THE BEHAVIOUR OF *ARENICOLA MARINA* L. IN SAND, AND THE ROLE OF SPONTANEOUS ACTIVITY CYCLES

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(Text-figs. 1–7)

In the laboratory, the lugworm shows two distinct types of spontaneous activity cycle. The question which the following paper sets out to answer is, have these laboratory results any bearing on the worm's normal life in the field?

The first type of cycle has tentatively been named the feeding cycle. The isolated oesophagus, suspended in sea water or the worm's body fluid, shows outbursts of rhythmic activity alternating with periods of rest. The intact worm, watched in a glass tube, generally shows periodic outbursts of proboscis extrusion and withdrawal, or of gulping and swaying of the head. These cycles, like those of the oesophagus, have an average period of about 7 min. By means of a series of dissected preparations of ascending complexity, one can show that the two rhythms are the same; the 'feeding rhythm' of the whole worm is the oesophageal rhythm, transmitted to the muscles of the proboscis and the anterior body wall (Wells, 1937).

The second type of cycle is of much longer period. The worms, in glass tubes, generally pump water through the tubes in a headward direction in rhythmically recurring bursts. Closer inspection shows that this headward irrigation is the second, and most prominent, phase of a 3-phase outburst; the first is tailwards locomotion, and the third is tailwards irrigation. The outbursts are not, as one might expect, reflexly elicited by oxygen exhaustion or CO_2 accumulation in the tube, but result from the activity of a second pacemaker, probably situated in the ventral nerve cord (van Dam 1937, 1938; Wells, 1949).

Now the intact worms, in all of these experiments, were watched under abnormal conditions. A glass tube differs, mechanically and chemically, from the sand in which the species normally lives; in order that their activities should be visible, the worms were illuminated; and they had mostly been fasting in the laboratory for days or even weeks. One might therefore suspect that the very regular periodicity, which so often characterizes their behaviour, is due to the artificial conditions and would not occur, or would be masked by reflex responses, in the more variable surroundings in the field.

To settle this point, one would have to watch or record the behaviour pattern of the worms in their natural habitat. This would be difficult. I have therefore

done the next best thing, and allowed worms to make burrows in sand in the laboratory, in which their behaviour could be recorded. The results are described below. The main conclusion is that the cycles appear with great regularity, and especially clearly when the worms are making funnels and faecal accumulations like those which signalize their presence on the beach.

THE FORM OF THE BURROW IN THE FIELD

The animal's mode of life has been described elsewhere (Wells, 1945).[1] The details of the burrow vary according to the nature of the beach, but there is
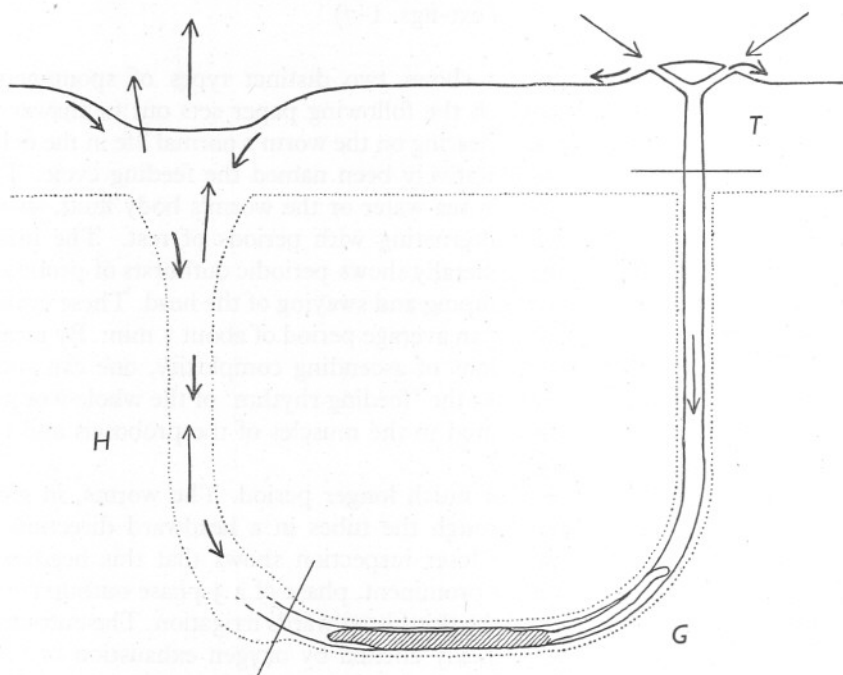

