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

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(Text-figs. 1–8)

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

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

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

METHODS

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

Method for Nereis

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

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

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

Method for Chaetopterus.

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

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

For closed-circulation experiments, cylinder *M* is sealed with liquid paraffin, as shown in the figure. The circulation can now be closed when desired, by passing rubber tube *I* over jet *L*. For feeding experiments, the paraffin seal is omitted, *M* is stirred and aerated by an air-jet, and *I* is kept permanently on *L*. The effect of adding diatom cultures, tow-nettings, etc., to *M* can now be recorded.

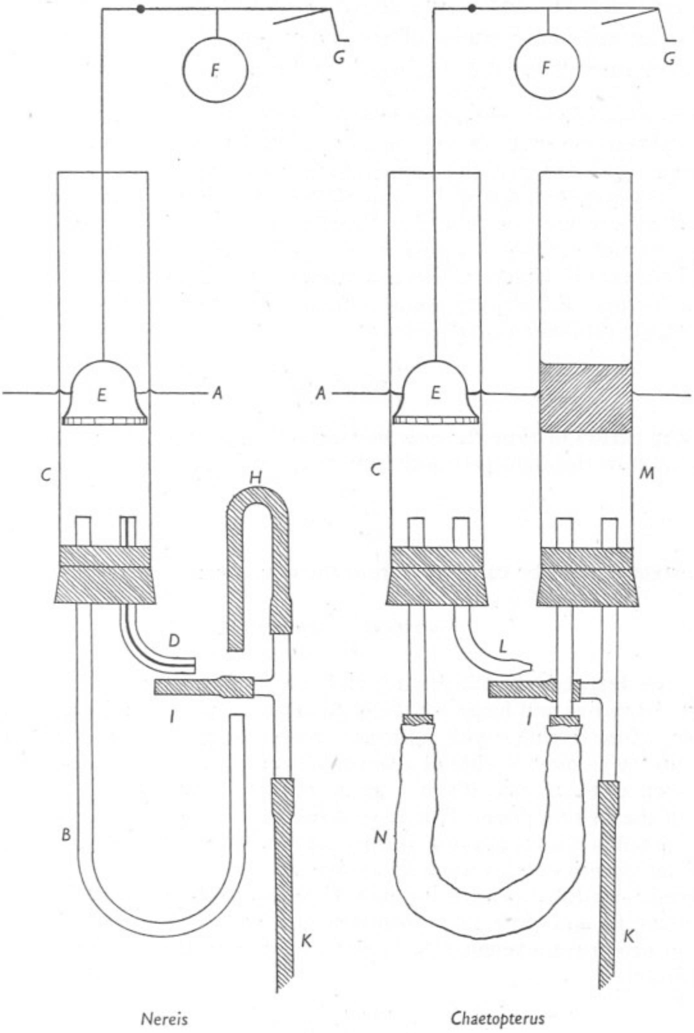

Fig. 1. Apparatus for recording the irrigation currents (see text).

Calculation of flow rates from the records

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

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

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

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

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

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

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

The constant j could be calculated from the equation:

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

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

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

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

Inserting the following rough but reasonable values: $\eta=0{\cdot}012$, $\rho=1$, $l=5$, $r=0{\cdot}07$, we get a value of 16·5 cm. for h_c. This is of course very much greater than the height to which the level in C can rise, so we may conclude that the linear relation will always hold when a capillary of dimensions suitable for such worms as *Arenicola* or *Nereis* is on the apparatus. However, h_c falls rapidly with an increase in r, and it also falls (through η) as the temperature rises. Where doubt exists, the linearity of the relation between pressure and flow rate can easily be checked during calibration. We found that the jets used for *Chaetopterus* gave turbulent flow even under ordinary working conditions, so we derived the flow rates for this worm from curves made by recording the lever excursions at various known flow rates.

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

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

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

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

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

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

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

CHAETOPTERUS VARIOPEDATUS

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

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

The fans normally drive water in a tailward direction, the only exception so far recorded occurring when irritating matter is being expelled from the tube (see below). The worm can reverse itself very rapidly in the tube, and produce a change in the direction of flow by this means; according to Enders, turning round can be completed in from 10 to 20 sec.

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

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

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

Expulsion of faeces. MacGinitie makes no mention of defaecation, and the following details are taken from Enders. The faecal masses 'are sometimes discharged from the anus singly, but more frequently by twos and threes... they remain until a fairly constant number has been discharged, then the palettes vibrate more strongly and expel them to the exterior. When the small specimens upon which I have made observations were well fed they expelled from ten to twenty masses at intervals of four minutes. The faeces are expelled with considerable force.' Even if the animal receives very little food, it produces faeces consisting largely of mucus. It is rather remarkable that the forcible performance described by Enders was not recorded by MacGinitie; the point is returned to below.

