200×10^{-9} μW	—	Kampa & Boden, 1957
Tunicata					
Pyrosoma atlanticum	$1{\cdot}18 \times 10^{-6}$ μW	10·8	$13{\cdot}8 \times 10^{-9}$ μW	14	Original
	17×10^{-6} μW	28·3	$1361{\cdot}5 \times 10^{-9}$ μW	23	Original
	8×10^{-3}–4×10^{-2} μW	1	800×10^{-9}–4000×10^{-9} μW	—	Kampa & Boden, 1957
Teleostei					
Searsia schnakenbecki	19×10^{-6} μW	9	150×10^{-9} μW	11	Original
	53×10^{-6} μW	9	430×10^{-9} μW	11	Original
S. koefoedi	98×10^{-6} μW	14·7	2117×10^{-9} μW	12–15	Original
	130×10^{-6} μW	14·7	2808×10^{-9} μW	12–15	Original
Myctophum punctatum	$0{\cdot}1 \times 10^{-6}$ μJ	9·5	$0{\cdot}925 \times 10^{-9}$ μJ	16	Original
	$5{\cdot}8 \times 10^{-6}$ μW	9·5	$52{\cdot}345 \times 10^{-9}$ μW	16	Original

receptor surface (Table 2). By assuming that the light intensity falls off with distance according to the inverse square law, values can be calculated for light intensities at a standard distance of 1 m in air, viz. $0{\cdot}55 \times 10^{-9}$ to $5{\cdot}34 \times 10^{-9}$ μW/cm^2 receptor surface (Table 3). Deviation from the inverse square law, owing to size of the source, decreases with distance. In the present instance, the error from this factor is small, and the flux calculated at 1 m may be considered a minimal estimate. The luminescence of these radiolarians appeared somewhat diffuse. If they were uniformly diffusing spheres, the total radiant flux from the entire surface of the animals would range from $0{\cdot}69 \times 10^{-4}$ to $6{\cdot}71 \times 10^{-4}$ μW/4π steradians.

No spectral emission curve is available for the light of radiolarians, and in the above calculations I have employed the spectral curve for *Chaetopterus* light as a substitute.



Text-fig. 4. Relative spectral emission curves for the light of four marine animals, namely, *Chaetopterus variopedatus*, *Vogtia glabra*, *Atolla wyvillei* and *Beroë ovata*.

Chaetopterus light is blue, and has a peak at about 465 mμ (Text-fig. 4) (Nicol, 1957*c*). Since the response curve of the photomultiplier is fairly flat below 500 mμ (Nicol, 1958*a*, fig. 2A), a difference of 10 or 20 mμ in the maximum of the spectral emission curve used in making the calculations would result in only a small change in estimated flux. I have calculated radiant flux on the basis of a spectral emission curve resembling that in Text-fig. 4, but displaced 20 mμ towards longer wavelengths; the result for the first response given in Table 2 is $2{\cdot}02 \times 10^{-6}$ μW/cm^2 receptor surface at 5·6 cm in air. This differs from the response given in the table ($1{\cdot}70 \times 10^{-6}$ μW) by 19%.

Cytocladus is widespread in the Atlantic and *C. major* has been found previously in a catch from 3000 m (Schröder, 1907). *Aulosphaera triodon* appears to be cosmopolitan (Haecker, 1907).

HYDROMEDUSAE

Crossota alba Bigelow. A single specimen was collected ('Discovery' Sta. no. 3376). The jellyfish was bell-shaped, and about 24 mm in diameter. When mechanically stimulated it gave a very weak bluish glow lasting about 1 sec. It soon fatigued, for a second and further stimuli evoked much weaker responses. The spectral emission curve for *Atolla* luminescence (see p. 718) was used to calculate radiant flux. *A. wyvillei* also emits a blue light, extending from about 410 to 600 mμ, with a peak at 470 mμ (Text-fig. 4, p. 714). According to Harvey (1952), the light of two other Hydromedusae (*Aequorea* and *Mitrocoma*), examined with a hand spectroscope, extends from about 460 to 600 mμ. At 1 m in air, estimated radiant flux for *Crossota alba* is $0{\cdot}4 \times 10^{-9}$ μW/cm^2 receptor surface.

This is the first report of luminescence in *C. alba*. It is a deep-water jellyfish known previously from the North Pacific and tropical Atlantic (Kramp, 1947, 1957).

Aeginura grimaldii Maas. Two specimens of this jellyfish were examined ('Discovery' Sta. no. 3376). With light mechanical stimulation they emitted a bluish glow lasting 1–4 sec (Text-fig. 3D). An estimate of light intensity was made, the calculation being based on the relative spectral emission curve for *Atolla* light (Text-fig. 4). At a distance of 1 m (in air), minimal estimated radiant flux is $9{\cdot}3 \times 10^{-9}$ μW/cm^2 receptor surface. *A. grimaldii* is a bathypelagic species of world-wide distribution (Russell, 1953), in which luminescence has not previously been reported.

Octophialucium funeraria (Quoy & Gaimard). This is a deep-sea medusa, reaching a diameter of about 4 cm. One specimen was examined ('Sarsia' Sta. no. 1, cruise 6/55). When mechanically stimulated by gently stroking it with a camel-hair brush, it emitted a bluish glow. No measurement of light intensity was made. Its luminescence is here noted, since it seems not to have been previously reported. *O. funeraria* has been found at various stations in the Atlantic and Mediterranean.

Colobonema sericeum Vanhöffen. One specimen was examined ('Sarsia' Sta. no. 5, cruise 3/57). This medusa is bell-shaped, up to 4 cm in diameter and height. It is a deep-water species, found in temperate and warm regions of the Atlantic, Pacific and Indian Oceans (Russell, 1953). When mechanically stimulated, the specimen of *C. sericeum* emitted a blue glow, lasting about 2 sec (Text-fig. 3E, F). A spectral emission curve was not obtained, and that for *Atolla* (Text-fig. 4) was used in calculating light intensity. At a distance of 1 m (in air), estimated radiant flux would be 7×10^{-9} to 9×10^{-9} μW/cm^2 receptor surface. This appears to be the first report of luminescence in *Colobonema sericeum*.

Other luminescent species of Hydromedusae are noted by Russell (1953). Certain physiological and histological observations on luminescence and photogenic tissue of *Aequorea* have been presented by Davenport and Nicol (1955).

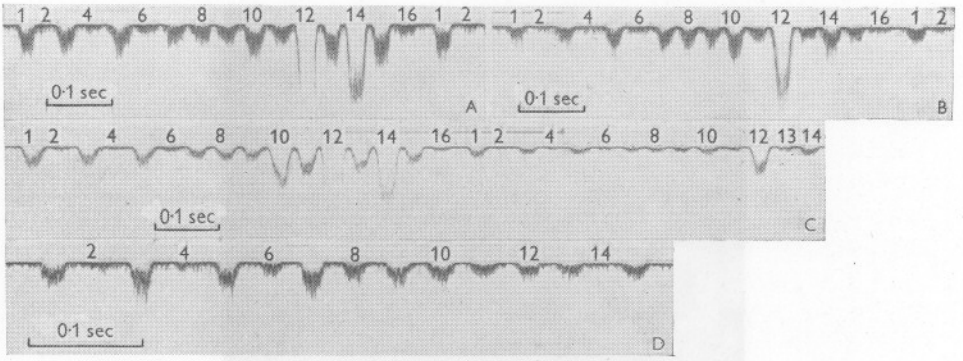
SIPHONOPHORA

Vogtia spinosa Keferstein & Ehlers. Specimens were obtained from 'Discovery' Sta. nos. 3374 and 3376. When examined in the dark, fragments of this species were found to be markedly luminescent. Light, evoked by mechanical stimulation, appeared as a bluish glow diffused through the fragment (nectophores or gastrozooids). The specimens appeared very sensitive to mechanical stimuli, and responded by glowing to roll of the ship, and slight tapping of the vessel in which they lay. Luminescence was not inhibited by exposure to light (60 W tungsten lamp at about 1 m). The glow lasts from 2 to 11 sec, depending on the strength of stimulus (Text-fig. 3G, H). To calculate light intensity, a spectral emission curve obtained for *V. glabra* was used (Text-fig. 4). At 1 m (in air), minimal estimates of radiant flux range from 14×10^{-9} to 321×10^{-9} μW/cm^2 receptor surface. This appears to be the first report of luminescence in *V. spinosa*, which is a widely distributed bathypelagic species known from the Atlantic, Pacific, and Mediterranean (Bigelow & Sears, 1937).

V. glabra Bigelow. A fragmented specimen was obtained ('Sarsia' Sta. no. 21, cruise 3/57). Fragments emitted a bluish luminescence under mechanical stimulation. The glow lasted some 4 sec (Text-fig. 3J). An approximate spectral emission curve was obtained with the aid of Disc II. This was spun at speeds of 1–2 rev./sec. The specimen was positioned close beneath the disc, and luminescence was evoked by gentle tactile stimulation (Text-fig. 5). Water temperature was 8° C. Spectral emission extends from about 430 to 590 mμ, with a maximum at about 470 mμ (Text-fig. 4). A single measurement of light intensity afforded an estimate of 120×10^{-9} μW/cm^2 at 1 m (in air) (Table 3). *V. glabra* is a bathypelagic species, found in the Mediterranean and the Atlantic (Leloup, 1955), and known to be luminescent (see Totton, 1954).

Rosacea plicata Bigelow. Fragments of a specimen were obtained ('Discovery'

Sta. no 3374). Luminescence was evoked by mechanical stimulation. The light had a blue hue, and the responses lasted 1–2 sec (Text-fig. 3K, L). The spectral emission curve of *V. glabra* (Text-fig. 4) was used in calculating light intensity. At 1 m (in air), estimated radiant flux is $2{\cdot}4 \times 10^{-9}$ to $13{\cdot}7 \times 10^{-9}$ $\mu W/cm^2$ receptor surface (Table 3). *R. plicata* has a world-wide distribution. Although usually obtained in catches from deeper waters, it has occasionally been found at the surface (Bigelow & Sears, 1937; Leloup, 1955).



Text-fig. 5. A, B. Oscilloscope deflexions obtained when Disc II was used to analyse the light of *Vogtia glabra*. Time scale, 0·1 sec. Filters in order: 1, 604; 2, OX 1; 3, 604; 4, 607; 5, 604; 6, 606; 7, 604, 8, 605; 9, 604; 10, 603; 11, 604; 12, 602; 13, 604; 14, 601; 15, 604; 16, OV 1. Temperature of sea water 8° C. Disc speed, *ca.* 1·7 rev./sec. C. Analysis of the light of *Atolla wyvillei* with Disc II. Numbering of filters as in A and B. Water temperature 20° C. Speed of rotation about 1·7 rev./sec. Time, 0·1 sec. D. Analysis of the light of *Beroë ovata* with Disc I. Filters in order: 1, 603; 2, 608; 3, 603; 4, 607; 5, 603; 6, 606; 7, 603; 8, 605; 9, 603; 10, 604; 11, 603; 12, 602; 13, 603; 14, 601; 15, 603. Temperature of sea water, about 19° C. Disc speed about 1 rev./sec.

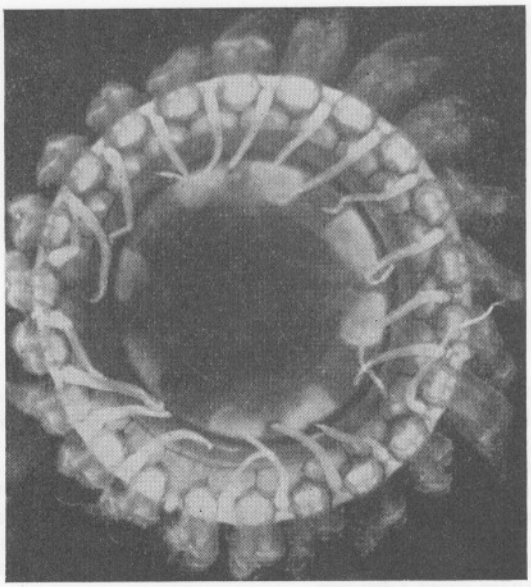
Hippopodius hippopus (Forskål). Fragments of a specimen were obtained ('Discovery' Sta. no. 3369). When mechanically stimulated the animal emitted a blue light lasting 1–2 sec (Text-fig. 3M, N). The spectral emission curve for the light of *Vogtia glabra* (Text-fig. 4) was used for calculating radiant flux. At 1 m (in air), estimated flux was $2{\cdot}6 \times 10^{-9}$ to $4{\cdot}2 \times 10^{-9}$ $\mu W/cm^2$ receptor surface. There are previous reports of luminescence in this species (Dubois, 1914; Totton, 1954). *Hoppopodius hippopus* occurs in the Mediterranean and in warmer regions of the three oceans (Totton, 1954; Leloup, 1955).

SCYPHOMEDUSAE

Atolla wyvillei Haeckel. Many specimens were examined from stations as follows: 'Discovery' Sta. nos. 3366, 3368, 3372, 3374, 3375 and 3376; 'Sarsia' Sta. no. 21, cruise 3/57. These jellyfish are umbrella-shaped, ranging up to 15 cm in diameter. When mechanically stimulated, some specimens emitted a faint bluish light all around the margin; some emitted only a weak point of

light in the immediate vicinity of stimulation; still others remained dark. These differences in behaviour possibly depend upon the condition of the specimen, amount of buffeting it has received in the net, etc. Luminescence has not hitherto been reported in this species.

Light appears as a brief flash or glow, lasting up to 2 sec (Text-fig. 3 O, P). Relative spectral composition of the light was determined by means of recording Disc II (Text-fig. 5C). The light is blue in colour, and emission occurs



Text-fig. 6. Dorsal view of *Atolla wyvillei*. From a colour transparency of a living animal.

at about 470 mμ, with hint of a secondary peak at about 570 mμ. Calculated values of light intensity are given in Tables 2 and 3. At a distance of 1 m (in air), minimal estimates of the intensity of *Atolla* luminescence range up to 200×10^{-9} μW/cm^2 receptor surface.

When a specimen of *A. wyvillei* was subjected to carefully localized mechanical stimulation with a probe, the light appeared in a thin streak just inside the peripheral edge of the thick coronal muscle, at the base of the rhopalar peduncle, between two tentacles (Text-fig. 6). It was visible from the upper surface, but not from the lower surface of the jellyfish. The thick coronal muscle of *Atolla* is opaque and white. The photogenic tissue must be above this muscle layer, which prevents the light from shining through to the lower surface. The white muscle band may also act as a reflector for the luminescence.

The white opacity of the coronal muscle extends throughout the thickness

of the latter. The white appearance is not destroyed by the following agents: water, formalin, ethanol, ether, 1 and 10% acetic acid, 1% HCl, 10% NH_3, and 0·1% NaOH. These negative results rule out the possibility that the white appearance is due to some deposit of purine material such as guanine, pterine, or even uric acid. It is probably a characteristic of the physical structure of the muscle or its contained connective tissue.

Histological sections were cut from the edge of the umbrella to search for luminescent tissue. The material was fixed in formalin, and post-fixed in Wittmaack's solution. Sections were cut in celloidin, and stained with Weigert's haematoxylin, Bordeaux red and aniline blue. A patch of tall columnar epithelial cells occurs in the floor of the rhopalar canal, and in its connexion with the canal running along the lateral wall of the rhopalar pedalium, opposite the nematocyst cushion. These columnar cells constitute a modified endodermal lining, which elsewhere in the canal consists of cuboidal cells. They have a very glandular appearance. The nucleus is almost central; the basal half of the cell is vacuolar, whereas the distal half is packed with small granules. The latter are stained mostly blue (with aniline blue), but some larger granules have taken up the Bordeaux red preferentially. Near the distal margin of each cell is a small spherical clear area, appearing like a lenticular organelle. Cellular dimensions are: height, about 45 μ; width, 12 μ; peripheral clear area, about 9 μ in diameter. The position and glandular character of these cells suggest that they may represent the luminous tissue.

A. wyvillei is a bathypelagic species having a cosmopolitan distribution (Kramp, 1947).

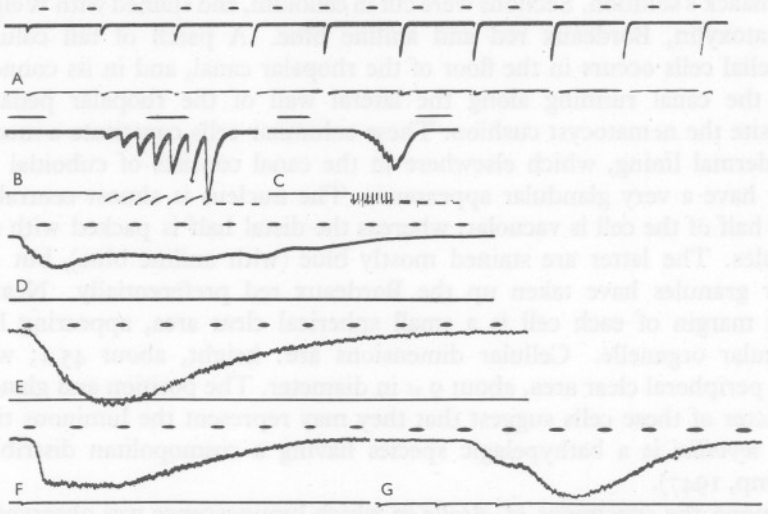
Among the specimens of *Atolla* in which luminescence was observed was one of *A. parva*, the new species recently described by Russell (1958).

Periphylla periphylla (Péron & Lesueur). Two specimens of this jellyfish were examined and were found to be luminescent ('Sarsia' Sta. no. 1, cruise 6/55). When mechanically stimulated they emitted a blue glow around the margin, either in the tentacles, or in the rim of the umbrella. The light was not recorded. There appears to be no previous notice of its luminescence. *P. periphylla* is bathypelagic and has a world-wide distribution (Kramp, 1947).

CTENOPHORA

Beroë ovata Bosc. (=*B. cucumis* Fabricius). Specimens were examined from 'Discovery' Sta. nos. 3366, 3368 and 3376; and from 'Sarsia' Sta. no. 5, cruise 3/57. The light of *Beroë* appears green to the eye (cf. Harvey, 1955). A few records, obtained with Disc I, gave enough data to make an approximate estimation of spectral composition (Text-fig. 5D). A strip of the animal, containing several combs, was pinned out in a black dish underneath the disc, and light was evoked by stimulating the preparation with a camel-hair brush. On analysing the results, it appears that light emission extends from about 440 to 650 mμ, with a peak around 510 mμ (Text-fig. 4, p. 714).

The relative spectral composition curve, shown in Text-fig. 4, was used to calculate light intensities. At a distance of 1 m (in air), estimated radiant flux is $1{\cdot}7 \times 10^{-8}$ to $8{\cdot}5 \times 10^{-6}$ μW/cm^2 receptor surface (Tables 2 and 3). Clarke & Backus (1956), using a different method, have measured the intensity of light emitted by the ctenophore *Mnemiopsis leidyi*. At 50 cm distance, radiant fluxes were $0{\cdot}5 \times 10^{-4}$ and at least $0{\cdot}75 \times 10^{-4}$ μW/cm^2 receptor surface (two determinations). When calculated for a distance of 1 m (in air), the equivalent intensities are $0{\cdot}1 \times 10^{-4}$ and $> 0{\cdot}2 \times 10^{-4}$ μW/cm^2 (Table 3).



Text-fig. 7. A, B, C. Flashes of *Beroë ovata* under electrical stimulation. Point responses. Stimuli intervals: A, 1·24 sec; B, 0·11 sec; C, 0·029 sec. Time scale above, 1/sec. Stimuli on lower line. Water temperature 20–21° C. D–G. Responses of *Pyrosoma atlanticum* to tactile and mechanical stimuli. D. Tactile stimulation. Local response and transmitted waves. Specimen 10 cm. long. Time scale, 0·98 sec. Water temperature 25° C. E. Local response to tactile stimulus. Time scale, 0·96 sec. Water temperature 25° C. F. Local response to an electric shock (shown on lower line). Water temperature 25° C. Time, 0·96 sec. G. Responses to burst of shocks at 1/sec. Water temperature, 24° C. Time, 1/sec. A low-pass filter was used when recording traces D–G to reduce noise.

When *Beroë* is mechanically stimulated, waves of luminescence run along the meridional combs. The conducting system is non-polarized, since transmission occurs with facility in either direction (Panceri, 1872). The same responses occur in *Mnemiopsis* (see Moore, 1924). The light appears in two closely spaced thin green lines along each of the combs, seemingly associated with paired strips of luminous tissue in the walls of the meridional canals (see Harvey, 1952). Under strong mechanical stimulation, the light has a flickering character, owing to repetitive flashing occurring along the length of the comb, such flashes continuing when stimulation has ceased. Multiple or repetitive flashing occurs also in *Beroë* under electrical stimulation (Nicol, 1955*a*), and it has been observed likewise in *Mnemiopsis* (see Chang, 1954).

The luminescence of ctenophores is inhibited by light, and specimens of *Beroë* were dark-adapted before use. Pieces containing one or several combs were pinned out on wax and were covered with sea water. Electrical stimuli were delivered through wire electrodes placed on the combs.

With local responses, i.e. those confined to the immediate vicinity of the electrodes, it is found that each shock above threshold produces a flash (Text-fig. 7A). With repetitive stimulation, the consecutive flashes increase progressively in intensity for some time (perhaps 8–12 flashes), and then reach maximum or plateau level, after which decline sets in. The increment of consecutive flashes is best seen when stimulation is at a rate slow enough for each response-record to return to base line, and for no summation of the light of successive flashes (Text-fig. 7A). In records of transmitted waves of light, obtained from long lengths of comb, the intensity relationships of single flashes are obscured by repetitive responses. At fast rates of stimulation (9/sec or more), the individual flashes tend to fuse together but they can still be distinguished at frequencies of 34/sec (Text-fig. 7B, C).

Under repetitive stimulation, augmentation of intensity can be produced by two factors, summation of light when the flashes recur at brief intervals, less than the duration of a single flash, and facilitation occasioned by build-up of an excitatory state such that one pulse leaves a residual condition enhancing second and later responses. Although the effect is somewhat irregular, there is a tendency for facilitatory increment to be greater at faster rates of stimulation (or shorter intervals), as shown in Text-fig. 8. The effect was also brought out as follows. Paired pulses were given at selected intervals and the responses measured. The ratios of the second to the first flash were:

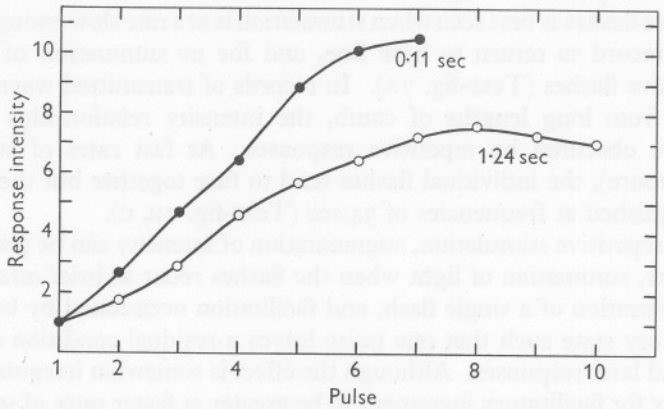
Interval between flashes (sec)	Ratio of intensity of second to first flash
120	1·3
60	1·2
12	1·4
4	2
1·68	2
1·24	1·8
0·62	1·8
0·24	2
0·11	2·7

Some residual facilitation is still detectable 2 min after a previous pulse. A similar increment of facilitation with rise in frequency appears to hold in *Mnemiopsis* (see Chang, 1954, p. 382, fig. 9). Continued stimulation leads to falling off in intensity, i.e. to fatigue. This becomes apparent after 10 or so pulses. A single flash, from a point area, has a duration of about 0·16 sec (20–21° C). Latent period is about 20 msec.

The progressive increase in intensity of consecutive flashes, shown in Text-fig. 7A, is one more manifestation of neuro-effector facilitation, so well documented in muscular responses of sea anemones and other coelenterates

(Pantin, 1952). It has also been detected in the luminous responses of hydromedusans and pennatulids (Davenport & Nicol, 1955; Nicol, 1955*b*). It is not known where the facilitatory process occurs in ctenophores, but there is evidence in polynoids that it can occur within the photocytes or light-generating cells (Nicol, 1957*a*).

Beroë ovata is a cosmopolitan form, found usually in upper waters (Chun, 1880; Bigelow, 1912; Mayer, 1912; Mortensen, 1912; Krumbach, 1927; Sears, 1954).



Text-fig. 8. Facilitatory increment in consecutive flashes of *Beroë ovata* at two frequencies (intervals shown). Ordinates show relative intensities. Temp. 20–21° C.

CRUSTACEA DECAPODA

Acanthephyra purpurea M.-Edw. Luminescence was observed in a deep-sea shrimp belonging to this species ('Sarsia' Sta. no. 5, cruise 3/57). This specimen appears to be *A. purpurea* sensu stricto, since it has only four pairs of dorso-lateral spines on the telson, and no tooth on the dorsal carina of the fourth abdominal segment (Kemp, 1939). *A. purpurea* is a widely distributed bathypelagic shrimp found in the Atlantic, south of 50° N., in the Pacific and in the Indian Oceans (Kemp, 1910, 1939; Stephenson, 1923; Balss, 1925).

Examined in the laboratory in darkness, *Acanthephyra* was found to discharge a luminous secretion from the head region into the surrounding sea water when the animal was excited mechanically. The light had a blue colour, and the discharge continued to glow for 1–5 sec (Text-fig. 3 s, t). Luminescence was soon exhausted under repeated stimulation, and it was not possible to determine spectral composition.

Since the light of *A. purpurea* has a bluish colour, I have used the relative spectral emission curve of *Cypridina* light, as determined by Coblentz & Hughes (1926), for calculating light intensity. *C. hilgendorfii* also discharges a luminous secretion and its light is blue in colour, with maximal emission at

about 480 mμ (Text-fig. 19A). The intensity of the discharge ranged from 2×10^{-9} to 8×10^{-9} μW/cm^2 receptor surface at a distance of 1 m (in air).

The discharge of a luminous secretion from the antennal glands or head glands of various other species has been observed repeatedly, e.g. in *Heterocarpus alphonsi*, *Plesiopennaeus* (=*Aristaeus*) *coruscans*, *Hoplophorus novaezealandiae*, *H. spinicauda* and *Systellaspis debilis*. The last-named is a species that also possesses integumentary photophores (Alcock, 1902; Dahlgren, 1916; Chace, 1940; Dennell, 1940, 1955; Harvey, 1952.)

TUNICATA

Pyrosoma. Specimens for observation and histology were collected as follows. *P. atlanticum* Péron—'Discovery' Sta. nos. 3344, 3354, 3355, 3365, 3366, 3374 and 3375; 'Sarsia' Sta. no. 23, cruise 3/57; one specimen from deep water off San Diego, California, 12 December 1953. *P. spinosum* Herdman—'Sarsia' Sta. no. 1, cruise 6/55.

Pyrosoma is one of the most brightly luminescent animals of the open ocean. Its light emission was first noted by Péron in 1804, and has been commented upon repeatedly—see descriptions by Bennett (1840), Huxley (1851), Moseley (1892), and Steuer (1910); and reviews of the literature by Neumann (1934), and Harvey (1952).

Pyrosoma is a colonial animal and light is emitted by each of the zooids. During a normal response an excited colony appears aglow from numerous points of blue light. Before presenting some original observations I would point out that the luminescence of *Pyrosoma* shows a combination of peculiarities not found in other animals. First there is a general agreement that the light of *Pyrosoma* is intermittent. Secondly, the light is transmitted as a wave along the colony, although nervous connexions between the zooids still await discovery. Thirdly, luminescence is evoked by illumination. Fourthly, the light is ascribed to luminescent symbiotic bacteria. This belief, fostered by Buchner (1914) and Pierantoni (1921), now appears to be generally accepted (Brien, 1948; Young, 1950; Caullery, 1952). Other luminescent bacteria, however, emit light continuously (discussion in Harvey, 1952).

Pyrosoma luminesces only when excited, and effective stimuli are mechanical, electrical, photic and chemical. The light appears in a punctate pattern over the whole surface; at each locus two closely spaced points of light can be resolved, which correspond to the pair of light organs at the entrance to the branchial sac of each zooid (*P. atlanticum*, cf. Panceri, 1873). In addition, there is a diffuse glow, the result of scattering and internal reflexion within the colony.

Light tactile stimulation of a fresh specimen produces a luminous wave, which spreads outwards from the stimulated region to the limits of the cylinder. A strong mechanical stimulus, such as squeezing the animal, causes the whole surface to lighten. Some recordings of the light emitted under mechanical stimulation are shown in Text-fig. 3 (U_1, U_2, V) (p. 712) and Text-fig. 7D.

With repeated tactile stimulation, the luminescent response becomes progressively weaker, transmission finally ceases, and the light is confined to the region of stimulation (Text-fig. 7E).

It has long been known that luminescence in *Pyrosoma* can be induced by illumination and a *Pyrosoma* in the dark will respond to the flash of another *Pyrosoma* by luminescing in turn. When a weak light from a torch is shone upon a colony, it responds by flashing (Nicol, 1955*a*, p. 312, fig. 9). The response to weak illumination appears to be of the same character as that induced by tactile stimulation; it begins with a local glow which spreads as a wave over the colony. An instance was observed in which the light, after proceeding from one end of the colony to the other, gradually retreated to the end first illuminated, where the light outlasted the response elsewhere.

The luminescent flashes of *Pyrosoma* are rather slow and prolonged compared with those of many other luminescent animals. The following measurements for *P. atlanticum* are given as examples.

Specimen 1 cm long. Tactile stimulation evoked transmitted luminous waves. Duration of response 13·8 sec. Time to maximum 1·06 sec; time to ½ maximum 0·41 sec; decay time 12·8 sec; ½ decay time 1·39 sec. Most of the response was finished (½ decay) by 2·5 sec (temp. 25·5° C).

Specimen 10 cm long. Tactile stimulation produced transmitted luminous waves. Time to maximum from first deflexion, 0·4–1·6 sec. For a response lasting 8½ sec, time to maximum lasted 1·6 sec; ½ maximum was reached in 1 sec; time for ½ decay was 2·9 sec (temp. 25·5° C).

Specimen 3 cm long. Local responses to electrical stimulation. Latency varied from 0·1 to 0·4 sec. In a response lasting 7·2 sec, maximum intensity was reached in 0·3 sec; ½ maximum in 0·15 sec; ½ decay from maximal deflexion occupied 3·3 sec (temp. 25·5° C).

For *P. elegans* (*P. atlanticum*), Polimanti (1911) found that the response varied from 5 to 30 sec (average 10 sec). Latencies varied from 1 to 5 sec; the average for photic stimuli was 5 sec. With very weak photic stimuli, the latency was prolonged; in general, the latency was shorter with stronger stimuli.

Nerves to the photogenic organs have not been detected, and it has been claimed that they are not innervated (Julin, 1912; Neumann, 1934). It is possible, of course, that the nerve fibres may be very fine, and may have been overlooked with the methods employed. The colonies are very sensitive to mechanical stimulation and, in the absence of innervation, would be acting as independent effectors. Following brief photic stimulation, transmission of luminescence across a colony can take place as a chain reaction, the light from one zooid stimulating its neighbours, and so on until the light wave has crossed the colony. As Burghause (1914) has shown, such transmission can occur even in the absence of nervous connexions. Pyrosomas often occur at the surface in shoals, and it seems likely that when one animal is excited, its light may cause other colonies nearby to luminesce.

For histological examination specimens of *P. atlanticum* and *P. spinosum* were fixed in various solutions, including formalin, Bouin's, Helly's, Heidenhain-Susa, 80% ethanol, and osmic acid. Sections cut in paraffin wax and celloidin were stained with Ehrlich's haematoxylin and eosin, Biebrich scarlet and erythrosin, Heidenhain's haematoxylin and van Gieson, Masson's trichrome, Heidenhain-azan, Giemsa and Bodian's activated protargol.

In *P. atlanticum* the photogenic organs lie on each side of the pharynx above the peripharyngeal bands. They consist of a mass of photogenic cells, one or several tiers in thickness, lying in the peripharyngeal blood sinus. The cells are closely spaced, cell boundaries are sometimes distinguishable, but in many places the limits of separate cells cannot be resolved (Pl. I). In shape they tend to be spherical, about 9–15 μ in diameter. In *P. atlanticum*, subsp. *giganteum*, cell size is given as 25–30 μ (Julin, 1912). The nucleus is peripheral, containing closely packed granular material; the cytoplasm is densely packed with inclusions, the presence of which is correlated with light production, and which constitute the photogenic paraplasm.

The paraplasmic inclusions are tubular structures, some 2 μ in thickness, containing fine particles or granules. The tubules appear curved, like half-rings, but they may actually, as Julin (1912, 1913) states, form a convoluted thread, only segments of which appear in focus at one time. This point is rather difficult to resolve. They stain with acid stains, eosin, erythrosin, Biebrich scarlet, orange G; diffusely and irregularly with haematoxylin; and with both xylidine ponceau and light green of Masson's trichrome stain in a spotty manner. In sections treated with Giemsa the inclusions are stained by the methylene blue. Their affinity for dyes is rather poor and they need to be overstained to confer much colour on them. Their structure is probably revealed as well, or better, by Bodian's silver proteinate, than by any of the more orthodox acidic dyes of the azo and xanthene groups. They are not dissimilar to the illustrations of Julin (1912), although much more densely packed than shown by him.

The photocytes of *P. spinosum* resemble those of *P. atlanticum*.

Pierantoni (1921) claimed that the inclusions were symbiotic bacteria, and he described and illustrated dividing bodies and spores inside the photocytes. I have not seen such reproductive bodies and spores in the photogenic cells of my material. It seems to me that dense areas and apparent nodes in the cytoplasmic inclusions can be ascribed to overlapping of inclusions, or end-views of the inclusions which are seen vertically rather than in profile. Julin (1912) suggested that the inclusions contained nuclein (i.e. nucleoprotein), since internal granulations stained with haematoxylin. To test this possibility, sections were treated with Feulgen's reagent for deoxyribose nucleic acid. The test was negative: the photogenic inclusions were not coloured. Therefore, I can offer no additional evidence for the existence of symbiotic light bacteria.

According to Julin (1912), ontogenetically the photogenic organs are formed from test cells, which are transmitted from one generation to the next. These test cells accompany the egg, and pass from cyathozooid to primary ascidiozooids. The test cells or follicular cells of the eggs of *Pyrosoma* are also luminous (Julin, 1913). In this developmental process, the photogenic inclusions (symbiotic bodies of Pierantoni) are supposed to be transmitted from the parent ascidiozooids to the luminous organs which develop in the ascidiozooids of the larval colonies (Buchner, 1914, 1953; Pierantoni, 1914). Development and budding are described by Berrill (1950*b*).

Measurements of light intensity were made from several specimens of *P. atlanticum*, and the results are presented in Tables 2 and 3 (pp. 711 and 713). For relative spectral composition I have used the spectral emission curve given by Kampa and Boden (1957, p. 88, fig. 8). According to these authors, the emission spectrum of *P. atlanticum* is bimodal, with a primary peak at about 480 mμ, and a smaller secondary peak near 525 mμ. The limits of this curve are far above the base-line, and it has been arbitrarily assumed that light emission extends from 420 to 600 mμ. In this respect it would resemble the blue light of other pelagic animals. Under mechanical stimulation, luminescence lasts up to 17 sec. At a distance of 1 m (in air), estimated radiant flux ranges from $1{\cdot}4 \times 10^{-8}$ to $1{\cdot}4 \times 10^{-6}$ μW/cm^2 receptor surface. Kampa & Boden (1957) report light intensities of $0{\cdot}8 \times 10^{-2}$ to 4×10^{-2} μW/cm^2 at a distance of 1 cm (recalculated, according to the inverse square law, as $0{\cdot}8 \times 10^{-6}$ to 4×10^{-6} μW/cm^2 receptor surface at 1 m in air).

Pyrosomids are warm-water planktonic organisms, usually found at depths of less than 500 m, but which have been taken as deep as 2850 m. *P. atlanticum*, in its various subspecies, is cosmopolitan in distribution. *P. spinosum* is found in the Atlantic, Indian and Pacific Oceans (Ihle, 1910; Metcalf & Hopkins, 1919; Thompson, 1948; Berrill, 1950*a*).

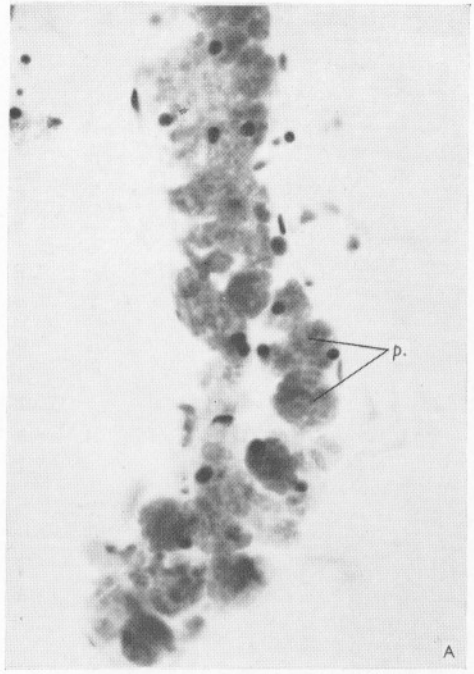
TELEOSTEI

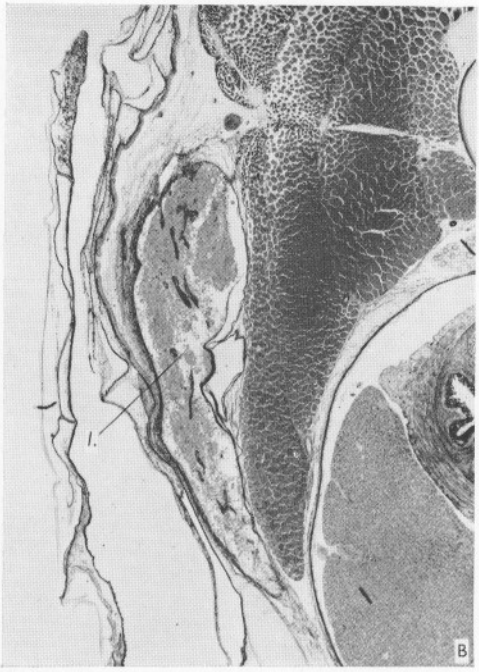
Searsia koefoedi Parr

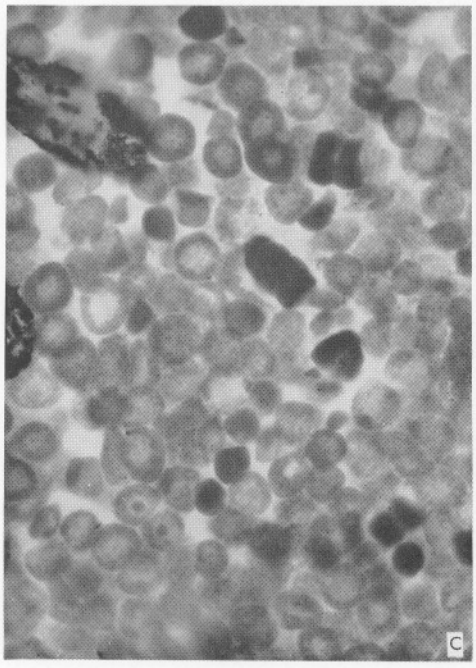
One living specimen was captured ('Sarsia' Sta. no. 23, cruise 3/57). This is a black, bathypelagic species, previously recorded from the North and South Atlantic, the Mediterranean and the Indian Ocean (Brauer, 1906; Norman, 1930; Beebe, 1933; Parr, 1937, 1951; Maul, 1948).

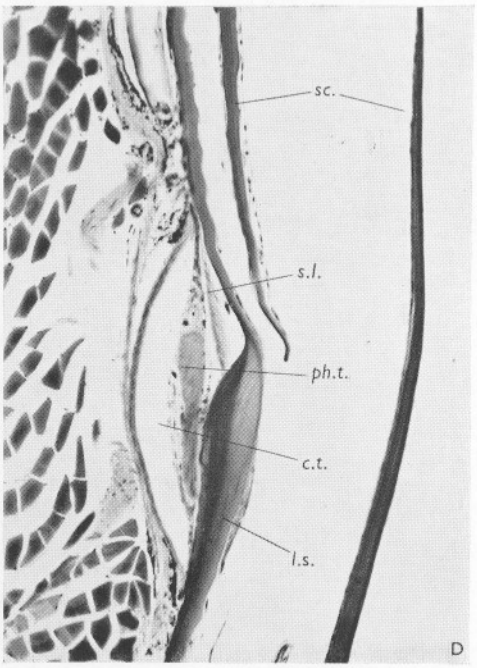
EXPLANATION OF PLATE I

Photomicrographs. A. Light organ of *Pyrosoma atlanticum*, showing photocytes. ×1650. B. Light gland (postclavicular organ) of *Searsia schnakenbecki*. ×25. C. Cellular contents of light gland of *S. schnakenbecki*. 'Red cells', light; 'blue cells', dark. ×1100. D. Photophore (anal organ, series *AO*) of *Myctophum punctatum*. ×265. *c.t.*, connective tissue; *l.*, light gland; *l.s.*, lenticular enlargement of scale; *p*, photocytes; *ph.t.*, photogenic tissue; *sc.*, scale; *sl.*, striated layer.