Fig. 1. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

a general pattern to which all of the variations conform (Fig. 1). Immediately below the well-known heap of castings, a 'tail shaft' descends vertically for several cm.; this houses the tail at the moment of defaecation. At its lower end,

[1] When I wrote that paper, I was unaware of two important works on the form of the lugworm's burrow. Häntzschel (1938) described burrows in sand. Linke (1939) described burrows in sand and mud, and gave much interesting information about the environment. Both accounts are illustrated by photographs and both stress the fact that the form of the burrow varies with the nature of the bottom.

the tail shaft widens into the 'gallery', a tube in which the worm moves to and fro, but always with its tail towards the tail shaft. The walls of the gallery are firm, due to impregnation with the worm's secretions (Osler, 1826; Häntzschel, 1938; Linke, 1939). The gallery descends more or less vertically, then swings round to become horizontal. Its lower ending communicates with the surface by the 'head shaft', a part of the burrow whose detailed structure varies greatly with the nature of the beach. Typically, the head shaft consists of a column of yellowish sand, without any lumen running through it, and its upper end is marked by a saucer-shaped depression of the surface. The chief forces by which the head shaft is set up and maintained are: (i) feeding from its lower end, causing its substance to slowly descend; (ii) upstreaming of the irrigation water, which helps to keep it soft; and (iii) occasional upward 'working' excursions of the worm.[1] If the conditions are favourable, a worm may live in the same burrow—irrigating, feeding and periodically defaecating—for months on end (Thamdrup, 1935; Linke, 1939).

Apparatus for Studying Behaviour in the Burrow

To watch the activities of a worm in sand is impossible. Even if one allows it to burrow between glass plates, so close that there is only just room for the worm, sand makes its way between worm and glass, and one gets only occasional glimpses of parts of the animal. The method used in this work was to record the water currents set up by the worms in their burrows, and to compare the resulting records with those produced by worms in glass tubes (Wells, 1949). The apparatus was as follows.

ABCD (Fig. 2) represents two squares of plate glass, about 38 cm. square. They are held apart by a U-shaped strip of rubber (shaded), which is of square section and about 1 cm. thick. This rubber is well greased with stopcock grease on the sides which meet the glass, and shorter pieces are put beside it at six points; at these places, the whole is held together by *G*-clamps, lightly applied through additional rubber pads external to the glass. Another greased rubber strip, in the centre, divides the upper part of the resulting vivarium into two.

When assembled, the vivarium is held upright in a wooden stand (not shown) and filled. The lower part contains, to a depth of about 20 cm., mud dug from the deeper layers of the beach (drawn black). On top of this is about 6 cm. of yellow surface sand (dotted), and 6 cm. of sea water. Aeration is through jet *E*. Finally a large, recently collected worm is added. The worm goes down into the mud at once, and one usually sees nothing more for a day or so; but the dimensions are such that it ultimately sets up a burrow with the funnel on one

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[1] Chapman & Newell (1947, 1948) believe that the thixotropy of muddy sand plays an essential part in the processes by which the worm enters the sand and sets up a burrow, but the writer is unable to see the necessity for this (Wells, 1948).

side of the centre partition and the faecal pile on the other, as shown in the drawing.