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

Irrigation patterns

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

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

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

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

The worm traces brief but very violent outbursts, during which the writing point moves up and down over a wide distance and with impressive speed, its strokes evidently corresponding to the 'kicks' of the fans. Between these bursts the worm is nearly or quite motionless. The bursts may follow each other fairly rapidly (as in the first part of Fig. 2), or at longer, and sometimes rather regular, intervals (as at the end of Fig. 2). The worm often reverses itself while registering this type of behaviour (this occurs four times in the first half of Fig. 2). The quantities of water driven during the outbursts can only be estimated very roughly from the records. The writing point, in the example of Fig. 2, often moved over 2 cm. at each stroke of the fans; this means an increase of the amount of water in the float chamber, at each stroke, of about 3 c.c. The strokes follow each other at intervals of about a second. We have named this pattern 'expulsion behaviour' because it appears to correspond with the violent ejections of irritating suspensions described by Enders. Its occurrence may be due to some disturbing mechanical or chemical factor. It was often seen at the beginning of an experiment, i.e. just after the tube had been tied to the apparatus, but it occasionally appeared later, without evident cause, after the worm had traced other patterns for many hours.

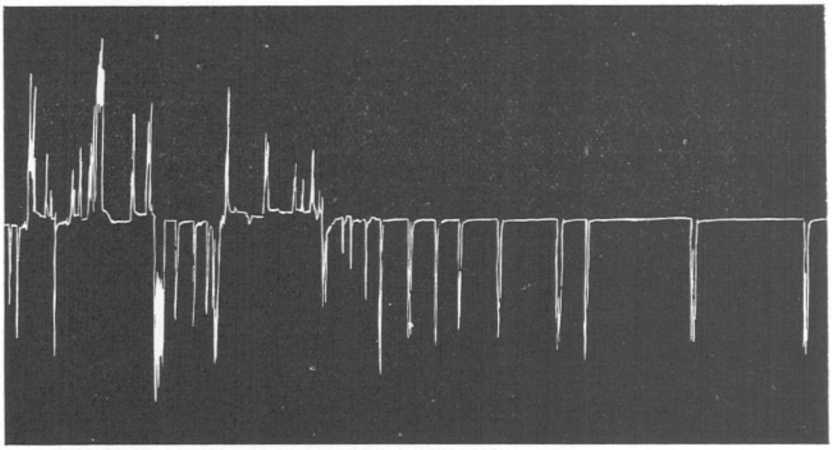

Fig. 2. *Chaetopterus variopedatus.* Irrigation record. The printed extract is 3 hr. long, and begins 1½ hr. after the tube was mounted on the apparatus. *Read all records from left to right.*

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

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

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

This pattern was traced from time to time by five of the worms. The base-line is given by the tips of the regularly spaced 'peaks', in the upper extract of Fig. 3. The worm is irrigating very steadily, except for brief pauses at the 'peaks', when the lever returns to the null position. The intervals between pauses average 18 min. The pattern agrees excellently with MacGinitie's account of mucous-bag feeding as summarized above, which it undoubtedly represents. A mucous bag is passed forwards to the mouth and swallowed at each pause. The following quantities can be got from Fig. 3. The flow rate, during the filtration periods, is 16 c.c./min., and the volume of water passed through each bag is about 290 c.c.

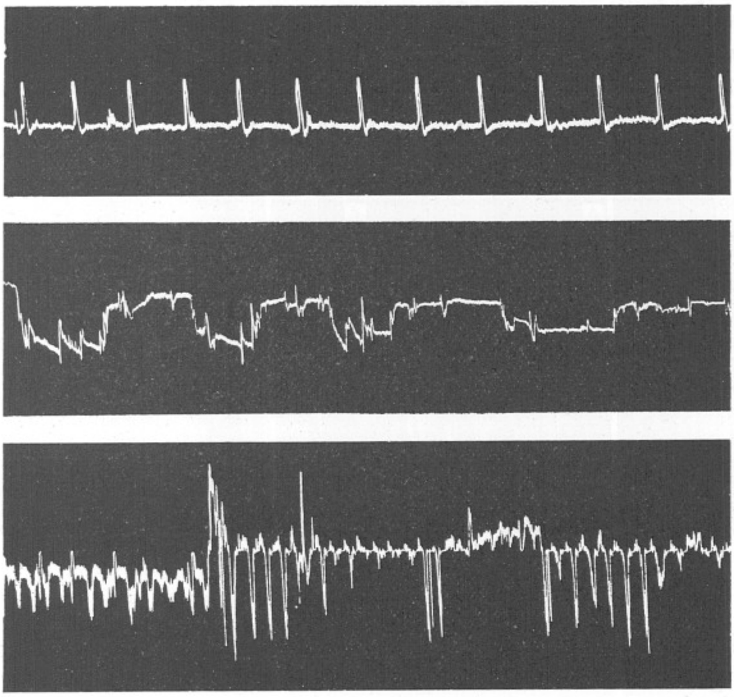

Fig. 3. *Chaetopterus variopedatus.* Extracts from the irrigation records of three individuals, all taken with the same lever magnification factor. Each extract is 4 hr. long.