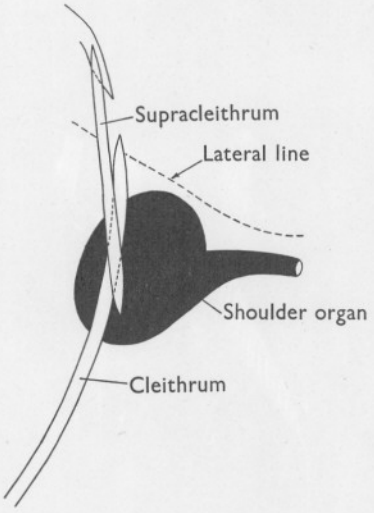






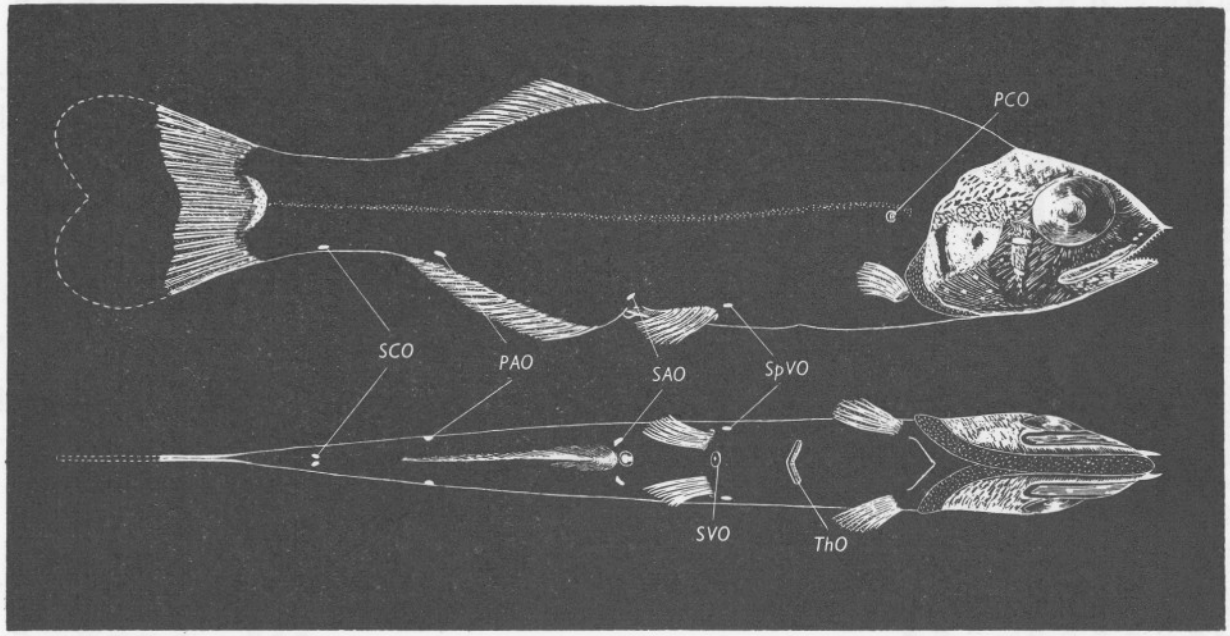
(*Facing p.* 726)

Light organs appear as follows (Text-fig. 10): a transverse linear thoracic organ (*ThO*), appearing as a depression with a white fleck at one end; a subventral V-shaped organ, black in hue (*SVO*); a pair of white supraventrals (*SpVO*); a pair of supra-anal organs (*SAO*); a pair of white postanals (*PAO*); and a pair of white subcaudal organs (*SCO*). The postclavicular organ (*PCO*) is obvious. Other reputed light organs, not clearly discernible in my specimen, are the submental and posterioventrals. Opercular and branchiostegal organs are faint. On the other hand, there appears to be a trace of a light organ on the basal portion of the posterior ray of the pectoral fin. Gunther (in Norman, 1930) observed that the light organs were red in life (see also Beebe, 1931; Parr, 1937). The shape of the supraclavicular process (=postcleithral or postclavicular organ) is illustrated by Beebe (1933) and shown in Text-fig. 9.



Text-fig. 9. Diagram of the postclavicular or shoulder luminescent organ of *Searsia* (=*Bathytroctes*) *rostratus*, copied from Beebe, 1933. The original drawing was made from a cleared specimen 32 mm long.

The animal was alive when brought to the surface, and it was seen to discharge a bright luminous cloud into the water when handled. The light appeared as multitudinous bright points, blue-green in colour. On repeated stimulation the light became weaker and ceased, and the fish died. Computation of radiant flux was carried out as described for *S. schnakenbecki* on p. 792). The luminous glow lasted about 4 sec. At a distance of 1 m (in air), light intensity was about 2×10^{-6} μW/cm^2 receptor surface (Tables 2 and 3). The light of this specimen of *S. koefoedi* was about 5 times brighter than that of *S. schnakenbecki*, as measured in these few instances.



Text-fig. 10. Lateral and ventral view of *Searsia koefoedi*. Legend for light organs: *PCO*, postclavicular (shoulder) organ; *ThO*, transverse thoracic organ; *SVO*, subventral organ; *SpVO*, supraventrals; *SAO*, supra-anal organs; *PAO*, post-anal organs; *SCO*, subcaudal organ. ½ natural size.

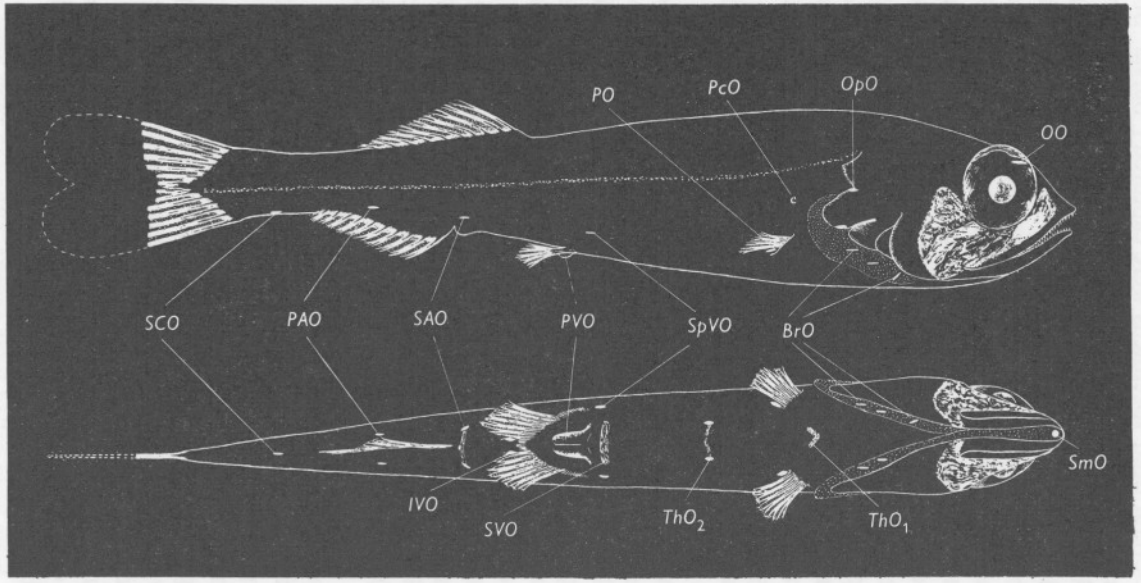
Searsia schnakenbecki Krefft

One living and several dead specimens were captured ('Sarsia' Sta. no. 5, cruise 3/57). This fish provided a spectacular luminescent display. When gently stimulated by being lightly pressed with the fingers, it suddenly shot forth myriads of blue-green sparks into the water. These brightly illuminated the whole dish with a glow lasting about 2 sec. The intensity of light was much greater than that usually recorded, and it was necessary to employ a piece of Chance neutral glass as a reducing filter when recording the responses. With repeated stimulation, the light gradually became weaker, and ceased after about six discharges. Since the fish lived only a short time, it was not possible to determine the spectral composition. In calculating light intensities, I made use of a spectral curve resembling that for *Beroë* light, but with the maximum displaced to 500 mμ. At a distance of 1 m (in air), estimated values for radiant flux are 150×10^{-9} and 430×10^{-9} μW/cm^2 (Tables 2 and 3, pp. 711 and 713. For light with maximal emission at 480 mμ, estimated radiant flux would range from 130×10^{-9} to 365×10^{-9} μW/cm^2.

Searsia schnakenbecki was described by Krefft (1953) from specimens captured in the region 63° 20′–40′ N., 11–12° W., depth of water 450–500 m. It is probably bathypelagic in habits. My specimen has the following suppositional light organs, which largely agree with comparable organs described in the type specimen (Krefft, 1953): submental (*SmO*); seven branchiostegal organs (*BrO*); eye organ (*OO*); opercular organ (*OpO*); pair of pectoral organs (*PO*); transverse thoracic organ 1 (ThO_1); transverse thoracic organ 2 (ThO_2); pair of supraventrals (*SpVO*); transverse subventral (*SVO*); a posterioventral (*PVO*); a pair of inferior ventral organs (*IVO*); a pair of supra-anal organs (*SAO*); a pair of postanals (*PAO*); and a subcaudal organ (*SCO*). In addition, there is a black shoulder organ (postclavicular organ). The position of these various organs is shown in Text-fig. 11.

Most of the surface of the fish is black, except for clear cheeks and cranial roof. The light organs *SmO*, *BrO*, *OO*, *OpO*, *PO*, *SpVO*, *IVO*, *PVO* and *SCO* appear as white spots or flecks on a black ground. Transverse thoracic organ 1 (ThO_1) is grey in colour, V-shaped, with the apex of the V pointing anteriorly. Transverse thoracic organ 2 is a grey transverse stripe with a white fleck at either end. The transverse subventral organ (*SVO*) is a broad grey transverse stripe. The posterioventral organ is a raised wedge-shaped mound, black in colour. The postcleithral organ *PcO*) is a raised papilla lying on the lateral body wall above the pectoral fin.

All these organs have been called light organs, although they have not been seen luminescing in the living fish. Parr (1951) described the shoulder or postcleithral organ of the Searsidae as a large sac lying underneath the skin, often extending forward partly underneath the upper posterior portion of the cleithrum, and opening to the exterior by a tube. The sac has a black lining,



Text-fig. 11. Lateral and ventral view of *Searsia schnakenbecki*. Legend for light organs: *SmO*, submental; *BrO*, branchiostegal; *OO*, eye organ; *OpO*, opercular organ; *PO*, pectoral organ. ThO_1, transverse thoracic organ 1. ThO_2, transverse thoracic organ 2; *SpVO*, supraventrals; *SVO*, transverse subventral; *PVO*, posterioventral; *IVO*, inferior ventral; *SAO*, supra-anal organ; *PAO*, postanal organs; *SCO*, subcaudal organ; *PcO*, postclavicular (shoulder) organ. $\frac{1}{2}$ natural size.

and is traversed from outer to inner wall by irregular strands or columns of soft tissue; it discharges through a tube, which also has a black lining. Parr (1951) and Tucker (1954) suggest that the function of this organ lies in the discharge of a luminous secretion, which I have observed.

Histological observations were made on the luminescent gland of *S. schnakenbecki*. The specimen of *S. schnakenbecki* was fixed in formalin initially, and some time later was post-fixed in Wittmaack's fluid. Sections were cut in celloidin at 15 μ, and treated with a trichrome stain (iron haematoxylin, Bordeaux red, and aniline blue).

The luminescent gland lies deep in the dermis, immediately outside the skeletal musculature (Pl. I B). It is elongated dorsoventrally, and is about one-fifth the height of the fish (about 2·3 mm high and 0·5 mm wide). The walls and internal trabeculae consist of a thick layer of dense connective tissue, staining with aniline blue. This tissue contains a dense population of yellowish black (by transmitted light) melanophores, some of which extend, as flattened cells, over the internal surface of the gland. There is no recognizable continuous epithelial lining.

In the connective tissue walls of the gland and in the trabeculae there are small 'violet cells' (Pl. I C). These are scattered individually, or grouped in clumps which give the impression of originating by division. Many of these cells also occur on the internal surface of the gland, and a few in the internal lumen; some of the cells seem to be in the process of migrating through the connective tissue into the lumen of the gland. The cells are coloured deep violet by the stain; the nucleus is very dense and dark, and the basophilic cytoplasm contains purple granules. These violet cells are only about 5 μ in diameter, and the cytoplasm is rather sparse.

Lying in the lumen of the gland are many spherical 'red cells'. These are large, ranging from 8 to 40 μ in diameter. The body of the cell or spherule (the 'cytoplasm') is packed with acidophilic granules, coloured pink by the dye; staining affinity is rather weak. In the centre of the spherule is a clear area, representing the nucleus, and containing a few fine chromatic threads.

A third cell type is found in the gland lumen, the 'blue cells'. These are smaller in size, around 6–8 μ, the nucleus is more prominent and deeply staining, and the basophilic cytoplasm contains blue granules. All kinds of transitional stages appear to exist between the 'blue' and 'red' cells, the nucleus in such intermediates becoming fainter, the cell volume increasing, and the cytoplasm shifting from basi- to acidophilic.

The picture that emerges is the following. The large acidophilic spherules appear to be the photogenic bodies. Presumably, when expelled, they become disrupted and activated and they then emit light. There is a reasonable degree of transition between the small 'violet' cells in the gland wall and the large 'red' cells in the gland lumen, and it is not improbable that the violet basophils represent the generative tissue. The latter cells, passing into the gland

lumen, gradually become transformed into the acidophilic spherules. This picture is rather an extraordinary one, and is offered with some hesitation, since a closely comparable situation has not been described in other luminescent animals producing a luminous secretion. Perhaps a distant analogy can be drawn with the proliferating epithelial tissue within the testis, or the sebaceous glands of mammalian skin. There is no continuous epithelial lining in the light gland of this specimen, however. Although this appearance may be an artifact, due to glandular discharge, fixation, etc., this is rather unlikely. Rather the generative cells appear to originate in the connective tissue itself, and subsequently pass into the gland lumen. In two other luminous teleosts (*Malacocephalus* and *Monocentris*), luminous secretion is produced by break down (cytolysis) of epithelial cells lining the light organs (Hickling, 1926; Okada, 1926); Harvey (1952) implicates bacteria in the luminescence of these two fish.

Myctophum punctatum Rafinesque

Lantern fish were attracted to the side of the boat by hanging a lamp over the side after dark. Fish which came to the surface were captured in a hand net. All specimens were *M. punctatum*. Position 47° 00′ N., 6° 05′ W. ('Sarsia' Sta. no. 8, cruise 3/57).

The myctophids examined were 8–9 cm in length (snout to tip of tail). This species possesses many large photophores on head and trunk, and the photophores have been labelled and numbered for systematic purposes (see Fraser-Brunner, 1949, fig. 2). Myctophids flash periodically when kept in aquaria. The light appears blue to the eye. To record luminescence, a fish was placed in a small dish beneath the photomultiplier, and was stimulated mechanically by handling it. With this treatment, the fish responds by lighting up all its photophores.

The spectral composition of myctophid light is not known, and I used the spectral curve of *Chaetopterus* light (Text-fig. 4, p. 714) for purposes of calculation. Since the light of both animals is blue, and since the photomultiplier has a fairly flat response below 500 mμ, any error occasioned by this procedure will be small.

Values for calculated radiant flux are given in Tables 2 and 3 (pp. 711 and 713). The light was measured at a distance of about 95 mm, and the recordings are of the light emitted by about half the photophores borne by the fish. The light is emitted in periodic flashes, sometimes grouped into rhythmic bursts. Each flash lasts about 0·5 sec and bursts of flashes last up to 3–4 sec (Text-fig. 3, W_1, W_2). At a distance of 1 m in air, minimal estimates of radiant flux are 1×10^{-9} μJ to 50×10^{-9} μW/cm^2 receptor surface. Owing to the large size of the source, viz. a lantern fish with all its photophores glowing, decrease of intensity with distance is less than that predicted by the inverse square law; consequently, these values for radiant flux may be slightly low. There is a further difficulty

owing to the circumstance that the photophores of lantern fish possess lenses or focusing devices, the optical characteristics of which are unknown; it is highly unlikely that all the photophores bring their light into focus in the same plane. For these various reasons, recalculated estimates of radiant flux at distances other than those actually measured can be regarded only as a rough estimate.

With regard to their histology, the photophores of *Myctophum* and *Scopelus* have been examined microscopically by earlier workers (Emery, 1884; Brauer, 1908; Ohshima, 1911). My own observations were made on the anal organs (series *AO*) of *Myctophum punctatum*. These were fixed in Bouin's, cut in celloidin, and stained with Ehrlich's haematoxylin and eosin, or with a trichrome stain containing iron haematoxylin, Bordeaux red, and aniline blue.

A photophore is overlapped externally by 1 or 2 scales, and the scale immediately overlying the organ is intimately associated with its structure (Pl. 1D). At the surface of the light organ the scale is thickened into a lenticular swelling; there is the usual epidermal covering. Beneath the scale lies a striated layer (the 'schüllelformige Organe' of Brauer and the 'peculiar membrane' of Ohshima). In section this shows transversely arranged striae or fibrils, which stain blue with haematoxylin. Underneath the striated layer is a patch of photogenic tissue, consisting of narrow elongated cells, with long axes directed dorsoventrally. These have narrow elongated nuclei, the cytoplasm has a somewhat indistinct fine granular appearance and stains blue with haematoxylin. The photogenic cells are in the neighbourhood of 40–50 μ long; although cell boundaries are difficult to distinguish, the cells seem to be about 5 μ broad.

The photogenic mass is invested with a thin limiting membrane of flattened cells, possibly a connective tissue sheath (Pl. 1D). Filling the intervening space, between the photogenic mass and the external sheath, is a loose connective tissue (mucous connective tissue of Emery, gelatinous layer of Brauer and Ohshima). This has a faintly eosinophilic ground substance, containing flattened nuclei. Investing the organ externally is a dense connective tissue sheath, consisting of an internal homogeneous eosinophilic layer, and an external dense basophilic layer. Occasional pigment cells, or extensive streaks of black pigment, are found behind the connective tissue sheath. The organ is ringed with pigment cells, which extend a short distance down over the dorsal face of the organ. The arrangement of the pigment and the asymmetrical arrangement of the lens and photogenic tissue all indicate that the light from these organs is directed downwards.

Since the lens system and aperture are wider than the actual photogenic tissue, they will have the action of enlarging the apparent source. In addition, the lens may have a collimating effect.

Leptostomias sp.

A *Leptostomias*, close to *L. macropogon* Norman, was captured alive, at 'Discovery' Sta. no 3344, on 18 October 1955. It was observed in the dark room. Notes made at the time read: 'The long chin barbel had an enlarged cream coloured tip. When the fish was sharply displaced, or the tentacle tip was gently stroked with a camel-hair brush, the tentacle tip gave off a faint bluish luminescence. Faint glow, lasting about a second.'

L. macropogon has been captured previously in the South Atlantic (Norman, 1930).

The barbel bulb is also yellow in fresh specimens of *L. gladiator* and *L. bermudensis*; the luminescence, apparently, has not been seen. The barbel of a living *Chirostomias pliopterus* gave off a steady pink glow anteriorly, and a white glow posteriorly. The bulb of a living male *Eustomias bibulosus* gave off a distinctly green light in three brilliant flashes (Beebe & Crane, 1939). Beebe (1935) observed red and blue lights in the barbels of deep-sea melanostomiatids during dives in his 'bathysphere'.

LUMINESCENCE AND REFLEXION OF LIGHT FROM ANIMAL SURFACES

It is well known that many animals from bathypelagic waters, below the level of light penetration, are black or red in colour, e.g., Scyphomedusae, nemertines, Crustacea, and teleosts. In upper, dimly lit waters, some animals are translucent, motley coloured, or have a silvery sheen. Thus silvery and pale-coloured fishes are mostly found in the upper 500 m, black and brown species at greater depths. This correlation of colour with depth is not absolute, but is striking enough when examining net hauls from various depths, and there has been much speculation concerning its significance (Murray & Hjort, 1912; Marshall, 1954). The commonest suggestion is that dark colours (red, black and brown) serve to reduce reflexion to a minimum in deep water, and thus decrease the animal's chances of being seen. With these ideas in mind it seemed worth while to make some actual measurements of reflexion from bathypelagic species.

Few attempts have been made to measure reflexion from animals, although many curves are available for reflexion characteristics of plants (leaves, flowers, etc.). Using a Hardy photoelectric recording spectrophotometer, Edwards & Duntley (1939) made a detailed study of pigments and colours of human skin. They measured reflexion from the skin surface, transmission through the skin and absorption by the skin and its contained pigments. Deanin & Steggerda (1948) have used the same instrument for measuring melanin dispersion in the frog.

Measurements of reflexion were made with a Unicam instrument, namely

the 'diffuse reflectance attachment' (S.P. 540) coupled to a 'photoelectric quartz spectrophotometer' (S.P. 500). This instrument measures diffuse reflectance, using a block of magnesium carbonate as a reference standard. The reflexion coefficient of $MgCO_3$ ranges from 0·967 at 450 mμ to 0·989 at 650 mμ (*Handbook of Chemistry and Physics*, 1949). The characteristics of the instrument were essayed by measuring reflectance from green leaves: two resultant curves for peony leaf (A) and *Euonymus* leaf (B) are shown in Text-fig. 12. The reflectance characteristics of these leaves are determined in large part by the properties of their chlorophylls and carotenoids; reflectance is less in the more glossy leaf of *Euonymus*, as might be anticipated. The instrument measures very little direct reflexion. At 450 mμ, reflexion from a disc of polished silver was 6%, compared with published values of 0·90 for reflexion factor (direct) (Walsh, 1953).

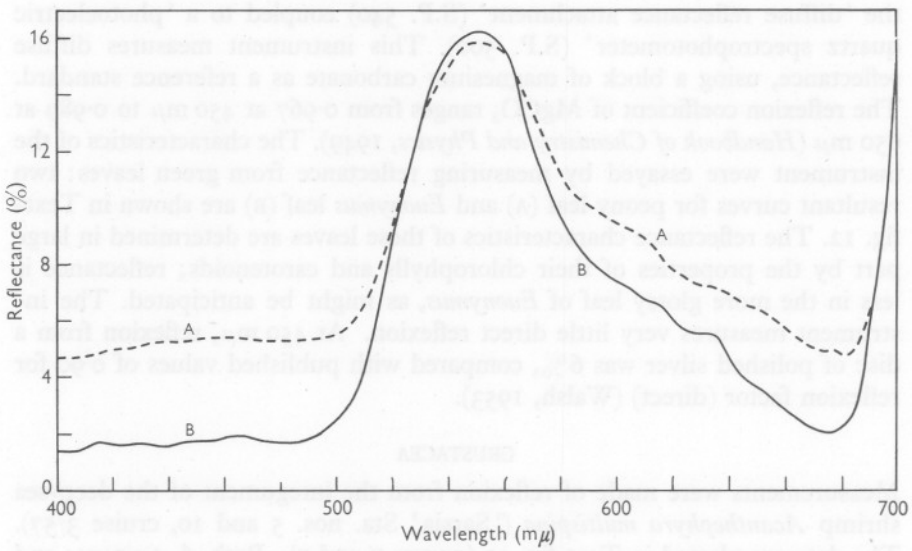
CRUSTACEA

Measurements were made of reflexion from the integument of the deep-sea shrimp *Acanthephyra multispina* ('Sarsia' Sta. nos. 5 and 10, cruise 3/57). The data are plotted in Text-fig. 13 (curves D and E). Both *A. purpurea* and *A. multispina* are deep red in colour, owing to a heavy deposition of carotenoids in the body coverings. Frozen specimens of *A. multispina* were saved for pigment extraction and treated as follows. After thawing the animals the integument was stripped off and extracted with acetone. Water and ethanol were added, and the pigment was transferred to petroleum ether (b.p. 40–60° C). Absorption was read in a spectrophotometer (Unicam S.P. 600). The solvent was evaporated *in vacuo*, and the pigment redissolved in CS_2. Absorption was read in the spectrophotometer. Absorption curves in petroleum ether and CS_2 are shown in Text-fig. 13 (A, B). These curves are identical with those for astaxanthin in the literature (Karrer & Jucker, 1948; Goodwin, 1952).

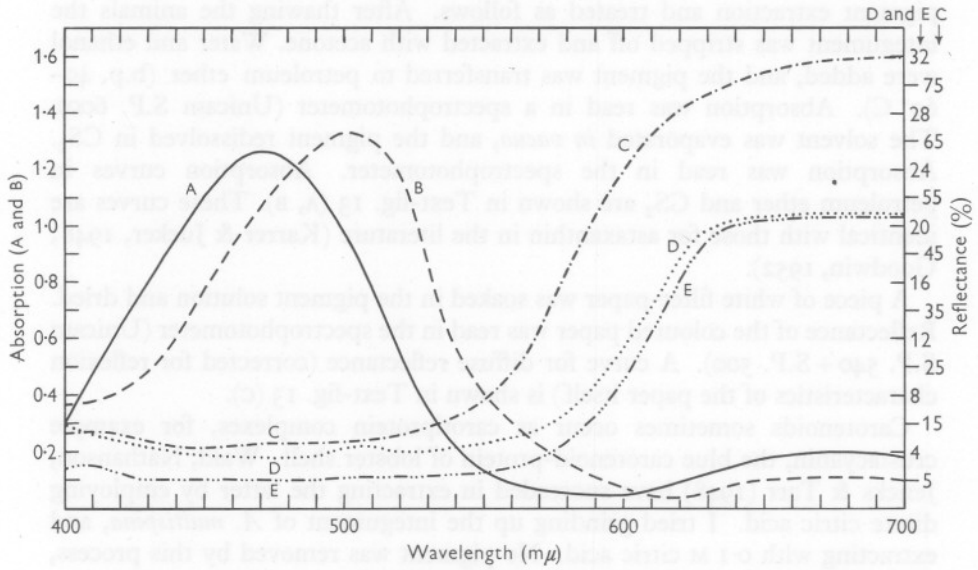
A piece of white filter-paper was soaked in the pigment solution and dried. Reflectance of the coloured paper was read in the spectrophotometer (Unicam S.P. 540 + S.P. 500). A curve for diffuse reflectance (corrected for reflexion characteristics of the paper itself) is shown in Text-fig. 13 (C).

Carotenoids sometimes occur as carotiprotein complexes, for example crustacyanin, the blue carotenoid-protein of lobster shell. Wald, Nathanson, Jencks & Tarr (1948) have succeeded in extracting the latter by employing dilute citric acid. I tried grinding up the integument of *A. multispina*, and extracting with 0·1 M citric acid. No pigment was removed by this process, indicating that the astaxanthin occurs in a free state.

A. purpurea and *A. multispina* are deep red in colour except for the black eyes. The entire surface of the body is covered with greatly expanded chromatophores having long filamentous processes. The cuticle itself is pigmented, appearing amber yellow between the chromatophores. In *Systellaspis debilis*,



Text-fig. 12. Reflectance curves for green leaves of peony (A), and Japanese *Euonymus* (B), as determined with the Unicam reflectance attachment (S.P 540).



Text-fig. 13. Spectral curves relating to *Acanthephyra multispina*. A and B. Absorption curves for carotenoid pigment (astaxanthin) extracted from the integument: A, in petroleum ether; B, in CS_2. 1 cm cells. Figures at the left for curve A (readings in petroleum ether), × 10; for curve B (readings in CS_2), × 5. C. Reflectance of filter-paper impregnated with astaxanthin. D, E. Reflectance from surface of the animal. Scales for C, D and E shown at the right.

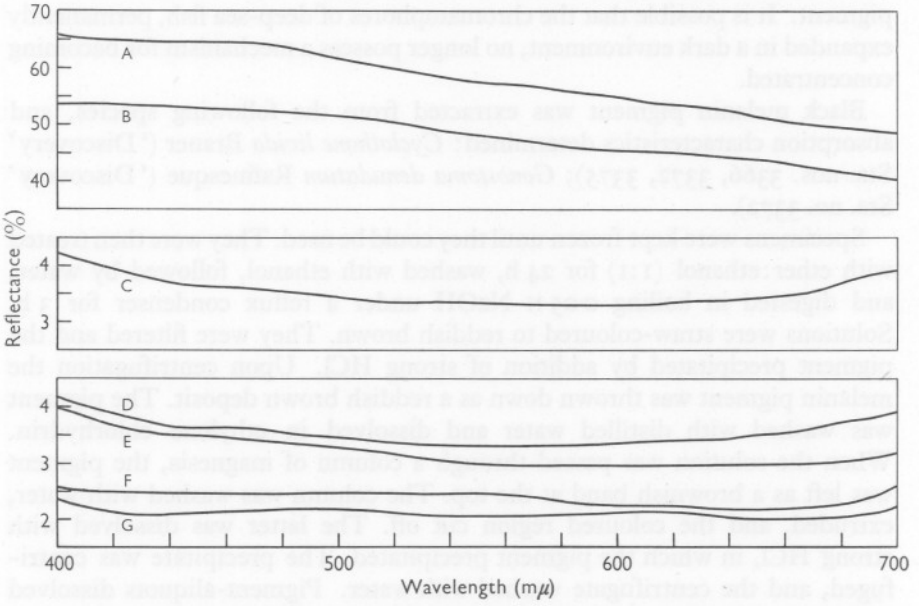
Dennell (1955) found that the deep red pigment of the body was confined to the cuticle.

The characteristics of the reflectance curves (Text-fig. 13) show good agreement with the absorption properties of extracted pigment, which seems to be astaxanthin. The reddish coloration of *Acanthephyra* is thus produced largely by the red astaxanthin pigment, located in red chromatophores and occurring freely in the cuticle.

TELEOSTS

The reflectance of several species of deep-sea fish was measured, and the data are assembled in the curves of Text-fig. 14. Specimens were: *Argyropelecus olfersi* Cuv. ('Sarsia' Sta. no. 5, cruise 3/57); *Cyclothone* sp. ('Sarsia' Sta. no. 6, cruise 3/57); *Xenodermichthys copei* Gill ('Sarsia' Sta. no. 10, cruise 3/57); and *Chauliodus* sp. ('Sarsia' Sta. no. 5, cruise 3/57).

The *Cyclothone* was a black bathypelagic species. Two sets of measurements showed low reflectance, ranging from 3 to 4% in the visible range (400–700 mμ). Reflectance is maximal in the blue, falls off slightly at longer wavelengths in the green and yellow, and shows a slight rise again in the red (above 650 mμ).



Text-fig. 14. Reflexion from the integument of some deep-sea fish. Measurements made with Unicam instrument (S.P. 540+S.P. 500). Ordinates, reflexion as percentage of $MgCO_3$ standard (maximum = 100). Abscissae, wavelength. A, B. *Argyropelecus olfersi* Cuv, abdominal wall and trunk. C. *Xenodermichthys copei* Gill, lateral abdominal wall. D, E. *Cyclothone* sp., flank of two specimens. F, G. *Chauliodus* sp., lateral peduncle and ventral surface of trunk, respectively. Note changes of scale on ordinates.

The black pigment in the skin of *Cyclothone* is contained in melanophores, which are densely distributed over the surface of the body. In freshly caught specimens these are all expanded, and their processes touch one another, thus forming a mosaic. Several shapes of melanophores can be recognized: cells with fine irregular, branching and radiating processes; cells with a dark pigmented centre from which radiate lobate processes; and more or less hexagonal-shaped pigmented cells, in which the processes are short or wanting. The melanophores lie in two layers, the more superficial cells having fine branching processes, while the deeper cells have coarser lobate processes, or are hexagonal in shape. The fin rays possess a layer of black pigmented cells on either side, and the ventral photophores lie in black pigmented capsules. There is no trace of other kinds of chromatophores, neither guanophores nor lipophores. Light shines through and between the processes of the cells, the latter being only partially absorbing. The muscles are translucent; the visceral region, owing to a black peritoneum, and much of the head, are opaque.

Pieces of fins of freshly caught (dead) specimens were placed in fish-Ringer, to which was added adrenaline to make 1/100,000 and 1/10,000. No contraction of the melanophores occurred in 1 h. Adrenaline is a strong stimulant of chromatophores of coastal and freshwater fish, causing concentration of the pigment. It is possible that the chromatophores of deep-sea fish, permanently expanded in a dark environment, no longer possess a mechanism for becoming concentrated.

Black melanin pigment was extracted from the following species, and absorption characteristics determined: *Cyclothone livida* Brauer ('Discovery' Sta. nos. 3366, 3372, 3375); *Gonostoma denudatum* Rafinesque ('Discovery' Sta. no. 3372).

Specimens were kept frozen until they could be used. They were then treated with ether:ethanol (1:1) for 24 h, washed with ethanol, followed by water, and digested in boiling 0·05 N NaOH under a reflux condenser for 3 h. Solutions were straw-coloured to reddish brown. They were filtered and the pigment precipitated by addition of strong HCl. Upon centrifugation the melanin pigment was thrown down as a reddish brown deposit. The pigment was washed with distilled water and dissolved in ethylene chlorhydrin. When the solution was passed through a column of magnesia, the pigment was left as a brownish band at the top. The column was washed with water, extruded, and the coloured region cut off. The latter was dissolved with strong HCl, in which the pigment precipitated. The precipitate was centrifuged, and the centrifugate washed with water. Pigment-aliquots dissolved in ethylene chlorhydrin and boric-borate buffer at pH 9; these were examined in a spectrophotometer (Unicam S.P. 500). Specimens of *Cyclothone*, preserved in formalin for 1 month, were extracted in a like manner (Gortner, 1911; Lea, 1945; Serra, 1946; Smyth, Porter & Bohren, 1951).

Representative absorption curves for the pigments are shown in Text-fig. 15.

They are typical of melanin curves: melanin is a reddish pigment showing high absorption in the blue, and minimal absorption at long wave-lengths. Visceral (peritoneal) and skin pigments are similar (Text-fig. 16); formol causes little or no change in the absorption characteristics of the melanin-pigment (Text-fig. 16).

When Text-figs. 14 and 15 are compared, it will be apparent that the melanin of the skin contributes very little to the spectral composition of the reflected light; the slight rise in the reflectance curves, about 600 mμ, amounting to about 1%, is caused by melanin in the skin. The surfaces of black bathypelagic species measured showed very low reflexion: *Chauliodus*, 2–2½%; *Cyclothone*, 3–4%; *Xenodermichthys*, 3–4%. Much of this reflexion probably originates in surface tissue lying between the chromatophores. Indirect reflexion is much higher in *Argyropelecus*, which possesses a silvery surface, around 40–65%.

DISCUSSION

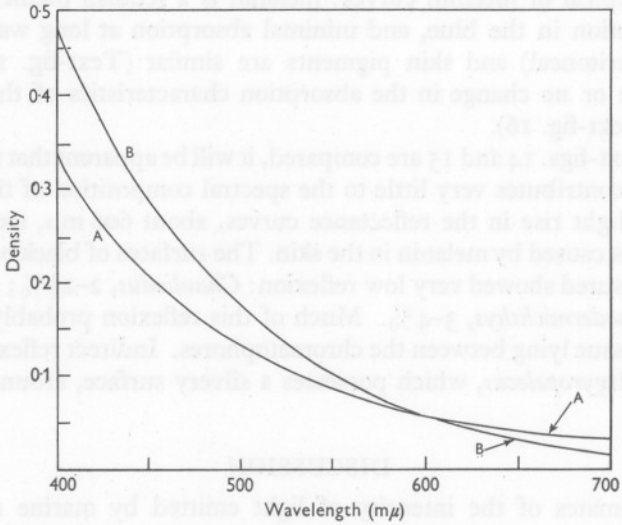
Recent estimates of the intensity of light emitted by marine animals are collated in Table 3 (p. 713). For comparison, they are brought to a common basis of energy units/cm^2 receptor surface at a distance of 1 m. Although this procedure involves some unknown degree of error, owing to probable deviation from the inverse square law, it at least provides rough estimates of orders of magnitude.

The estimates in Table 3 are all derived from photoelectric measurements. There are, in the literature, some earlier estimates of the brightness of animal light, based on visual comparison.

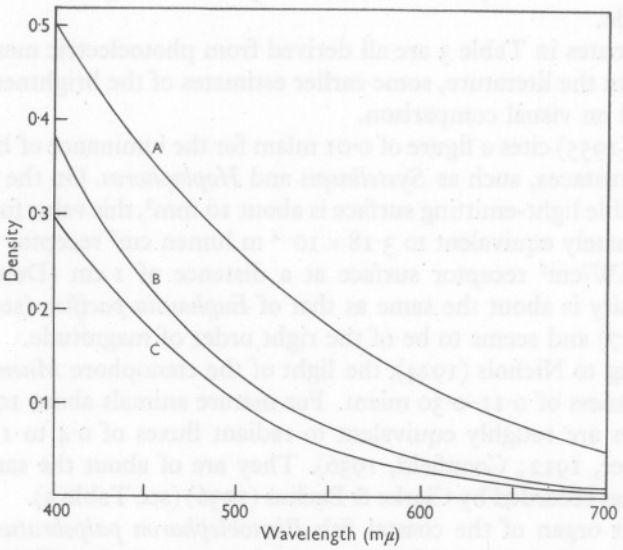
Dennell (1955) cites a figure of 0·01 mlam for the luminance of bathypelagic decapod Crustacea, such as *Systellaspis* and *Hoplophorus*. On the assumption that the visible light-emitting surface is about 10 mm^2, this value for luminance is approximately equivalent to $3{\cdot}18 \times 10^{-4}$ m lumen cm^2 receptor surface and $2{\cdot}3 \times 10^{-3}$ μW/cm^2 receptor surface at a distance of 1 cm (Dennell, 1940). This intensity is about the same as that of *Euphausia pacifica* (see Kampa & Boden, 1957) and seems to be of the right order of magnitude.

According to Nichols (1924), the light of the ctenophore *Mnemiopsis leidyi* has a brightness of 0·11–0·30 mlam. For mature animals about 100 mm long, these values are roughly equivalent to radiant fluxes of 0·4 to 1 μW/cm^2 at 1 cm (Mayer, 1912; Coonfield, 1936). They are of about the same order of magnitude as recorded by Clarke & Backus (1956) (see Table 3).

The light organ of the coastal fish *Photoblepharon palpebratus*, according to Steche (1907), has a brightness equivalent to a surface illuminated with 0·0024 Meter-Kerze, or 0·0022 lx. The light organ has a flattened oval shape, 11×5 mm in dimensions; the light is produced by symbiotic luminescent bacteria. The light is reported to be greenish blue in colour, and probably is not greatly different in relative spectral composition from the curve for the



Text-fig. 15. Absorption characteristics of the melanin pigment from the integument of *Gonostoma denudatum*. 1 cm cuvette in Unicam spectrophotometer, S.P. 500. A, in boric-borate buffer, pH 9; B, in ethylene chlorhydrin.



Text-fig. 16. Absorption characteristics of the melanin pigment from the deep-sea fish *Cyclothone livida*. A, from entire animal, in ethylene chlorhydrin; B, formol-preserved integument, in ethylene chlorhydrin; C, viscera, in ethylene chlorhydrin. 1 cm cuvette in Unicam spectrophotometer, S.P. 500.

relative luminous efficiency of radiation (human scotopic vision). An estimation of equivalent radiant flux is about 3×10^{-4} μW/cm^2 receptor surface at a distance of 1 cm.

The light of most pelagic animals is blue in colour, although there are notable exceptions. Actual measurements of spectral composition give maximal emission peaks (approximately) as follows: *Gonyaulax polyedra*, 478 mμ (Hastings & Sweeney, 1957); *Atolla wyvillei*, 470 mμ; *Vogtia glabra*, 470 mμ; *Beroë ovata*, 510 mμ; *Euphausia pacifica*, 476 mμ (Kampa & Boden, 1957); *Pyrosoma atlantica*, 482 mμ (Kampa & Boden, 1957). Of these animals only the light of *Beroë ovata* is green. Symbiotic bacteria from the deep-sea fish *Coelorhynchus* (*kishinouyei*?) emit light with a maximum $\nu = 21{,}200$ cm^{-1} or $\lambda = 472$ mμ (Takase, in Harvey, 1952). The bacterial light of *Malacocephalus laevis*, another macrourid, is said to have an emission maximum around 510 mμ (Haneda, in Harvey, 1952). Harvey (1952) cites some instances of lights of other colours in pelagic animals: *Thaumatolampas diadema* is a squid having photophores emitting red light; *Echiostoma tanneri* is a teleost possessing cheek organs which shine with a pink *or* blue glow (cf. Beebe & Crane, 1939). The smaller photophores of *Echiostoma* and those of *Argyropelecus olfersi* are said to emit a yellowish or yellow-green light (see Harvey, 1952).

Attenuation of light from a point source in sea water depends both upon distance (operation of the inverse square law) and absorption (given by the extinction coefficient). Clarke & James (1939) give the following values for absorption in (preserved) Sargasso Sea water:

λ (mμ)	Transmission/m (%)	Remarks
405	97·2	Filtered
436	99	Filtered
490	97·2	Filtered
—	90	Shaken
505	95·5	Filtered
546	95·8	Filtered
550	87	Shaken

A measurement made at sea of surface water (Sargasso Sea) gave a value of 96·1 % at 550 mμ.