Water currents are produced by the worm in various ways—by irrigation, or by creeping along the tube—and will clearly tend to displace the levels of the water in the two top compartments. The muddy sand is practically impermeable to water. The compartments are connected by capillary siphon *F*,
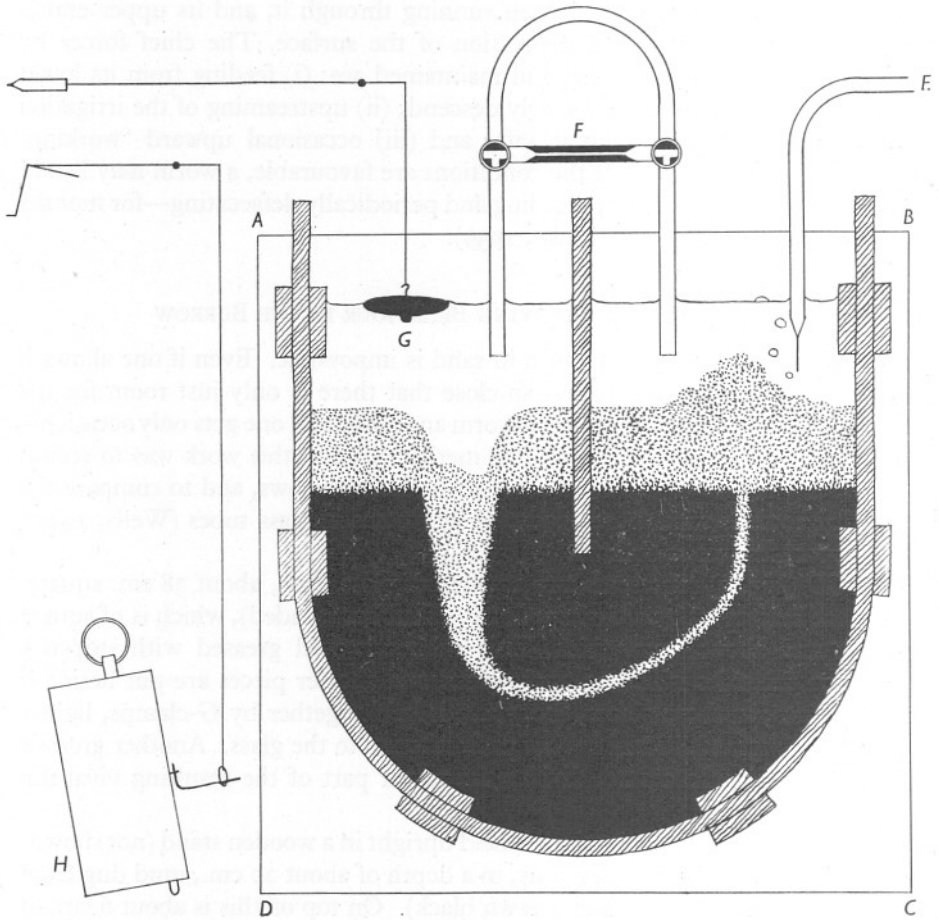

Fig. 2. Apparatus for recording the behaviour of the worm in the burrow (see text).

provided with a by-pass of wide bore to facilitate the daily routine, described below. The capillary prevents excessive piling up of water on either side, but offers enough resistance to allow the fluctuations in level to be recorded. This is done by means of float *G*, made of paraffin wax moulded on silver wire, and connected to a light isotonic lever writing on smoked paper.

The following values were found satisfactory: capillary bore about 1·5 mm.; lever magnification about 12; paper moves at about 25 mm./hr. The time trace was made by clock *H*, connected to a lever with a frontal writing point and tracing 1 cycle per hr.; it has been omitted from the illustrations to save space.

Once a day, the following routine was carried out. The smoked paper was changed, the wide by-pass siphon was opened, the sea water was topped up with distilled water to a gauge mark to compensate for evaporation; the faeces were removed and fresh sand was added to the funnel. Except for this daily operation, which took about 5 min., recording was continuous and the apparatus ran itself.

Altogether, six worms were studied, for periods ranging from 5 to 21 days; they yielded an aggregate of 72 recorded 'worm-days'. None of these worms died during the experiments and five of them were still in good condition in the sand when their records were stopped. The sixth ended its experiment by coming out on the surface of the sand on the 11th day and refusing to go down again (though apparently in good condition) for 36 hr.; this was probably due to some kind of organic decomposition in the sand. I have noticed, on other occasions, that the worms tend to leave very foul sand, and when the vivarium of this particular individual was dismantled it was unusually evil-smelling.