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

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

There is fairly continuous activity on which a cycle is evidently superposed, having a period of about 5 min. (5·3 min. in the extract of Fig. 3). The cycle varies somewhat in its expression, as the extract shows, but it often appears as a series of brisk, but by no means maximal, outbursts of the expulsion type. The picture agrees reasonably well with Enders's account of the forcible ejection of faeces from the tube every 4 min., as summarized above.

Now a striking feature of the upper line of Fig. 3 is the absence of anything which could be interpreted as faecal ejection, neither does MacGinitie mention such an act as interrupting the mucous-bag feeding process. On the other hand, the description of Enders is very clear and convincing. The available facts suggest that *Chaetopterus* has more than one method of feeding. We know that *Nereis diversicolor* can take relatively large pieces of animal or plant material with its jawed proboscis, or ingest the surface mud, or filter-feed with a mucous plankton net (Linke, 1939; Harley, 1950); and there seems no reason why *Chaetopterus* should not ring the changes too. Perhaps the MacGinitie method is chiefly used when the suspended particles are few and fine, and the Enders method when they are coarser and more numerous; the first might result in the production of light, mucoid faeces which would drift away with the filtration current, and the latter of heavier ones which would have to be kicked out.

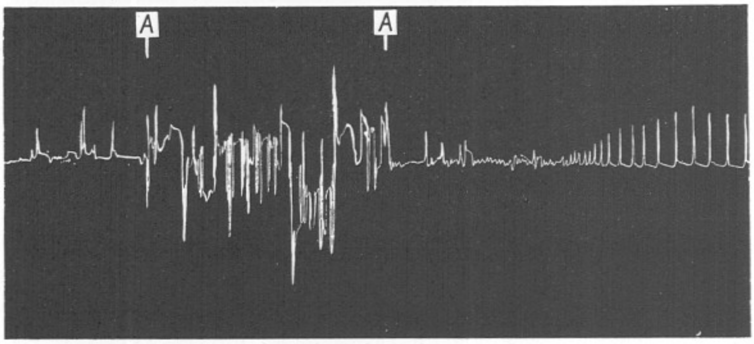

Fig. 4. *Chaetopterus variopedatus*. Irrigation record. The circulation was closed for 3 hr., between the marks *A*. Total length of extract, 10 hr.

Response to closure of the circulation

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

The effect of closure was to produce a sharp increase in the water currents, which lasted during the whole closure period (Fig. 4). The movements consist in the main of violent expulsion bursts, superimposed on periodic reversal in the tube; that is to say, they suggest a generalized state of irritation rather than a specific increase of respiratory irrigation. Re-opening of the circulation was invariably followed by a prolonged period in which the water movements were very slight, or even ceased altogether.

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

Response to 'feeding'

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

Dependence of the patterns on external conditions

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

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

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

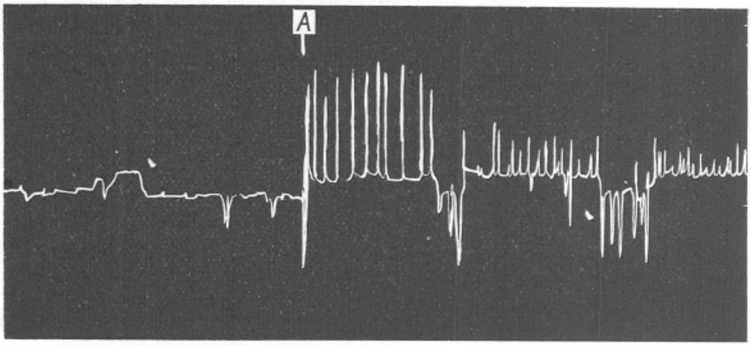

Fig. 5. *Chaetopterus variopedatus*. Irrigation record. A suspension of organisms was added at *A*. Total length of extract, 10 hr.

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

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

Behaviour of isolated fan segments

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

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

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

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

We have not traced any detailed correspondence between the time-patterns of the isolated fan segments and those of the intact worm; but it seems clear that the former afford a good supply of material from which the latter could be constructed. There is also, of course, the likelihood of other spontaneous centres, elsewhere in the nervous system.