Jerlov (1951), from measurements at sea, found that transmission/m depth for blue daylight in the Atlantic Ocean varied from a minimum of 91·5 % (surface) to a maximum of 98 % (at 25–50 m) (various stations). Selected values for transmission at various stations (0–50 m) are

λ (mμ)	Mean transmission/m depth (%)
400	93·3–96·8
475	95·6–96·8
500	95·1–96·8
525	93·4–94·9
550	91·3–93·7

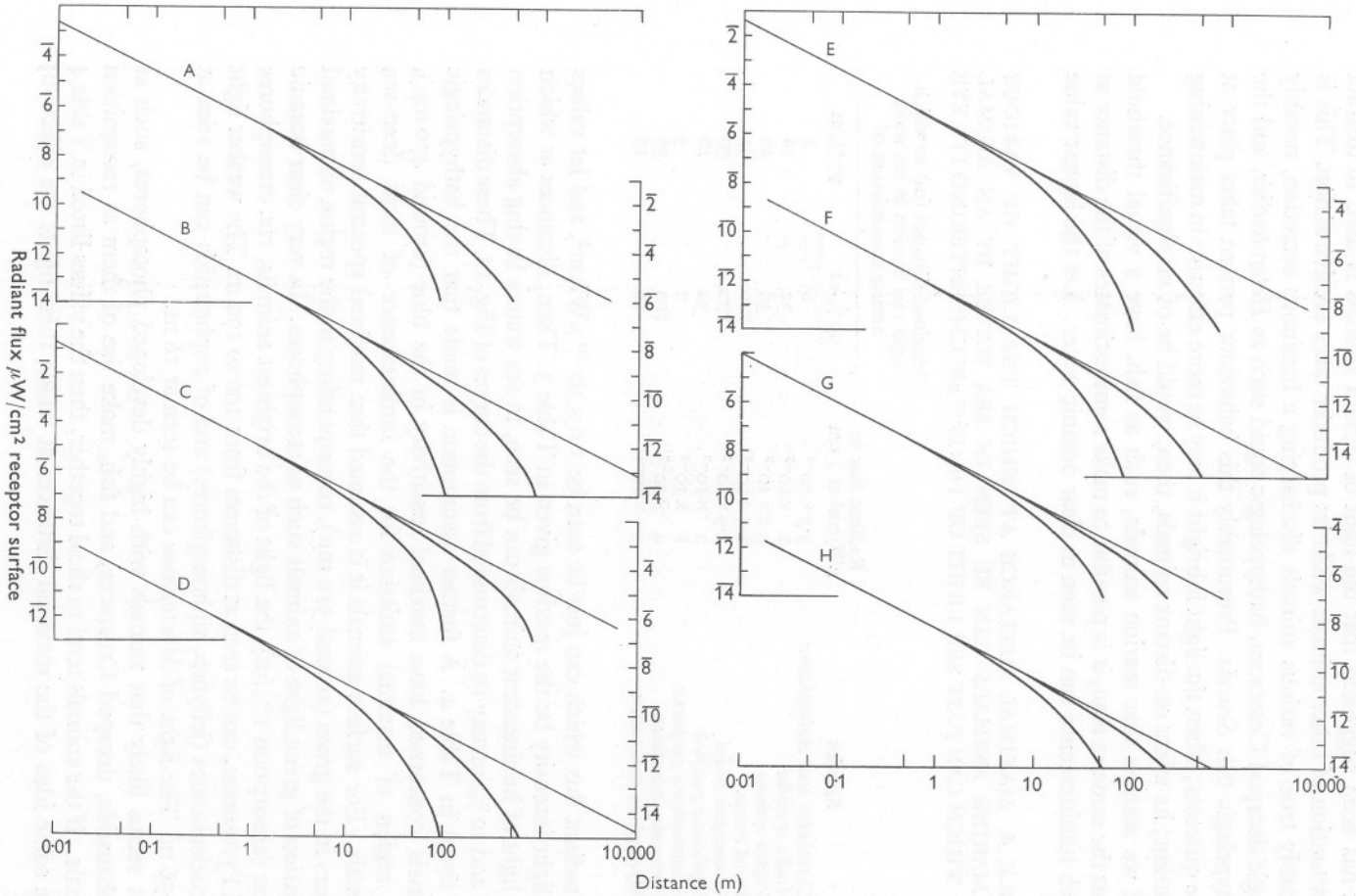
It would seem, then, that transmission in oceanic waters for blue and green light (spectral range of about 460–510 mμ) lies between 91 and 99% (transmission/m depth), and for purposes of illustration, arbitrary limits of 1 and 10% absorption/m depth have been selected, as representing two extremes for oceanic water.

Estimates of light intensities at various distances from a point source are illustrated in Text-fig. 17. The light intensities illustrated are selected from Table 3, and represent the maximal measured output of several luminescent animals in terms of radiant flux/cm^2 receptor surface at an initial distance of 1 cm, viz. of radiolarians *Cytocladus* and *Aulosphaera*; a siphonophore *Vogtia spinosa*; a scyphomedusan *Atolla wyvillei*; ctenophores *Beroë ovata* and *Mnemiopsis leidyi*; crustaceans *Euphausia pacifica* and *Acanthephyra purpurea*; *Pyrosoma*; and the lantern-fish *Myctophum punctatum*. The three curves in each figure show decrease of light intensity with distance according to the inverse square law alone, and decrease according to the inverse square law in sea water having transmission values of 99 and 90%/m depth. For these values it will be observed that the curve for 90% transmission only begins to diverge markedly from that for the inverse square law at distances greater than 10 m, and that for 99% transmission, above 100 m.

It is unfortunate that so little information exists about visual threshold or minimal intensities that can be perceived by marine animals. Earlier estimates of visual threshold for fish have made use of Grundfest's observations (1932) on *Lepomis*, a freshwater fish. These indicated that the lower limits of light intensity for fish vision were similar to those for the human eye, viz. 1×10^{-6} mlam. For an estimated pupillary area of 0·1 cm^2, equivalent radiant flux would be about $1{\cdot}2 \times 10^{-8}$ μW falling into one eye. *Lepomis* is most sensitive to the green region of the spectrum, around 530–550 mμ (Grundfest, 1932; Clarke 1936; Strickland, 1957).

The threshold of the human eye, when dark-adapted, for a small steady light source, has been estimated at 200 quanta/sec at 510 mμ (selected from values ranging from 170 to 830 quanta/sec) (Pirenne, 1956). For a just detectable flash of duration $\geqslant 1$ sec, the human eye needs 200 quanta $= 8 \times 10^{-10}$ erg to fall in the pupil, area 0·5 cm^2 in 1 sec. Pirenne (1956) suggests that the high retinal sensitivity of man is similar to that of other rod-bearing vertebrates, and that some invertebrates may also be equally sensitive. *Dendrocoelum lacteum*, a fresh-water planarian, responds to light having an energy flux of 15×10^{-9} erg/sec falling in one eye (Pirenne & Marriott, 1955).

The brightest luminescent animals known in the sea are ctenophores, Pyrosomas, and the deep-sea fish *Searsia*, all of which have a measured light output in excess of 2×10^{-7} μW/cm^2 receptor surface at a distance of 1 m. In the first two, luminescence is intracellular; the latter discharges a bright luminous secretion.



Text-fig. 17. Curves for estimated decrease in intensity of animal light at increasing distances from source. Intensities taken from Table 3. The three curves in each figure refer, from above downwards, to decrease from a point source according to the inverse square law alone; decrease in sea water having an absorption of 1 %/m; and decrease in sea water having an absorption of 10 %/m. A, *Vogtia spinosa*; B, *Beroë ovata*; C, *Mnemiopsis leidyi*; D, *Atolla wyvillei* and *Euphausia pacifica*; E, *Pyrosoma atlanticum*; F, *Myctophum punctatum*; G, *Acanthephyra purpurea*; H, *Cytocladus* and *Aulosphaera*. Scale for A on left, for B on right, and so on.

It has been suggested that the light of certain animals is used to distract the attention of other animals while its producer takes evasive action. This is probably true of various animals discharging a luminous secretion, notably pelagic decapod Crustacea, bathypelagic squid such as *Heteroteuthis*, and the bathypelagic fish *Searsia*. Presumably this behaviour pattern takes place at close quarters; when the light is bright it may be more effective in maintaining attention; its effect on distant animals, then, would be of no significance.

If we assume that marine animals, such as fish, have a visual threshold about the same as man, it is possible to make some estimates of the distance at which luminescence can be seen in clear oceanic water. Let the lowest value

TABLE 4. MAXIMAL DISTANCE AT WHICH THE LIGHT OF VARIOUS MARINE ANIMALS CAN BE SEEN IN SEA WATER BY AN ANIMAL WHICH CAN JUST SEE LIGHT OF $1{\cdot}6 \times 10^{-10}$ μW/CM^2 ENTERING ITS EYE

Species	Radiant flux in μW/cm^2 at 1 cm	Maximal distance (m) at which light can be seen in sea water having transmission of	
		99 %/m	90 %/m
Cytocladus and *Aulosphaera*	$5{\cdot}3 \times 10^{-5}$	6	4
Atolla wyvillei	2×10^{-3}	32	16
Vogtia spinosa	$3{\cdot}2 \times 10^{-3}$	36	20
Beroë ovata	$8{\cdot}5 \times 10^{-2}$	120	41
Mnemiopsis leidyi	$1{\cdot}9 \times 10^{-1}$	170	50
Euphausia pacifica	2×10^{-3}	32	16
Acanthephyra purpurea	8×10^{-5}	7	5
Pyrosoma atlanticum	4×10^{-2}	100	36
Myctophum punctatum	5×10^{-4}	16	10

for radiant flux which can just be seen be $1{\cdot}6 \times 10^{-10}$ μW/cm^2, and let values for light intensity be the maxima given in Table 3. Then, distances at which the light of luminescent animals can be seen, in sea waters having absorption of 1 and 10 %/m may be determined from the curves of Fig. 17. These distances are listed in Table 4. A further assumption is made that the bathypelagic animals concerned have maximal sensitivity in the blue (around 470 mμ), the region of maximal emission for the luminescence of most deep-sea animals. For surface animals it is assumed that maximal spectral sensitivity occurs in the green (around 510 mμ), corresponding to the region of maximal emission of green light of animals such as ctenophores. In very clear oceanic water (absorption 1 %/m), the light of the brightest animals, viz. ctenophores and Pyrosomas, can be seen at distances from 100 to 170 m. The weaker light of coelenterates (jellyfish, siphonophores) and of euphausiids can be seen at 32–36 m. The light of *Myctophum* can be seen at 16 m.

It seems likely that animals with highly developed photophores, such as euphausiids, decapod Crustacea, and fish, make use of them as recognition signals. If the animals tend to shoal together, then the values listed in Table 4 give some idea of the maximal distances at which their lights are effective;

they can also be correlated with estimates of population density. Dennell (1955) has made an estimate of the distance at which the light from the photophores of a deep-sea shrimp can be seen by another shrimp. He gives a minimal value of 0·01 mlam for brightness, and he quotes values of 1×10^{-6} to 1×10^{-7} mlam for visual threshold of a crustacean (*Cambarus*?). Using an extinction coefficient of $u_v = 0{\cdot}0920$ for clear oceanic water, he has estimated that the light of decapod photophores may well be mutually perceived at distances of 100 m. Assume that the eye of a shrimp has an area of 0·05 cm^2; then the minimal light entering that eye which can just be seen has an intensity around 1×10^{-8} μW. One shrimp can be treated as a point source, the light from which decreases with distance according to the inverse square law. For waters having transmissions of 99 and 90%/m, the estimated maximal distance at which one shrimp could see the light of another shrimp is about 1 m. If the visual threshold of the shrimp lies at about the same level as that of man (dark adapted), the equivalent maximal distance would lie around 16–32 m.

Estimates have been made of the average spatial distribution of deep-sea shrimp, based on towing data. It is suggested that, if the animals are evenly distributed, *Systellaspis debilis* occurs at intervals of about 14 m and *Hoplophorus grimaldii* at 40 m. For a visual threshold value of 2×10^{-7} $\mu W/cm^2$, these distances are excessive for mutual perception of photophore luminescence. It is known that euphausiids occur in shoals, and, from the estimates given above, it can be argued that their lights can be mutually seen at distances of about 1 m. Since these animals appear to flash spontaneously in their natural habitat, it is likely that their lights tend to promote shoaling. There are a great many variables in these estimates. Thus, the photophores possess lenses, the optical properties of which may greatly alter the geometry of the light beam, and firmer values are desirable for visual threshold.

There remains for speculation a consideration of the optics of photogenic organs. Many photogenic organs obviously lack focusing devices, and the light which they emit radiates outwards more or less uniformly over some solid angle determined by the morphological configuration of the light organs. Various examples are the unicellular radiolarians and dinoflagellates; luminescent tissues of coelenterates and ctenophores; light organs of Pyrosomas; organs of Pesta (luminous liver tubules) of *Sergestes*; disc-like organs of squid *Abralia* and *Leachia*; luminous tentacles and bulbs of bathypelagic teleosts. From organs of this kind it is reasonable to assume that the light will conform to the inverse square law. In sea water, intensity will decrease in a predictable manner according to distance and transparency of the water.

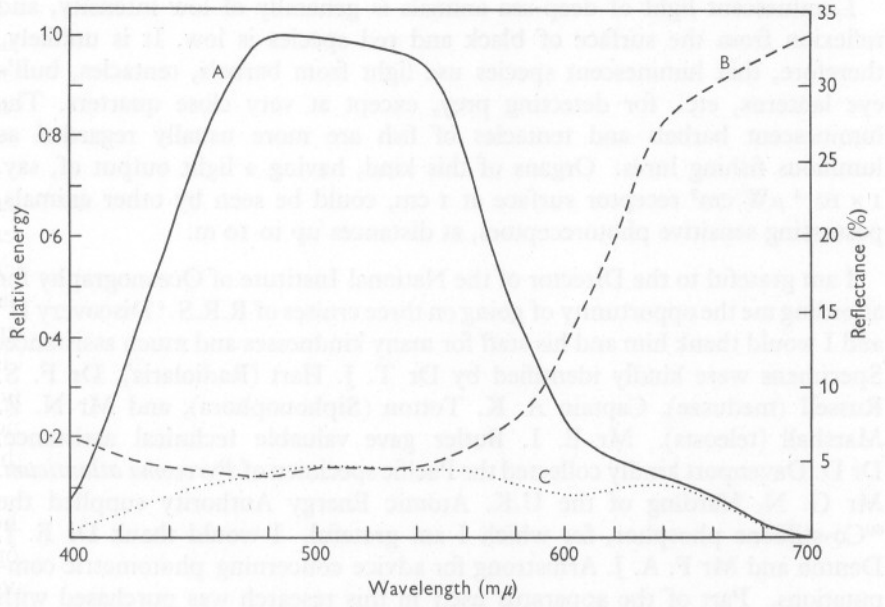
Many other animals possess very complex light organs, containing reflectors and lens systems. Very little is known about the optics of these structures. If the action of the lenses is to produce a parallel beam of light, then intensity would fall off much less rapidly with distance. Trojan (1907) has ventured some conclusions concerning the optic properties of the photophore of the

euphausiid *Nyctiphanes couchi*. He has found that the light is brought to a focal point immediately in front of the light organ; the light, therefore, could radiate forth from that focal point as a point source. In order to get further information about this effect, it would be desirable to make simultaneous measurements at varous distances of the light from organized photophores, containing lenses, if a suitable preparation or preparations could be found.

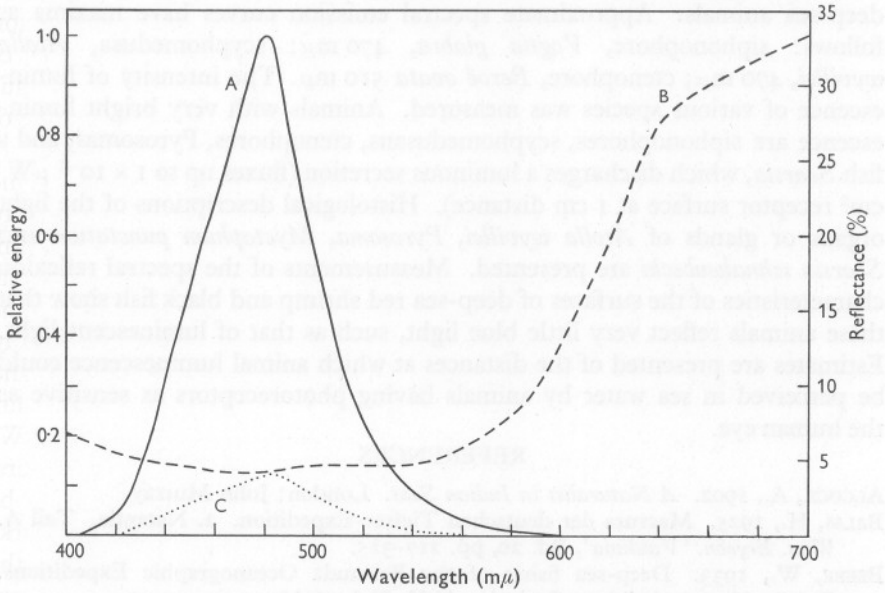
Data have been presented for reflectance of light from some deep-sea animals (Text-figs. 13 and 14, pp. 736 and 737). Reflexion curves for deep-sea fish *Cyclothone* and *Chauliodus* are fairly flat in the visual range (400–700 mμ), so that there is little change in relative reflexion at different wave-lengths (Text-fig. 14). Quite otherwise is the reflexion curve for the deep-sea shrimp *Acanthephyra* (Text-fig. 13). Reflexion from the integument of this animal is minimal in the blue, below 500 mμ, and maximal in the red, above 650 mμ. Oceanic waters are most transparent to blue light, with a maximum around 475 mμ and, owing to differential absorption, this is the only effective light in deeper regions (Text-fig. 18).

The relative spectral energy of light reflected from a surface depends on the reflectance characteristics of that surface, and the relative spectral composition of the incident light. In Text-figs. 18 and 19 are presented curves for relative spectral composition of light in clear oceanic water (from Sverdrup, Johnson & Fleming, 1942), relative spectral composition of *Cypridina* light (from Coblentz & Hughes, 1926), diffuse spectral reflectance of *Acanthephyra multispina*, and product curves (C) of incident light and reflectance. It will be seen that the integument of *Acanthephyra* reflects least light in the blue region of the spectrum, and it is this region that contains most of the energy of daylight and luminescent light in the sea. The colour of *Acanthephyra* thus seems well suited to reducing reflexion, and therefore the animal's chance of being seen.

The following estimates for *Acanthephyra* are presented to illustrate some of the factors involved in computing light reflexion from the surface of animals. Assume a luminescent fish has a light output of 1×10^{-8} μW/cm^2 receptor surface at 1 m distance, and let this light be blue, with maximal emission at 480 mμ. An *Acanthephyra*, 9 cm long, has a surface area, on one side, of approximately 12 cm^2; at 480 mμ let its reflexion be 10%. At 1 m distance, that *Acanthephyra* will receive 1×10^{-8} μW/cm^2 body surface, and reflect back $1{\cdot}2 \times 10^{-8}$ μW. At a distance of 1 m, estimated radiant flux reflected from the surface of *Acanthephyra* will be only about $2{\cdot}5 \times 10^{-13}$ μW/cm^2 receptor surface, well below visual sensitivity of known photoreceptors. In terms of the above energy values, the *Acanthephyra* would have to be within about 20–30 cm of the fish to be seen by the latter. Since the dark-coloured bathypelagic fishes also have very low reflectance throughout the visible spectrum (Text-fig. 14), similar considerations would apply to these animals.



Text-fig. 18. Curves: A, relative spectral composition of daylight transmitted through clear oceanic water, scale for ordinates on left (from Sverdrup, Johnson & Fleming, 1942); B, spectral reflexion curve for *Acanthephyra*; C, product curve of A and B. Scale for B and C on right.



Text-fig. 19. A, relative spectral composition of *Cypridina* light (from Coblentz & Hughes, 1926). B, spectral reflexion curve for *Acanthephyra*; C, product curve of A and B. Scale for A on left; for B and C on right.

Luminescent light of deep-sea animals is generally of low intensity, and reflexion from the surface of black and red species is low. It is unlikely, therefore, that luminescent species use light from barbels, tentacles, bull's eye lanterns, etc., for detecting prey, except at very close quarters. The luminescent barbels and tentacles of fish are more usually regarded as luminous fishing lures. Organs of this kind, having a light output of, say, 1×10^{-4} μW/cm^2 receptor surface at 1 cm, could be seen by other animals, possessing sensitive photoreceptors, at distances up to 10 m.

I am grateful to the Director of the National Institute of Oceanography for affording me the opportunity of going on three cruises of R.R.S. 'Discovery II' and I would thank him and his staff for many kindnesses and much assistance. Specimens were kindly identified by Dr T. J. Hart (Radiolaria), Dr F. S. Russell (medusae), Captain A. K. Totton (Siphonophora), and Mr N. B. Marshall (teleosts). Mr E. I. Butler gave valuable technical assistance. Dr D. Davenport kindly collected the Pacific specimen of *Pyrosoma atlanticum*. Mr G. N. Harding of the U.K. Atomic Energy Authority supplied the ^{60}Co-stilbene phosphor, for which I am grateful. I would thank Dr E. J. Denton and Mr F. A. J. Armstrong for advice concerning photometric computations. Part of the apparatus used in this research was purchased with grants from the Royal Society.

SUMMARY

Miscellaneous observations have been made on the luminescence of pelagic deep-sea animals. Approximate spectral emission curves have maxima as follows: siphonophore, *Vogtia glabra*, 470 mμ; scyphomedusa, *Atolla wyvillei*, 470 mμ; ctenophore, *Beroë ovata* 510 mμ. The intensity of luminescence of various species was measured. Animals with very bright luminescence are siphonophores, scyphomedusans, ctenophores, Pyrosomas, and a fish *Searsia*, which discharges a luminous secretion (fluxes up to 1×10^{-1} μW/cm^2 receptor surface at 1 cm distance). Histological descriptions of the light organs or glands of *Atolla wyvillei*, *Pyrosoma*, *Myctophum punctatum* and *Searsia schnakenbecki* are presented. Measurements of the spectral reflexion characteristics of the surfaces of deep-sea red shrimp and black fish show that these animals reflect very little blue light, such as that of luminescent light. Estimates are presented of the distances at which animal luminescence could be perceived in sea water by animals having photoreceptors as sensitive as the human eye.

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THE BUOYANCY OF BATHYPELAGIC FISHES WITHOUT A GAS-FILLED SWIMBLADDER

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(Plates I and II, and Text-figs. 1–3)

INTRODUCTION

The upper reaches of the deep ocean contain many bathypelagic fishes with a capacious, gas-filled swimbladder. But living within and below this region are also numerous species in which this hydrostatic organ is absent or markedly regressed (Marshall, in preparation). In the neritic province nearly all the fishes that swim freely at the various water levels (and can stay poised at a particular level without undue effort) have a well-developed swimbladder, the capacity of which is about equal to 5% of the body volume (Jones & Marshall, 1953). Having this amount of gas, these fishes are able to keep their weight in water close to the vanishing point. If such a fish were deprived of its swimbladder, it could keep at a constant level only by exerting a downward force equivalent to 5% of its weight in air. The swimbladder thus saves the fish the energy needed for such effort, which is quite appreciable.

The advantage to a fish of being in neutral buoyancy can be illustrated by the following simple calculations. A fish deprived of the gas in its swimbladder would have a reduced weight in water of 5–8% of its weight in air (depending on whether it were a a marine or freshwater fish). To stay at constant level it would have to exert a downward force equal to its reduced weight (and unlike terrestrial animals, pelagic creatures only exert forces on the surrounding medium by making movements). When it is remembered that even an active pelagic fish seldom exerts a force of more than 25–50% of its weight in air for more than a very brief period (Gray, 1953), the force necessary for a fish to maintain its level appears to be considerable.

How considerable an economy the swimbladder allows can be further evaluated by realizing that the drag of the water opposing a fish's movement is proportional to $(\text{velocity})^{\frac{3}{2}}$ for laminar flow and approximately $(\text{velocity})^2$ for turbulent flow (Kermack, 1948; Hill, 1950). Thus for some active pelagic fish a force of 7% of the body weight would enable a fish to *sustain continuously* a horizontal velocity of 43% or 53% (depending on whether the flow is laminar or turbulent) of that velocity which it would have if it exerted *continuously* a force of 25% of its body weight, a force fishes *seldom* exert. (If we take our reference velocity as that given by a fish exerting 50% of its body weight then 7% would give a sustained velocity of 27% or 37% of this velocity). The above calculations were made by E. J. Denton and T. I. Shaw.

The mackerel (*Scomber scombrus*) is one of the few freely swimming fishes from the neritic region without a swimbladder, and it is noticeable that it can only maintain its level in the water by restless and vigorous activity. This unceasing motion is perhaps the price paid for a facility of moving up and down quickly in the top layers of the sea; for to come quickly to the surface from 20 m would increase the volume of a swimbladder threefold, and, apart from the danger of internal damage, the fish would have to exert an upward force equal to about 10% of its weight in order to go down again.[1].

The 5% relation between the swimbladder and body volume is also found in bathypelagic teleosts (Kanwisher & Ebeling, 1957). This might suggest that the species without a swimbladder were faced with the same problems as the mackerel. But many of these fishes have fragile, lightly ossified skeletons, the scales are reduced or absent, and the muscle layers of the trunk and tail are thin. This must lead to some reduction of their weight in water and it has been suggested (Marshall, 1954, 1955) that they are not much heavier than their surroundings. Measurements by one of us (E.J.D) have shown this is certainly true of two fairly common bathypelagic fishes without a swimbladder, *Gonostoma elongatum* (order Isospondyli, suborder Stomiatoidea) and *Xenodermichthys copei* (order Isospondyli, suborder Clupeoidea). Analysis of their chemical composition has revealed how this reduction of specific gravity is achieved. However, in evading, or almost evading, the buoyancy problem, it is the muscles used in propulsion that are particularly reduced. Nevertheless, the proportion of muscle (as indicated by total protein) falls less than does the downward force which has to be exerted to keep the fish in a given horizontal plane. Because of loss of speed, this might, however, seem to be like 'jumping from the frying pan into the fire', but consideration of the biology and environment of the bathypelagic fishes without a swimbladder reveals much of how this problem seems to have been met.

MATERIAL AND METHODS

The buoyancy of the fish

These experiments were made in the Bay of Biscay aboard R.V. 'Sarsia'. The deep-sea fish were caught in an Isaacs-Kidd mid-water trawl, the live fish being put into sea water previously cooled to about 10° C. A piece of cotton was threaded through the lower jaw of a fish and the fish was weighed in air on a 100 g spring balance, and in sea water using a torsion balance of 1 g full-scale deflexion. The torsion balance was on a gimbal table and it proved possible to measure the weight of the fish in sea water to a few milli-

[1] Dr G. Hughes (private communication) has noted that a considerable fraction of a fish's metabolism may be devoted to providing the flow of water across the gills. A fish like a mackerel which uses its forward motion to provide much of this flow may not be at such a disadvantage as simple calculation might suggest.

grams. Great care was taken for the weighing under sea water to have no bubbles of air on or inside the deep-sea fish and both spring balance and torsion balance were frequently checked with known weights. After checking the weight in sea water several times the fish was taken out of sea water, gently dried and placed in a dry honey jar or Kilner jar and stored in a deep-freeze. Before using the fish for chemical analysis the jar and fish were weighed and after removing the fish and drying the jar this was weighed alone. The difference between these two weights gave a check on the accuracy of the weighing of the fish which had been made at sea. At sea the temperature of the sea water used was noted and samples of the sea water were taken in sealed jars. The specific gravities of the samples were measured with a hydrometer on returning to Plymouth.

The common bathypelagic fish *Chauliodus sloanei* has a thick transparent gelatinous envelope around its body. It was thought that this might be less dense than sea water and thus provide some positive buoyancy. Pieces of this material cut away from the fish were, however, found to be heavier than sea water.

Direct measurements were made of the contribution of the swimbladder gases to the buoyancy of the coastal fish *Ctenolabrus rupestris*. Specimens of this fish, freshly killed, were weighed in air and in sea water after opening the fish, puncturing the swimbladder and squeezing out its gas. These measurements showed that such a fish without the gas in its swimbladder would have a weight in sea water of about 5·4% of its weight in air. This weight must in very large part be attributed to the muscles (the largest single tissue component), for isolated pieces of muscle had in sea water about 5% of their weight in air. Experiments on coastal fish of different species showed that the density of muscle varies appreciably; the weight of hake (*Merluccius merluccius*) muscle in sea water was only 3·2% of its weight in air. These experiments suggested that a variation in the proportion of protein might be an important variable in the 'buoyancy balance sheet' of fishes. That this is so was borne out by the determinations of chemical composition described below.

Chemical analysis

The chemical analyses were made with the advice and help of Mr E. I. Butler. Not all fishes were analysed in the same way but the most complete analyses were made in the following way:

The fish were ground with sand and anhydrous calcium sulphate and Soxhlet extracted with 40°–60° petroleum ether. The residue was reground and dried in an oven for several hours when further extracts were made until no further material could be extracted. The residue, insoluble in petroleum ether, was extracted in a Soxhlet apparatus with 96% alcohol to constant weight of extract. The nitrogen in the final residue was estimated, and the alcohol extract refluxed with 40°–60° petroleum ether and filtered. The filtrate contained only that fraction of the animal's fat which was extractable by

alcohol but not petroleum ether and this was estimated by drying the filtrate to constant weight. The alcohol-soluble ether-insoluble nitrogen was estimated using the method of Kjeldahl.

As a check on this method the procedure was varied. On occasions total nitrogen was estimated using whole fish, whilst on other occasions the fat was extracted after grinding with sand fish which had been oven dried (105° C) to constant weight. The various methods used gave results which were in good agreement with one another. The dry weights given in this paper are those of fish cut into very small pieces and dried in an oven at 105° C to constant weight.

RESULTS

The buoyancy of Gonostoma *and* Xenodermichthys

All the fishes used were caught alive and in very good condition. The values for the (weight in sea water/weight in air) × 100 were for, 6 *Gonostoma* 0·54, 0·68, 0·90, 0·34, 0·40, 0·90 (average 0·63) and for 6 *Xenodermichthys* 1·4, 1·1, 1·4, 1·1, 1·2, 1·3 (average 1·25).

The sea water used for these buoyancy measurements was found to have a salinity close to that in which the fish live, i.e. about 35·5 g of salt in 1000 g of sea water. These fish are usually found down to 1000 m and, in the water of the Atlantic from which they were taken, there is little change in salinity between the surface and 1000 m (Cooper, 1952). The maximum error in the above figure for (weight in sea water/weight in air) which might be attributed to differences in salinity was 0·05 and this is disregarded.

Radiographs

The radiographs (Pls. I and II) show that the skeletons of *Chauliodus*, *Gonostoma* and *Xenodermichthys* are very poorly ossified in comparison with specimens of coastal fish *Gadus minutus* of comparable weight. The deep sea myctophid *Diaphus rafinesquei* which *has* a swimbladder is seen to have a skeleton as well ossified as that of a *Ctenolabrus rupestris* of about the same weight. Pl. II shows the remarkable difference in ossification between *Gonostoma elongatum* and *Gonostoma denudatum* both bathypelagic fish, the former without, and the latter with, a gas-filled swimbladder.

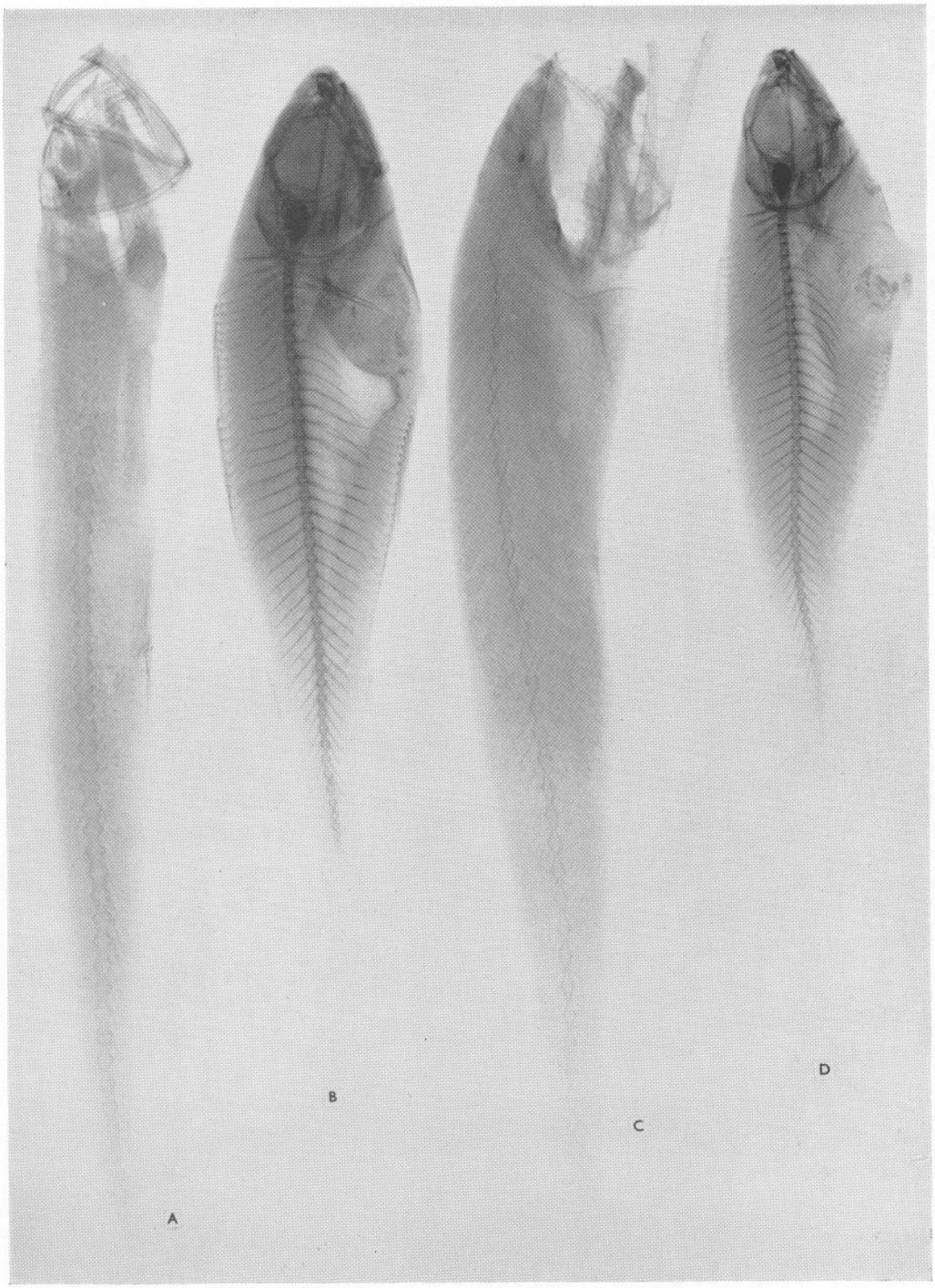
EXPLANATION OF PLATES

PLATE I

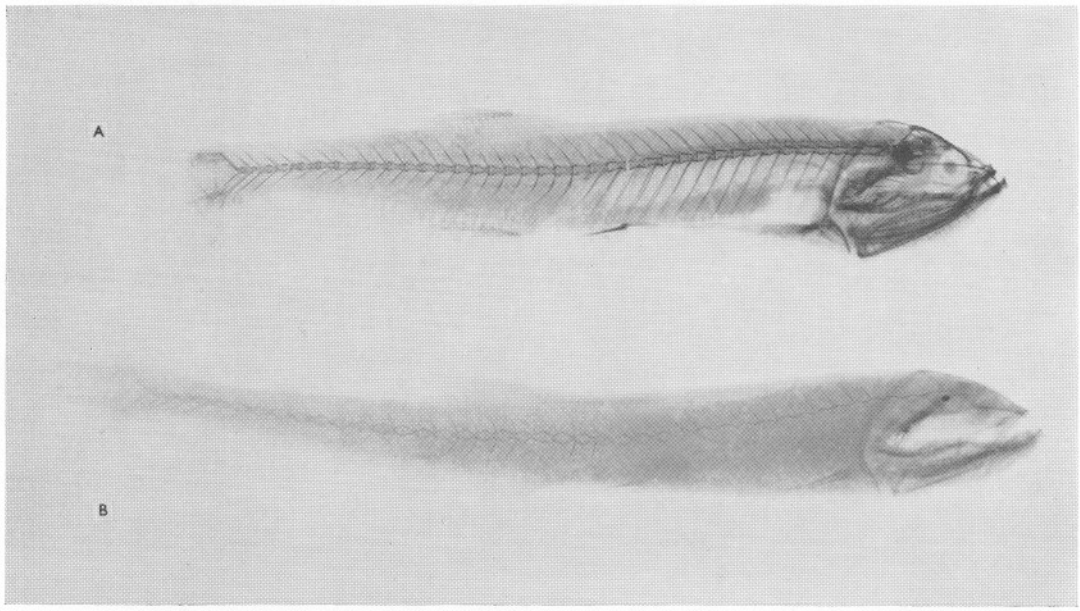
Radiographs comparing the degree of ossification of (A) *Chauliodus sloanei*, (B) *Gadus minutus*, (C) *Gonostoma elongatum*, and (D) *Gadus minutus*. Of the two specimens of *G. minutus* the second (D) is much smaller than either of the bathypelagic fish. The swimbladders of *G. minutus* appear as light areas in the body. Magnification × ⅔.

PLATE II

Radiographs (above) showing the difference in ossification between (A) *Gonostoma bathyphilum* and (B) *G. elongatum*; and (below) comparing the degree of ossification of (C) *Ctenolabrus rupestris*, (D) *Diaphus rafinesquei*, (E) *Xenodermichthys copei*, and (F) *Gadus minutus*. Magnification × ⅔.



(*Facing p.* 756)


A
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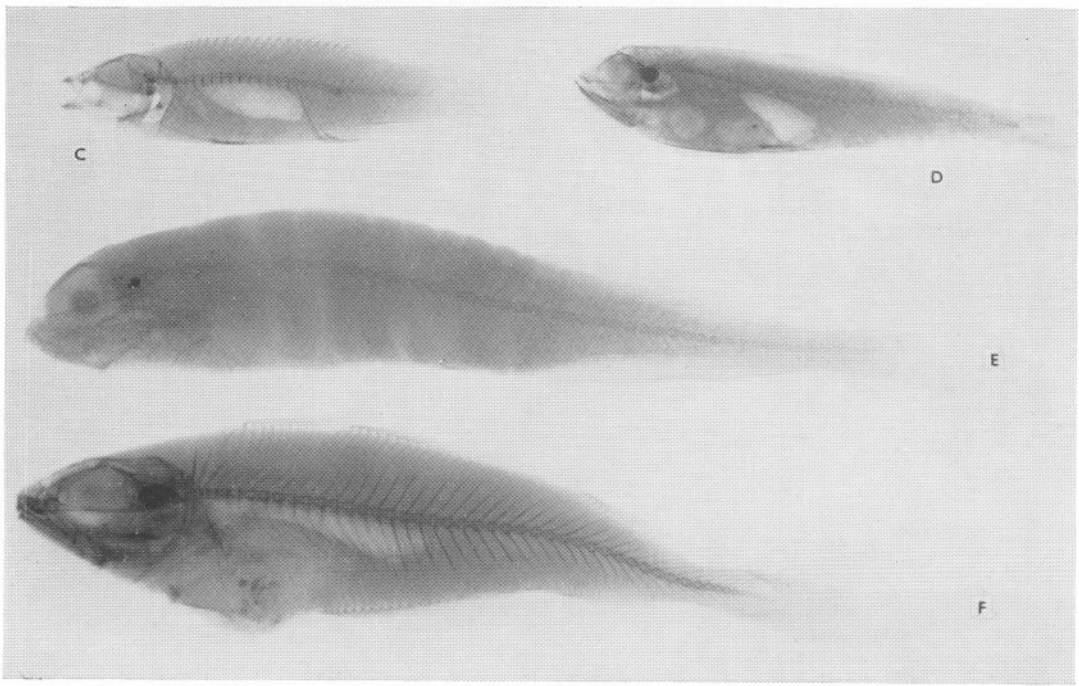
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The otoliths of the bathypelagic fish without swimbladders are very small when compared with those of the fish with swimbladders. Particularly striking is the contrast between the large otoliths of the small fish *Diaphus rafinesquei* with the tiny otoliths of *Chauliodus sloanei*.

Chemical analyses

The principal results of the chemical analyses are given in Table I. Components are given as percentage of wet weight. The protein is taken as being 6·025 × the total nitrogen (see Love, 1957).

TABLE 1. CHEMICAL ANALYSES

Fish	Fat extractable in 40°–60° petroleum ether	Total N_2	Protein	Dry weight	$\frac{\text{Wt. in sea water}}{\text{Wt. in air}} \times 100$
Gonostoma elongatum	2·6	—	—	—	0·68
,,	5·3	—	—	—	—
,, *	3·4	0·71	4·3	12·6	0·34, 0·4
,,	—	1·01	6·0	—	0·54
,,	—	0·87	5·2	—	—
Xenodermichthys copei	0·51	—	—	—	—
,,	0·55	—	—	—	—
,,	—	1·2	7·2	—	—
,,	—	—	—	9·8	—
,, *	—	1·2	7·2	11	1·1, 1·2
Ctenolabrus rupestris	—	2·76	16·6	—	—
,,	—	—	—	28	—
,,	—	—	—	26	—
,,	0·5	—	—	—	—
Labrus bergylta†	—	2·72	16·4	—	—

* Two fish taken together. † These fish have a gas-filled swimbladder.

Part of the lipid material in fish is bound in such a way as not to be extractable in petroleum ether. This is a small fraction of the total lipid in fish which have a good deal of fat but an important fraction when there is little fat (Lovern, 1955). After extracting with petroleum ether some fish were therefore further extracted with 96% alcohol to constant weight of extract. This alcohol was shaken with petroleum ether and the residue from the ether, after evaporation, was taken as the ether inextractable fat. Part of the total nitrogen of the fishes was non-protein nitrogen and this was estimated on the alcohol extract after shaking it with petroleum ether. For one *Gonostoma* the extra fat corresponded to 0·5% of the wet weight and for two *Gonostoma* the non-protein nitrogen to 0·05 and 0·04% of the wet weight. For *Xenodermichthys* the extra fat corresponded to 0·7% of the wet weight and the

non-protein nitrogen to 0·04% of the wet weight. These are figures which would give only very small corrections and they are not taken into account in the Discussion below.

DISCUSSION

Buoyancy properties

The buoyancy measurements were made at around 10° C which is close to the normal environmental temperature for these fishes. They were left for some time in sea water at this temperature before the measurements were made.