The Form of the Burrow in the Apparatus

The configuration of the burrows in the apparatus (as shown by a yellow stain on the black sand) resembled that found in the field. The worms fed from conical head shafts (whose upper surfaces subsided rather more rapidly than usual owing to the small sectional area of the apparatus) and piled up heaps of faecal cylinders. They appeared, however, to be rather more restless than worms kept under less cramped conditions. The head shafts often shifted a little in position from day to day, and the worms sometimes reversed their burrows, converting the old tail shaft into a head shaft, and vice versa. Both of these changes are occasionally seen in larger vivaria (and they undoubtedly occur in the field), but they were rather more frequent in the apparatus here described.

The Defaecation Cycle

Whenever the worms were feeding regularly from the head shaft, and piling up their faeces in the other compartment of the apparatus, the pattern shown in Fig. 3 was traced on the record. The obvious feature is a series of prominent diphasic excursions with a sharp, short peak followed by a broader one in the opposite direction. They occur about once every 40 min.

Now this record can very readily be interpreted by means of the experiments with worms in glass tubes. The cycles traced in Fig. 5 of my previous paper

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(Wells, 1949) are evidently identical with those now under consideration.[1] We may safely conclude that the movements responsible for the tracings are the same in both cases. The sharp first peak is due to a tailward excursion of the worm, and the broad second peak is due to vigorous headward irrigation accompanied by gentle headward creeping. The third 'rebound' phase, which was sometimes very conspicuous in glass tubes, is seldom visible on the records got from actively feeding worms in sand.

If one watches the experiments with worms in sand, one sees that a faecal cylinder is suddenly shot out of the burrow at (or a moment before) the apex of each of the sharp peaks. In other words, the tailward excursion, which
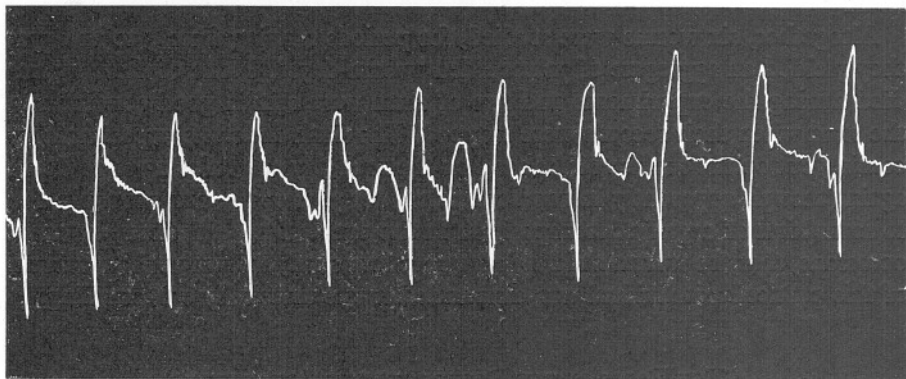

Fig. 3. Record (7 hr. long) traced by an actively feeding worm, with its tail towards the float. The worm defaecates at the tip of each of the prominent downward peaks. Read from left to right. (Worm 'Violetta'.)

begins the whole outburst, has carried the worm to the surface of the sand, and serves as a defaecatory excursion. The worm presumably creeps back to the point where it feeds, at the lower end of the head shaft, during the phase of headward irrigation.

One might have thought that the tailward excursion which brings the worm into position for defaecation is a reflex response to a full rectum, but this does not seem to be the case. Exactly similar excursions were often seen in glass tubes, in worms which had been fasting for days and whose tails were consequently empty.[2] We must therefore conclude that the tailward trip is simply an expression of one of the phases of the triphasic cycle, which is very beautifully suited to the worm's normal way of life.

[1] The worm in Fig. 3 of the present paper has its tail to the float, while that in Fig. 5 of the previous one is the other way round; so the patterns are traced the opposite way up.