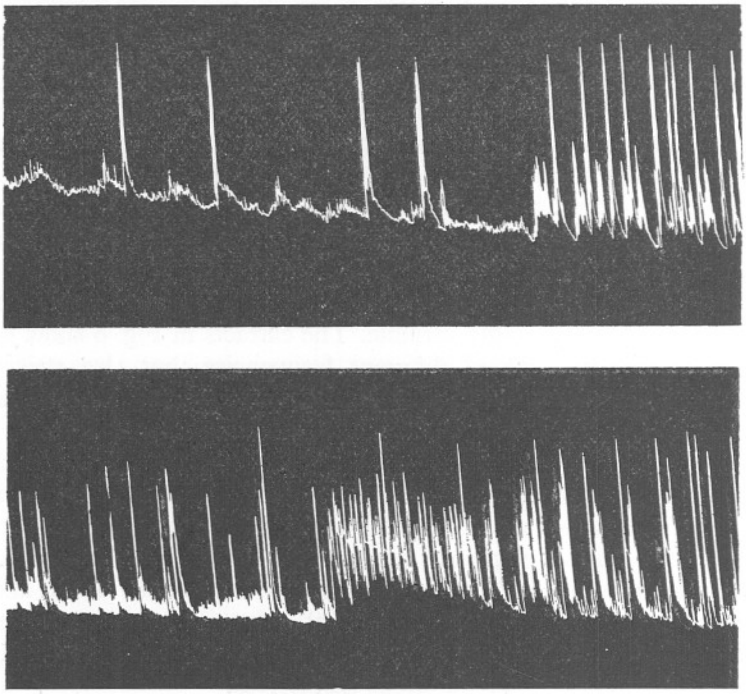

Fig. 6. *Chaetopterus variopedatus.* Movements of the isolated 14th segment, recorded with a light isotonic lever. Each extract is from a different individual. Duration of extracts, 4 hr.

NEREIS DIVERSICOLOR

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

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

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

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

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

Irrigation patterns on open circulation

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

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

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

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

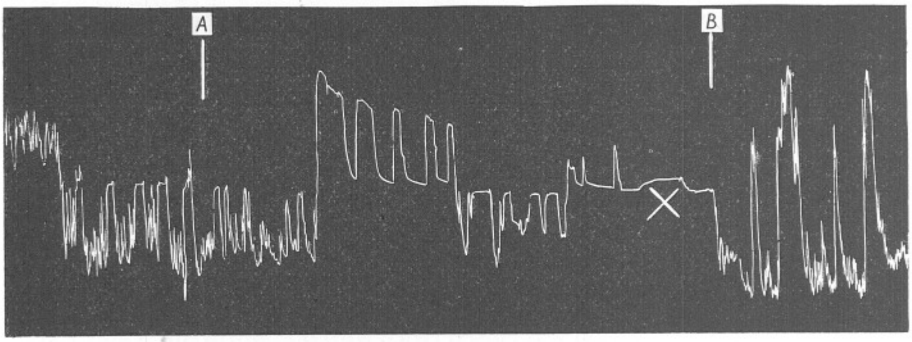

Fig. 7. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 22 hr.; length from *A* to *B*, 12½ hr. The slight rise at *X* is an artefact due to a temporary change in level of the water in the outer tank.

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

Response to closure of the circulation

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

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

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

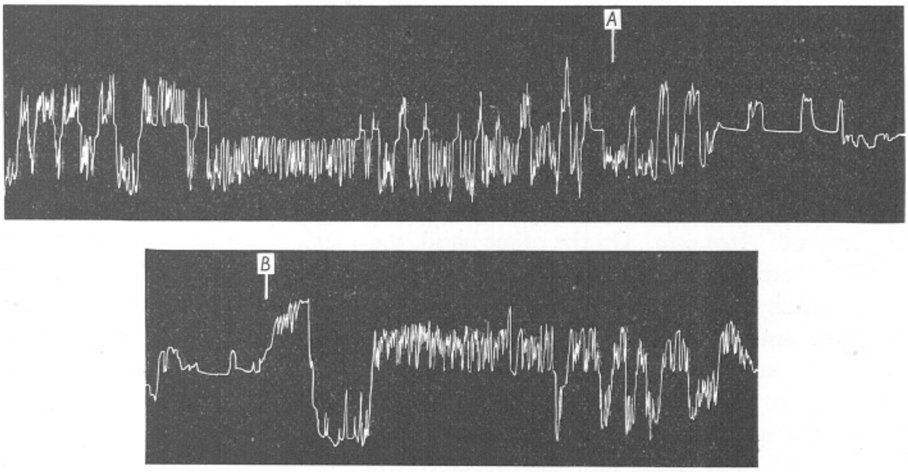

Fig. 8. *Nereis diversicolor*. Irrigation record. The circulation was closed between *A* and *B*. Total length of extract, 38 hr.; length from *A* to *B*, 10½ hr.

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

SPECIFICITY OF THE IRRIGATION PATTERNS

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

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

SUMMARY

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

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

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

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

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

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

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

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