The measurements were made in the laboratory on R.V. 'Sarsia' with the fish under sea water at atmospheric pressure, but the fish are often caught at depths around 500 m where they are subject to pressures of around 50 atmospheres. This change in pressure can, however, make very little difference to the buoyancy of the fish, for the change in volume of water when the pressure is raised from 1 to 50 atmospheres is only one of about 0·2% and the volume of the fish will change in much the same way as does the sea water, leaving a residual change in buoyancy which is only a small fraction of 0·2%. We can therefore accept the surprising fact that *Gonostoma* is often within $\frac{1}{2}$% and *Xenodermichthys* within 1·2% of neutral buoyancy despite the fact that neither fish has a gas-filled swimbladder.

The chemical analyses show quite clearly how this is achieved. These are extremely watery fishes with poorly ossified skeletons. The dry weight of *Gonostoma* and *Xenodermichthys* are only 12·5 and 10% respectively of their weights, whereas the *Ctenolabrus rupestris*, used as a control, had a dry weight of about 28% of its wet weight. The fat content of the deep-sea fishes is not particularly high, averaging about 3%, but the protein content of about 5% of their dry weight is very low indeed when compared with the corresponding 16% for the typical coastal fishes, *Ctenolabrus rupestris* and *Labrus bergylta*.

Most of the data in the literature is for edible portions of fish (see Vinogradov, 1953, pp. 463–566). Shewan (1951) gives total nitrogen figures varying from 2·42 to 3·78% for skeletal muscles of many teleosts. These values may be compared with the 2·76–2·74 given here for whole wrasse used for control experiments. The protein content of the principal organs of higher vertebrates is shown in the *Handbook of Biological Data* (1956) as varying from about 10% for brain and spinal cord through about 20% for skeletal muscle to 30% for skin.

Marine fishes normally derive a considerable degree of buoyancy from the fact that their body fluids are considerably more dilute than sea water. The figures given by Krogh (1939) for the extracellular fluids of marine teleosts suggest that these have an approximate osmotic pressure of about 40% that of sea water. The intracellular fluids will be in osmotic equilibrium with the extracellular fluids, although the components will be different. The principal

intracellular cation is probably potassium rather than sodium (this in itself will affect the density little), and most of the anions will be organic compounds such as the organic phosphates of muscle and the haemoglobin of red blood cells whose contribution to density has to some extent been included in the organic analysis. The intracellular concentration of chloride will

TABLE 2. BALANCE SHEET FOR *GONOSTOMA ELONGATUM*

Component	% wet weight	Specific gravity	Weight in sea water/100 g of fish
Fat	3·7	0·91*	−0·5
Protein	5·0	1·33†	+1·1
Body fluids (water + dissolved salts)	87·6	1·013	−1·2
Other components including bone	3·2‡		+1·1‡

Buoyancy. These fish had no gas-filled swimbladder and their average weight in sea water was approximately +0·5 % of their weight in air. (Wet weight)

* *Handbook of Biological Data* (1956).
† Höber, (1954). Specific gravity taken as the reciprocal of the partial specific volume.
‡ These values are given by difference.

TABLE 3. BALANCE SHEET FOR *CTENOLABRUS RUPESTRIS*

Component	% wet weight	Weight in sea water/100 g of fish
Fat	0·5	−0·1
Protein	16·6	+3·8
Body fluids	73·3	−0·9
Other components including bone	9·2*	+2·6*

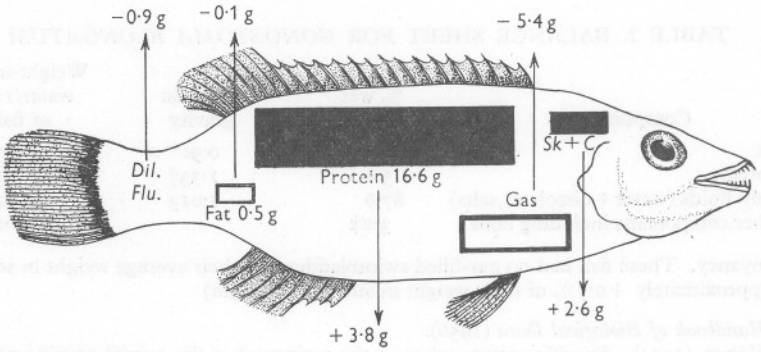
Buoyancy. This fish without its swimbladder has a weight in sea water of +5·4 % of its weight in air

* These values are given by difference.

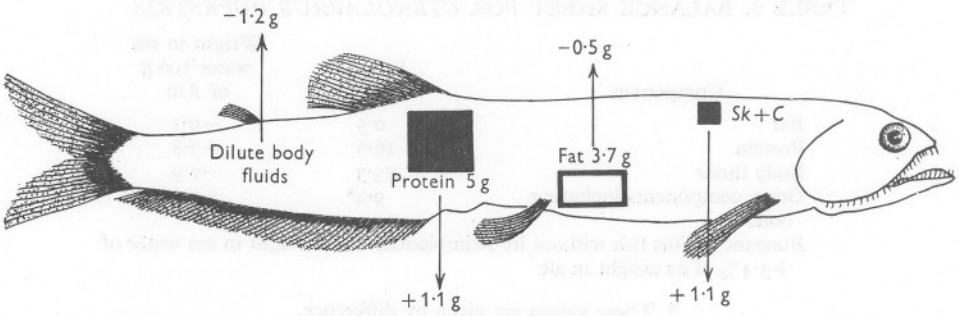
almost certainly be very much lower than the extracellular concentration. We will, however, in the absence of good analyses, make the assumption that both the deep-sea fish and the wrasse have body fluids whose density lies half way between that of distilled water and sea water. [Preliminary analyses indicate that this cannot (in terms of density) be very seriously in error.] It is now possible to draw up balance sheets to explain the buoyancy properties of a deep-sea fish and a wrasse (Text-fig. 1, Tables 2 and 3). The negative weights imply that the component has a positive buoyancy in sea water.

Some idea of the contribution of the mineral components of bone is given by ashing the fish. Ashings in a platinum crucible of whole deep-sea fish (*Xenodermichthys copei*) gave for a high temperature (around 1000° C) an

ash of 1·2% and for a low temperature (around 450° C) an ash of 1·9%. The corresponding figures for ash from wrasse (*Ctenolabrus rupestris*) were both 4·5%. The ash from wrasse contains large recognizable fragments; skull, vertebrae, etc., whilst that of the deep-sea fish is very much less in amount and much more powdery (Text-fig. 2). Some of the ash is sodium, potassium



Ctenolabrus rupestris



Gonostoma elongatum

Text-fig. 1. Diagram of the 'buoyancy balance sheet' for a bathypelagic fish *Gonostoma elongatum* without a swimbladder (below) and a coastal fish *Ctenolabrus rupestris* with a swimbladder (above). Positive values are given for those components of the fish which are heavier than the sea water which they displace and thus tend to 'sink' the fish, whilst negative values are given for those components which displace more sea water than their own weight and thus tend to 'float' the fish. Weights given per 100 g of fish. *Dil. Flu.*, dilute body fluids; *Sk+C*, skeleton and other components.

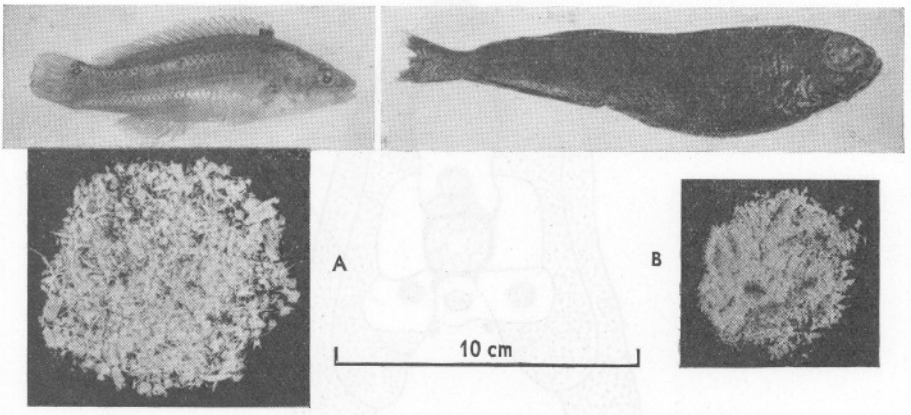
and chloride. Estimates made of these components on water extracts from the ashes indicate that the remaining mineral components account for 1·2% and 0·7% of the two deep-sea fish ashed. The densities of salts found in bone, e.g. apatite, (Harrow, 1954) are close to 3 (*International Critical Tables*, 1928) so that the contribution of this material to the buoyancy of the

fish will be about +0·6 g/100 g of fish for *Xenodermichthys*, which is a value rather smaller than that given in the above table on *Gonostoma* for 'other components including bone'.

General biological considerations

While these findings are striking in themselves, they may be seen in better perspective against a more general biological background.

Bathypelagic fishes without a gas-filled swimbladder are quite diverse. The main groups in the order Isospondyli are Melanostomiatidae, Stomiatidae,



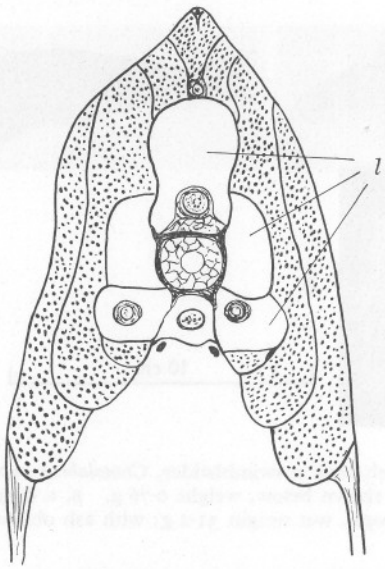
Text-fig. 2. A, a coastal fish with a swimbladder, *Ctenolabrus rupestris*, wet weight 16·7 g; with ash obtained from it shown below, weight 0·76 g. B, a deep-sea fish without swimbladder, *Xenodermichthys copei*, wet weight 31·2 g; with ash obtained from it shown below, weight 0·33 g.

Chauliodontidae, Idiacanthidae, Malacosteidae (stomiatoids), Alepocephalidae (clupeoids) and Bathylogidae (salmonoids). Of the order Iniomi, the entire suborder Alepisauroidea consists of fishes without any known trace of a gas-filled swimbladder at any stage of their life history (Marshall, 1955), and the same is true of the ceratioid angler-fishes (Bertelsen, 1951). Finally, there are the fishes of the small orders, Giganturoidea, Lyomeri, Cetunculi and Miripinnati, the last having a functional gas-filled swimbladder during the larval phase (Bertelsen & Marshall, 1956). These groups and a few not mentioned, make up nearly half of the bathypelagic fish fauna.

In these fishes the nature and extent of the tissues appear to be very similar to the two species we have analysed in detail. The stomiatoid species certainly have lightly ossified skeletons (the scales are absent or poorly developed) and a correspondingly reduced musculature. Concerning the melanostomiatids and *Idiacanthus*, Beebe & Crane (1939) remark that '. . . as usual in deep-sea fish, the jaws are the only really strongly ossified parts of the body, the gill

arches usually come next, then the tip of the caudal penduncle, while the skull proper, the rest of the vertebral column and the supports of the vertical fins are ossified very late, and then usually weakly.'

These observations also apply to the alepisauroid fishes (Marshall, 1955) and particularly to the Lyomeri, which have a persistent notochord and a very reduced skeleton (Tchernavin, 1947). The weak lateral muscles in one species (*Eurypharynx pelecanoides*) is well shown in transverse sections figured by Nusbaum-Hilarowicz (1923). The vertebral column is not immediately surrounded by the myotomes, but by extensive fluid-filled cavities, which



Text-fig. 3. Transverse section through the fore-part of the trunk of the gulper-eel, *Eurypharynx pelecanoides*, showing the extent of the muscle (dotted) and the lymphatic spaces (*l*). (After Nusbaum-Hilarowicz, 1923).

appear to be lymphatic in nature (Text-fig. 3). The ceratioid angler-fishes also have weakly developed lateral muscles and lightly ossified skeleton (Bertelsen, 1951).

But, as we have already seen, such weakness of the skeletal and muscular systems is not true of bathypelagic fishes with capacious gas-filled swim-bladders (for instance, the Myctophidae). Here we need only draw attention to the radiograph (Pl. II) of *Gonostoma elongatum* and *G. denudatum*. Earlier reference has been made to this (Marshall, 1954), but the plate gives more striking proof than words of the difference in ossification between these two related deep-sea fishes. The skeleton of *G. denudatum* (the outline of the swim-bladder can also be seen) stands out sharply beside that of *G. elongatum*, in which the swimbladder is regressed and invested with fat. (It should be

stressed that both fish are of adult size and that this difference between them can also be readily appreciated when they are handled).

While the bathypelagic fishes with a well developed, gas-filled swimbladder tend to be concentrated at depths above 1000 m, those lacking this organ are found at all mid-water levels known to contain fish. Of the groups listed above, most of the stomiatoids, bathylagids, alepisauroids, giganturoids and Miripinnati tend to occur above the 1000 m level, while the Lyomeri and ceratioid angler-fishes are mostly fished below this depth (for a review of the vertical distribution and references, see Marshall, (1954)). The latter seems to be also true of many alepocephalids,[1] but not of such forms as *Searsia* (Grey, 1956).

Turning now to the physical nature of their environment, most species of bathypelagic fishes are found in the tropical and temperate regions of the ocean between depths of about 250 m down to at least 3000 m. Owing to the rapid fall of temperature below the thermocline there is a corresponding increase in viscosity (between the above levels the laminar viscosity will be increased by a maximum factor of about 1·66). At the cooler, lower levels, a fish will thus gain more support from the surrounding water. If heavier than water it will sink more slowly, but it will find movements more difficult to make. At all events, it is interesting that the ceratioid angler-fishes, which appear to be little more than floating traps, make up most of the fish fauna at these lower levels.

Except for the Cetunculi and Miripinnati, which take small prey, particularly copepods (Bertelsen & Marshall, 1956), most of the bathypelagic fishes without a swimbladder consume a wide range of food organisms. Considering only their larger prey, the stomiatioid groups, the alepisauroids (excluding the paralepidids), the giganturoids, the Lyomeri and the ceratioid angler fishes are able to capture and master relatively large fishes, which may even be longer than themselves.

It is thus perfectly clear that these deep-sea predators are not handicapped by their relatively feeble muscular system. And, as we have seen, the main structures for holding and swallowing the prey, the jaws and gill arches, are supported by the most firmly ossified parts of the skeleton. Sections through the lower jaws of *Gonostoma elongatum* and *Diaphus rafinesquei* (a lantern fish with a capacious swimbladder) showed that the degree of ossification was much the same, but that the bone was thinner in the former. (This fish has a standard length of 205 mm and a lower jaw length of 36 mm, the bone of the latter having a maximum thickness of 0·03 mm. The corresponding measurements in the lantern fish are, 74, 16 and 0·12 mm). However, just beneath the tooth-bearing surface of the lower jaw and continuing to the angle, the bone in the gonostomatid has a honeycomb-like structure, which must give extra strength along the biting edge.

[1] Judging from trawl catches, a number of species appear to live close to the deep sea floor.

But while the jaws and associated structures have a relatively robust framework, the fish (or squid) has first to be caught. Observations on the capture of large prey have yet to be made, although both Mackintosh and Gunther (Clarke, 1950) watched a silvery stomiatoid fish attacking a swarm of krill at the surface. Gunther wrote: 'In its manner of lurking and snapping prey it resembled the freshwater pike.' Beebe & Crane (1939) observed that melanostomiatid fishes brought up alive '...swam about and snapped with all the accuracy of balance and swiftness of surface fish'.

However, fishes with thin lateral myotomes are hardly fitted to be tireless hunters, and this is borne out by their body forms and fin patterns. Like the pike, or better still the garfishes (Belonidae), the melanostomiatids, stomiatids and malacosteids have slim, elongated bodies and the dorsal and anal fins are opposed and set well back, close to the caudal fin. As in the species that Gunther saw, they are fishes which hover and dart after their prey. The combined dorsal, anal and caudal fins must form a powerful swimming organ (Beebe & Crane, 1939). Even more important, this fin arrangement will not only enable the fish to get away quickly from a hovering position but also confer stability during the dart (see Harris, 1952).

Dr S. Smith has noted from the radiographs that the myotomes are of relatively constant width along the length of the fish. We may compare the rapidly diminishing width of myotome on moving close to the tail of *Gadus minutus* with the almost constant width of myotome of the deep sea fish. The deep sea fish have not therefore flexible tails adapted for delicate movements.

The alepisauroids also tend to have an elongated pike-like form (the paralepidids are known as barracudinas), but only the anal fin has a posterior setting. One species, *Paralepis rissoi*, was observed from a bathyscaphe by Furnestin (1955), who describes it as hovering in a vertical position with the head or tail uppermost, apparently keeping its level by the flickering of the small dorsal fin. Then, from this position, the fish would suddenly 'jack-knife' and dart off. At least some of the other paralepidids may be expected to behave in a similar way, while a hovering-darting habit is likely to be common to all alepisauroids.[1]

The ceratioid angler-fishes achieve even greater economy of effort by luring their prey to within striking distance (Bertelsen, 1951). They are clearly floating traps *par excellence*. Brauer (1908) thought that the luminous chin barbels of stomiatoid fishes might also be used as lures, while in *Chauliodus* the long second ray of the dorsal fin, which is tipped with luminous tissue, also appears to be an angling device (Tchernavin, 1953). Some of the stomiatoids even have light organs within the mouth. It is also conceivable that the spongy luminous tissue on the tail of the gulper-eel, *Saccopharynx*, may also act as a lure.

[1] The scopelarchids and evermannellids have upwardly directed, tubular eyes and thus might be expected to adopt a horizontal position when hovering.

Lastly, it should be emphasized that these fishes live in the quieter parts of the ocean under the thermocline, which has an average depth of about 75 m. Above the thermocline the currents are relatively fast and wind-driven; below this level the (density) currents are more sluggish and the water is much less turbulent. In these deeper reaches a fish with relatively reduced propulsive powers can use these to greater effect (during a sudden dart) than under more boisterous conditions.

To summarize, bathypelagic fishes without a swimbladder often radically reduce their weight in water by developing lightly ossified skeletons, which are associated with reduced muscular systems, particularly along the trunk and tail.[1] In spite of this many of them are able to capture and swallow large prey. However we must add that this tendency is not invariable among such predacious fishes. Certain of the Astronesthidae and *Chiasmodon* (the great swallower) have well developed swimbladders (together with firm skeletons and fairly thick lateral myotomes). A closer comparison between these bathypelagic fishes and those without a swimbaldder would clearly be interesting.

We should like to thank Mr G. Parish for advice and help with the radiography, and Captain C. A. Hoodless and the crew of R.V. 'Sarsia' for their co-operation. We are grateful to Mr R. G. Maddock for excellent technical assistance.

SUMMARY

Gonostoma elongatum is often within 0·5%, and *Xenodermichthys copei* within 1·2%, of neutral buoyancy despite the fact that neither of these fish has a gas-filled swimbladder.

The dry weights of *Gonostoma elongatum* and *Xenodermichthys copei* are only about 12·6 and 10% of their wet weights compared with 28% for a typical coastal marine fish *Ctenolabrus rupestris*.

The fat content of *Gonostoma elongatum* and *Xenodermichthys copei* is not particularly high, averaging about 3% of their wet weight, but their protein content which is only about 4–7% of their wet weight is very low indeed when compared with the corresponding 16% for a typical coastal marine fish.

Radiographs of *Gonostoma elongatum*, *Xenodermichthys copei* and *Chauliodus sloanei* show that their skeletons are poorly ossified when compared with that of *Gadus minutus* a typical coastal marine fish of the same size, whereas the skeleton of *Diaphus rafinesquii* is ossified as well as that of *Ctenolabrus rupestris* a coastal marine fish of similar size. The skeleton of *Gonostoma*

[1] It is difficult to imagine a much weaker skeleton without much weaker muscles for, as A. V. Hill (1950) writes: 'Athletic animals in fact, have rather a small factor of safety...if a man's muscles could be altered without altering his general design, so as to allow him to run 25% faster or jump 50% higher, athletics would become a highly dangerous pastime; pulled tendons, torn muscles, even damaged bones, would be so frequent as to make it prohibitive.'

denudatum, a bathypelagic fish with a swimbladder, is shown to be very well ossified in contrast with that of the related species *Gonostoma elongatum*.

The ash of *Xenodermichthys* was found to be about 1·5% of the wet body weight, whilst that of *Ctenolabrus rupestris* was about 4·5%.

The 'design' of these fish in relation to the life they lead is discussed. The muscular system is particularly reduced along the trunk and tail; whilst the jaws and gill arches, the main structures for holding and swallowing their prey, are supported by the most firmly ossified parts of the skeleton. These fish are almost certainly not tireless hunters, but rely on quick darts, often using luminous lures to attract their prey. Many of them could be simply described as floating traps.

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OBSERVATIONS ON THE LITTORAL ALGAE OF THE ISLE OF WIGHT

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(Text-figs. 1–4)

As a result of the geological formation of the Isle of Wight there is a great variety in the type of shore. Although much of the coastline is unsuitable for the establishment of algal communities there are some parts where a few species can exist, and others where full zonation is achieved. It therefore seemed worth making some study of the algal distribution. Towards this end a general survey was made of the south coast of the island in April 1955, with more detailed studies of the places of interest by means of transects in April and July 1955.

Previous observations on the algal flora include a list of records given by Morey (1909), and additions to it made by Delf & Grubb (1923) and Norkett (1947). In the present investigation the nomenclature used is that given in the Check Lists of Parke (1953) and of Hendey (1954). The observations presented are limited to the most common algae.

The behaviour of the tide around the Isle of Wight is unusual. In the English Channel the shallow water produces a quarter-diurnal harmonic curve superimposed on the semi-diurnal. From Swanage to the Nab Tower the phases are in a relationship such that a double or prolonged high water is produced. In the Isle of Wight the effect is strongest in the west, where also the tidal range is lowest. At Freshwater there is a distinct double high water at springs but a single prolonged one at neaps. In the east, at Bembridge, the effect is hardly apparent, high water at springs being only slightly prolonged. As low water is always about 6 h after the first high water in these areas, it follows that the ebb, once it has begun, is faster than the flood.

GEOLOGICAL STRUCTURE

The main geological regions of the Isle of Wight are shown in Fig. 1. The southern half of the island is composed of Cretaceous beds affected by two anticlines which run roughly east and west and overlap west of the centre. The uppermost beds, which are of Chalk, rise steeply as a ridge across the centre of the island. The Chalk thus extends to the coast at the Needles and at Culver Cliff. On the south-west coast the Upper, Middle and Lower Chalk are followed south-eastwards by Upper Greensand, Gault, Lower Greensand

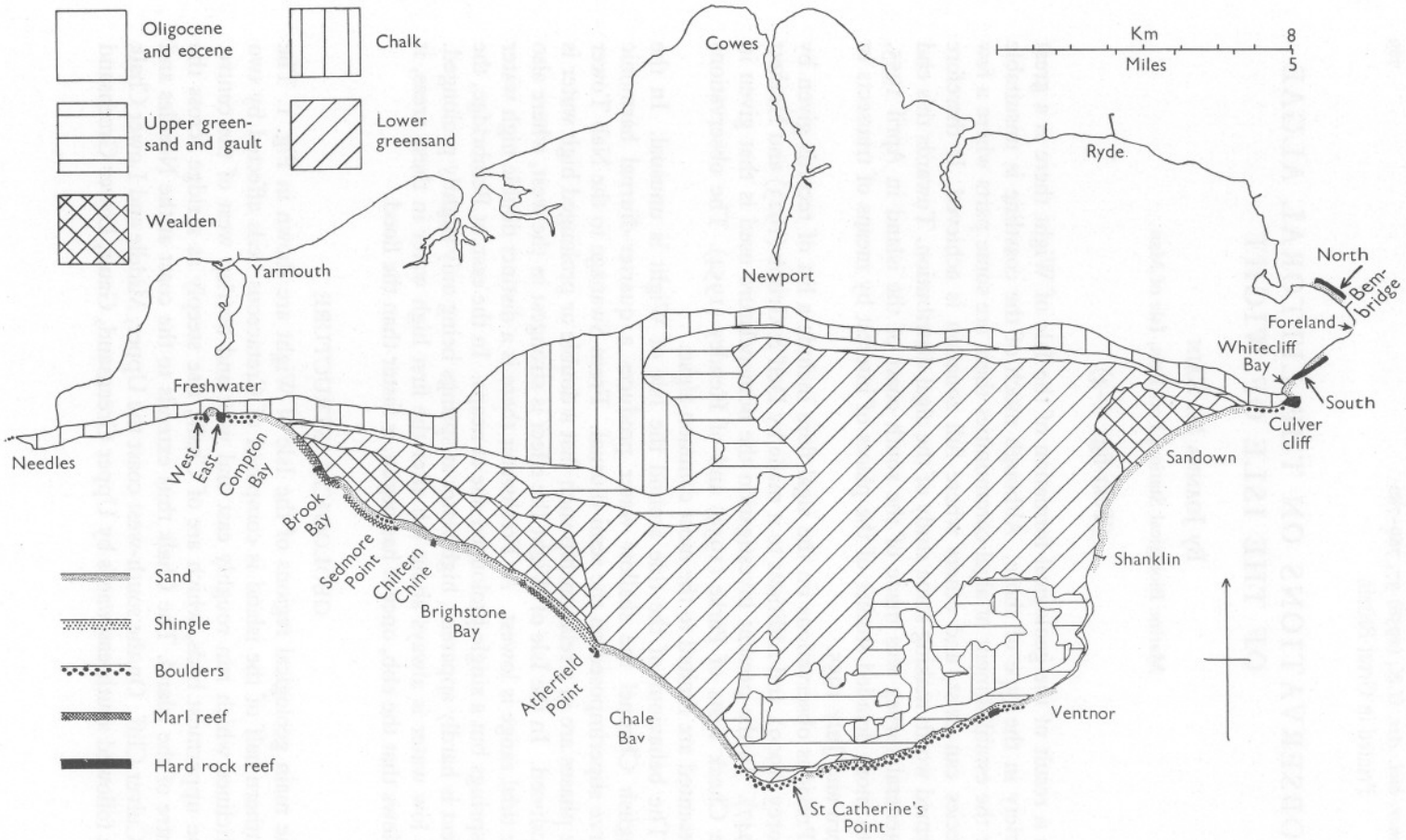

Fig. 1. Map of the Isle of Wight showing the geological structure (taken mainly from Chatwin, 1948) and the nature of the shore along the south coast. The arrows indicate the positions of transects.

and Wealden, the lowest beds being exposed at about Sedmore Point. The series then ascends to St Catherine's Point. The south-east coast shows a similar sequence passing north-eastwards, the lowest beds being exposed in Sandown Bay. The southern limb of the anticline has a gentle slope, and where the Chalk reappears inland of St Catherine's Point the beds are almost horizontal. The soft underlying Gault has resulted in large sections of these Downs slipping down.

GENERAL SURVEY

A general survey of the type of shore and the distribution of the principal algae was made by walking along the shore and noting the substrata and the species present. Only the southern coast was studied. The northern shores are mostly of mud or sand, with some boulders in places.

From the Needles to Freshwater the cliffs of hard Upper Chalk drop almost sheer down to the sea. On either side of Freshwater Bay there are hard Chalk reefs which support fairly rich algal communities. These were studied with the use of transects (p. 775). The Middle and Lower Chalk cliffs of Compton Bay have boulders at their bases. Below the narrow belts of Upper Greensand, Gault and Lower Greensand the shore is sand or shingle. From the centre of Compton Bay to Sedmore Point most of the shore is occupied by a grey and purple Wealden Marl reef. This rock is smooth and very soft, but a number of algae are able to colonize it. The most common are *Polysiphonia nigrescens*, *Corallina officinalis* and *Cladostephus spongiosus*. *Cladophora*, *Fucus vesiculosus*, *F. serratus*, *Ceramium rubrum*, *Ulva lactuca*, *Rhodochorton* and some diatoms are also present. From Sedmore Point to the centre of Brighstone Bay is mostly sand except for a hard reef opposite Chiltern Chine. This supports a flora similar to that on the Marl, with the exception of *Polysiphonia nigrescens*, but with the addition of *Lomentaria articulata*, *Chondrus crispus*, *Rhodymenia palmata*, *Laurencia pinnatifida*, *Furcellaria fastigiata* and *Ptilota plumosa*. The Marl reefs of Brighstone Bay are for the most part covered with sand and support no algae. The hard reef off Atherfield Point was not accessible when it was visited but clearly supported fucoids. Chale Bay has a beach of fine sand and shingle.

Between St Catherine's Point and Ventnor the shore is strewn with boulders, sometimes forming a complete covering and sometimes mainly in the bays, in patches alternating with sand or shingle. There is usually a band of shingle at the top of the beach just below the cliff. The boulders support fairly extensive algal communities. The more detailed study of St Catherine's Point was of a fairly representative section (p. 775).

The shore between Ventnor and Shanklin was not visited. From there to the beginning of Culver Cliff, where the Chalk reappears on the shore, is sandy. Boulders lie at the base of the cliff and a Chalk reef extends from it. This supports a fairly extensive flora. Just north of the sand of Whitecliff Bay

the ledges of Bembridge Limestone around the Foreland begin. These are more extensive on the south side than the north, where there is a greater proportion of sand. Both places were studied in more detail (p. 776).

Of the 25 miles of coast visited, 9 miles have hard reefs or boulders and 3 miles have Marl reefs. The rest of the coast is sandy.

SHORE TRANSECTS

Five shores were selected for more detailed study by means of transects: the Chalk boulders west of and the Chalk reef east of Freshwater Bay, the boulders below St Catherine's Point lighthouse, some limestone reefs north of Whitecliff Bay ('Bembridge South') and limestone reefs at Bembridge Point ('Bembridge North'). These are marked in Fig. 1.

Levelling apparatus

A simple form of levelling apparatus was developed for the use of the single-handed worker. As it is very cheap to assemble it will be described in some detail.

The sighting level is shown in Fig. 2A–D. It consists of a carpenter's level with wooden sides added to support a partly silvered piece of glass (to reflect the bubble) in the centre, a fine wire horizontally across one end and a brass plate, with a pinhole, across the other end. In order to adjust the sighting line between the hole and the wire so that it is parallel to the level itself, the brass plate is moved up or down until readings of height taken in opposite directions with the instrument are identical.

It is usual with this type of instrument to have it at a fixed height and to read the height on a staff in the position to be measured. But as this involves another worker holding the staff the proceeding has been reversed: the staff is fixed in one position with a clear triangular marker, and the heights of the positions to be measured are determined by sliding the instrument up or down a graduated movable staff until it is level with the marker and then reading its height on the movable staff.

The fixed staff is shown in Fig. 2E, F. It is constructed mainly of 0·6 m lengths of 1·2 × 2 cm wood bolted together in such a way that it can be folded to a length of 0·7 m. The staff is 2·1 m high and is marked at 0·5 m intervals from the ground. The pointer can be attached at any of the four marks by means of a bulldog clip. The staff is held upright by two legs, each a metre long and with a hinge at the top end which can be bolted through any of a number of alternative holes. It can thus be set up on uneven ground. The bottom ends of the legs and the staff itself have strap hinges with flat pieces of leather attached. Stones can be placed on these so that the whole is stable and rigid. The movable staff is shown in Fig. 2G, H. It is marked in centimetres.

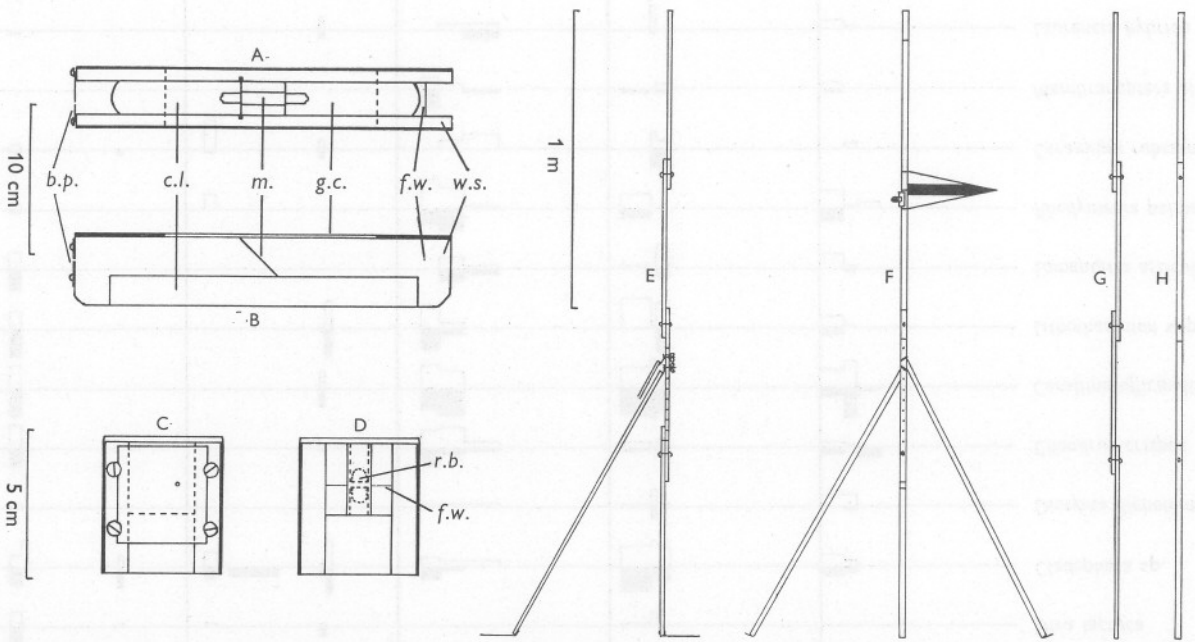

Fig. 2. Diagrams of the sighting level (A–D), fixed staff (E and F) and movable staff (G and H). A, top view of level; B, side view; C, end view with brass plate in place; D, end view with plate removed; E, side view of fixed staff; F, front view; G, side view of movable staff; H, front view. *b.p.*, brass plate; *c.l.*, carpenter's level; *f.w.*, fine wire; *g.c.*, glass cover; *m*, mirror; *r.b.*, reflexion of bubble; *w.s.* wooden sides.

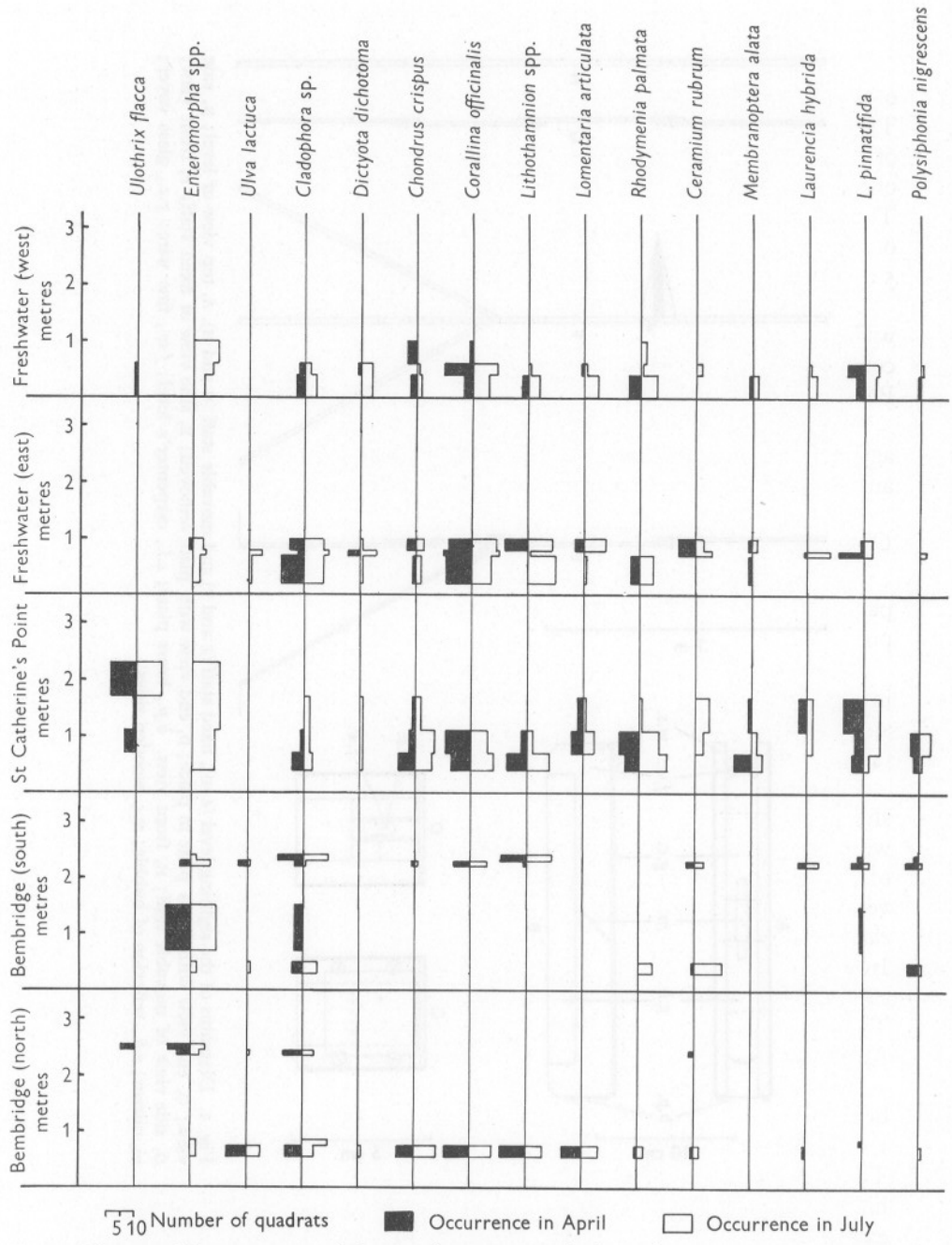

Fig. 3. Diagram of the occurrence of the most important species in quadrats at various levels in the five localities, in April and July.

Method of survey

A marked line was run out down the selected part of the shore. The level of each major irregularity was determined and sketches made of the profile. The limits of the main algal communities were noted and at about the centre of each a 10 m line was placed at right angles to the profile line. At each metre on this line a 25^2 cm quadrat was placed and the species present in it noted. The limits of the *Fucus* and *Laminaria* were determined by taking the level of the highest and lowest (if accessible) plant in each metre-wide band for 5 m on one side of the profile line.

The heights were referred to chart datum by measuring the level of low water and calculating its height from the predicted low water for the locality corrected for the deviation on that particular day, shown by the tide gauge at Portsmouth.

The original survey was made in April. In July the same line was visited again, quadrats taken in the same places to the nearest metre, and the *Fucus* and *Laminaria* zones similarly noted.

Observations

The nature of the transect method resulted in a very limited area of a particular shore being studied. Although it was made as representative as possible it clearly cannot be taken as a description of the whole shore.

A total of sixty-five macroscopic and twenty-five diatom species occurred in the quadrats, in April and July together. There were more brown and red species in July than in April, and this was the true for all the five locations taken individually.

The most important species, other than *Fucus* and *Laminaria* spp., are shown in Fig. 3. The levels over which they extended are approximate and were determined from the levels (given by the profile diagram) of the limits of the communities noted on the shore. It is clear that *Enteromorpha* was very much more abundant in July than April. *Dictyota dichotoma*, *Ceramium rubrum* and possibly *Laurencia hybrida* were also more abundant in July. In addition to these *Leathesia difformis*, *Cystoclonium purpureum*, *Ceramium ciliatum* and *C. diaphanum* occurred in a number of quadrats only in July. The distribution of the other species shown was similar in July to that in April, especially that of *Corallina officinalis* and *Lithothamnion*.

At Freshwater the height to which the species could extend seems to have been limited by the nature of the substratum, which was sheer cliff above 1 m. The exposed nature of the shore probably rendered this uninhabitable. The species therefore all had similar ranges. At St Catherine's Point the higher boulders were occupied by *Enteromorpha* and *Ulothrix*, other species extending up to about mid-tide. At Bembridge (South) it may have been the flat slow-draining ledge which enabled many species to extend to 2·2 m above

chart datum, whereas the same species were limited to 1·7 m at St Catherine's Point where the slope was steep and drainage fast. At Bembridge (North) only a few species existed on the ledge at about 2·5 m, the rest being limited to a lower ledge below a belt of sand.

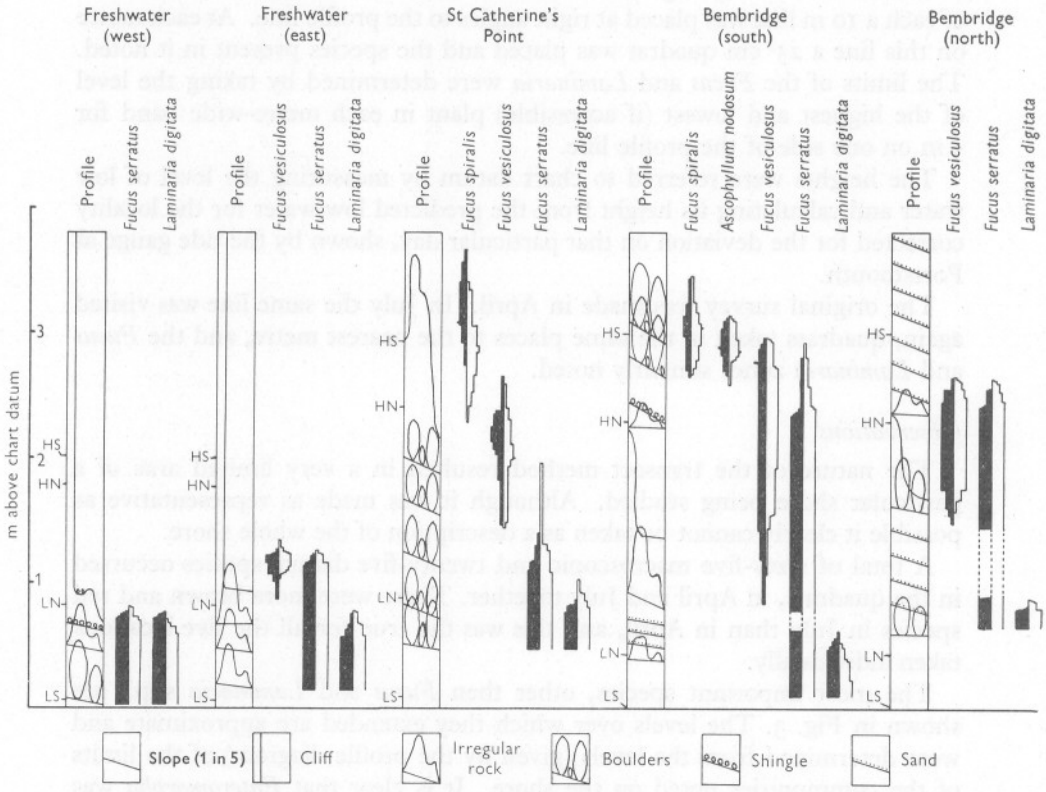

Fig. 4. Diagram of the summarized profiles in the five localities, together with the limits to which the fucoids and *Laminaria* extended, in April and July. HS, HN, mean high water springs and neaps; LN, LS, mean low water neaps and springs. See text for further explanation.