[2] The worms occasionally produced faeces in the U-tubes but only if studied within 24 hr. of collection, and unfortunately never while they were being watched. The worm O 48 (in Fig. 5 of the previous paper) was collected on 11 January 1949, kept in a glass tank of clean sea water, and then put in the apparatus on 14 January 1949; its behaviour was recorded for 48 hr., during which two exposures to 'no air' were tried. The record shown in the illustration was taken in the evening of 15 January 1949.

ALTERNATIVE BEHAVIOUR PATTERNS

The pattern just described invariably accompanied feeding and defaecation. Having once set in, it was generally written on the drum with great regularity for many hours at a stretch, while the faeces steadily piled up and the funnel subsided. During the rest of the time, records were obtained which can be classified into three groups.

Fig. 4. Two records (each 4½ hr. long) traced by a worm which was not actively feeding and defaecating. The extracts were given on two different days. In both cases the worm's head is towards the float. The horizontal lines give the resting water levels at the beginning and end of the day. The difference is due to evaporation, which also causes the gradual upward trend of the other figures. (Worm 'Fasolt'.)

(i) *Irrigation cycles without a pronounced tailward excursion.* In sand, as in glass U-tubes, the three phases of the typical cycle can vary greatly in their relative prominence. The two records of Fig 4 were taken from the same worm, on different days, and in both cases its head was towards the float. They represent irrigation cycles in which the first phase is barely perceptible on the

tracing, while the second and usually the third are well marked (compare Wells, 1949, second part of Fig. 6). Now and again, one sees an outburst in which the third, 'rebound', phase is dropped out, and the same thing can be seen in the records got from glass tubes. With this curious exception, it may be stressed that the outbursts in any single series have an extremely constant form. The various types are modifications of an underlying triphasic pattern; having made up its mind, so to speak, which type to register, the worm sticks to that type very steadily for hour after hour. On another day, of course, it may choose another.

(ii) *Periods of apparently complete quiescence.* The lever sometimes traces a horizontal line, with barely perceptible oscillations if any, for many hours on end. One would like to know what the worm is doing, and especially how it gets oxygen, at such times. One knows only that it is inside the sand, whose untroubled surface gives no clue to what goes on below. Quiescence may continue for 24 hr. or even longer, after which vigorous activity begins again and the regular rhythmic patterns reappear.

(iii) *Periods of unexplained activity.* The lever shows excursions, often of very great amplitude, but the tracings are confused and have successfully defied all attempts at interpretation. This may continue for many hours.

Taking together all of the six worms which were studied in sand, their total time was divided between the various patterns as follows: defaecation cycles, 45 %; other irrigation cycles, 5 %; quiescent spells, 15 %; periods of unexplained activity, 35 %. It will be seen that only about half of the records obtained have been satisfactorily interpreted.

These results can be extrapolated, with due reservation, to the behaviour of the worms in the field. It may, I think, be fairly safely assumed, that every saucer and pile of faeces on the beach is the outcome of a cyclic behaviour pattern like that seen in Fig. 3. Mrs D. M. Kermack, who is studying the feeding and digestion of *Arenicola*, informs me that under favourable conditions the worms in the field defaecate about once every 45 min. This agrees well with the timing of the peaks in my records. My results also suggest that, at any moment, a considerable proportion of the worms is giving no surface signs at all—but the relative magnitude of the 'hidden population' will presumably vary with conditions. Newell (1948) assessed the density of lugworm populations by digging up areas of 1 sq.yd., and wrote 'This rather tedious method of sampling was found to be essential, since counting the number of casts per square yard is a most unreliable index of the number of worms, varying as it does with, among other conditions, the state of the tide'. There was, of course, no tide in my experiments. The time spent in active feeding and defaecation varied in different individuals from 32·5 to 68 %; so it may be that the conditions determining activity are not entirely environmental. I have already described great differences in feeding activity between worms kept individually in aquaria (Wells, 1945).

THE FEEDING CYCLE

As stated in the opening paragraphs, two distinct types of behaviour cycle are shown by lugworms in glass tubes. There is the irrigation-defaecation cycle already dealt with, and there is a cycle of anterior end activity, of period averaging about 7 min., which has been tentatively named a feeding cycle (Wells, 1937). Now the records got from worms in sand often show a considerable amount of 'background' activity between the irrigation-defaecation outbursts, and sometimes this has an obviously cyclic pattern, with a period of the same order as that of the feeding cycle. The extract of Fig. 5, for example,
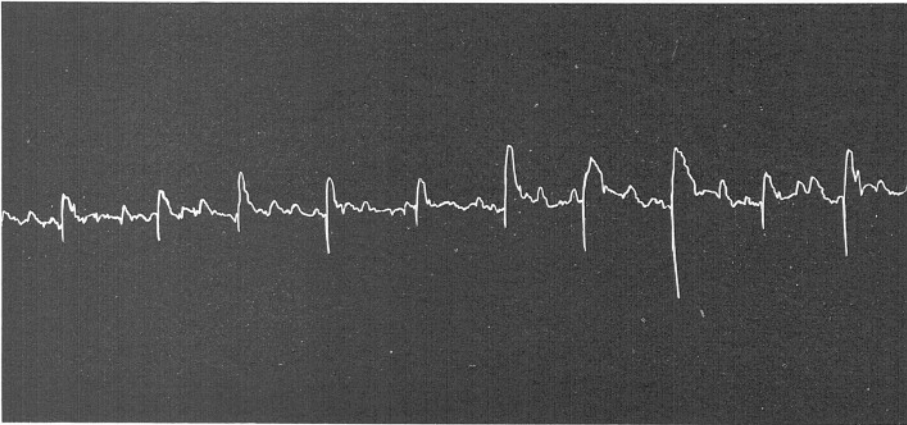

Fig. 5. Record (6 hr. long) traced by an actively feeding and defaecating worm, with its tail towards the float. The record shows a short-period cycle imposed on the main one. (Worm 'Sieglinde'.)

shows defaecatory excursions at intervals of about 35 min., and minor oscillations with a period of about 7–8 min. These may well be due to the oesophageal pacemaker, but it remains to be shown how the feeding outbursts could write themselves on the drum, with the apparatus of Fig. 1.

Just (1924) pointed out that there is a functional differentiation between the nineteen chaetigerous segments in the lugworm's body. The first three participate in the movements of the head and especially in proboscis activity, while the wave movements, which run along the body in irrigation or creeping, are the concern of the remaining sixteen. I showed in an earlier work that the excitations responsible for the feeding outbursts spread from the oesophagus to the body-wall muscles of the more anterior segments, which play a direct part in proboscis activity (Wells, 1937). The experiments now to be described were made to find out whether any influence of the oesophageal rhythm could be traced in the wave-carrying segments farther back.