The fucoid and *Laminaria* zones are shown in Fig. 4. Included with them are the diagrams summarizing the profile of each shore. These were constructed from profile drawings in which the horizontal scale was a fifth of the vertical. The slope is thus much steeper than in reality. Each line representing the slope on the diagram refers to the region above the line, and the type of shore in that region is indicated diagrammatically.

The existence of *Fucus spiralis* at Freshwater was probably precluded by the exposed nature of the vertical cliff at the level it would have occupied. It was present on another part of the shore where there were boulders at this level. On the east side *F. vesiculosus* occupied the tops of the rock irregularities,

while the flatter parts were dominated by *F. serratus*. At St Catherine's Point four zones were present, but the shore was apparently too exposed and steep for *Ascophyllum*. The steepness was presumably responsible for preventing *Fucus serratus* from extending higher, as it did on the gentle slopes of the Bembridge shores. At Bembridge (South) *Ascophyllum* was also present on the flat reef, but *Fucus vesiculosus* extended farther down the steeper part, where the surf was probably too strong for *Ascophyllum*. Here the upper limit of *Laminaria* was lower than at the other places, as a belt of sand prevented its extension upwards. Sand also severely limited zone-formation on the northern Bembridge shore, *Fucus vesiculosus* and *F. serratus* occupying the upper ledge.

A complete list of the species encountered is given in Tables 1 and 2 (pp. 779–80). The frequencies in the quadrats of the macroscopic forms are given (Table 1).

Finally it must be said that no definite conclusions can be reached on the factors determining the distribution on these shores without more prolonged observations or experiments. It is possible that similar studies made after several years might reveal important differences in the distribution of many species.

My thanks are due to Mr A. C. Kain for the design and construction of the levelling apparatus and to the Hydrographer (Admiralty) and the Assistant Queen's Harbour Master, Portsmouth, for tidal information. I am also indebted to Dr E. M. Burrows, Dr P. J. Dixon, the late Dr K. M. Drew Baker, Dr N. I. Hendey, Dr and Mrs D. E. G. Irvine and Dr M. W. Parke for the identification of various algae. Dr Hendey was entirely responsible for the identification of the diatoms given in Table 2, and I am extremely grateful to him.

SUMMARY

The southern coast of the Isle of Wight, though mainly sandy, is composed in parts of marl reefs bearing a few algae and in other parts of boulders or hard reefs which bear full algal zonation.

Transect and quadrat studies showed that in 1955 there were more species present in July than April and several species showed a marked increase in cover in July. The vertical distribution of the common species showed little change.

The levels or existence of the fucoid zones are dependent on the slope of the substratum.

A levelling technique suitable for single-handed work is described.

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APPENDIX

TABLE 1. LIST OF ALGAE

The species (other than diatoms) recorded in this work at Freshwater West (F.W.-W.), Freshwater East (F.W.-E), from Compton Bay to Brighstone Bay (S.W.), at St Catherine's Point (St. Cath.), from St Catherine's Point to Ventnor (S.E.), at Bembridge South (Bemb.-S.) and at Bembridge North (Bemb.-N.) in April and July. The occurrence in quadrats is expressed as a percentage of the total number of quadrats taken at that place.

	F.W.-W.		F.W.-E.		S.W.	St Cath.		S.E.	Bemb.-S.		Bemb.-N.	
	Apr.	July	Apr.	July	Apr.	Apr.	July	Apr.	Apr.	July	Apr.	July
Number of quadrats...	30	30	30	30		40	40		35	35	50	50
Zostera nana	–	–	–	–	–	–	–	–	–	–	4	–
Blidingia minima	–	–	–	–	–	–	–	–	–	–	–	2
Chaetomorpha aerea	–	–	–	–	–	23	–	–	–	–	–	–
Cladophora spp.	17	20	50	77	+	13	18	+	54	34	30	44
Codium tomentosum	–	–	–	–	–	–	–	–	3	6	+	2
Enteromorpha spp.	+	67	3	40	+	–	90	+	37	54	10	14
Ulothrix flacca	–	–	–	–	–	35	23	–	–	–	10	–
Ulva lactuca	6	–	–	20	+	–	–	+	9	6	16	18
Ascophyllum nodosum	–	–	–	–	–	–	–	+	+	3	–	–
Asperococcus fistulosus	–	–	–	–	–	–	–	–	6	–	2	10
Chorda filum	–	–	–	–	–	–	–	–	–	–	–	6
Cladostephus spongiosus	3	7	–	3	+	10	3	+	–	6	–	–
Colpomenia peregrina	–	–	–	–	–	–	–	–	–	–	14	–
Dictyota dichotoma	3	27	13	20	–	–	8	–	–	–	–	6
Fucus serratus	13	20	40	40	+	28	28	+	49	43	22	20
F. spiralis	–	–	–	–	–	+	+	+	+	+	+	–
F. vesiculosus	–	–	+	+	+	5	8	+	6	3	4	6
Halidrys siliquosa	–	–	–	–	–	–	–	–	6	3	2	–
Halopteris scoparia	–	–	–	–	–	–	–	–	–	–	–	4
Laminaria digitata	7	10	+	20	–	20	23	+	+	+	4	10
L. saccharina	–	–	–	3	–	–	3	–	–	–	6	4
Leathesia difformis	–	13	–	30	–	–	–	–	–	6	–	–
Petalonia fascia	–	–	–	–	–	–	–	+	3	–	–	12
Pylaiella littoralis	–	–	–	–	–	–	5	–	11	–	8	–
Sphacelaria fusca	–	–	–	–	–	–	–	–	–	6	–	–
S. radicans	–	–	–	–	–	–	–	–	–	6	–	–
Ahnfeltia plicata	–	–	3	3	–	–	3	–	–	–	–	–
Callithamnion hookeri	–	–	–	–	–	5	–	–	–	–	–	–
C. tetricum	–	–	–	–	–	–	3	–	–	–	–	–
Ceramium ciliatum	–	20	–	20	–	–	–	–	–	–	–	–
C. deslongschampsii	–	–	–	–	–	–	–	+	–	–	–	–
C. diaphanum	–	3	–	7	–	–	5	–	–	–	–	–
C. flabelligerum	–	–	–	–	–	3	5	–	–	–	–	–
C. rubrum	–	7	7	30	+	–	20	+	11	23	16	12
Chondrus crispus	17	10	13	17	+	23	38	+	3	3	24	34
Corallina officinalis	47	50	90	87	+	40	35	+	17	17	30	34
Cystoclonium purpureum	–	7	–	–	–	–	5	–	–	–	–	4
Dumontia incrassata	–	–	–	13	–	5	–	–	3	–	12	–
Furcellaria fastigiata	3	–	7	7	+	–	–	–	6	–	7	6
Gastroclonium ovatum	–	7	3	–	–	–	8	–	–	–	–	–
Gelidium coinale	–	–	–	–	–	–	–	–	–	–	–	2
G. latifolium	–	–	–	–	–	–	–	–	–	–	2	4
Gigartina stellata	–	–	–	–	–	–	–	+	3	–	–	–
Griffithsia flosculosa	–	–	–	–	–	–	–	–	–	–	2	4
Halopitys incurvus	–	–	–	–	–	–	–	–	3	–	12	6
Jania rubens	–	–	–	–	–	–	–	–	–	–	2	10
Laurencia hybrida	–	13	3	27	–	8	10	+	9	11	2	–
L. pinnatifida	30	30	33	20	+	35	35	+	20	6	4	4
Lithothamnion spp.	7	17	60	67	–	23	25	+	29	26	36	28
Lomentaria articulata	3	20	10	30	+	15	13	+	–	–	20	24
Membranoptera alata	3	7	7	7	+	20	13	+	–	–	2	10
Phyllophora membranifolia	–	–	13	20	–	–	–	–	6	–	14	10
Plocamium coccineum	–	–	13	7	–	–	3	–	–	–	14	20
Polyides caprinus	–	–	–	–	–	–	–	–	11	11	–	–
Polysiphonia denudata	–	–	–	–	–	–	–	–	–	–	–	4

TABLE 1 (*cont.*)

	F.W.-W.		F.W.-E.		S.W.	St Cath.		S.E.	Bemb.-S.		Bemb.-N.	
	Apr.	July	Apr.	July	Apr.	Apr.	July	Apr.	Apr.	July	Apr.	July
P. fibrata	–	–	3	–	–	–	–	–	–	–	–	–
P. lanosa	–	–	–	–	–	–	–	+	–	3	–	–
P. nigrescens	3	3	–	7	+	13	13	+	29	3	–	4
P. urceolata	–	–	–	–	–	–	–	+	–	3	–	–
Porphyra umbilicalis	–	–	–	–	–	–	–	+	–	–	–	–
Pterosiphonia thuyoides	–	7	+	–	+	–	–	–	–	3	–	2
Ptilota plumosa	–	–	–	–	+	–	5	–	–	–	–	–
Rhodochorton floridulum	–	–	–	–	+	–	–	+	–	–	4	6
Rhodomela confervoides	–	–	–	–	–	–	–	–	–	–	–	2
Rhodymenia palmata	13	30	10	17	+	30	45	+	+	11	14	22
Spermothamnion barbatum	–	–	20	–	–	–	–	–	–	–	–	–
Spyridia filamentosa	–	–	–	–	–	–	–	–	–	–	–	10

TABLE 2. LIST OF DIATOMS

The diatom species recorded in this work at Freshwater West (F.W.-W.), Freshwater East (F.W.-E.), from Compton Bay to Brighstone Bay (S.W.), from St Catherine's Point to Ventnor (S.E.) and at Bembridge South (Bemb.-S.) in April.

	F.W.-W.	F.W.-E.	S.W.	S.E.	Bemb.-S.
Actinoptychus senarius	+	+	–	–	–
Amphipleura rutilans	–	+	–	+	–
Amphora arenicola	–	–	–	+	–
A. exigua	+	–	–	–	–
Biddulphia alternans	+	–	–	–	–
B. aurita	+	+	+	+	–
B. mobiliensis	–	–	–	+	–
Cocconeis costata	+	–	+	–	–
C. dirupta	–	–	+	–	–
C. scutellum	–	–	–	+	–
C. scutellum var. *stauroneiformis*	–	–	–	+	–
Coscinodiscus excentricus	+	–	–	+	–
Diploneis bombus	+	–	–	+	–
Grammatophora oceanica	–	–	+	–	–
Licmophora gracilis	+	–	+	+	–
L. lyngbyei	+	–	–	–	–
Mastogloia binotata	–	–	+	–	–
Navicula cluthensis	–	–	–	+	–
N. cyprinus	–	–	–	+	–
N. distans	+	–	–	+	–
N. grevillei	+	+	–	+	+
N. mollis	+	–	+	+	+
N. ramosissima	+	+	+	+	+
Nitzschia acuminata	–	–	–	+	–
N. angularis	+	–	–	+	–
N. lanceolata	–	–	–	+	–
N. panduriformis	–	–	–	+	–
N. punctata	+	–	–	+	–
N. punctata var. *coarctata*	–	–	–	+	–
N. sigma var. *rigidula*	+	–	–	+	+
Paralia sulcata	+	–	–	+	–
Podosira stelliger	–	–	–	+	–
Rhabdonema arcuatum	–	–	+	–	–
R. minutum	–	–	+	–	–
Rhaphoneis amphiceros	+	–	–	+	–
R. surirella	–	–	–	+	–
Rhoicosphenia curvata	+	–	–	+	–
Rhopalodia musculus	–	–	–	+	–
Synedra affinis	+	–	+	+	–
S. gaillonii	–	–	+	+	–
S. investiens	+	–	+	+	–
S. tabulata	–	–	–	+	–
Thalassiosira decipiens	+	–	–	+	–
Trachyneis aspera	+	–	–	–	–

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STUDIES ON THE GROWTH OF MARINE PHYTOPLANKTON

II. *ISOCHRYSIS GALBANA* PARKE

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(Text-figs. 1–8)

A good deal is known about the growth in culture of *Phaeodactylum tricornutum* Bohlin (*Nitzschia closterium* W. Sm. forma *minutissima* Allen & Nelson) (see Spencer, 1954; Harvey, 1955; Provasoli, McLaughlin & Droop, 1957). This organism, however, is a somewhat aberrant member of the Chrysophyta, and other marine and brackish-water representatives of the group, e.g. *Syracosphaera carterae* Braarud & Fagerland (Braarud & Fagerland, 1946; Provasoli, McLaughlin & Pintner, 1954), *Prymnesium parvum* Carter (Reich & Kahn, 1954; Droop, 1954), and certain other species (Droop, 1954, 1955*a*, *b*) have been studied much less intensively from this point of view. It has therefore seemed worth while making a general study, similar to that reported in the first paper of this series for the diatom *Asterionella japonica* Cleve & Müller ex Gran, of the growth requirements of a representative of the Chrysophyceae. *Isochrysis galbana* Parke, a flagellate of some importance as a food organism of the oyster, has been selected for this purpose. Johnston (1955) has used unialgal cultures of this species in studies of dissolved organic matter in sea water and, since the investigation being described was carried out, Droop (1957) has reported that it has a requirement for cobalamin.

MATERIALS AND METHODS

The culture of *Isochrysis* used was isolated by Dr M. W. Parke from Port Erin fish ponds in 1938 (Parke, 1949). It was obtained from the Plymouth collection shortly after it had been partly freed of bacteria by phototaxis. It was not purified further.

The methods used for the culture and study of this organism were almost the same as those used for *Asterionella* (see Kain & Fogg, 1958). In stagnant culture a glass bead was included in each boiling tube to help in the removal of cells adhering to the bottom. Media were autoclaved at 15 lb. for less than 1 min instead of for 15 min. The media used were identical to those used for *Asterionella*, omitting sodium silicate and the buffer. They are denoted AO

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(similar to AK for *Asterionella*), AQ_N (similar to AR_N) and AQ_A (similar to AR_A). AO and AQ_N, containing natural sea water and soil extract in the case of AO, presumably contained cobalamin though it cannot be certain that the amount of this was always sufficient to maintain the optimum growth of *Isochrysis*. Vitamins were sometimes added to AQ_A.

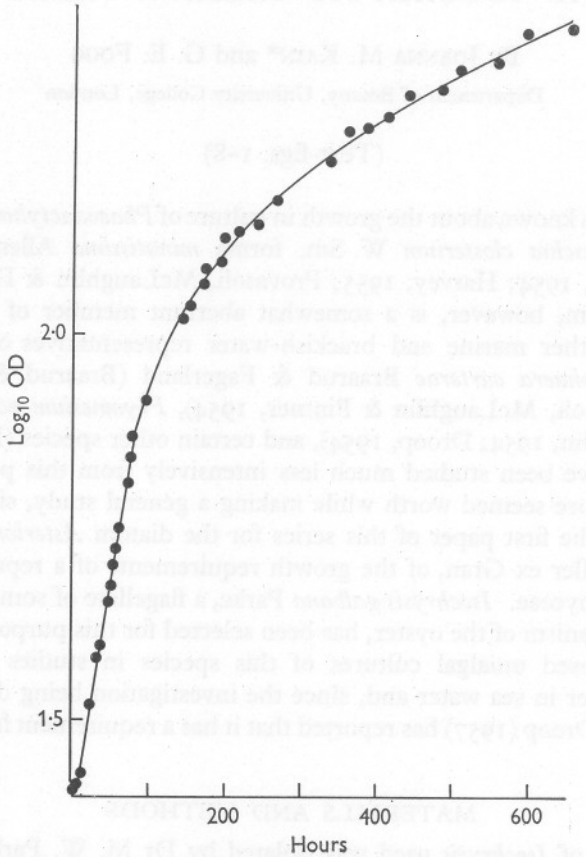

Fig. 1. The mean growth curve, determined by optical density readings, of two cultures of *Isochrysis*.

EXPERIMENTS

Growth

An example of the growth curve of *Isochrysis* in stagnant Erdschreiber medium is shown in Fig. 1. There was normally a lag period of up to 24 h after which growth was exponential, with a relative growth constant (defined as $(\log_e N_t - \log_e N_0)/t$ in days) of $k = 0{\cdot}25$ to $0{\cdot}55$. After 100–150 h growth was limited by the availability of carbon dioxide but continued slowly for up to 500 h, giving final populations of the order of 10,000 cells/mm^3. During the

growth of *Isochrysis* in stagnant culture the pH of the medium rose to a higher level than for *Asterionella*, pH 9 being exceeded after 400 h.

Nitrogen supply

Isochrysis was grown in a series of concentrations of potassium nitrate in the artificial sea water medium (AQ_A), from an inoculum that had been washed in nitrate-free artificial sea water. Cell counts were made after 700 h and the cell crop in each culture calculated by subtracting the cell concentration in the controls to which no nitrate had been added from the cell concentration in the culture itself. This is shown plotted against the initial nitrate concentration in Fig. 2, which also gives the quantity of nitrate added to the medium divided by the crop obtained from it. The two lowest concentrations were evidently limiting and in these the mean nitrogen content was 0·0507 $\mu\mu$g-atom N/cell ($0{\cdot}7 \times 10^{-9}$ mg N/cell).

Phosphorus supply

An analogous experiment on the phosphorus requirement was made with a series of concentrations of dipotassium hydrogen phosphate. The results are shown in Fig. 3. The mean quantity of phosphorus in the cells in the lowest three concentrations, where it was limiting, was 0·000972 $\mu\mu$g-atom P/cell ($0{\cdot}03 \times 10^{-9}$ mg P/cell).

Salinity

The relative growth constant of *Isochrysis* in natural sea water was reduced to 0·27 at 10‰ S but showed no statistically significant deviation from a mean value of 0·36 over the range 15–40‰ S.

Artificial sea water

In medium AQ_A, composed principally of the major constituents of sea water and the trace elements with EDTA as used by Provasoli *et al.* (1957), the growth of *Isochrysis* was normal only when soil extract was present. This may be at least partly explained by its requirement for cobalamin. Unpublished work by Miss S. Arregger has shown that *Isochrysis* grows well in a synthetic medium, S50 of Droop (1958), in which 0·25 g/l. of glycylglycine seems to be an important component.

Temperature

The relative growth constants at different temperatures in medium AO, expressed as percentages of the mean of those of control cultures at 25° C, are plotted in Fig. 4. Between 20° and 25° C was optimal; at 30° C no growth

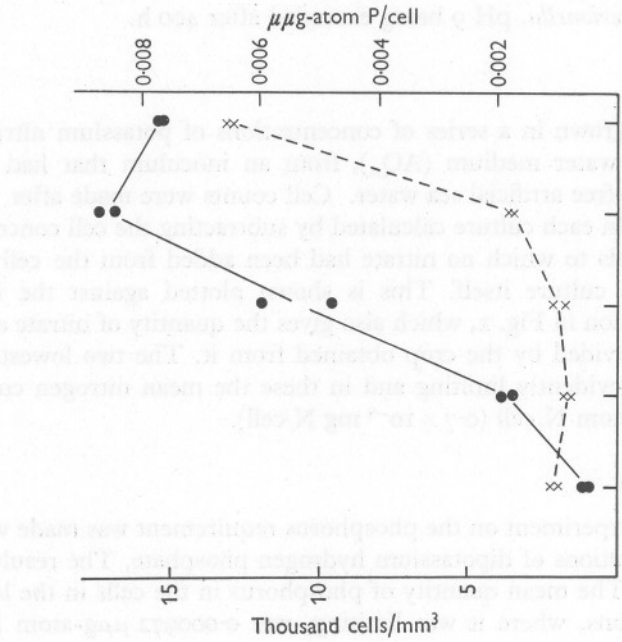

Fig. 3. The cell crop and phosphorus per cell of *Isochrysis* in relation to concentration of dipotassium hydrogen phosphate. –●—●–, cell crop; – – × – – × – –, phosphorus/cell.

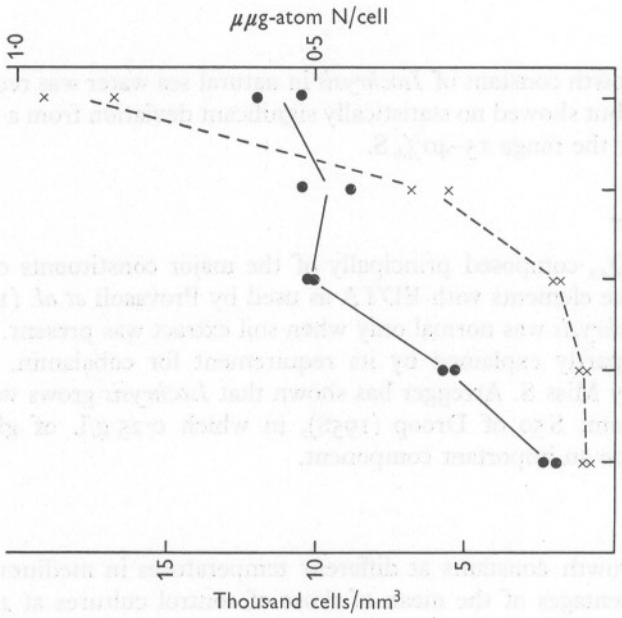

Fig. 2. The cell crop and nitrogen per cell of *Isochrysis* in relation to concentration of potassium nitrate. –●—●–, cell crop; – – × – – × – –, nitrogen/cell.

took place, but exposure for a week to this temperature was not lethal as cultures returned to 20° C were able to grow.

Light

The results of two experiments to determine the relative growth constants at various light intensities in medium AQ_N are shown in Fig. 5. Saturation was reached at about 1500 lux, an intensity of the same order as that saturating

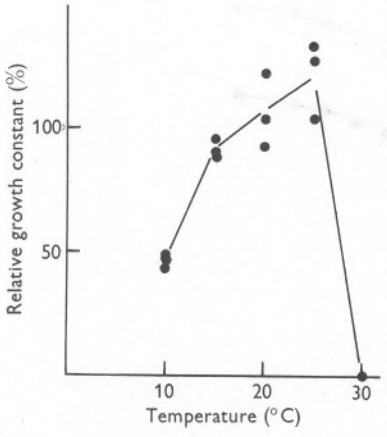

Fig. 4

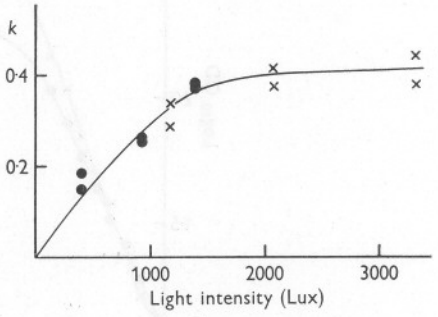

Fig. 5

Fig. 4. The relative growth constant, as % of controls, of *Isochrysis* at different temperatures. (See text for further explanation.)

Fig. 5. The relative growth constant (k) of *Isochrysis* in different intensities of fluorescent light. ●, Expt. 1; ×, Expt. 2.

for the growth of *Chlorella pyrenoidosa* (Myers, 1953); there was no inhibition at 3000 lux. In both experiments the optical density per cell at the end of the exponential phase was considerably lower at higher than at lower light intensities.

Aeration

The mean growth curves of triplicate aerated and stagnant cultures in medium AQ_A are shown in Fig. 6. The mean relative growth constant was higher under aerated ($0{\cdot}526 \pm 0{\cdot}025$) than under stagnant ($0{\cdot}446 \pm 0{\cdot}026$) conditions, but the difference between the values was scarcely statistically significant at the 5% level. It is clear, however, that growth at the initial rate was continued to a much higher cell concentration (about 14,000 cells/mm^3) under aerated than under stagnant conditions (about 6000 cells/mm^3). A final population of 24,000 cells/mm^3 was attained in aerated culture on occasion.

Hydrogen-ion concentration

In determining the optimum pH for the growth of *Isochrysis* it was not possible to use the buffer tris(hydroxymethyl)aminomethane at a really effective concentration as this was inhibitory (see below). Instead 1·65 mM of tris was used and daily adjustments made to the pH of the medium (AQ_A), by means of the dummy tube method previously described (Kain & Fogg,

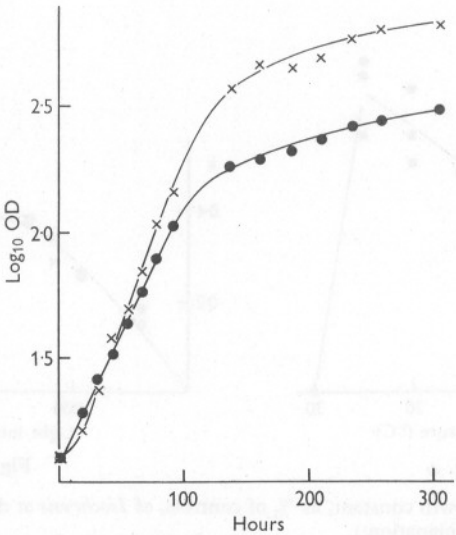

Fig. 6. The growth curves, determined from optical density readings, of *Isochrysis* in stagnant and aerated culture. -●—●-, stagnant; --×---×--, aerated.

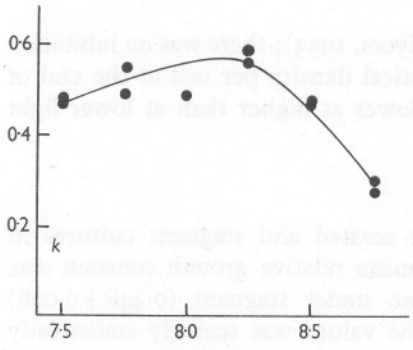

Fig. 7

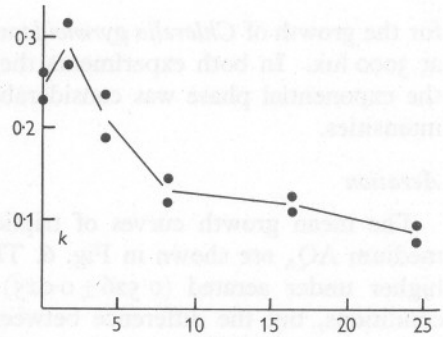

Fig. 8

Fig. 7. The relative growth constant (k) of *Isochrysis* in media adjusted to various pH's.

Fig. 8. The relative growth constant (k) of *Isochrysis* in relation to concentration of the buffer tris.

1958). The maximum variation observed was 0·3 pH units at pH 7·5. It was mostly about 0·1 pH unit. The pH of each experimental tube was determined at the end of the exponential phase and found not to differ by more than 0·12 pH units from that of the corresponding dummy tube. The relative growth constants are shown in Fig. 7. There was clear inhibition at pH 8·75 only.

The relative growth constants in a range of tris concentrations are shown in Fig. 8. There was a marked inhibition at 8·25 mM and above. The difference between the k values for 1·65 mM and for the controls is not statistically significant. In a further experiment using triplicate cultures k values of $0{\cdot}446 \pm 0{\cdot}026$ and $0{\cdot}446 \pm 0{\cdot}017$ were obtained for control and 1·65 mM tris cultures respectively. It therefore appears that low concentrations of tris have no appreciable stimulatory effect on *Isochrysis*. The marked inhibition of the growth of *Isochrysis* in 8·25 mM of tris shows that this organism differs from those tried by Provasoli *et al.* (1957) which were all tolerant of 0·1% (8·25 mM) of the buffer.

These results will be discussed together with those for other species on a later occasion.

This work has been carried out under extra-mural contract with the Institute of Seaweed Research. We are grateful to the Institute for a maintenance grant made to one of us (J. M. K.). We are also grateful to Dr M. W. Parke for the culture of *Isochrysis* and for helpful suggestions.

SUMMARY

The flagellate *Isochrysis galbana* has been grown in unialgal culture under controlled conditions and its growth has been measured by means of optical density determinations and cell counts.

The relative growth constant has been found to be 0·55 $\log_e$ units per day under optimum conditions. Waters with salinities from 15 to 40‰ S supported rapid growth. The optimum temperature was 20° to 25° C and the optimum light intensity from 1500 to at least 3000 lux. The rate of growth was inhibited at pH 8·75 and above. The buffer tris(hydroxymethyl)aminomethane had an inhibitory effect at concentrations of 8 mM and above. Final yields of the order of 24,000 cells/mm^3 could be obtained in cultures aerated by bubbling air. The minimum nitrogen requirement per cell was 0·0507 $\mu\mu$g-atom N/cell and the minimum phosphorus 0·000972 $\mu\mu$g-atom P/cell.

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NEUROMUSCULAR ACTIVITY IN SEA ANEMONE *CALLIACTIS PARASITICA* (COUCH)

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(With Text-figs. 1–7)

In a recent study (Ross, 1957) isolated marginal sphincter preparations of the sea anemone, *Calliactis parasitica*, showed two distinct responses to stimulation: (1) a quick contraction in response to stimuli at frequencies from 0·2 to 3·0 sec, the facilitated response of Pantin (1935*a*) beginning only on the second stimulus of a series, with a latent period of about 0·1 sec; (2) a smooth slow contraction in response to stimuli at lower frequencies, with a latent period of not less than 30 sec, and beginning only after several stimuli. This slow movement of the marginal region had not been detected in work on whole animals, but it is similar to the contractions of the 'slow' muscles of *Calliactis* (Pantin, 1935*b*) and *Metridium* (Batham & Pantin, 1950*a*). However, *Calliactis* sphincter shows almost no spontaneous activity.

Both quick and slow contractions had previously been observed in excised sphincters and mesenteric retractors of *Metridium* (Batham & Pantin, 1954), the chief muscles utilized in the closure of that animal. In all these cases, the quick contraction would seem to be a specialized mechanism for sudden withdrawal superimposed upon, and perhaps developed from, a more primitive and general slow contractile mechanism. As part of a programme to investigate and compare the properties of quick and slow contractions in these muscles it seemed desirable to see what part, if any, slow contractions of the marginal sphincter play in the life of *Calliactis*. This involved us in a wider study of the neuromuscular activity of this anemone which normally lives on shells inhabited by the hermit crab, *Eupagurus bernhardus*. We report the results here as an additional contribution to the analysis of behaviour in the Actinozoa, supplementing the similar studies on *Metridium* by Batham & Pantin (1950*a*, *b*).

METHODS

As in the work of Batham & Pantin (1950*b*, 1954), this investigation required the use of several methods of recording and observing the movements of the animals. Kymograph records, together with visual and photographic records, were used for information on the frequency, size and form of certain periodic activities. A short film record supplemented these observations. Preparations

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of *Calliactis* consisting of several rings joined to a strip of column were studied for information on innate rhythmic activity and on the timing and co-ordination of movements at different levels of the column. Responses to electrical and other forms of stimulation were also studied, both in whole animals and preparations, in order to see how they resembled the natural movements without stimulation.

RESULTS

With its thicker and tougher integument and mesogloea, *Calliactis* does not show the extremes of shape and posture observed in *Metridium*. It can close down to a flattish cone but it never assumes the wrinkled and shrivelled appearance that is seen so commonly in *Metridium*. It can extend itself or bend to the side only to moderate degrees, and local contractions of the circular muscle of the column never produce in *Calliactis* the conspicuous deep furrows so clearly seen in *Metridium* (Batham & Pantin, 1950*a*). Moreover, unlike *Metridium*, *Calliactis* does not 'walk'; once it becomes firmly fixed on a plate or a stone, it may remain in the same place for months. It only moves by detaching itself altogether and creeping or rolling about the tank in a prone position.

Close observation of *Calliactis* shows, as Batham & Pantin (1950*b*) have remarked, that this anemone, like *Metridium*, is in a state of continual activity. Although most of the movement is too slow to be visible and the changes in appearance are less conspicuous than in *Metridium*, shape and posture are often quite different from one minute to the next. Moreover, there are periods when an exceptional amount of activity seems to be taking place and these periods are repeated at regular intervals.

Besides slowly changing in posture and shape, *Calliactis* closes up from time to time, even in the absence of any obvious stimulus. In order to find out how often it does so, ten animals were observed closely for 5 min periods at hourly intervals, ten times every day for a week. This gave us a record of the number of closing movements in 350 min observation time. In fourteen of the seventy observation periods, all ten animals remained open the whole time. The total number of closures recorded was 108, and on two occasions, four different animals exhibited closing movements during the whole or part of the same 5 min period. There were big differences in individuals. One was closed twenty-one times; another was never seen to close during the seventy observation periods. Thus closure may occur in some animals several times an hour, but in the majority it occurs with a frequency of about once an hour, and in some it is a very rare event indeed.

Two kinds of closing movement were evident in these animals. Some, like the responses to mechanical and electrical stimulation, were of short duration, with little loss of water or change of volume and the animal expanded again

within a minute or two (Pantin, 1940; Chapman, 1949). Others were long-lasting. Animals closed at the beginning were frequently still closed at the end of an observation period, and some of these were also closed at the next and even later observation periods as well. From occasional checks in between, we know that in many of these cases no opening occurred in the intervening periods. These closures, which may be sustained for several hours, comprised about one-third of the total, and since the contraction of the animal in these closures was more complete and water loss greater, relaxation and opening were very much slower than in the familiar closing responses of short duration.

Since one of the objects of the investigation was to find out if slow contractions of the sphincter play any part in the normal behaviour of *Calliactis*, the closing movements were followed closely to see if slow contractions of the margin could be detected in them. It may be significant in this connexion that the first stages of these closing movements were not often seen. Closures beginning with a quick contraction were spotted only seven times. In the remaining 67 closures, the animals were already partly closed before any movement was detected. This may mean either that an observer tends to miss an initial quick contraction or that the movement begins slowly and only becomes apparent later. Subsequently, smooth flowing movements of the margin could be seen taking part in completing the closing movement, though occasionally the jerky movements of a quick contraction might be inserted into the sequence. Relaxation after many of these closures and partial closures was slow, resembling the time-course of relaxation after slow contractions of sphincter preparations (Ross, 1957) rather than the dramatic opening which follows quick closures. We concluded, therefore, that slow contractions of the sphincter contribute substantially to the spontaneous closing movements that occur from time to time in unstimulated *Calliactis*.

Closing movements are not the only feature of the behaviour of unstimulated *Calliactis*. The margin is frequently thrown into graceful folds by local contractions in certain radii. Changes in length and local constriction and peristalsis in the column produce a variety of shapes, some of which are illustrated in Fig. 6. Defaecation, with its gaping mouth and shapeless appearance, is easily recognized in *Calliactis* as in *Metridium* (Batham & Pantin, 1950). Many of these phases involve considerable shortening of the margin without quick sphincter contractions. Thus slow movements of the sphincter seem to be involved in these activities also.

RHYTHMIC CYCLES OF ACTIVITY IN *CALLIACTIS*

Some of the movements seen in *Calliactis* over a period seemed to have a repetitive character. Kymograph recordings gave clear evidence of this, and often showed a slow rhythm of remarkable regularity. Fig. 1 is a 3 hr record

of *Calliactis* attached to a light gimbal lever. The big downward movements represent slow contractions of the submarginal and marginal regions culminating in a shortening of the column. This took 3–4 min to complete and was repeated every 10–15 min. The regularity, frequency and size of the main movement in the cycle vary greatly from one animal to another, and in the same animal at different times. But repetitive movements are always a feature of the records and they usually have marginal and submarginal components which are repeated several times per hour.

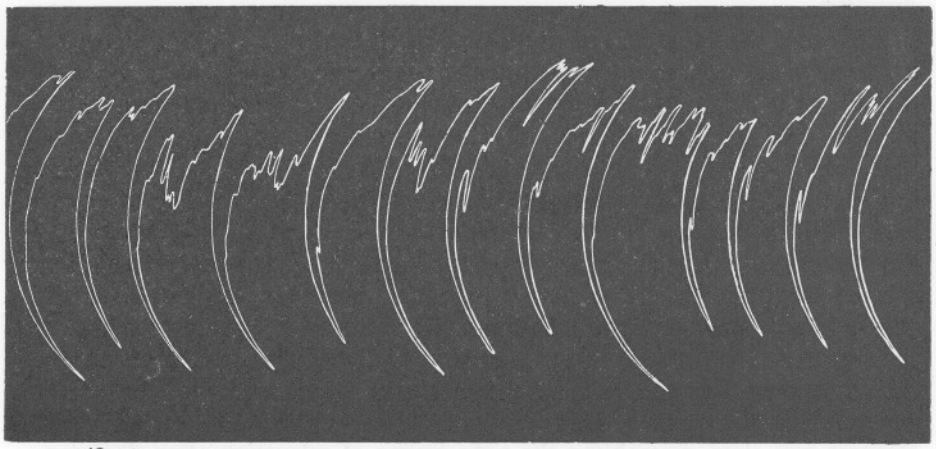


Fig. 1. Continuous record of movements of *Calliactis* during 3 h. Thread inserted in margin and attached obliquely to gimbal lever.

It is not easy to relate these cycles of activity to the closing movements which occur intermittently in unstimulated animals. The cycles recorded on the kymograph occur more frequently than visible closing movements. Moreover, the recorded movements sometimes produce a condition corresponding to partial closure, but full closure and sustained closure are almost never seen, though this may simply be due to the pull of the lever. We know also that a good many animals show visible closing movements very infrequently, yet in our experience all *Calliactis* give evidence of repeated activity cycles on the kymograph. It seems to us that the closing movements may be regarded as one form that the main movement of the repetitive cycle may take in some animals at certain times. Further data on this matter will be presented later.

The detailed picture of these low-frequency 'beats' varies greatly from one animal to another and from day to day in the same animal. There are periods, however, usually lasting several hours, when the rate is constant and then the form is remarkably constant too. Each cycle normally consists of one

main series of contractions followed by a partial relaxation and then by one or more subsidiary cycles. In typical cycles, like those shown in Figs. 1–3, ten or more distinct movements may be involved. The main movement often begins, as in Fig. 2, with a small quick contraction of the sphincter, and even when this does not appear in the record, a slight twitch or bristling of the tentacles and marginal edge is often detected visually, just before the slow downward movement of the lever starts. The main components in this movement are a slow contraction of the submarginal region, and an even shortening of the column and depression of the disk, presumably by the longitudinal mesenteric and parietal muscles. In Fig. 3 the final pull on the lever is due to a slow sphincter contraction which is powerful enough to mask the relaxation of the column taking place at the same time. Most of the big movements of the cycles consist of combinations of at least two of these components but a variety of additional minor movements may be involved in various sequences.

In the subsequent relaxation, the column lengthens, presumably by the contraction of the circular muscles, but before relaxation is complete it is generally interrupted by a subsidiary cycle. This is characterized by the constriction and twisting of the column at the level of the cinclides, initiating a peristaltic wave of contraction which moves up the column and which may involve the margin.

Electrical stimuli giving a quick contraction of the sphincter can reproduce a good deal of this activity, and generally initiate a complete cycle conforming to the pattern of repetitive activity at the time. This suggests that the small sphincter contraction or tentacular twitching, so often seen just prior to the beginning of a cycle, may be a signal that the cycle is about to start, or may act as its trigger. Low-frequency stimuli, which elicit only slow contractions, do not initiate new cycles, possibly because several muscle systems which normally work independently are brought into action simultaneously so that the sequence is disrupted.

Activities of isolated preparations of Calliactis

Two kinds of preparation have been studied: (1) simple rings taken from the column at all levels; (2) preparations consisting of three loops taken from the margin, the submarginal region and the lower column at the level of the cinclides, joined together by a connecting strip of column.

The simple ring preparations showed that the circular muscle of the column is rhythmically active at all levels below the sphincter. Moreover, the timing of the 'beats' is very close to that observed in the movements of whole animals, usually with several main movements and rather more subsidiary movements occurring per hour (Fig. 4). Such rings give slow contractions to stimuli like those obtained from *Metridium* preparations (Batham & Pantin, 1954), and these contractions are similar to the main movements of the cycles

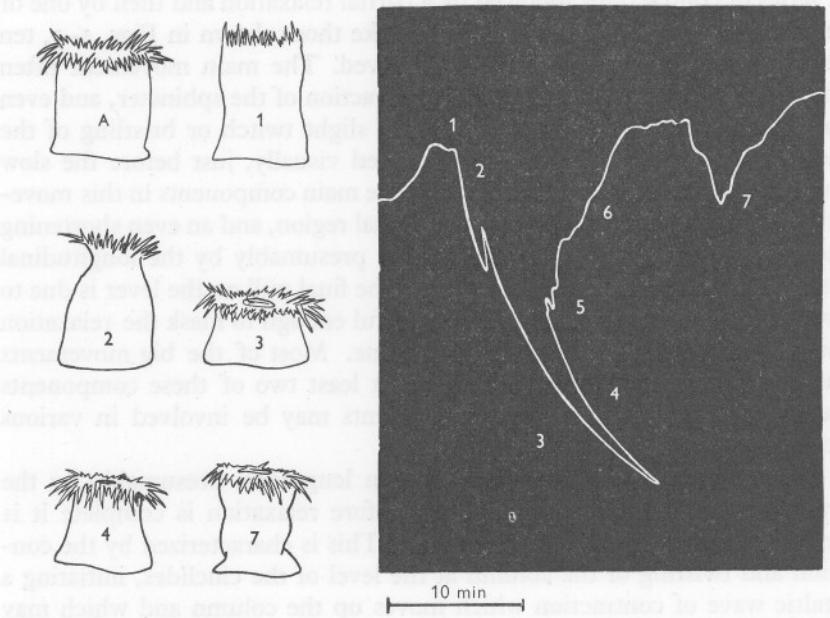


Fig. 2. Record of a single cycle in the rhythmic activity of *Calliactis* during 35 min. Numbers refer to the following distinct stages recognized visually and depicted in the accompanying sketches: (1) quick sphincter contraction; (2) submarginal contraction; (3) column shortening; (4) column extension; (5) brief submarginal contraction followed by (6) expansion of disc; (7) subsidiary cycle with transitory changes in length and peristaltic movements of the column. A shows the animal in the non-active stage.

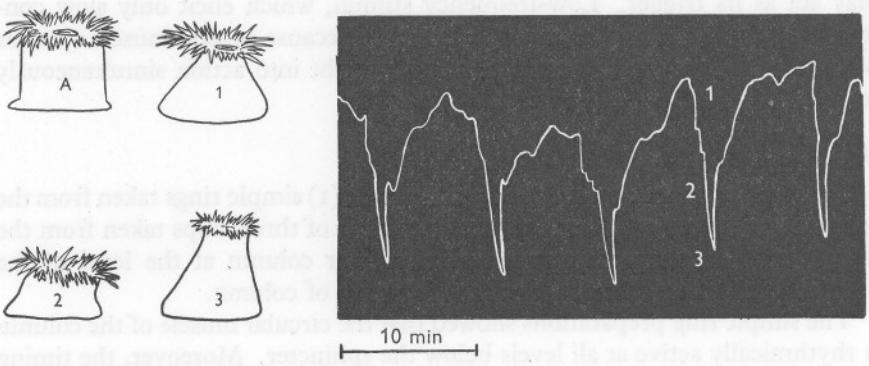
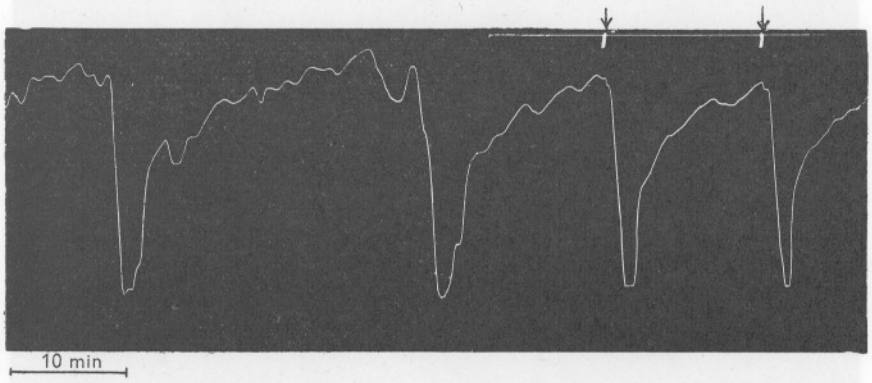


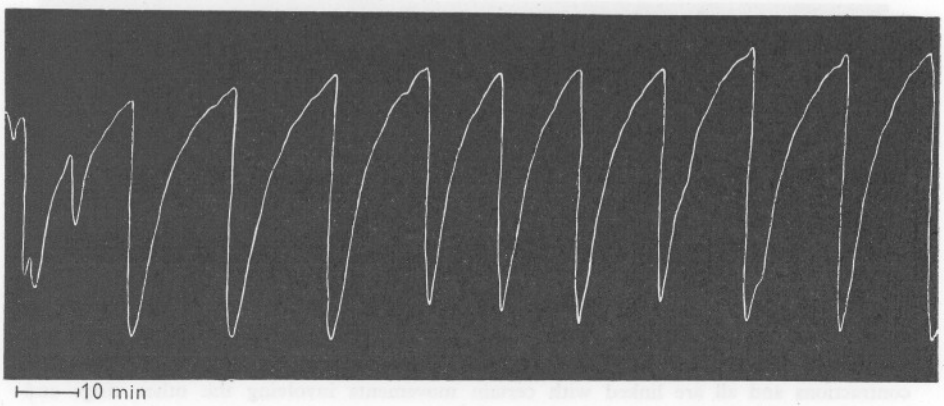
Fig. 3. Record of five cycles in the rhythmic activity of *Calliactis* during 39 min. Numbers on record and sketches refer to the following distinct stages in the movement: (1) submarginal contraction; (2) column shortening; (3) slow sphincter contraction merging into column extension. A shows the non-active stage.

(Fig. 4). As a rule ten or more stimuli are required to start such a movement and the latent periods are usually at least 1 min.

The triple-loop preparations gave evidence of co-ordinated activities. Movements occurred about every 10–20 min as in the intact animal, and in these movements, all three loops came into action in a definite sequence. Since the longitudinal strip of column joining the loops was firmly fixed to a cork plate with pins and held firmly in position by strips of glass pressed down by rubber bands, there was no possibility of the movement of one loop pulling mechanically on the next. The co-ordination seems to be based,



A



B

Fig. 4. Activity of simple ring preparations of *Calliactis* column. A, Preparation taken from submarginal region. 40 min record of activity without stimulation followed by period of 35 min. during which electrical stimuli (10 stimuli at 1·2 sec) were applied at 12 and 26 min (arrows). The slow delayed contractions in response to stimuli are preceded by small contractions on the stimuli probably due to residual sphincter tissue in the preparation. B, Preparation taken from lower region of column. Record of activity during 2½ h without stimulation.

therefore, on nervous, or perhaps intramuscular conduction. In the bigger movements involving all three loops, the submarginal region almost always took the lead. It began to move from 30 sec to 1 min before the sphincter and about 1 min or more before the loop from the lower part of the column. In the latter, independent movements frequently occurred. Fig. 5 shows records which illustrate these points. The general picture is similar to that found by Batham & Pantin (1954) in *Metridium*, where there is a gradient of spontaneity from the sphincter to the pedal edge, though *Calliactis* is more

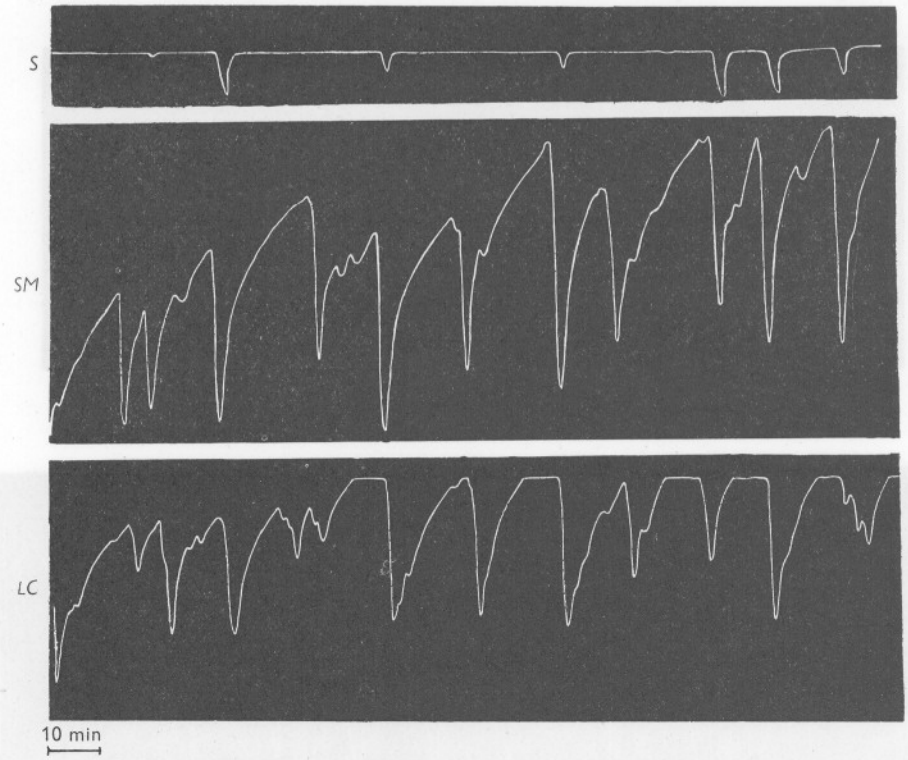


Fig. 5. Three-ring preparations of *Calliactis* with connecting strip of column recorded over 2½ h. *S*, sphincter ring attached to spring lever; *SM*, submarginal ring; and *LC*, lower column ring attached to weighted levers. The sphincter movements here recorded are slow contractions and all are linked with certain movements involving the other rings and beginning with the submarginal ring.

consistent in showing the submarginal region leading the co-ordinated movements. From the kymograph records of preparations alone, one might postulate that the pace-maker for these movements is located in the submarginal region, but we must recall that in the whole animal, a marginal twitch, often too small to be recorded, frequently precedes the main recorded

movement. Therefore, the location of the pacemaker must remain an open question.

The effects of stimuli on the triple-loop preparations also showed the submarginal region taking the lead in the slow responses to stimuli at frequencies of 6·1 and 7·5 sec. Even when the electrodes were nearer to the loop at the cinclide level, the submarginal loop began to contract about 30 sec before either of the other two loops.

Special experiment on five Calliactis

The results presented so far refer to an assortment of *Calliactis* studied at different times and places. In order to obtain more definite information based on a few animals studied in detail, an additional experiment was set up. Five *Calliactis* on plates were placed in a bath and visual, photographic (still) and film records of their activities were made over a period of 3–4 weeks. They were fed once weekly with chopped *Mytilus* muscle and the sea water was changed one day after feeding. After thus observing the animals under aquarium conditions, each one was removed in turn and by means of threads inserted into the marginal, submarginal and cinclide regions of the column, 3-lever kymograph records were taken to show the movements of the whole animals over periods of about 2 days. After this, 3-loop preparations were made from each animal (after 4–6 h anaesthesia in 0·4 M-$MgCl_2$) and their movements recorded on the same levers as long as the preparations survived in good condition, usually 1½–2 days.

One feature of the observations was that each animal was found to have certain individual characteristics of attitude, posture and activity which it displayed throughout the experiment. The animals are shown in Fig. 6, and they were labelled A to E from left to right. Animal A usually kept its column moderately extended and its disk depressed below the level of the margin. Its tentacles were well extended but rather limp and trailing, and from the amount of movement of the margin, the number of closures observed, and the frequency of peristalsis, it was designated 'active'. In animal B the tentacles invariably rose stiffly from the margin, the column was always elongate and erect, with the margin kept in a near-vertical position. In this animal, activity was intense for short periods, with long periods of apparent immobility in between, and it was therefore described as 'intermittently active'. *Calliactis* C showed an asymmetrical posture, with the tentacles and margin slightly lifted on one side, *Calliactis* D a squat posture, with a deeply depressed disk and very short column, and *Calliactis* E an erect posture with almost no basal expansion, and a disk tending to project above the margin. *Calliactis* C was very active from time to time and so was classed as 'intermittently active'; *Calliactis* D and E moved infrequently and showed little variation in shape and were described as 'inactive'.

Photographs *a–f* in Fig. 6, taken at 1 min intervals, illustrate the characteristic

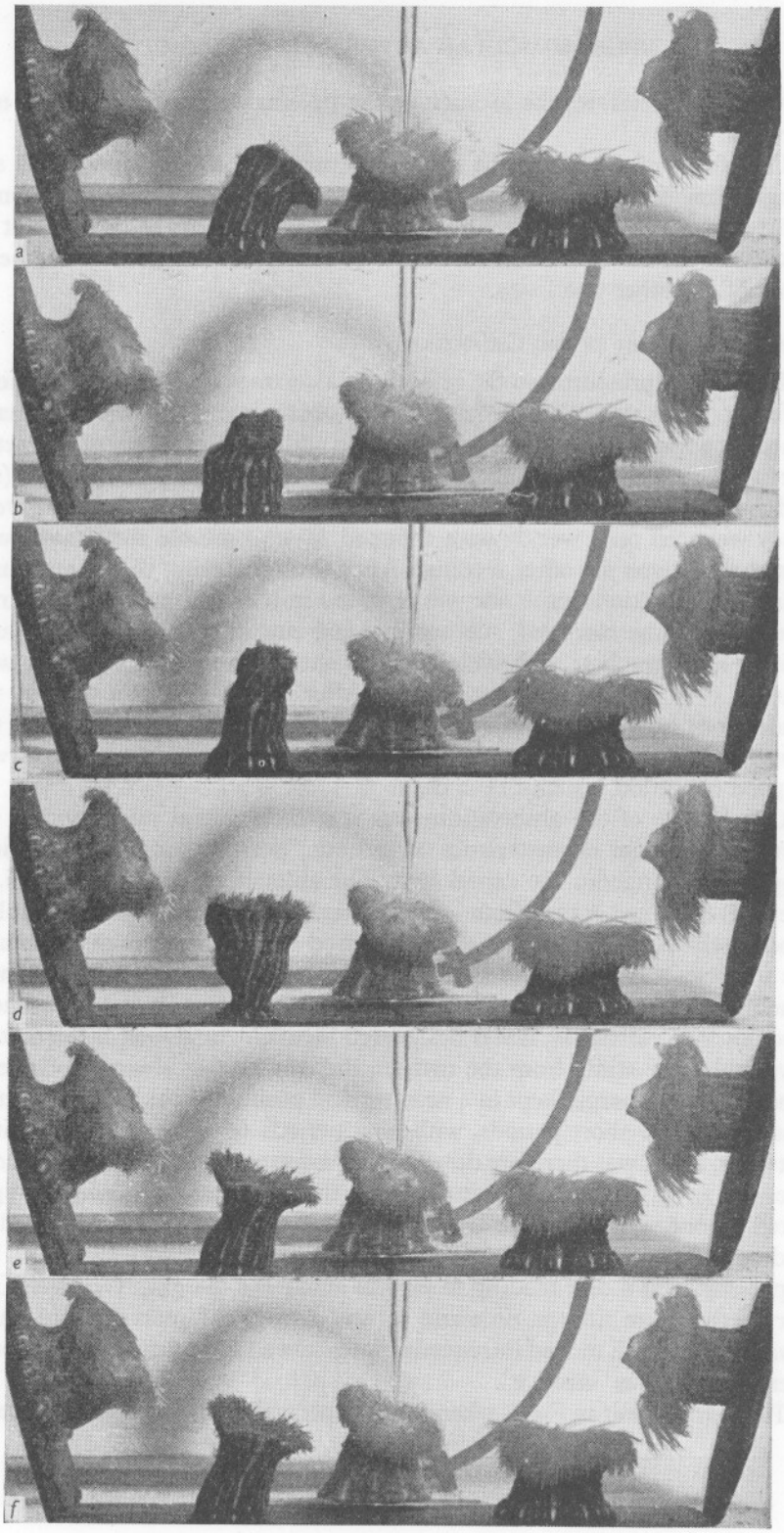


Fig. 6. For legend see opposite page.

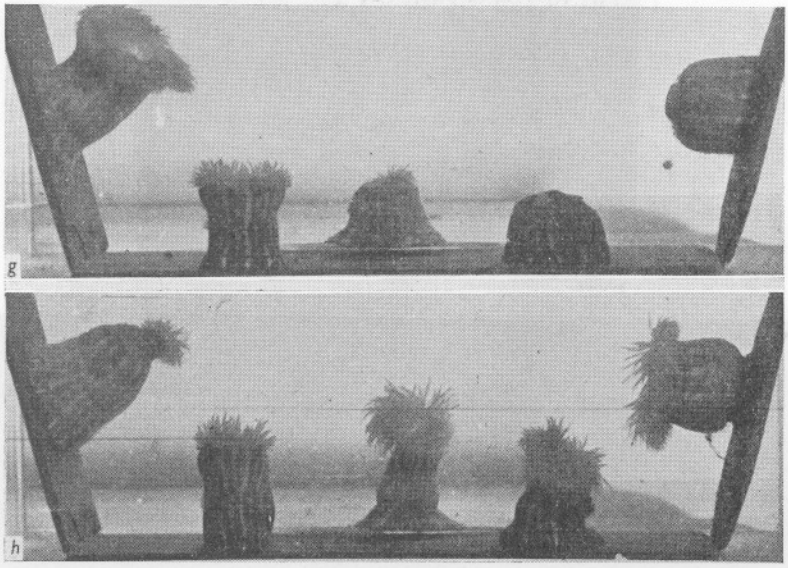


Fig. 6. Group of five *Calliactis* used in experiments described on pp. 797–803. Animals designated A, B, C, D, E from left to right. *a–f*, photos taken at intervals of 1 min showing 'normal posture' of animals A, C, D and E and active phase in animals B. *g*, 'normal posture' of animal B and active phases in animals A, C, D and E. *h*, 2½ min after feeding.

postures of *Calliactis* A, C, D, E, and an activity cycle in *Calliactis* B corresponding to the description given earlier. The position in (*b*) was produced by a slow contraction of the margin which was maintained while the column was extended (*c*). Positions (*d*) and (*e*) marked the beginning and end of a peristaltic wave in a subsidiary cycle. The characteristic posture of *Calliactis* B is shown in (*g*). Under normal conditions, not more than 1 or 2 of these animals were active at once. Photograph (*g*), in Fig. 6 shows one instance, however, when all these animals except *Calliactis* B were either closed or in active movement, in two cases due to defaecation. Feeding, as might be expected, initiates an outburst of activity which goes on for at least 15 min. Several closing movements take place in quick succession and various distorted or asymmetrical positions are taken up before the animal returns to its normal posture and behaviour pattern. Photograph (*h*) shows the group 2½ min after feeding. As far as could be seen, the normal rhythmic cycles were resumed within an hour or two, and were continued without marked change until defaecation initiated another outburst of activity about 2 days later.

Three-lever kymograph records of the activities of three of these *Calliactis* (A, C and E) and of 3-loop preparations made from them are shown in Fig. 7. These show the normal patterns of activity in periods outside feeding cycles lasting for 2 or 3 h. The descriptions 'active', 'intermittently active' and

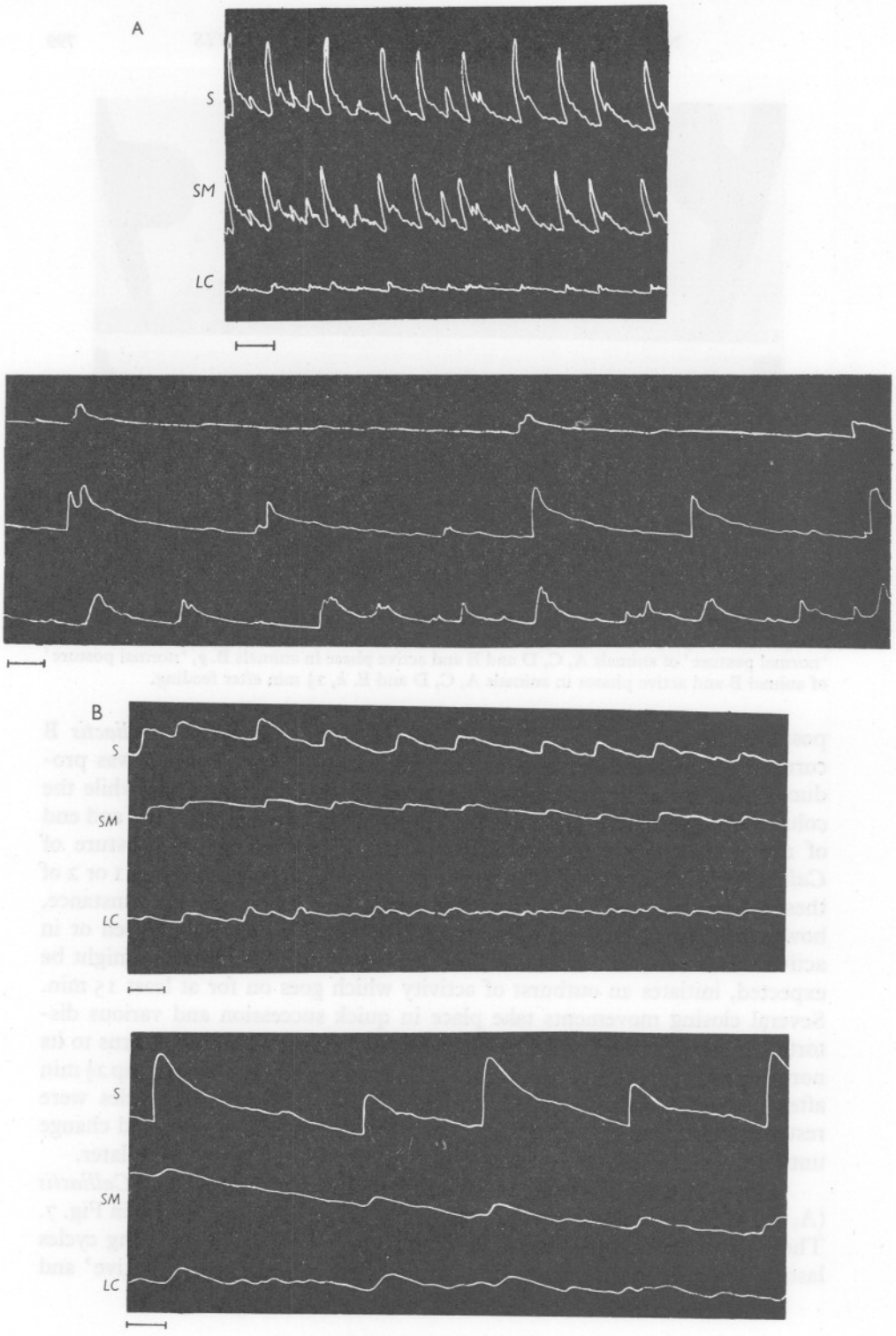


Fig. 7. For legend see opposite page.

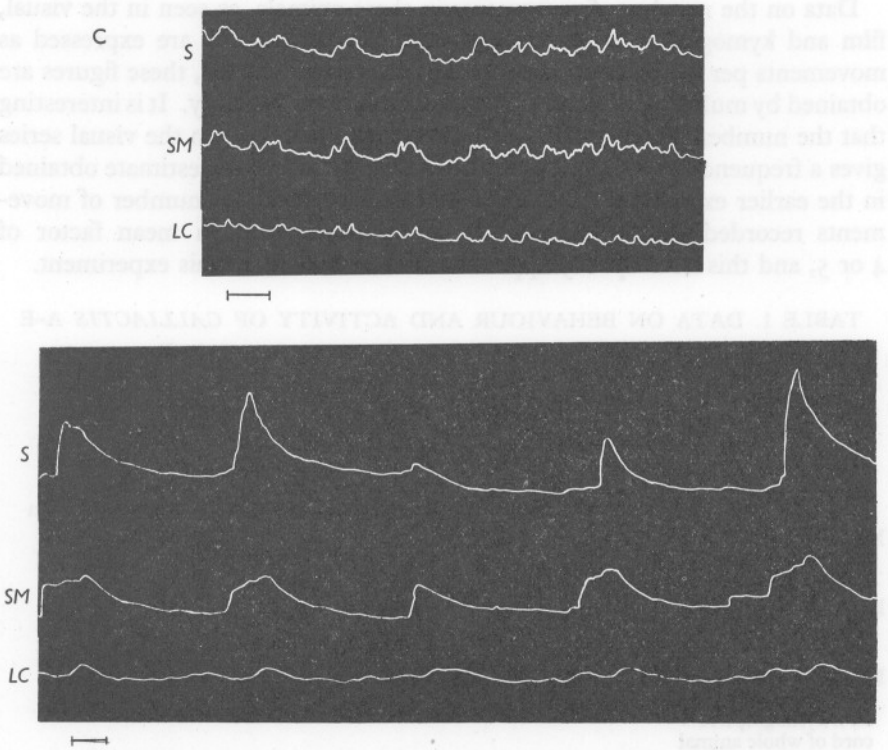


Fig. 7. Records of activity of intact *Calliactis* from the group of five experimental animals (cf. Fig. 6), with threads attached to marginal, submarginal and lower column regions, and records of three-loop preparations made later from the same animals. A, Intact *Calliactis* A (cf. Fig. 6) for 2 h and its 3-loop preparation for 4 h (7 days later); B, intact *Calliactis* C for 3 h and its preparation for 3 h (4 days later); C, intact *Calliactis* E for 2 h and its preparation for 4 h (6 days later). *S*, *SM* and *LC* indicate tracings from sphincter, submarginal and lower column regions in each recording. The scales represent a period of 10 min.

'inactive', which were applied to *Calliactis* A, C and E respectively from their behaviour over many days, are seen here to apply also to some extent to their tracings.

It is not easy to distinguish between active and passive movements at a given region in the intact animal. Big movements of the animal at any level must lead to passive movements of a lever attached to a neighbouring level, and thus the marginal and submarginal levers usually show more or less identical movements in the upper tracings in Fig. 7. In four of the five animals A–E, the submarginal region took the lead in all movements except those which began with a quick contraction, but in animal C, the regular movements began with the margin. Near the base there were many independent movements though the amplitude of these was generally much smaller than at the other levels.

Data on the number of movements in these animals, as seen in the visual, film and kymograph records, are given in Table 1. They are expressed as movements per 24 h, though for the film and visual records, these figures are obtained by multiplying up results for 6 and 20 hr respectively. It is interesting that the number of marginal closing movements observed in the visual series gives a frequency of about 1 per h which is very close to the estimate obtained in the earlier experiment. But this figure falls short of the number of movements recorded in the film and on the kymograph by a mean factor of 4 or 5, and this descrepancy applies to all the animals in this experiment.

TABLE 1. DATA ON BEHAVIOUR AND ACTIVITY OF *CALLIACTIS* A–E

Calliactis	A	B	C	D	E	
Behaviour, posture, etc.	Active, tentacles relaxed, disc depressed	Intermittently active, tentacles erect, disc depressed	Intermittently active, asymmetrical posture	Inactive, tentacles relaxed, disc depressed	Inactive, tentacles trailing, disk level or raised	Mean
No. of closures and partial closures in 24 h visual observation*	35	43	31	12	15	27
No. of marginal movements in 24 h film record†	111	204	105	27	291	148
No. of repetitive marginal movements in 24 h kymograph record of whole animal	74	177	97	211	95	131
No. of co-ordinated movements in 24 h kymograph record of 3-loop preparations	34	49	48	51	32	43

* Calculated from 20 h actual observation.
† Calculated from 6 h film record.

Difficulties in relating kymograph records to visually observed activity were encountered earlier, and it was hoped that the experiment with five *Calliactis* would clarify the matter. Instead, it has only emphasized the individual and phasic differences in the form and frequency of repetitive activity. In *Calliactis* C, D and E, the basic pattern of activity consists of movements hardly visible to the eye, appearing as slight twitches in the film and as small movements of the kymograph levers (Fig. 7 B, C). In *Calliactis* A and B, movements like those in the rhythmic cycles described above, which are associated with fairly conspicuous changes of shape or partial closure, dominate the kymograph records (Fig. 7 A), but with a frequency two or three times as great as the same movements in the visual observations. It is unlikely that such movements would have been overlooked, so it must be assumed that the kymograph records in A and B coincided in time with phases of exceptional activity.

The functions of these movements can only be surmised. However, from the changes of shape and volume accompanying the more conspicuous activity cycles, it might be inferred that some water is expelled from the coelenteron and replenished by fresh water at such times. The smaller repetitive movements of the levers seen in Fig. 7 B and C are due to small movements in the animal which lift the margin and constrict the submarginal region and other parts of the column. These movements are probably carrying out minor pumping and circulating activities, and the pattern is interrupted only at long intervals by the larger movements and closures which could provide for an exchange of water on a bigger scale.

The records of preparations made from these animals differ from those of the whole animals in many respects (Fig. 7). The frequency of the co-ordinated movements is much reduced and, although much closer to the frequency of closing movements as observed visually (Table 1), the preparations show much more regularity. Four out of the five preparations examined gave movements that were very much larger than the movements at the same level in the intact animal, though as the figure shows, the enhancement was not always the same at all levels. However, this may only mean that as preparations the loops were freer to move than in the intact column.

It is interesting that in the preparations, the individual differences noted in the intact animals tend to disappear. The timing and general form of activity in these five preparations were not very dissimilar from one animal to another and bore little relation to the record taken from the whole animal. In the co-ordinated and independent activities of the different loops, these preparations behaved like the preparations described earlier, the submarginal loops being the first to move in all except *Calliactis* C, and the loops at the level of the cinclides showing many movements of their own.

DISCUSSION AND CONCLUSIONS

The activities observed in *Calliactis* provide another example of an apparently almost immobile animal showing a great deal of co-ordinated behaviour occurring at a very slow time scale. But there is nothing simple or stereotyped about these activities. Patterns of behaviour in *Calliactis* are extremely variable with individual differences amongst animals and phasic differences in single animals at different times.

All the observations indicate that in the aquarium the quick closing response is a relatively infrequent occurrence, but it may happen more frequently when the animal is living on the shell with *Eupagurus*. Inconspicuous slow movements comprise most of the neuromuscular activity of the animal, and even a good deal of the activity of marginal sphincter itself. In the study of actinian nerve and muscle, work on the physiology of the slow activities is

obviously very important. Quick facilitated contractions, notwithstanding their many interesting physiological features, are highly specialized activities in which some of the more typical and general properties of the actinian neuromuscular system may be obscured.

We feel that our observations should be regarded chiefly as another contribution to the growing literature on slow-periodic activities in invertebrate neuromuscular systems. Although the evidence from preparations suggests that these activities are co-ordinated, it is difficult to envisage appropriate mechanisms of conduction in the nerve net or intramuscular slow conduction processes to account for the exceptionally slow passage of the co-ordinated movement through the animal. But slow periodicity is a feature of many processes in which neuromuscular activity is not generally regarded as being involved. Dr L. J. Hale of Edinburgh has made a film of the growth of an *Obelia* colony by time-lapse cinematography, and the results seem remarkable to us and highly relevant to the phenomena seen in the activities of anemones. Apparently the growth of the colony is a pulsating process in which advancing movements are followed by partial withdrawals in a rhythmical way. Moreover, the timing of these 'beats' or 'pushes' is of the same order as the timing of the recorded 'beats' in both *Metridium* and *Calliactis*, occurring every few minutes (Hale, personal communication). Perhaps the notion that there is an underlying slow periodicity in the lives of certain organisms, involving their growth and development as well as their behaviour, is one that might be borne in mind in this connexion.

Slow periodic activities are now known to be involved in the behaviour of widely different groups of animals, in burrowing worms (Wells, 1950), in tunicates (Hoyle, 1952), as well as sessile coelenterates. Although these activities are generally described as spontaneous because they often have no obvious external or internal causes, and particularly because they are often seen in isolated preparations, they have many features that deserve further investigation. Koshtoyantz & Smirnova (1955) reported a relationship between the availability of sulphydryl groups and the initiation and maintenance of slow rhythmic movements in *Actinia*. We repeated their experiments on ring preparations of *Calliactis* but did not find that cadmium chloride inhibited, or that cysteine re-started, slow periodic movements in the way they had described. Yet this approach could be very useful if applied generally to this problem. Experiments aiming to reveal the properties of these spontaneous slow periodic activities by testing the action of a wide range of treatments, using metabolic as well as neuromuscular agents, might produce results throwing a great deal of light on this still obscure corner of comparative physiology.

We acknowledge with very warm thanks the help we received from the Director and Staff of the Plymouth Laboratory where much of the work was

carried out. We have also had invaluable assistance from Mr W. Brackenbury, who did the photography, and from Mr Norman MacQueen of the MacQueen Film Organization, who took the film sequence. One of us (M.N.) also thanks Prof. P. B. Medawar, F.R.S., for the facilities and hospitality received at the Zoology Department, University College, London, during several months spent there in 1954–55 as a visiting research worker from Canada.

SUMMARY

Features in the behaviour of the sea anemone, *Calliactis parasitica*, as seen in visual, photographic and kymograph records, are described.

As well as occasional and aperiodic closures, sometimes maintained for several hours, this anemone shows slow, complex, co-ordinated activity cycles whose main components are repeated at fairly regular intervals. These occur several times per hour in most animals, but their form and frequency show many individual and phasic variations. Slow movements of the marginal sphincter contribute to these activities.

Contractions of the submarginal region generally lead the slow co-ordinated movements in whole animals and 3-loop preparations, but tiny marginal twitches often precede them in whole animals. Loops and ring preparations taken near the base show most independent activity.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ABBOTT, B. C., HILL, A. V. & HOWARTH, J. V., 1958. The positive and negative heat production associated with a nerve impulse. *Proc. roy. Soc.*, B, Vol. 148, pp. 149–87.

'Initial' heat production in non-medullated nerve (*Maia*) has been re-examined with improved instruments. A single impulse at 0° C gives an observed deflexion corresponding to two distinct phases of heat: (*a*) heat production of about 9×10^{-6} cal/g nerve within 20 msec of the impulse, immediately followed by (*b*) heat absorption of about 7×10^{-6} cal/g nerve lasting about 300 msec. The net heat of 2×10^{-6} cal/g nerve confirms previous estimates. Heat is contributed by many fibres of varied diameter and velocity of propagation. As a result the positive and negative phases of heat production are, to some extent, masked by the asynchronous arrival at the thermopile of impulses of different velocity. Using probable assumptions for propagation velocity the corrected positive and negative heat production becomes about 14×10^{-6} and 12×10^{-6} cal/g nerve respectively.

In the discussion some possible sources of the heat are considered. The discharge and subsequent recharge of the membrane capacity, though giving positive and negative heat of the observed magnitude have the wrong time relations to be the source of the heat recorded in the present experiments. Heat of mixing in the trans-membrane exchange of Na and K ions may contribute part of the positive heat. The heat production accompanying chemical events in the membrane during its cycle of permeability change is suggested as a likely source of heat, positive and negative.

J.V.H.

ABBOTT, B. C. & LOWY, J., 1958. Contraction in molluscan smooth muscle. *J. Physiol.*, Vol. 141, pp. 385–97.

Certain mechanical and thermal events during activity of long-fibred smooth molluscan muscles have been studied. In all cases the speed of shortening was found to be related to load during isotonic contraction in a manner approximating closely to Hill's characteristic equation. It was also observed that shortening of stimulated muscle is accompanied by extra heat production proportional to shortening. In the smooth muscles studied, the constant *a* for shortening heat differs from the value *a* in the characteristic equation.

The smooth muscles develop greater tensions, have a slower maximal shortening velocity, a smaller maintenance heat rate, and relax more slowly than any other type of muscle hitherto studied.

Following a release during the plateau of an isometric tetanus, re-development of tension decreases with speed of release. Fall of tension after stretch of tetanised muscle also decreases with speed of stretch. For a given extent of lengthening, the maintained tension increase above isometric is more pronounced than in vertebrate skeletal muscle, i.e. the active smooth muscles show a greater rigidity.

The ability of the smooth muscles to maintain high tensions economically is discussed in terms of their slow relaxation, small maintenance heat rate, and the extent of 'setting' within the contractile material as a result of activity. Tension is assumed to be maintained by spontaneous random excitation of the muscle, rather than by a special 'catch' mechanism.

J.L.

ABBOTT, B. C. & LOWY, J., 1958. Mechanical properties of *Helix* and *Mytilus* muscle. *J. Physiol.*, Vol. 141, pp. 398–407.

Experiments with smooth muscle preparations from *Helix* and *Mytilus* have shown that maximum isometric tension is developed at about the longest length reached by the muscles in the animal's body (reference length). When stretched beyond reference length, the muscles exert resting tension. This is not due to spontaneous activity.

Relaxation, following isometric contraction, and stress relaxation (decay of tension following rapid stretch of resting muscle) are not identical processes as claimed by Bozler. Their time courses differ and stress relaxation is not significantly affected by changes in temperature. J.L.

CARLISLE, D. B., 1958. Niobium in Ascidians. *Nature, Lond.*, Vol. 181, p. 933.

Niobium has been shown to be present in some species of Ascidians. In *Molgula manhattensis* some individuals possess vanadium, others niobium. The two elements do not appear to be present in significant amounts in the same individual. D.B.C.

CARLISLE, D. B. & HUMMERSTONE, L. G., 1958. Niobium in sea-water. *Nature, Lond.*, Vol. 181, pp. 1002–3.

There is enough niobium in inshore sea water to supply the needs of those ascidians which have been shown to contain it. The method is described for detecting small amounts of the element in sea water. The different samples vary between 0·005 and 0·1 μg/l. D.B.C.

DENTON, E. J. & WALKER, M. A., 1958. The visual pigment of the conger eel. *Proc. roy. Soc.*, B, Vol. 148, pp. 257–69.

New methods of studying the spectral absorption of intact retinae are described. Using these methods the retina of *Conger conger* (L.) has been studied and the retinal spectral absorption curves are compared with those obtained on retinal extracts made with digitonin solution. The retina of the conger, like that of deep-sea fish, is golden in colour, its absorption curve being similar in shape to that of frog rhodopsin but with its maximum displaced about 16 mμ towards the blue end of the spectrum. The absorption curve of unbleached retinae is displaced about 4 mμ towards the red end of the spectrum from the absorption curve of unbleached retinal extract, but, when an estimated correction for possible yellow impurities in the extract is made, this displacement is only one of 2 mμ. The change in optical density of the dark-adapted retina on bleaching with strong white light is 0·6 at $\lambda = 484$ mμ: this probably represents a retinal density for unbleached pigment of about 0·8. The visual pigment in the intact retina is approximately twice as effective as simple calculations based on extracts would predict. The absorption of light by the retina is dominated by the principal photosensitive pigment, whilst the screening of the rods, due to the absorption of light by the layers of retina lying between the rods and the internal limiting membrane, is trivial. E.J.D.

NORTH, W. J. & PANTIN, C. F. A., 1958. Sensitivity to light in the sea-anemone *Metridium senile* (L.): adaptation and action spectra. *Proc. roy. Soc.*, B, Vol. 148, pp. 385–96.

The sea-anemone *Metridium senile* responds to illumination by local contraction of the longitudinal musculature, particularly of the parietal system. No specific receptors have so far been identified for this response. The phenomena of light and of dark adaptation are shown by the photoreceptive mechanism. The action spectra of white individuals show a maximum at about 490–520 mμ. Relative to this the sensitivity in the region 550–600 mμ varies in different individuals. The possible presence of two distinct photosensitive systems is mentioned. Sensitivity decreases very rapidly beyond 600 mμ. Action spectra of the white, red and brown coloured varieties of the species are compared in relation to the absorption spectra of tissues obtained from the three types. It is concluded that the pigments which give the characteristic body colour in the red and brown varieties act as filters. Comparison with the white variety indicates that these pigments probably do not act as specific photosensitive substances. It is pointed out that the differential sensitivity of the coloured varieties appears to have no selective influence on the occurrence and distribution of the different coloured varieties.

C.F.A.P.

ROBSON, ELAINE A., 1957. The structure and hydromechanics of the musculo-epithelium in *Metridium*. *Quart. J. micr. Sci.*, Vol. 98, pp. 265–78.

Musculo-epithelial cells in the mesenteries of the sea-anemone *Metridium senile* contribute both to the muscle-field above the mesogloea and to the epithelium. The epithelial elements are connected to the muscle fibres by vertical protoplasmic strands, and the intervening space is occupied by fluid. This subepithelial fluid forms a thin layer between the epithelium and muscle-field.

Epithelial elements from contracted mesenteries are taller than those from stretched tissue. As the area of the mesentery decreases during contraction, a reversible change from pavement to columnar epithelium takes place. The epithelium is able to follow rapid contractions without delay, owing to the hydrostatic action of the subepithelial fluid in thrusting it outward. Although considerably elastic, the epithelium does not appear to be active during contraction or relaxation and is moved passively.

Only the coelenterates possess true musculo-epithelium, and it may be modified, as in certain regions of *Metridium*. Analogous systems occurring in higher animals are discussed. It is possible that the subepithelial fluid of *Metridium* not only functions hydrostatically, but that it and the mesogloeal fluid together form an 'internal medium' providing some degree of biochemical co-ordination.

E.A.R.

SUTTON, MURIEL F., 1957. The feeding mechanism, functional morphology and histology of the alimentary canal of *Terebella lapidaria* L. (Polychaeta). *Proc. zool. Soc. Lond.*, Vol. 129, Part 4, pp. 487–523.

The food of *Terebella lapidaria* is collected by the mucus-secreting tentacles and passed to the upper lip and thence to the mouth. The lower lip is not concerned with food ingestion; its function is to provide mucus and cement for tube building.

The complex musculature of the lower lip has been described and separate coelomic cavities within upper and lower lip regions noted. The musculature of upper and lower

lips together with the varying pressures of the coelomic fluid in upper and lower lip regions and in the thorax are responsible for lip movements.

The structure of the alimentary canal has been described in some detail, and, in particular, an account has been given of a complex type of mucous secretion involving a glandular epithelium and an adjacent glandular tissue. In no part of the alimentary canal is there a peritrophic membrane, *sensu stricto*.

The possible course of evolution of the arthropod alimentary canal from that of a polychaete ancestor is discussed. M.F.S.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1957–58

The Council have to report with regret the death of two distinguished members of the Association: Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O., who represented the Fishmongers' Company on the Council from 1937 to 1946 and was a Vice-President of the Association from 1948 until his death; and Prof. H. U. Sverdrup, Director of the Norwegian Polar Institute, who was elected an Honorary Member of the Association in 1949.

The Council and Officers

Four ordinary meetings of the Council were held during the year, two in the rooms of the Royal Society, one at Fishmongers' Hall, and one at Plymouth. At these the average attendance was sixteen. The Council wish to record their thanks to the Prime Warden and Court of the Fishmongers' Company for their hospitality in entertaining members of the Council to lunch on 23 October 1957, and making their Court Room available for the meeting on that afternoon.

It has been a source of much pleasure to the Council that our Honorary Treasurer, Mr Harrison S. Edwards, has been Prime Warden of the Fishmongers' Company during the year.

The Plymouth Laboratory

During the year the new outside circulation tanks have been completed and the new pumps installed. The circulation from the new sea-water reservoirs has now come into operation, and this supplies the research tanks on the first floor of the main laboratory as well as most of the outside tanks.

Minor alterations have been made to enlarge the room in the north building adjoining the dark-room, and it has now been fully equipped for photography.

Aquarium

During the year structural alterations were made in the old sea-water reservoirs whereby silt from the water returning from the aquarium is trapped in one of the reservoirs. From this reservoir clean water overflows into the other, from whence it is pumped back to the aquarium. As a result of this the water in the aquarium tanks is now exceptionally clear.

Owing to the breaking up of their slate walls several tanks on the south side of the aquarium have developed serious leakages. Two of them had to

be emptied and put out of use during the busiest period in the summer. Temporary repairs to four tanks have been effected, but it is evident that rebuilding of the tanks cannot be much longer delayed.

Plans are in preparation for rebuilding, and Dr D. P. Wilson, in company with our architect, Mr F. L. Preston, F.R.I.B.A., of Messrs Easton and Robertson, visited the recently reconstructed aquarium of the Oceanographical Institute at Monaco in September.

Work on reconstruction of the tanks will probably begin in the autumn of 1958 and this has been made possible by generous grants from the Nuffield Foundation and other sources which are recorded on page 23 of this report.

Research Ships

The three research ships have operated regularly throughout the year. R.V. 'Sarsia' has satisfactorily completed her first four years' continuous machinery survey and special survey required by Lloyd's Register of Shipping. R.V. 'Sula' has also satisfactorily completed her second four-year continuous machinery survey. During the year a new rudder stock was fitted, and a heat exchanger has been fitted enabling the engine to be cooled by fresh water.

M.V. 'Gammarus' has been running continuously, but a thorough inspection of her hull will soon be necessary.

Ray Lankester Investigator

The Council have pleasure in reporting that Prof. J. E. Harris, F.R.S., has been appointed Ray Lankester Investigator to work at the Plymouth laboratory in 1958.

Staff

Dr H. W. Harvey, C.B.E., F.R.S., retired from the staff of the Plymouth laboratory on 31 March 1958. The Council wish to record their deep appreciation of Dr Harvey's services to the Association over a period of nearly 37 years. His distinguished researches on the productivity of the sea and the physiology of diatoms have added much to the international reputation of the Plymouth laboratory. The good wishes of the Council go with him on his retirement. Dr Harvey was appointed Commander of the Order of the British Empire in the New Year Honours for 1958.

Miss D. Ballantine resigned from the staff of the Plymouth laboratory in January 1958 on her marriage.

Dr E. D. S. Corner joined the staff of the Plymouth laboratory as Senior Scientific Officer on 1 September 1957. He has been seconded to the International Paints Research Fellowship for the year ending 31 August 1958.

Dr B. C. Abbott left in August 1957 on special leave of absence to work in the University of California at Los Angeles.

Mr B. R. Jewell has been appointed temporary Scientific Officer on the staff of the Plymouth laboratory during Dr Abbott's absence.

Dr L. H. N. Cooper attended meetings of the International Union of Geodesy and Geophysics in Toronto and of the International Council for the Exploration of the Sea in Bergen, in September and October 1957.

Dr D. B. Carlisle attended the second International Symposium on Neurosecretion in Lund in July 1957. He also visited the Kristineberg Marine Laboratory and the Max-Planck Institute for Biochemistry in Munich during the year.

Mr F. A. J. Armstrong attended the meeting of the International Council for the Exploration of the Sea held in Bergen in September and October 1957.

Dr T. I. Shaw attended a Colloquium on the Ecology of Marine Algae held at Dinard in September 1957 under the auspices of the Centre National de la Recherche Scientifique.

Occupation of Tables

The following one hundred and forty-eight workers have occupied tables at the Plymouth laboratory during the year:

E. Adams, Plymouth (Library).
V. P. Agrawal, London (Mouthparts and feeding of amphipods).
R. McN. Alexander, Cambridge (Swim bladder of teleosts).
Dr J. S. Alexandrowicz, Plymouth (Crustacean nervous system).
T. D. Allan, Cambridge (Geology of continental shelf).
Dr Daphne Atkins, Plymouth (Ciliary mechanisms of brachiopods).
T. B. Bagenal, Millport (Fecundity of plaice).
R. Bassindale, Bristol (Barnacle morphology).
Dr J. S. Bradshaw, La Jolla (Foraminifera).
Dr Anna M. Bidder, Cambridge (Digestive system in cephalopods).
E. J. Binyon, London (Tonic regulation in *Asterias*).
Dr P. E. Brockman, Plymouth (Library).
Miss S. M. L. Bocks, London (General).
Q. Bone, Oxford (Feeding mechanisms and neurosecretion in *Amphioxus*).
A. D. Boney, Plymouth (Ecology of red algae).
Dr Eleanor M. Brown, London (Parasitic protozoa).
Sir Edward Bullard, F.R.S., Cambridge (Geology of continental shelf).
Dr C. Burdon-Jones, Anglesey (Gastropods).
Miss E. A. M. Burley, Leicester (Library).
R. F. Burton, London (General).
Mrs P. A. Caldwell, Plymouth (Library).
Dr P. C. Caldwell, Beit Memorial Fellow; Alan Johnston, Lawrence and Moseley Research Fellow (Muscle and nerve physiology).
G. W. Cambridge, Leeds (Pharmacology of lamellibranch muscle).
L. Carter, Brixham (Library).

P. E. CLOUD, Jr., Washington (Oceanography).
J. W. COLES, London (Nematodes parasitic on sea-weeds).
D. J. COLLINS, Plymouth (Library).
R. G. COLLINS, Penzance (Library).
Dr E. D. S. CORNER, International Paints Research Fellow (Effects of toxic substances on marine organisms).
Miss W. A. M. COURTNEY, London (Respiration and feeding of cirratulids).
W. D. G. COX, Plymouth (Library).
Dr D. J. CRISP, Anglesey (Ship design).
C. J. CROFT, Plymouth (Library).
Dr R. I. T. CROMARTIE, Cambridge (Quinone pigments of *Antedon*).
R. I. CURRIE, N.I.O. Wormley (Productivity of the sea).
K. W. DAISLEY, Shinfield (Vitamin B_{12} in sea water).
Dr R. PHILLIPS DALES, London (Metabolism of polychaetes).
P. M. DAVID, Godalming (Oceanic squid).
B. N. DESAI, Anglesey (Gastropods).
P. S. B. DIGBY, London (Tissue culture; plankton).
Miss E. J. DIMELOW, New Brunswick (Physiology of *Antedon*).
Dr D. T. DONOVAN, Bristol (Submarine geology).
Capt. J. T. DUNBAR, Kingsbridge (Library).
Dr E. ELKAN, Watford (Pituitary and saccus vasculosus of fishes).
Dr R. ENDEAN, Brisbane (Vanadium and iron in ascidians).
D. ETHERINGTON, London (*Phascolion*).
Mrs D. ETHERINGTON, London (*Ectocarpus*).
Surg.-Lt. R. J. FALLON, R.N., Plymouth (Library).
Dr L. R. FISHER, Reading (Vitamin A in zooplankton).
L. H. FLAVILL, Cambridge (Geology of continental shelf).
R. F. H. FREEMAN, London (Respiration of *Scrobicularia*).
Dr VERA FRETTER, Reading (Prosobranchs).
Dr T. GASCOIGNE, London (*Pelta*).
Dr J. B. GILPIN-BROWN, Yelverton (*Nereis*; experimental light trapping).
E. GOTTLIEB, Haifa (General).
Prof. A. GRAHAM, Reading (Prosobranchs).
Dr J. GREEN, London (Parasites of crustacea).
D. N. F. HALL, Colonial Office (Penaeid prawns).
R. HAMOND, Holt (Library).
Dr J. P. HARDING, London (Harpacticid nauplii).
M. G. HARDY, Reading (Rhythmical activity in bivalves).
Prof. J. E. HARRIS, F.R.S., Bristol (Vertical migration of copepods).
D. HEDDLE, Oxford (Behaviour and histology of asteroids).
Dr R. H. HEDLEY, London (Foraminifera).
B. T. HEPPER, Conway (Lobster marking).
E. F. HERMANN, Copenhagen (Physical oceanography).
Prof. A. V. HILL, F.R.S., London (Heat production in nerve).
Dr M. N. HILL, Cambridge (Structure of the continental Shelf).
M. HORNSEY, Cambridge (General).
R. V. HOWARTH, London (Heat production in nerve).
Dr D. I. D. HOWIE, Dublin (Culture of *Bucephalopsis*).
Dr G. M. HUGHES, Cambridge (Respiratory movements of teleosts).
D. J. HUME, Teignmouth (Library).
O. D. HUNT, Newton Ferrers (Library).

Dr C. H. JELLARD, Plymouth (Library).
Dr JANET JELLARD, Plymouth (Library).
Miss P. M. JENKIN, Bristol (Library).
Miss J. M. JOHNSON, London (General).
Dr JOANNA M. KAIN, Port Erin (Isolation of *Prorocentrum*).
P. J. KEADY, Galway (Plankton; Library).
Dr G. Y. KENNEDY, Sheffield (Porphyrins and chlorophyll).
Dr R. D. KEYNES, Cambridge (Nerve physiology of squid).
M. C. KINGWELL, South Brent (Library).
Prof. L. H. KLEINHOLZ, Oregon (Crustacean endocrinology).
Sir FRANCIS G. W. KNOWLES, Bart, Marlborough (Crustacean endocrinology).
Miss A. KUKU, London (General).
Dr MARIE V. LEBOUR, Plymouth (Decapod crustaceans).
Dr J. LLEWELLYN, Birmingham (Trematode parasites of fishes).
Dr G. A. C. LYNCH, Plymouth (Library).
Prof. IRENE MANTON, Leeds (Marine flagellates).
Dr SHEINA M. MARSHALL, Millport (Respiration of *Calanus*).
A. L. MARTIN, London (Feeding and digestion in gammarids).
D. H. MATTHEWS, Cambridge (Geology of continental shelf).
R. B. MAYNE, Plymouth (Library).
Prof. J. L. MOHR, Los Angeles (Protozoan parasites of crustacea; Mesozoa).
Miss F. M. E. MOLLOY, Harpenden (Digestion in mysids).
Mrs B. BEECHER MOORE, London (Digestive glands of *Idotea*)
Dr J. E. MORTON, London (Mollusca).
L. A. MOUND, London (General).
Dr MARGARET NAYLOR, Hull (Cytology of *Phaeophyta*).
Prof. LILY NEWTON, Aberystwyth (Algae).
Dr C. I. O. OLANIYAN, Nigeria (Library).
Mrs E. OLDFIELD, Guildford (Embryology of *Lasaea*).
Dr A. P. ORR, Millport (Respiration of *Calanus*).
Prof. F. PAUTSCH, Gdynia (Chromatophores of crab zoeas).
C. R. PEARSON, Brixham (Library).
Miss C. S. PEARSON, Oxford (Brains of fish).
Dr R. B. PIKE, Millport (Decapod larvae).
Dr W. T. W. POTTS, Birmingham (Adductor muscle of *Pecten*).
Cdr. C. F. B. POWELL, R.N. (Rtd), Plymouth (Library).
J. D. PYE, London (Nervous chromactivation in teleosts).
A. M. QURESHY, London (Blood parasites of fishes).
Miss P. M. RALPH, Wellington, N.Z. (Hydroids and medusae).
Dr F. A. RICHARDS, Woods Hole (Chemical oceanography).
Dr F. H. RIGLER, Toronto (Ion exchange in *Bryopsis*).
Prof. P. ROA MORALES, Venezuela (Chemistry of sea water).
M. B. V. ROBERTS, Cambridge (*Myxicola* muscle).
A. H. W. ROBINSON, Leicester (Shallow water morphology in Start Bay)
G. RODRIGUEZ, Venezuela (Ecology of sandy shores).
Prof. FINDLAY E. RUSSELL, Los Angeles (Toxins of weevers).
M. SALEEM, Manchester (Crustacean mouth parts).
Miss R. S. M. SAVAGE, London (General).
R. J. SKAER, Cambridge (General).
Dr EVE C. SOUTHWARD, Plymouth (Polychaetes).
Dr S. SMITH, Cambridge (Library).

B. W. SPARROW, Newton Ferrers (Library).
Miss F. A. STANBURY, Plymouth (*Cladophora*).
O. SUDDABY, Plymouth (Library).
Dr MURIEL F. SUTTON, London (Embryology of salps).
Dr T. K. SZELA, Kettering (Library).
H. THIEL, Hamburg (General).
G. E. WALSTER, Plymouth (Glycolysis in *Maia*).
Dr B. WERNER, List a Sylt (Hydroids and medusae).
Dr MARY WHITEAR, London (Proprioreceptors in crustaceans).
Prof. W. F. WHITTARD, F.R.S., Bristol (Submarine geology).
J. H. WICKSTEAD, Colonial Office (Plankton).
Dr J. J. WOLKEN, Pittsburg (Photoreception).
M. YOSHIDA, London (Naphthaquinone pigment in *Psammechinus*).

Among the many other scientists who have visited Plymouth during the year to see the general work of the laboratory and to discuss problems with members of the scientific staff, the following have come from overseas: Dr G. J. Schuringa (Holland), P. de Wolf (Holland), A. M. Christensen (Copenhagen), Prof. K. Sembrat (Poland), Dr D. Goldmann (U.S.A.), S. Nagappa (India), Prof. Dr Gunnar Thorson (Copenhagen), Prof. F. E. Eggleton (U.S.A.), Dr J. Verwey (Holland), Dr P. Korringa (Holland), Dr Windemuller (Holland), Dr H. Holtedahl (Bergen), Prof. S. F. Bush (Natal), Dr P. Radoman (Yugoslavia), Prof. R. A. Jasper (Canada), Dr P. Gurtner (Rome), Mrs N. Tirmizi (Pakistan), Miss M. Kalk (Johannesburg), Dr E. Lisitzin (Finland), Dr F. D. Ommanney (Hong Kong), Dr Irving Friedman (Washington), Dr V. Worthington (U.S.A.), F. P. Mendes (Lisbon), Prof. L. R. Richardson (Wellington), Dr A. G. Wurtz (France), Mr and Mrs Foster (U.S.A.), Mrs E. Finch (Australia), V. Krishnamurthy (India), Dr Katherine Tansley (U.S.A.), S. J. Holt (Rome), J. W. Brodie (New Zealand), Dr Talbot H. Waterman (U.S.A.), W. G. Morison (Sarawak), J. L. Reid, Jr. (U.S.A.), Prof. J. Tokida (Japan), Dr R. W. Hiatt (Hawaii), Dr M. S. Gordon (U.S.A.).

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by forty students from the following Universities: Oxford, Cambridge, Glasgow, Aberdeen, London, Liverpool, Sheffield, Reading, Southampton, Exeter, University College of North Wales, Aberystwyth and Regent Street Polytechnic.

Also during the Easter Vacation Mr J. F. Eggleton and Miss J. Kenworthy brought a party of thirteen from Hinckley Grammar School; Mr K. W. Wilkes brought four boys from Harrow School; Mr G. Thomas brought three boys from Ilford County High School, and Dr Margaret Christianson a party of nine girls from Harrow County Girls School.

Prof. J. E. Smith, F.R.S., Dr. G. E. Newell and Dr J. E. Morton conducted a course in marine biology in September for twenty-two students, mainly from Queen Mary College. Also during September Dr Margaret Naylor, of the University of Hull, conducted a course in marine botany for fifteen students.

Scientific Work of the Plymouth Laboratory Staff

Sea Water and Plankton

Dr L. H. N. Cooper has continued his study of the effect of deep oceanic circulation upon the biological productivity of shallow seas. He has prepared four papers by invitation. One was for 'Travaux du Centre de Recherches et d'Etudes Océanographiques' on 'Experimental Oceanography in the Mediterranean'. He has suggested that the sea area off the Italian Riviera, including the Capraia Channel, may be used as a small-scale model for studies on the formation of North Atlantic deep water. Another on radioactive tracers as tools for the oceanographer was delivered before the Geophysical Section of the Royal Astronomical Society. The third under the title 'The effect of continental slopes upon vertical and horizontal circulation and upon energy transfer at depth in the North Atlantic Ocean' was written to be presented at the Toronto meeting of the International Association of Physical Oceanography. It was then found that at least a part of the variations in oxygen upon which conclusions hung was due to absorption by corrosion products in the reversing bottles. Though the conclusions are probably sound, publication must be postponed pending repetition of the work with bottles which are above suspicion. This experience was reported in lieu of the paper planned. It was possible also to report that within three weeks in June 1956 all the water in the north-eastern Bay of Biscay between 300 and 3800 m was uplifted bodily by 75 m. The cause is not understood.

At the symposium held at Bergen under the auspices of the International Council for the Exploration of the Sea on Measurement of Primary Production in the Sea Dr Cooper reported on the measurement of production by means of the consumption of nutrients. This method, once so powerful, is not easily adapted to assess the fine structure of events which we now need to know. In the English Channel it has served its turn and other means of attack need now to be sought.

At the Toronto meeting Dr Cooper was appointed chairman of a committee of the International Association for Physical Oceanography, on Chemical Oceanography, one of whose assignments is to consider standardizing methods for the analysis of sea water. He favours the devising of standards of performance with which methods must comply. Standards of this kind do not hinder advance whilst inspiring confidence in results. It remains to be seen whether the necessary intercomparison of methods between laboratories is feasible.

Dr Cooper and Dr T. I. Shaw have carried out a theoretical study on the state of iodine in sea water. The oxidized form of the element, which various authors have shown to co-exist with iodide in the sea, is probably hypoiodous acid. This hypothesis accounts for a wide range of observations, such as the

ratio of oxidized to reduced forms, the iodine content of the atmosphere and the distribution of iodine between partially enclosed sea areas. The work should prove of value in predicting the oxidation states of other marine materials which undergo ready reactions with iodide and iodine.

Mr F. A. J. Armstrong has continued the monthly cruises to Station E 1, and analyses for phosphate, total phosphorus and silicate up to the end of 1956. Since then this work has been done by Mr E. I. Butler. In 1956 the winter maximum phosphate concentration was 0·51 μg atom P/l., a normal value in recent years, and markedly lower than the exceptional high value in 1955. The station was worked four times in four weeks in March and April, when there was a period of bright settled weather; changes in nutrient concentrations were observed during the spring outburst of plankton. There is good reason to suppose that the water mass at the station did not change during this period. Consumption of phosphate was first rapid and then slowed down. Silicate fell sharply and linearly during the first three weeks, to exceptionally low values (0·08–0·09 μg atom Si/l. even below the photosynthetic zone). This requires explanation, since at the time there was a thermocline and vertical mixing should not have had much effect in impoverishing the whole water column. Moreover, phosphate was not unusually low in the deeper water. During these three weeks, the ratio Si:P consumed was about 10:1 by weight. If the phytoplankton were mainly diatoms, this would suggest that they were deficient in silicon, and it is possible, since they sometimes sink rapidly in spring, that they continued, at least for a while, to remove silicon from the deeper water, even if unable to make normal growth. A week later silicate in the deeper water had increased markedly. These results are being prepared for publication. In 1957 Mr Armstrong has done analyses for ammonia by distillation followed by the indophenol blue method, and for total inorganic nitrogen by determination of ammonia after reduction with Raney nickel. The results at Station E 1 show maximum inorganic nitrogen concentrations of about 10 μg atom N/l., with ammonia about 3 μg atom N/l. Minimum values were about one-tenth of these. The results resemble those got by Dr Cooper in 1933. Simpler methods for ammonia and nitrate are being sought, and some success has been achieved in the reduction of nitrate to nitrite under ultra-violet irradiation. In distilled water, 80% reduction has been attained in the presence of urea, with manganese as catalyst, but in sea water recovery is only about 50%. Further work on this and on changes in nitrogen contents of sea water during storage is in hand.

The method and results of analysis for iron content of sea water have been published in Vol. 36, No. 3, of the *Journal*. The final model of the filter absorptiometer has been made and tried out at sea. An account of it is in preparation.

Dr E. D. S. Corner, in collaboration with Dr F. H. Rigler of Toronto

University, has made a study of the behaviour of mercury in sea water. Experiments with ^{203}Hg-labelled mercuric chloride have shown that stored sea-water solutions of this compound lose mercury at a fairly rapid rate which is significantly increased when nutrients favouring the growth of bacteria are added to the sea water, and greatly diminished when the sea water is treated with various bactericides. The conditions under which bacteria develop in solution also influence the loss of mercury qualitatively. For whereas most of the mercury lost from plain sea water is in the form of a product which volatilizes from solution, a large amount of the mercury lost from sea water containing added nutrients is taken up by the walls of the glass storage vessel. An account of this work has been published in Vol. 36, No. 3, of the *Journal*.

Dr H. W. Harvey has continued experiments on rate of growth of *Phaeodactylum tricornutum* under different environmental conditions, with the aim of indicating factors, other than those already recognized, which may affect the growth rate of phytoplankton in nature. Experiments in which *Phaeodactylum* was grown in alternating periods of 12 h light and 12 h darkness showed a greater rate of carbon assimilation during illumination than when grown in continuous light. The increase was more than was accounted for by the increase in chlorophyll during darkness, and indicated that there was also a build-up during the dark periods of the substance, or its substrates, which actuates the Blackman dark reaction. This indication, based on crude experiment, was found to conform with the conclusion arrived at by Tamiya in Japan from extensive experiments with a freshwater *Chlorella*.

In cultures of *Phaeodactylum* a marked physiological change takes place in the cells when the pH rises above 8·8, resulting in much slower growth rate and the accumulation of fatty material in the cells. Experiment indicated that this was in part due to reduced availablity of iron in the medium. This marine alga, notably unexacting in its requirements for growth, was trained to grow in 1% sea water diluted with 0·024N sodium bicarbonate; it raised the pH of this medium to 11·5 before growth ceased. An account of these exploratory experiments has been circulated to colleagues in other laboratories who are engaged upon allied problems.

A second edition of Dr Harvey's book, *Chemistry and Fertility of Sea Waters*, containing a summary of advances made since the book was written in 1954, has been published by the Cambridge University Press.

Dr Mary W. Parke has continued her study of the form range in the genus *Chrysochromulina* (Chrysophyceae), and a further paper, in collaboration with Prof. Irene Manton and Mr B. I. Clarke of Leeds University, was published in Vol. 37, No. 1 of the *Journal*. In this paper a description is given of the anatomy of the haptonema which shows that its structure differs from that of a flagellum in having seven peripheral strands and none in the centre, as compared with nine peripheral and two central in a flagellum.

Throughout the year monthly samples of sea water have been taken at E 1, at the same time as the hydrographic samples were taken. From these samples the seasonal distribution of the already described nanoplankton forms, and of those known only by a serial number in her collection, has been recorded. Several new forms were observed and some of these have been isolated in unialgal culture. The samples have also been used for testing out methods for quantitative and qualitative estimations of these small forms as a preliminary to doing routine monthly counts. With the co-operation of Mr E. I. Butler the number of samples taken for examination has now been increased and the first series taken from L 2–L 6 and E 1 (surface to 73 m) in September has already been examined and cultured, and interesting information on the range of distribution of some species has been obtained.

Under the supervision of Dr Parke, Miss I. Adams has maintained the collection of unialgal cultures of marine phytoplankton organisms throughout the year. She has also isolated a considerable number of new forms, belonging mainly to the classes Chrysophyceae and Dinophyceae, for the use of Dr Parke and Miss Ballantine. From January to the end of November, 160 cultures had been distributed for research purposes to institutions in this country and abroad, in addition to well over 100 l. of cultures of different organisms that had been grown for use by scientists working in the laboratory.

Dr S. T. Cowan, director of the National Collection of Type Cultures of the Medical Research Council, very kindly offered to try out the freeze-dry method on four cultures, representing four different algal classes, to test whether or not these marine organisms would survive this treatment. Unfortunately, however, it was unsuccessful for the organisms tested.

A paper, in collaboration with Miss D. Ballantine, on a dinoflagellate, *Exuviaella mariae-lebouriae*, n.sp., which has been maintained in culture at Plymouth since 1949 has been published in Vol. 36, No. 3, of the *Journal*.

Through the kindness of the Director, Dr D. J. Crisp, it was possible for Miss D. Ballantine to work at the Marine Biology Station, Menai Bridge, for two months, in collaboration with Dr C. P. Spencer, on the purification of extracts of the toxin from *Gymnodinium veneficum*. The preliminary extraction had been done previously at Plymouth by Dr B. C. Abbott and Miss Ballantine. Some degree of purification was attained, and the properties of the toxin indicate that it is probably a saponin. Further work on this has been abandoned for the present due to the variable toxicity of the cultures. A variety of substances (vitamins, amino-acids, etc.) have been added to cultures in an attempt to increase the growth rate of the organism and/or the toxicity, but no success has been obtained, and the experiments have been discontinued.

Miss Ballantine is now testing for toxicity to fish all the cultures in the Plymouth Collection. As yet only *G. veneficum* and *Prymnesium parvum* have been found to be toxic. She is also continuing work on the marine dino-

flagellates, both on the collection of records from observation of water samples, and on systematic and taxonomic problems in some genera.

Dr F. S. Russell, in continuation of his observations on medusae collected from deep water, has described a new species of scyphomedusa, *Atolla vanhöffeni*. He has also described a new hydromedusa, *Krampella dubia*, whose systematic position is not yet clear. This medusa has the peculiar strands of tissue running through the mesogloea from the radial canals to the exumbrella surface also seen in *Amphinema krampi*. Such strands have never been described in any other medusae. The above descriptions have been published in Vol. 36, Nos. 2 and 3, of the *Journal*. Dr Russell is now beginning to collect the necessary data for the preparation of a monograph on British Scyphomedusae.

Mr G. M. Spooner has continued examination of Amphipoda from the deep-water stations worked by R.V. *Sarsia*. These are mostly of the suborder Hyperiidea, a group widely spread in plankton and in the deep water of the oceans, but virtually unrepresented amongst the littoral or benthic fauna. The scattered literature of the group has been indexed, and, as sorting and identification of samples proceeds, a synopsis is being made of the chief descriptions and illustrations of individual species, and a simplified working key for the identification of the known world species is being compiled. Existing literature is still predominantly taxonomic or distributional. Other biological data are normally hard to obtain, for instance, on specialized feeding habits and on the peculiar commensal relationships between hyperiids and medusae or salps. The new facilities for working at sea may afford chances for advancing this knowledge.

Mr P. G. Corbin has continued his examination of the regular stramin ring trawl collections. No change in the low level of macroplankton production associated with the prevailing *Sagitta setosa* conditions has been observed in 1957.

Dr. A. J. Southward has made some preliminary observations on the distribution of plankton animals in the western Channel. It is hoped that new sampling techniques will allow rapid surveys to be made of the chief indicator species. Earlier attempts to use cirripede larvae for this purpose will be continued.

Dr D. P. Wilson has been able to amplify the account of the biology of *Ianthina janthina* (L.) which was published in Vol. 35, No. 2, of the *Journal*. A large shoal of young specimens of this species stranded in the Scilly Islands in March and April 1957 and nearly 200 perfect specimens less than half an inch high were obtained. Measurements of these small shells fully confirmed the conclusion previously reached, based mainly on large shells, concerning the change in shape of the shell as it ages. A note has been published in Vol. 37, No. 1, of the *Journal*.

Dr Wilson and Mr Armstrong have completed an account, in Vol. 37, No. 1,

of the *Journal*, of the work they did in 1954 and 1955 on biological differences between sea waters. Whilst several new facts emerged, these do not appear to lead any nearer to the discovery of the main cause of the differences. The most interesting observation was that sea waters filtered at the time of collection, and proved bacteriologically sterile until use, were very little different as a medium for rearing *Echinus esculentus* larvae than were the same sea waters collected at the same time in the ordinary way and not sterile. These observations, whilst incomplete, give no support to the view that bacteria present in the water at the time of collection, and multiplying in it before use, make that water unsuitable for larvae subsequently reared in it.

Macro-Flora and Fauna

'Corrections and Additions II, 1956' to 'A Preliminary Check-List of British Marine Algae' (1953, Vol. 32, of the *Journal*) has been compiled by Dr Parke and published in *Phycological Bulletin*, No. 5, pp. 36–7, May 1957.

Additions have been made during the year to the herbarium of marine algae by all members of the botanical section to try to fill the gaps in the collection, and for this purpose visits have been made to the shores of Cornwall and the Isles of Scilly.

The final stages of editing the third edition of the *Plymouth Marine Fauna* continued to occupy much of Dr Wilson's time until its publication in June 1957. Final proof correcting was very tedious and involved checking very many references. The new volume is larger than its predecessor and lists many more species.

Much of Mr Spooner's time has also been taken up in the production of the new fauna list. Accumulated records of the burrowing fauna from the collecting grounds in the Salcombe Estuary have been collated by him, and these results have been expressed in a summarized form in the introduction to this new edition.

Mr Corbin has continued to collect data on the Lucernarians, certain of the smaller fishes and the hermit-crabs. The new *Lucernariopsis* sp. found at Wembury in 1951 has for some time presented a puzzle in regard to its distribution. In a very small area on Church Reef it has always been quite plentiful and at any one visit throughout the year some two dozen or fifty or more specimens can easily be collected without stripping the locality. Elsewhere in the south-west Mr Corbin could not find it, nor did it occur in collections examined from other parts of the British Isles. In September this year, however, material from the Scilly Isles collected by Prof. L. A. Harvey of Exeter University contained two specimens among larger numbers of *Haliclystus* and *L. campanulata*. This Scilly record thus establishes the distribution of the species over an area and that it is not limited, as formerly appeared to be so, to a single point site. The species is not a recent

immigrant: the British Museum collection contains specimens from Plymouth collected before 1929.

Although absent for much of the year due to illness, Mr N. A. Holme has continued working up bottom samples obtained in previous years off southern Brittany and the south-west coast of Ireland. Some observations have been made on the mode of life of members of the Tellinidae which indicate that these lamellibranchs lie buried in the sand in a horizontal position, with the left valve down. This indicates the possibility of horizontal migrations through the sand, as was suggested by earlier work on the spacing of individuals of *Tellina tenuis* on a sandy beach. Mr Holme has translated from the French, and adapted for British coasts, the book *La vie étrange des rivages marins* by E. le Danois, and this has now been published under the title *Marine Life in Coastal Waters (Western Europe)*.

Mr G. R. Forster has continued work on sponges collected by diving. A collection is slowly being built up of specimens of the genus *Haliclona*, with the aim of providing more satisfactory descriptions of some of its numerous species, of which very few are well established. Spicule measurements are being taken to find out the range of variation within a species, which may well be greater than many of the small differences in spicule dimensions on which new species have been erected.

Two new sponge records for the Plymouth area have been made: *Crella inflata* (Bowerbank) twice taken from the Mewstone dredging ground, and an unusual bright red sponge, tentatively identified as *Raspaciona aculeata* (Johnston), which was found on a gulley wall at 14 fathoms off Stoke Point.

Many sponges were collected from the neighbourhood of Santander during the course of five days diving in June. These dives were made from the launch of the Laboratorio Oceanographico thanks to the co-operation of the Director, Dr J. Cuesta, and the Ministerio de la Marina.

Some observations have been made on the browsing of *Echinus esculentus* in aquarium tanks. These animals will feed on a variety of encrusting organisms, including some sponges, but they do not touch *Corynactis*. One *Echinus* on which a close watch was kept was seen to move away whenever it came into contact with a stone covered with *Corynactis*. This apparent distastefulness of *Corynactis* to *Echinus* may account for the general abundance of the former at depths of 10–15 fathoms where *Echinus* is also very common.

During the summer more diving has been carried out by Mr Forster in the vicinity of Plymouth; several rare species have been found. *Phoronis hippocrepia* colonizing considerable areas of *Pomatoceros* tubes have been discovered in a gulley near Penlee Point. In the same gulley and also near Revelstoke Point several *Balanophyllia regia*, Gosse's gold cup-coral, have been observed. A few specimens of *Lima* spp., burrowing lamellibranchs, have been taken by turning over boulders.

With the Robot camera some underwater pictures of sponges and various

sessile animals have been taken with the aim of showing how much more expanded many of these animals are in their natural habitat than when they are living in aquaria. A waterproofed Minifon recorder has also been tested which it is hoped will greatly facilitate making quantitative estimates or counts of the rock fauna over a fairly large area.

Several rock samples from outlying submerged reefs have been obtained by diving by Mr Forster for the Department of Geology of the University of Bristol.

Dr A. J. Southward has continued his studies on the distribution and breeding of barnacles and other intertidal animals; work is in progress on cinematographic and other techniques for studying their behaviour. The results of several years' field investigations have been published in a joint contribution with Dr D. J. Crisp in Vol. 37, No. 1, of the *Journal*. The distribution of intertidal organisms along the Channel coasts is described and discussed in some detail in relation to temperature and other environmental factors, and it is concluded that most trends in distribution can be explained by temperature factors, modified by effects of substratum and larval dispersal. An accompanying article deals with temperatures in the intertidal zone and the extremes of temperature tolerated by some intertidal animals. Work on the population dynamics of limpets and sea weeds in the Isle of Man was completed by publication of a final note in *Annual Report*, No. 68, of the Marine Biological Station at Port Erin. A review of more recent trends in intertidal zonation studies, with a discussion on the causes of zonation, is being published in *Biological Reviews*.

Dr Southward has made further observations on the deep-sea barnacle *Hexelasma*, including the examination of specimens obtained by the Cable Ship *Marie Louise Mackay* off the south-west of Ireland, and preserved material at the British Museum (Natural History). So far, living examples have been obtained only north of the Little Sole submarine promontory, by R.V. *Sarsia*, although old shell compartments were dredged up off La Chapelle Bank. Deep water dredging is a tedious process, and it is hoped to try new methods in future. More experiments on living *Hexelasma* support the previous suggestion that there is some connexion between this species and deep sea water currents.

Dr G. A. Steven has continued to make replicate trawl hauls as regularly as possible at international Station L4 in the vicinity of Plymouth in order to obtain records of short- and long-term changes in the demersal fish fauna. At the same time he is studying the biology and life-history of *Arnoglossus laterna*, *Trigla cuculus* and *Trachurus trachurus*.

Arnoglossus laterna is a small flatfish—the most abundant flatfish in the Plymouth area—that seldom exceeds 14 cm in total length. It appears to be short lived, reaching a length of 6–9 cm at 1 year, 10·5–11·5 cm at 2 years, about 12·5 cm at 3 years and just over 13 cm at 4 years. The total life span

probably does not often exceed 6–7 years. Its numbers on the trawling ground remain fairly constant throughout the year.

Trigla cuculus is also present throughout the year, but may be scarce in the winter months. It enters the trawl catches as the O-group, usually by the beginning of October. It attains a total length of 11–16 cm at 1 year, 20–25 cm at 2 years, 28–32 cm at 3 years and 34–38 cm at 4 years. Its growth rate at greater ages has not yet been determined.

Trachurus trachurus is a pelagic fish which at times can also be taken near the sea floor in a trawl. Until recent years this fish was seldom caught in the trawl in the vicinity of Plymouth, but it is now fairly common except during the months of July–September. It reaches a length of 9–13 cm at 1 year, 16–19 cm at 2 years, 21–24 cm at 3 years and 25–27 cm at 4 years. Its growth rate at greater ages has not yet been determined.

In collaboration with Miss Barbara Whitaker, warden to the Lundy Island Field Society, Dr Steven has examined collections of regurgitated food pellets of shags in order to ascertain what the birds in the Lundy breeding colonies were feeding on during the breeding season. The food remains in the pellets were found to consist almost entirely of fish bones and otoliths (mostly *Ammodytes* sp.) in the breeding seasons of both 1956 and 1957. A few crustacean fragments were found, but they appeared in every instance but one to have come from the stomachs of fish eaten.

Physiology of Marine Organisms

Dr T. I. Shaw has continued his experiments upon iodine uptake by the sea-weed *Laminaria digitata*. Many agents, among them tyrosine, catechol and pyruvate, have been found to act as reversible inhibitors for ^{131}I accumulation. In every case the inhibitors have been found to prevent the weed from liberating I_2 from iodide. These findings reinforce the view that I_2, or a related oxidation state of the element, is involved in the process of iodide accumulation. The rate of uptake varies with the iodine content of the medium in a way that parallels the expected concentration of hypoiodous acid rather than I_2 and it seems likely that HIO is the form that enters the tissues.

The oxygen consumption of the weed during iodine accumulation has been shown to be too rapid, in comparison with the known diffusion constant of oxygen and the thickness of the weed, to occur uniformly throughout the tissues. It must be principally localized at the surface of the plant. Since an increase in the partial pressure of oxygen does little to hasten its consumption, the localization cannot be simply due to the slow diffusion of O_2 through the tissues.

Analyses are being made of the likely intermediates of carbohydrate metabolism in the weed, both in the presence and absence of iodide. The object is to identify the rate-limiting reaction in sugar breakdown, a reaction

which must also be involved in iodine accumulation. Pyruvate, α-ketoglutarate and citrate have already been studied. The most interesting observation so far is that pyruvate decreases when iodide is supplied aerobically, but increases if I_2 is supplied anaerobically.

Many pelagic animals are luminescent and, in deeper water, they are exclusively responsible for producing the light which is used in visual perception. The majority of these animals possess well-formed eyes, and it is desirable to know how effective is this animal light in permitting vision among deep sea species. Measurements have been made of the intensity of luminescence at sea, and data are now being gathered for the light output of single animals. In furtherance of this research, Dr J. A. C. Nicol has been measuring the spectral composition and absolute intensities of the light emitted by various coastal and pelagic species, including Protozoa, jellyfish, sea-pens, ctenophores, polychaetes, *Pholas*, *Pyrosoma*, and fish. Special apparatus has been devised for analysing flashes of short duration, and thereby obtaining spectral emission curves. This apparatus has been used successfully at sea, on board R.V. *Sarsia*. Luminescence has been recorded from a number of pelagic species for the first time (various radiolarians, jellyfish and fish). Absolute values for light intensities (radiant flux) have also been secured for many species. Some representative values are as follows. *Noctiluca*, a protozoan, has a blue light, with maximal emission at 470 mμ. The flux from a single cell at 1 cm is about 1×10^{-8} microjoule/1 cm² receptor surface. A deep-sea jellyfish, *Atolla wyvillei*, emits blue light with a peak at 470 mμ; light intensities range up to 1×10^{-4} μW/cm² receptor surface at 1 cm. Other animals emitting blue light are Radiolaria, Hydromedusae, *Chaetopterus*, *Pholas* and lantern fish (myctophids). Intensity measurements for myctophids give values up to 5×10^{-4} μW/cm² receptor surface at 1 cm. Ultimately it should be quite possible to correlate this information with that secured for the sensitivity of photoreceptor systems of marine animals. Part of this work has been published in the *Journal* (Vol. 35, pp. 529 and 629) and other parts are being prepared for publication.

Dr E. J. Denton has continued observations on vision in fishes and other marine animals. Some results of this research have been published in Vol. 36, No. 3, of the *Journal*, showing that deep-sea fish should be able to see daylight at a depth of more than 1000 m in the open ocean. At this depth light from luminescent organisms is probably already becoming predominant.

The apparatus referred to in last year's Report of Council has been modified to give absorption curves for unbleached retinae. It has been shown on a number of fishes, including deep-sea and freshwater species, that the absorption curves for whole retinae are almost the same as those given by very pure retinal extracts. It appears that most of the 'impurities' so commonly found in extracts are manufactured during extraction. It has been confirmed that the retinal densities of chrysopsin in fresh deep-sea fish are often around

1·0 for the wavelength most absorbed. A short account of this work has been published in the proceedings of the National Physical Laboratory symposium on colour vision.

In collaboration with Miss M. A. Walker of the Institute of Ophthalmology, London, Dr Denton has made a detailed comparison of the absorption of light by intact retinae and by retinal extracts of the conger eel. The retinal pigment, which is of the golden deep-sea type, is approximately twice as effective at absorbing light *in situ* than in extracts, whilst the absorption curve for the extract is shifted a few mμ towards the shorter wavelength end of the spectrum. The results of this research have been published in the *Proceedings of the Royal Society* B, Vol. 148.

Dr Denton and Dr D. B. Carlisle have found that the retina of the fresh-water eel, purple in the immature form, becomes golden as the eel metamorphoses in preparation for its return to the deep sea. This golden pigment has an absorption curve identical with that of the conger eel and is typical of the retinal pigment of a deep-sea fish. The retinal density of pigment in the mature form is higher than in the immature form.

With the help of Mr F. J. Warren, Dr Denton has shown that the mid-water oceanic fish have crystalline lenses which are transparent down to 310 mμ. The majority of diurnal shallow-water fish have previously been shown to have lenses in which the light below about 400 mμ is absorbed. This may be an adaptation to improve acuity or to protect the photoproducts of bleaching against further photochemical action. Oceanic squid show similar differences in lens transparency.

Through the kindness of Dr S. K. Kon, of the Development Commission's Fisheries Biochemical Unit, Dr Denton has been able to use their fluorescence microscope at Reading. He has confirmed that the visual white (probably vitamin A) in the bleached retina of the frog remains in an organized state within the retinal rods for at least $2\frac{1}{2}$ h after bleaching. The fluorescence of the molecules of visual white within the rods is polarized in such a way as to support the hypothesis that these molecules are orientated with their axes of resonance along the axes of the rods.

With Mr N. B. Marshall of the British Museum (Natural History) Dr Denton is starting a study of the biology of deep-sea fish. He has made experiments on board R.V. *Sarsia* on deep-sea fish caught alive which show that these fish can be within $\frac{1}{2}\%$ of hydrostatic equilibrium with sea water, although they have no air-filled swim-bladder. This surprisingly high buoyancy does not appear to be achieved by any one modification but by having more fat, a more fragile and lighter skeleton, and less protein than usual. Mr E. I. Butler is assisting in the fat and protein analysis.

Experiments upon the swim-bladders of fish have been started by Dr Denton and Dr Shaw. They have developed a new method, suitable for use at sea, which gives an accurate measure of the gas content of fish *in vivo*. Using this

apparatus in Plymouth and on board R.V. *Sarsia* it has been found, contrary to expectations, that fish do not necessarily secrete gas in response to an increased hydrostatic pressure. The fish, conger eels and *Diaphus rafinesquei* (Cocco), were lowered to various depths (the congers down to 1000 m) and recovered 12–72 h later. The congers lowered to 500 m or more died whilst the others failed to show any increase, indeed most showed a decrease, in gas volume.

Control of gas loss by the pneumatic duct has been studied in conger eels. It has been found that in decapitate and living fish gas escaped whenever swim-bladder volume increased to approximately twice that required for neutral buoyancy, a condition in which the swim-bladder becomes a disadvantage to the fish.

The histology and gross anatomy of the swim-bladder and related structures are also receiving attention.

Dr D. B. Carlisle has directed most of his attention this year to the endocrinology of Crustacea and continued his fruitful collaboration with Sir Francis Knowles of Marlborough. Their review of 'Endocrine control in the Crustacea' appeared in November 1956 issue of *Biological Reviews*, while a book on the subject of crustacean hormones is in the press and is to be published shortly by the Cambridge University Press as one of the series of monographs on experimental biology.

Dr Carlisle's investigations of moulting in Crustacea have this year been mainly directed at elucidating the nature of the control of the termination of moulting in crabs. The spider crab, *Maia*, is not sexually mature until it has undergone its last moult: thereafter it never moults again. The shore crab, *Carcinus*, moults 10 or 11 times after the moult of puberty and then ceases to moult. The edible crab, *Cancer*, can apparently continue to moult indefinitely. Two endocrine organs are concerned in the control of moulting: the X organ-sinus gland complex, which secretes a hormone tending to inhibit moulting, and the Y organ, which, besides a hormone necessary for the moult process to take place, also secretes a hormone responsible for the maturation of the juvenile gonad. In *Maia*, at the moult of puberty the Y-organ degenerates, as soon, that is, as the gonads are mature; thereafter moulting is no longer possible in the absence of the necessary hormone. In *Carcinus* the Y organ persists, but after the final moult the X organ produces far more moult-inhibiting hormone than at any stage earlier in the crab's life. This effectively prevents further moulting from taking place, but removal of the X organ-sinus gland complex from these crabs, after the final moult, allows moulting to begin once more with the production of 'giant' crabs. In *Cancer*, the Y organ does not degenerate nor does the X organ produce excess moult-inhibiting hormone; moulting can therefore continue without let. Some of the results of this work have been published in Vol. 36, No. 2, of the *Journal*. In connexion with this work Dr Carlisle has been employing diving equipment

in an attempt to study the biology of crabs in their natural habitat. The information gained has made the interpretation of experiments easier.

On a second visit to Sweden, to attend the International Symposium on Neurosecretion, Dr Carlisle took the opportunity to extend further his investigations of the endocrine basis of sex reversal in *Pandalus*, and to take specimens of the endocrine organs of this species for histological study. While in Sweden he also began an investigation in collaboration with Prof. L. H. Kleinholz into the hormone responsible for provoking the proximal migration of the distal pigment of the eye of Natantia. This investigation was continued later in Plymouth, with Sir Francis Knowles joining in the collaboration, and led to the demonstration that the principle responsible is distinct from any of the known chromactivating substances.

Dr P. Karlson, of Munich, and Dr Carlisle have shown that a chromactivating substance active upon *Leander* and comparable to substance A of that species, is present in impure samples of ecdyson obtained from silkworms, *Bombyx* sp. It is not yet clear whether it is ecdyson itself which has this action or whether it is some impurity.

Dr Carlisle has devised a cell whereby the pituitary stalk of *Lophius* may be examined alive under the microscope when it is still attached to the pituitary and the brain. Under these conditions neurosecretory transport may be observed, particularly by the use of polarized light, and the phenomenon has been filmed. A note on this is being published in the Reports of the Second International Symposium on Neurosecretion.

Dr Abbott and Dr Carlisle have been investigating the electrophysiology of the pituitary stalk of *Lophius* and preliminary results suggest that it is capable of propagating normal action potentials.

Dr B. C. Abbott has continued experiments on the properties of invertebrate smooth muscle in collaboration with Dr J. Lowy of the Biophysics Research Unit, King's College, London. Further measurements have been made on the opacity changes which occur in the mantle muscle of squid, with emphasis on the scattered light. Polar diagrams for the forward scattering have been plotted under conditions of rest, of twitch and tetanic activity, and after death. The influence of wavelength of the light on the scattering has also been studied. Preliminary experiments have also been carried out on the properties of the funnel retractor of the squid.

The results of experiments in collaboration with Prof. A. V. Hill and Mr J. V. Howarth of University College London have been published in the *Proceedings of the Royal Society* B, Vol. 148: following a single impulse in a crab nerve at 0° C there is a rapid burst of heat, followed by the reabsorption of the majority of this heat. The initial burst of heat is comparable in value with the heat of mixing resulting from the movement of ions across the membrane during activity. Measurements have been made of the loss of potassium ions when crab nerve at low temperature is stimulated: ^{42}K exchange was measured

over a range of stimulus frequencies. A value for the potassium efflux for an isolated impulse was estimated.

Experiments were also begun to find whether the crab nerve will continue for a reasonable period of time to conduct action potentials in a bathing medium where the sodium ion is replaced by lithium: this was attempted because the heat of mixing due to ion movements should then be appreciably different from that with normal sea water.

Thermal measurements on the electric organ of the electric ray *Torpedo* have been made at the Station de Biologie Marine d'Arcachon in collaboration with Prof. A. Fessard from the Collège de France, Paris, and with Dr X. M. Aubert from Louvain. Organs were isolated with their nerves and mounted in a thermostat in air between rectangular non-polarizable (Ag–AgCl) plates which were as large as the organ surface. A small thermistor was inserted into the organ and connected to a galvanometer–photocell–cathode-ray tube system. Temperature changes following stimulation were studied at various temperatures, and with different external load resistances connected between the plates. A rapid heating, larger than the internal Joule effect, was followed by a long-lasting cooling such that the overall effect was often a cooling. Control experiments showed that this effect could not be due to dead tissue. More experiments are required to be quite sure of the quantities of heat involved.

Dr E. D. S. Corner, International Paints Research Fellow, in collaboration with Mr B. W. P. Sparrow (International Paints Research Laboratory, Newton Ferrers), has completed an investigation of the factors influencing the toxicities of various mercury compounds to certain crustacea. An account of this work has been published in Vol. 36, No. 3, of the *Journal*.

This study has been continued in collaboration with Dr F. H. Rigler, of Toronto University. Tracer isotopes have been used and the experiments have shown that differences between the susceptibilities of *Artemia salina* and *Elminius modestus* to ^{203}Hg-labelled mercuric chloride and *n*-amylmercuric chloride are directly related to the rates at which the poisons are accumulated: they do not reflect the quantities of these compounds which the animals can tolerate in their tissues. Thus, mercury is taken up at approximately the same rate from equitoxic solutions of the two poisons; and the rates at which mercury is accumulated by the two species from equitoxic solutions of either poison are of the same order. Experiments in which the poisoned animals have been washed with reduced glutathione have given results consistent with the view that most of the mercury taken up by either species penetrates into the tissues of the test animals and does not act simply by becoming attached to their surfaces. Direct evidence of the penetration of mercury compounds into a crustacean has been obtained in experiments with the prawn *Leander serratus*. Both mercuric chloride and *n*-amylmercuric chloride have been detected in various organs of the poisoned animals, a large quantity of the poison being

present in the antennary gland. In addition it has been found that both mercury compounds concentrate in the gills of the test animals. An account of this work has been published in Vol. 37, No. 1, of the *Journal*.

Further studies on mercury poisoning have been carried out by Dr Corner, using *Maia squinado*. In these experiments it has been found that when the animals are immersed in sea water containing ^{203}Hg-labelled mercuric chloride the poison accumulates in the blood, antennary gland, and, eventually the urine. In addition, it has been found that the urine of *Maia* poisoned with mercuric chloride contains greatly increased quantities of α-amino nitrogen. Evidence has also been obtained that the gills of the poisoned animals are heavily contaminated with mercury and it is hoped to carry out further work in order to see what effect the poison has on their normal function.

The Library

The thanks of the Association are again due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association.

The Council wish to record their thanks to Dr Mary Parke for a gift to the library of a number of important botanical works, chiefly on marine algae.

Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

The Library has again been much used by visiting members of the Association.

Published Memoirs

Vol. 36, No. 2 of the *Journal* was published in June, Vol. 36, No. 3 in November 1957 and Vol. 37, No. 8 in February 1958.

The following papers, the outcome of work done at the Plymouth laboratory, have been published elsewhere than in the *Journal* of the Association:

Abbott, B. C., Hill, A. V. & Howarth, J. V., 1958. The positive and negative heat production associated with a nerve impulse. *Proc. Roy. Soc.*, Ser. B, Vol. 148, pp. 149–87.

Alexandrowicz, J. S., 1957. Notes on the nervous system in the Stomatopoda. V. The various types of sensory nerve cells. *Pubbl. Staz. zool. Napoli*, Vol. 29, pp. 213–25.

Bidder, A. M., 1957. Evidence for an absorptive function in the 'Liver' of *Octopus vulgaris* Lam. *Pubbl. Staz. zool. Napoli*, Vol. 29, pp. 139–50.

Boden, B. P. & Kampa, E. M., 1957. Records of bioluminescence in the ocean. *Pacif. Sci.*, Vol. 11, pp. 229–35.

Caldwell, P. C., 1957. The sensitivity to pH of the inhibitory effects of dinitrophenol on squid giant axons. Proc. biochem. Soc., 19 July 1957. *Biochem. J.*, Vol. 67, 1–2P.

CALDWELL, P. C. & KEYNES, R. D., 1957. The utilization of phosphate bond energy for sodium extrusion from giant axons. Proc. physiol. Soc., 29–30 March 1957. *J. Physiol.*, Vol. 137, 12–13*P*.

COOPER, L. H. N., 1957. Death of a channel herring fishery. *New Scientist*, 4 pp., 2 May.

DALES, R. PHILLIPS, 1957. Pelagic polychaetes from the Bay of Biscay. *Ann. Mag. Nat. Hist.*, Vol. 10, pp. 661–64, (12th Ser.).

DARTNALL, H. J. A., 1957. The spectral variation of the photo-sensitivities of some visual pigments. *Paper* 3, *Symposium on Visual Problems of Colour held at Nat. Phys. Lab., Teddington, Middx. from* 23*rd to* 25*th September*, 1957, 26 *pp.*

DENTON, E. J. & WALKER, M. A., 1958. The visual pigment of the conger eel. *Proc. Roy. Soc.*, Ser. B, Vol. 148, pp. 257–69.

FRANKENHAEUSER, B. & HODGKIN, A. L., 1957. The action of calcium on the electrical properties of squid axons. *J. Physiol.*, Vol. 137, pp. 218–44.

HANSON, JEAN & LOWY, J., 1957. Structure of smooth muscles. *Nature, Lond.*, Vol. 180, pp. 906–9.

HODGKIN, A. L., 1958. Ionic movements and electrical activity in giant nerve fibres. The Croonian Lecture. *Proc. Roy. Soc.*, Ser. B, Vol. 148, pp. 1–37.

HODGKIN, A. L. & KEYNES, R. D., 1957. Movements of labelled calcium in squid giant axons. *J. Physiol.*, Vol. 138, pp. 253–81.

JONES, W. C., 1957. The contractility and healing behaviour of pieces of *Leucosolenia complicata*. *Quart. J. micr. Sci.*, Vol. 98, pp. 203–17.

MACDONALD, J. D., PIKE, R. B. & WILLIAMSON, D. I., 1957. Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). *Proc. zool. Soc. Lond.*, Vol. 128, pp. 209–57.

MARINE BIOLOGICAL ASSOCIATION, 1957. *Plymouth Marine Fauna*, Third Edition, pp. i–xliii, 1–457, with 4 charts.

NORTH, W. J. & PANTIN, C. F. A., 1958. Sensitivity to light in the sea-anemone *Metridium senile* (L.): adaptation and action spectra. *Proc. Roy. Soc.*, Ser. B, Vol. 148, pp. 385–96.

NICOL, J. A. C., 1957. Observations on photophores and luminescence in the teleost *Porichthys*. *Quart. J. micr. Sci.*, Vol. 98, pp. 179–88.

ROBSON, ELAINE A., 1957. The structure and hydromechanics of the musculo-epithelium in *Metridium*. *Quart. J. micr. Sci.*, Vol. 98, pp. 265–78.

SUTTON, MURIEL F., 1957. The feeding mechanism, functional morphology and histology of the alimentary canal of *Terebella lapidaria* L. (Polychaeta). *Proc. zool. Soc. Lond.*, Vol. 129, pp. 487–523.

SHAW, T. I. & COOPER, L. H. N., 1957. State of iodine in sea water. *Nature, Lond.*, Vol. 180, p. 250.

STOTT, F. C., 1957. Observations on the food canal and associated structures in the holothurian *Holothuria forskali* Delle Chiaje. *Proc. zool. Soc. Lond.*, Vol. 129, pp. 129–36.

MEMBERSHIP OF THE ASSOCIATION

The total number of members on 1 March 1958 was 994, being 94 more than on 31 March 1957; of these the number of life members was 115 and of annual members 879. The number of associate members is four.

During the year Dr Å. Vedel Tåning was elected an Honorary Member.

GRANTS FOR AQUARIUM RECONSTRUCTION

The Council wish to record their grateful thanks for the following generous grants towards the cost of reconstructing the aquarium.

Nuffield Foundation	£12,000
Royal Society	£500
Imperial Chemical Industries	£200

In addition there will be a sum of approximately £500 from donations placed by the general public, over the past ten years, in the collecting box in the aquarium.

GRANT FOR CULTURE COLLECTION

The Council wish to record their thanks to the International Union of Biological Sciences for a grant of $500 towards the cost of upkeep of Dr Mary Parke's culture collection of marine micro-organisms kept at the Plymouth laboratory.

FINANCE

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Capital Grants. The Council wish to record their thanks to the Development Commissioners for a substantial capital grant to meet the cost of constructing two new sea-water reservoirs, and the building of new outside circulation tanks. They also wish to record their thanks for a grant towards the cost of publication of the third edition of the *Plymouth Marine Fauna.*

Private Income. The Council gratefully acknowledge the following generous grants received during the year:

Fishmongers' Company (£400), The Royal Society (£100), British Association (£50), Physiological Society (£50), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s.*), Leeds (£20), Durham (£10. 10*s.*), Manchester (£10. 10*s.*), Sheffield (£10. 10*s.*), Southampton (£15. 15*s.*), Reading (£10. 10*s.*), Nottingham (£10. 10*s.*), Hull (£10. 10*s.*), Exeter (£10. 10*s.*), Leicester (£10. 10*s.*), the Imperial College of Science and Technology (£10), Gonville and Caius College, Cambridge (£5), and the Zoological Society of London (£10. 10*s.*).

PRESIDENT, VICE-PRESIDENTS, OFFICERS AND COUNCIL

The following is the list of those proposed by the Council for election for the year 1958–59:

President

Prof. A. V. HILL, C.H., O.B.E., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of IVEAGH, K.G., C.B., C.M.G.
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., F.R.S.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.
Major E. G. CHRISTIE-MILLER
MORLEY H. NEALE, C.B.E.
The Earl of VERULAM
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S.

COUNCIL

To retire in 1959

G. E. R. DEACON, C.B.E., D.Sc., F.R.S.
M. N. HILL, Ph.D.
O. D. HUNT
Prof. R. J. PUMPHREY, Sc.D., F.R.S.
Prof. G. P. WELLS, Sc.D., F.R.S.

To retire in 1960

Prof. E. BALDWIN, Ph.D.
C. H. MORTIMER, Dr.phil., D.Sc., F.R.S.
C. F. A. PANTIN, Sc.D., F.R.S.
Prof. J. E. SMITH, Sc.D., F.R.S.
H. G. VEVERS, M.B.E., D.Phil.

To retire in 1961

H. A. COLE, D.Sc.
G. E. FOGG, Ph.D.
Prof. J. E. HARRIS, Ph.D., F.R.S.
C. E. LUCAS, C.M.G., D.Sc.
Prof. C. M. YONGE, C.B.E., D.Sc., F.R.S.

Hon. Treasurer

HARRISON S. EDWARDS, Westhumble Lacey, Near Dorking, Surrey

Secretary

F. S. RUSSELL, C.B.E., D.S.C., D.F.C., LL.D., F.R.S.

The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of Council:

R. G. R. WALL (Ministry of Agriculture, Fisheries and Food)
The Worshipful Company of Fishmongers:
The PRIME WARDEN
Major E. G. CHRISTIE-MILLER
HARRISON S. EDWARDS
Prof. Sir ALISTER HARDY, Kt., D.Sc., F.R.S. (Oxford University)
S. SMITH, Ph.D. (Cambridge University)
EDWARD HINDLE, Sc.D., F.R.S. (British Association)
N. B. MARSHALL (Zoological Society)
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S. (Royal Society)

BALANCE SHEET 1957–8

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET

31 MARCH 1958

	£	£
CAPITAL RESERVE ACCOUNT:		
As at 31 March 1957	176,084	
Add: Expenditure on fixed assets recovered	1,670	
	177,754	
Less: Transfer to surplus account being an amount equivalent to the depreciation provided on assets acquired out of Development Fund grants	3,700	174,054
SURPLUS ACCOUNT:		
As at 31 March 1957	6,782	
Add: Excess of income over expenditure for the year	3,160	
Transfer from Capital Reserve Account	3,700	
	13,642	
Deduct: Increase in provision for diminution in value of General Fund investments	120	13,522
		187,576
BALANCES ON SPECIAL FUNDS (see annexed statement)		7,669
CURRENT LIABILITIES:		
Sundry creditors and accrued expenses	1,997	
Subscriptions and grants received in advance	184	
		2,181
		£197,426

Note: Capital commitments outstanding amount to £1,200 (1957 £10,400) no part (1957 £9,300) of which will be recoverable under Development Fund grants.

M. N. HILL }
O. D. HUNT } *Members of the Council*

	£	£	£
FIXED ASSETS:	Cost or Valuation	Depreciation	
Boats and equipment:			
At cost:			
R.V. 'Sarsia'	137,761	3,270	134,491
M.F.V. 'Sula'	12,500	420	12,080
R.L. 'Gammarus'	200	10	190
	150,461	3,700	146,761
Laboratory apparatus, equipment and machinery:			
At cost	16,169	4,019	12,150
Library at valuation in 1941 plus additions as valued by the Director...	23,100	—	23,100
	£189,730	£7,719	
			182,011
INVESTMENTS:			
General Fund (including Composition Fees) at book amount (Market value £1,220; last year £1,277)		1,672	
E. T. Browne Bequest Funds at cost (Market value £3,086; last year £3,346)		4,582	
		6,254	
Less: Provision for diminution in value of investments		1,948	
			4,306
CURRENT ASSETS:			
Stocks on hand as valued by the Director		3,467	
Sundry debtors and prepayments		4,470	
Balances at bankers and cash in hand		3,172	
			11,109
			£197,426

AUDITORS' REPORT TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31 March 1958 and of its excess of income over expenditure for the year ended on that date.

We have obtained all the information and explanations which we considered necessary. In our opinion the Association has kept proper books and the said accounts which are in agreement with them and with the said information and explanations, give in the prescribed manner the information required by the Companies Act 1948.

Norwich Union House
2 St Andrew's Cross
Plymouth
16 May 1958

PRICE WATERHOUSE & Co.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT

FOR THE YEAR ENDED 31 MARCH 1958

	£	£
SALARIES (including additional for previous year) NATIONAL INSURANCE AND SUPERANNUATION SCHEME CONTRIBUTIONS		35,788
LABORATORY AND BOATS' CREWS' WAGES (including additional for previous year), NATIONAL INSURANCE, SUPERANNUATION SCHEME CONTRIBUTIONS AND EMPLOYERS' LIABILITY INSURANCE		32,593
UPKEEP OF LIBRARY		874
SCIENTIFIC PUBLICATIONS, *less* SALES		2,255
UPKEEP OF LABORATORIES:		
Buildings and machinery	827	
Electricity, gas, coal and water	1,133	
Chemicals and apparatus	1,761	
Depreciation of Laboratory apparatus, equipment and machinery	1,351	
Rents and insurance	295	
Travelling expenses	833	
Audit fee	138	
Stationery, postage, telephone and sundries	1,192	
Specimens	225	
Collecting expenses and upkeep of truck	235	
		7,990
MAINTENANCE AND OPERATION OF BOATS:		
Petrol, oil, paraffin, etc.	1,549	
Maintenance and repairs	6,905	
Depreciation	3,700	
Insurances	2,460	
Hire of Decca Navigator—R.V. 'Sarsia'	395	
		15,009
ENTERTAINMENT EXPENSES		50
BALANCE being excess of income over expenditure for the year ...		3,160
		£97,719

	£	£
GRANTS AND TABLE RENTS:		
Ministry of Agriculture, Fisheries and Food Grant from Development Fund	88,703	
Fishmongers' Company	400	
Miscellaneous (including Royal Society £100, British Association £50, Physiological Society £50, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s*., Leeds £20, Southampton £15. 15*s*., Durham £10. 10*s*., Exeter £10. 10*s*., Leicester £10. 10*s*., Manchester £10. 10*s*., Nottingham £10. 10*s*., Hull £10. 10*s*., Reading £10. 10*s*., and Sheffield £10. 10*s*., Imperial College, £10, Zoological Society of London £10. 10*s*., Ministry of Works £96, Imperial Chemical Industries Ltd. £52. 10*s*., International Paints Ltd. £52. 10*s*., Gonville and Caius College, Cambridge £5)	1,267	
		90,370
SUBSCRIPTIONS		856
SALES:		
Specimens	2,971	
Fish	712	
	£	
Nets, gear and hydrographical apparatus	715	
Less: Cost of materials	366	
	349	
		4,032
SUNDRY PUBLICATIONS		291
INCOME FROM INVESTMENTS		55
INTEREST ON BANK DEPOSITS, *less* CHARGES		182
AQUARIUM:		
Admission Fees	2,124	
Sale of guides	47	
	2,171	
Less: Maintenance, printing and advertising	238	
		1,933
		£97,719

MOVEMENTS ON SPECIAL FUNDS DURING THE YEAR TO 31 MARCH 1958

	Aquarium Reconstruction Fund	E. T. Browne Bequest			Rockefeller Foundation Fund	Library Extension and New Dogfish House Fund	'Plymouth Marine Fauna' Fund	Reservoir and Sea Water Tanks Fund	Algal Culture Fund	Research Funds*	TOTAL
		Library	Special Apparatus	Scientific Publications							
	£	£	£	£	£	£	£	£	£	£	£
BALANCE AT 31 MARCH 1957 (after providing £1,151 for diminution in value of investments)	431	1,051	2,052	464	269	1,187	(3)	1,163	—	288	6,902
Add: Income during year											
Grants	700	—	—	—	2,631	—	500	8,330	178	3,571	15,910
Income from investments	—	40	83	21	—	—	—	—	—	—	144
Bank deposit interest	15	—	—	—	—	—	—	33	—	—	48
Other income	26	—	—	85	—	—	—	—	—	—	111
Stock of 'Plymouth Marine Fauna' at 31 March 1958	—	—	—	—	—	—	1,100	—	—	—	1,100
Transfer between Special Funds	—	—	—	—	(125)	—	125	—	—	—	—
	1172	1,091	2,135	570	2,775	1,187	1,722	9,526	178	3,859	24,215
Deduct: Expenditure during year	—	31	82	—	2,761	508	622	8,692	—	3,505	16,201
Increase in provision for diminution in value of investments	—	85	218	42	—	—	—	—	—	—	345
BALANCE AT 31 MARCH 1958	£1,172	£975	£1,835	£528	£14	£679	£1,100	£834	£178	£354	£7,669

* Including International Paints Ltd. Research Fellowship.

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1958

GOVERNORS

THE BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE, Burlington House, W. 1
THE UNIVERSITY OF OXFORD
THE UNIVERSITY OF CAMBRIDGE
THE WORSHIPFUL COMPANY OF CLOTHWORKERS, 48 Fenchurch Street, E.C. 3
THE WORSHIPFUL COMPANY OF FISHMONGERS, London Bridge, E.C. 4
THE PRIME WARDEN. (**Council,** 1886→)
EDWARDS, HARRISON S., Westhumble Lacey, near Dorking, Surrey. (**Council,** 1950→; **Hon. Treasurer,** 1956→)
CHRISTIE-MILLER, Major E. G., 38 Hyde Park Street, W. 2. (**Council,** 1941→; **Hon. Treasurer,** 1941→56; **Vice-President,** 1951→)
THE ZOOLOGICAL SOCIETY OF LONDON, Regent's Park, N.W. 1
THE ROYAL SOCIETY, Burlington House, Piccadilly, W. 1
MINISTRY OF AGRICULTURE, FISHERIES & FOOD, 3 Whitehall Place, S.W. 1
BAYLY, ROBERT (the late). (**Council,** 1896–1901)
BAYLY, JOHN (the late)
BROWNE, E. T. (the late). (**Council,** 1913–19; 1920–37)
THOMASSON, J. P. (the late). (**Council,** 1896–1903)
BIDDER, G. P., Sc.D. (the late). (**Council,** 1899–1953; **President,** 1939–45; **Vice-President,** 1948–53)
THE LORD MOYNE, P.C., D.S.O. (the late). (**Vice-President,** 1929; 1939–45; **President,** 1930–39)
ALLEN, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary). (**Council,** 1895–1942; **Secretary,** 1895–1936; **Hon. Governor,** 1937–42)

FOUNDERS

1884 THE CORPORATION OF THE CITY OF LONDON, The Guildhall, E.C. 3
1884 THE WORSHIPFUL COMPANY OF MERCERS, Mercers' Hall, 4 Ironmonger Lane, E.C. 2
1884 THE WORSHIPFUL COMPANY OF GOLDSMITHS, Goldsmiths' Hall, Foster Lane, E.C. 2
1884 THE ROYAL MICROSCOPICAL SOCIETY, B.M.A. House, Tavistock Square, W.C. 1
1884 BULTEEL, THOS. (the late)
1884 BURDETT-COUTTS, W. L. A. BARTLETT (the late)
1884 CRISP, Sir FRANK, Bart. (the late). (**Council,** 1884–92; **Hon. Treasurer,** 1884–88)
1884 DAUBENY, Captain GILES A. (the late)
1884 EDDY, J. RAY (the late)
1884 GASSIOT, JOHN P. (the late)
1884 LANKESTER, Sir E. RAY, K.C.B., F.R.S. (the late). (**Hon. Secretary,** 1884–90; **President,** 1891–1929)

1884 Lord MASHAM (the late)
1884 MOSELEY, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord AVEBURY, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 POULTON, Prof. Sir EDWARD B., F.R.S. (the late). (**Council**, 1888–94)
1884 ROMANES, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 WORTHINGTON, JAMES (the late)
1885 The 15th EARL OF DERBY (the late)
1887 WELDON, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 BURY, HENRY, (the late)
1888 THE WORSHIPFUL COMPANY OF DRAPERS, Drapers' Hall, E.C. 2
1889 THE WORSHIPFUL COMPANY OF GROCERS, Grocers' Hall, Princes Street, E.C. 2
1889 THOMPSON, Sir HENRY, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord REVELSTOKE (the late)
1890 RICHES, T. H. (the late). (**Council**, 1920–25)
1892 BROWNE, Mrs E. T. (the late)
1898 WORTH, R. HANSFORD, M.Inst.C.E. (the late)
1899 The EARL OF IVEAGH, K.G., C.B., C.M.G., 11 St James's Square, S.W. 1 (**Vice-President**, 1929→)
1902 GURNEY, ROBERT, D.Sc. (the late). (**Council**, 1932–5)
1904 SHAW, JOSEPH, K.C. (the late)
1909 HARDING, Colonel W. (the late)
1910 MURRAY, Sir JOHN, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 SWITHINBANK, H. (the late)
1913 SHEARER, Dr CRESSWELL, F.R.S. (the late)
1913 HERON-ALLEN, E., F.R.S. (the late)
1918 EVANS, GEORGE (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 MCCLEAN, Capt. W. N., 39 Phillimore Gardens, W. 8
1920 Lord BUCKLAND OF BWLCH (the late)
1920 LLEWELLYN, Sir D. R. (the late)
1921 HARMER, F. W. (the late)
1924 THE MACFISHERIES, LTD., Ocean House, Pudding Lane, E.C. 3
1924 Lady MURRAY (the late)
1925 THE INSTITUTION OF CIVIL ENGINEERS, Great George Street, Westminster, S.W. 1
1925 DISCOVERY COMMITTEE
1927 BIDDER, Miss ANNA M., Ph.D., 2A Cavendish Avenue, Hills Road, Cambridge. (**Council**, 1948–51, 1954–57)
1933 PEEL, Col. Sir EDWARD T., K.B.E., D.S.O., M.C., c/o Messrs Peel and Co., Ltd. P.O. Box 331, Alexandria, Egypt. (**Vice-President**, 1936→)
1938 BUCHANAN, Dr FLORENCE (the late)
1945 BROWN, ARTHUR W. W. (the late)

MEMBERS

* Life Members

1949 ABBOTT, B. C., Ph.D., F.Inst.P., Dept. of Zoology, University of California, Los Angeles 24, Calif., U.S.A.
1945 ABERDEEN UNIVERSITY LIBRARY, The University, Aberdeen
1934 ADAM, Mrs K. M. G., 84 Lasswade Road, Edinburgh 9

1951 ADAMS, E., 2 Woodford Crescent, Marsh Mills, Plympton, Devon
*1954 ADAMS, Miss M. N. E., 11 Milner Road, Kingston-on-Thames, Surrey
1957 ADCOCK, N. W., Rossignol, Harlaxton Drive, Long Eaton, Notts
1940 Lord ADRIAN, O.M., M.D., D.Sc., LL.D., F.R.S., The Master's Lodge, Trinity College, Cambridge
1947 AFFLECK, R. J., 1 Helmsdale Road, London, S.W. 16
1957 AGRAWAL, V. P., Dept. of Zoology, Queen Mary College, Mile End Road, London, E. 1
1957 AKKESHI MARINE BIOLOGICAL STATION: Akkeshi, Hokkaido, Japan
1950 ALEXANDROWICZ, J. S., Ph.D., M.D., The Laboratory, Citadel Hill, Plymouth, Devon
1957 ALLEN, Miss D. M., Cedars, Furzedown College, Welham Road, Tooting, London, S.W. 17
1954 ALLEN, G. L., The Nook, 87A Bury Old Road, Sedgley Park, Prestwich, Manchester
1951 ALLEN, J. A., Dove Marine Laboratory, Cullercoats, Northumbs
1952 ALLEN, Miss J. M., Tenements Farm, Chipperfield, Herts
1953 ALVARIÑO, Señora A., Doce de Octubre 11–1 °C, Madrid, Spain
*1927 AMIRTHALINGAM, C., Ph.D., 2 Dickmans Path, Colombo, Ceylon
1957 ANGUS, L. H., A.R.I.C., Three Gables, Torridge, Plympton, Plymouth, Devon
1956 ANSELL, A. D., 22 Mannion Road, Henley-on-Thames, Oxon
1950 ARNOLD, D. C., Gatty Marine Laboratory, The University, St Andrews, Fife
1944 ASHBY, D. G., c/o P.O. Box 61, Stellenbosch, Cape Province, S. Africa
1954 ASHHURST, Miss D. E., Heron Court, Alexandra Road, Epsom, Surrey
1958 ATHERTON, D., Ph.D., J. S. Craig & Co. Ltd., 87 Portman Street, Glasgow, S. 1
1957 ASTON, C. E. J., 23 Beechcroft Avenue, Harrow, Middx
*1929 ATKINS, Miss D., D.Sc., c/o The Laboratory, Citadel Hill, Plymouth, Devon
*1939 ATKINS, W. R. G., C.B.E., O.B.E. (mil.), Sc.D., F.R.I.C., F.Inst.P., F.R.S., The Old Vicarage, Antony, Torpoint, Cornwall
*1910 ATKINSON, G. T., Gresham House, Esplanade, Lowestoft, Suffolk
1951 ATLANTIC BIOLOGICAL STATION, St Andrews, N.B., Canada

1948 BAAL, H. J., 3 Bel Royal Villas, Jersey, C.I.
1957 BAER, Prof. J. G., Institut de Zoologie, Rue Emile Argand, Neuchâtel, Switzerland
1950 BAERENDS, Prof. G. P., Zoölogisch Laboratorium, Rijksstraatweg 78, Haren (Gron.), Holland
*1949 BAGENAL, T. B., Marine Station, Millport, Isle of Cumbrae, Scotland
1956 BAILEY, Miss J. A., 110 Cambridge Road, North Harrow, Middx
*1952 BAILY, JOSHUA L. Jr., 4435 Ampudia Street, San Diego 3, Calif., U.S.A.
1950 BAINBRIDGE, R., Ph.D., 43 Strathmore Avenue, Hull
1953 BAINBRIDGE, V., Fisheries Laboratory, Lowestoft, Suffolk
1957 BAKER, C. J. E., 34 St John's Road, Oxford
*1920 BAKER, J. R., D.Sc., F.R.S., Dept. of Zoology and Comparative Anatomy, University Museum, Oxford
1936 BALDWIN, Prof. E., Ph.D., Dept of Biochemistry, University College, Gower Street, London, W.C. 1 (**Council**, 1946–48, 1957→)
1955 BALLANTINE, W. J., A3 Downing College, Cambridge
1953 BARKER, J. A., 8 Hillside Avenue, Friern Barnet, London, N. 11
1949 BARNARD, E. E. P., 7 Webster Gardens, Ealing, London, W. 5

1956 BARNARD, J. LAURENS, Ph.D., Allan Hancock Foundation, University of California, Los Angeles 7, Calif., U.S.A.
1939 BARNES, H., D.Sc., F.R.I.C., Marine Station, Millport, Isle of Cumbrae, Scotland
1954 BARNES, M. McC., Mandeville, Rosebank Crescent, Pennsylvania, Exeter, Devon
1955 BARNETT, P. R. O., Cloudshill, Eaton Avenue, Allestree, Derby
1953 BARNS, H. N., Spearwood, Combpyne, near Axminster, Devon
1957 BARR, W. A., 238A Main Street, Bellshill, Lanarkshire, Scotland
1939 BARRINGTON, Prof. E. J. W., D.Sc., Dept. of Zoology, The University, Nottingham
1951 BARRON, H., 65 Sumerton Road, Belfast, N. Ireland
1939 BASSINDALE, R., Dept. of Zoology, The University, Bristol
1946 BATHAM, Miss E. J., Ph.D., Portobello Marine Biological Station, Portobello, Otago, New Zealand
1939 BAXTER, E. W., Biology Dept., Medical School, Guy's Hospital, London, S.E. 1
*1929 BAYLIS, L. E., Ph.D., Dept. of Physiology, University College, Gower Street, London, W.C. 1
1934 BEADLE, L. C., Dept. of Biology, University College of East Africa, P.O. Box 262, Kampala, Uganda
1955 BEALL, I. D., 19 Beresford Street, Stoke, Plymouth, Devon
1957 BEARD, D. M. MacG., 123 Northcote Road, Downend, Bristol
1928 BEER, Sir GAVIN DE, Kt., D.Sc., F.R.S., British Museum (Natural History), Cromwell Road, London, S.W. 7
1955 BEESON, Miss G., Redgate, 216 Unthank Road, Norwich, Norfolk
1954 BELCHER, J. H., 197 Risley Avenue, Tottenham, London, N. 17
1950 BELL, Mrs E. B., Solva, Glanford Road, Brigg, Lincs
1958 BELLAIRS RESEARCH INSTITUTE of McGill University, St James, Barbados, B.W.I.
1957 BENNETT, D. P., 15 Pickering Road, Cheltenham, Glos
1954 BERNER, L. D. Jr., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1958 BERNHARD, Dr MICHAEL, c/o Istituto di Genetica, Universita di Pavia, Pavia, Italy
1947 BERRILL, Prof. N. J., F.R.S., Dept. of Zoology, McGill University, Montreal, Canada
1955 BERRY, R. J., Group for Experimental Research in Inherited Diseases, University College, Gower Street, London, W.C. 1
1947 BEST, A. C. G., The Laboratory, Citadel Hill, Plymouth, Devon
1953 BHATTACHARYYA, Dr R. N., 44/B Kalighat Road, Calcutta 26, India
1956 BHAVANARAYANA, P. V., Zoological Laboratories, Andhra University, Waltair, S. India
1953 BHIMACHAR, B. S., D.Sc., F.N.I., Central Inland Fisheries Research Station, 47/1 Strand Road, Calcutta 7, India
1958 BHUPENDRA, P., Marine Biology Station, Menai Bridge, Anglesey
1903 BIDDER, Col. H. F., The Malting House, Nettlebed, near Henley-on-Thames, Oxon
*1945 BINGLEY, F. J., Flatford Mill Field Centre, East Bergholt, near Colchester, Essex
1955 BINYON, E. J., 44 Kendall Avenue South, Sanderstead, Surrey
1957 BIERI, R., Ph.D., 116 Glen Street, Yellow Springs, Ohio, U.S.A.
1925 BIRKBECK COLLEGE, The Library, Malet Street, London, W.C. 1
1951 BIRKETT, L., Fisheries Laboratory, Lowestoft, Suffolk

1947 BISHOP, M. W. H., Meadow Farm, Waterbeach, Cambs
1951 BLACKBURN, Prof. M., D.Sc., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1957 BLAKE, J. W., Dept. of Zoology, University of North Carolina, Chapel Hill, North Carolina, U.S.A.
1955 BLAKE, M. L., Picket Piece, Avening, near Stroud, Glos
1930 BLASCHKO, Dr H., Dept. of Pharmacology, South Parks Road, Oxford
1952 BLAXTER, J. H. S., Marine Laboratory, Victoria Road, Torry, Aberdeen
1957 BLOOD, M. J., Ravenscourt, Coopers Green, Uckfield, Sussex
1955 BLOOM, Miss J. L., 12 Belsize Square, Hampstead, London, N.W. 3
1910 BLOOMER, H. H., Longdown, Sunnydale Road, Swanage, Dorset
1953 BOALCH, G. T., c/o The Laboratory, Citadel Hill, Plymouth, Devon
1957 BOCKS, Miss S. M., 29 Milford Street, London, S.W. 8
1951 BODEN, B. P., Ph.D., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1947 BOËTIUS, Dr JAN, Fysiologisk Laboratorium, Danmarks Akvarium, Charlottenlund, Denmark
1936 BOGUE, Prof. J. YULE, D.Sc., Heyscroft, Hartley Road, Altrincham, Cheshire
1932 BOLITHO, Capt. R. J. B., Gorey, Jersey, C.I.
1957 BOND, Miss A. J., 51 Coleridge Vale Road North, Clevedon, Som
1945 BONEY, A. D., 24 Ford Park Road, Mutley, Plymouth, Devon
1954 BONHAM, Dr K., Applied Fisheries Laboratory, University of Washington, Seattle, Wash., U.S.A.
1957 BOOLOOTIAN, R. A., Ph.D., Dept. of Zoology, University of California, Los Angeles 24, Calif., U.S.A.
1957 BOOTH, Miss M. A., 21 Pinfold Lane, Penn, Wolverhampton
*1933 BOSCHMA, Prof. Dr H., Rijksmuseum van Natuurlijke Historie, Leiden, Holland
1947 BOSSANYI, J., 22 Field End Road, Eastcote, Pinner, Middx
1954 BOWERS, A. B., Marine Biological Station, Port Erin, Isle of Man
1955 BRADLEY, D. J., 71 Linden Drive, Evington, Leicester
*1954 BRADSHAW, J. S., P.O. Box 891, Del Mar, Calif., U.S.A.
1957 BRAILSFORD, J. D., 328 London Road, Wokingham, Berks
1940 BRAMBELL, Prof. F. W. ROGERS, D.Sc., F.R.S., Dept. of Zoology, University College of North Wales, Bangor, Caern. (**Council**, 1944–47, 1948–51)
1954 BREHAUT, R. N., La Canurie, Collings Road, St Peter Port, Guernsey, C.I.
1924 BRIGHTWELL, L. R., East Cliff Cottage, West Portholland, Portloe, Truro, Cornwall
1958 BRIMSON, P. W., The Rectory, Old Cleeve, Minehead, Som
1933 BRISTOL UNIVERSITY, Dept. of Zoology, Bristol
*1941 BRITISH CELANESE LTD., Celanese House, Hanover Square, London, W. 1
1939 BRITISH ROPES LTD., Western Avenue, Cardiff
1958 BRITISH SUB-AQUA CLUB, TAUNTON BRANCH, The Secretary, Two Lilac Cottage, Trull, Taunton, Som
1955 BRITISH SUB-AQUA CLUB, Scientific Section, The Close, Newport Pagnell, Bucks
*1946 BROCK, Mrs C. H., Ph.D., 32 Barton Road, Cambridge
1946 BROUGH, Prof. JAMES, D.Sc., Dept. of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff
1955 BROWN, C. A., 26 Sydney Road, Newquay, Cornwall
1928 BROWN, Miss E. M., Ph.D., 6 Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey

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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, and, since that date, a new library and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; 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. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. 27 (p. 761) and Vol. 31 (p. 193) of this *Journal*.

The laboratory is open throughout the year and its work is carried out by a fully qualified research staff under the supervision of the Director. 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, physiology and other branches of science. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

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