The worm was pinned on a cork sheet under sea water, ventral side down

(Fig. 6). The first few segments were laid open and the extrovert was dissected as described in my earlier paper (Wells, 1937). The oesophagus was cut across and its oral end was connected to a light isotonic lever. The movements of this lever are mainly due to the proboscis muscles acting under the influence of the oesophageal pacemaker, though the muscles of the surrounding body wall also contribute to some extent. One or two of the branchiate segments were
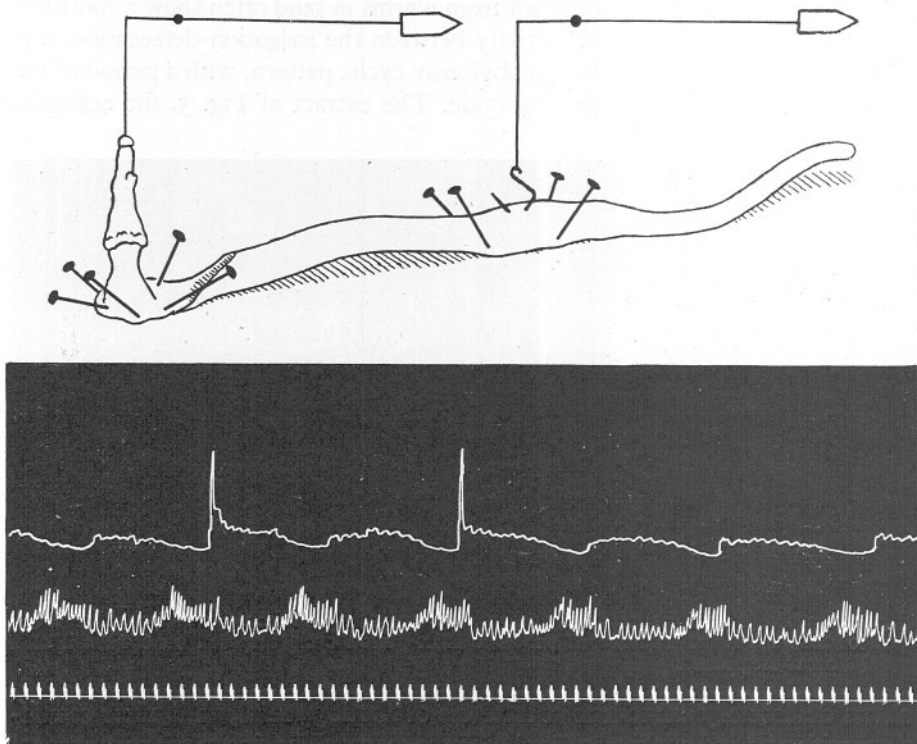

Fig. 6. Method for studying the influence of the oesophageal outbursts on the branchiate segments (above), and a record obtained in this way (below). The lower line of the tracing was made by the extrovert, and the upper by the body wall. Read from left to right; time scale in minutes. (Worm E/I 8.)

immobilized by pins inserted latero-ventrally (but avoiding the nerve cord), and a hook inserted mid-dorsally in the same region was connected to a second lever.

The results were rather capricious. In most of the worms so treated, an inhibitory influence of the oesophageal outbursts on the branchiate region could be detected. Fig. 6 gives a typical tracing; the lower line (from the oesophagus) shows the outbursts of extrovert activity, following each other in this case at intervals of 12 min., and the upper trace (from the body wall) shows very clearly how the body wall relaxes and suspends its slight spontaneous movements at each of the oesophageal outbursts. In two of the cycles, there

is an upstroke of the body-wall lever as the oesophageal outburst passes off; and this effect was seen from time to time in several of the worms.

Fig. 7 shows an experiment in which the body wall was unusually active; one can see very clearly that the inhibitory effect of the extrovert is on the amplitude, not the frequency, of contraction in the body wall.
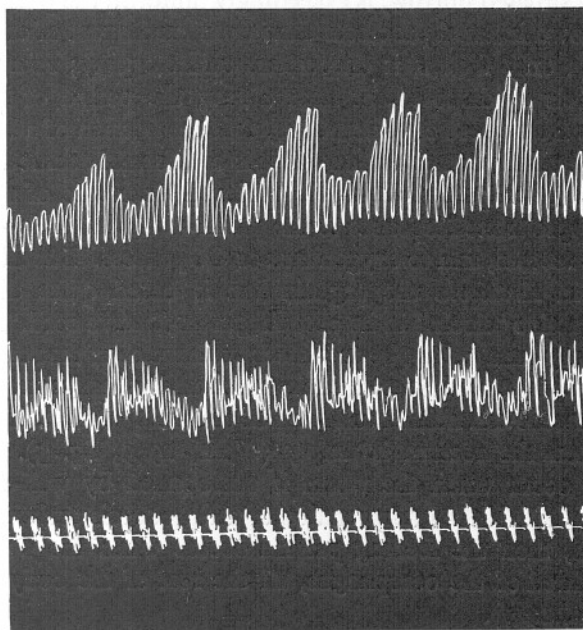

Fig. 7. Record, got by the method of Fig. 5, showing decrease in amplitude of the body-wall contractions (above) at each outburst of the extrovert (below). Time scale in minutes. (Worm E/I 4.)

These results show that the oesophageal pacemaker influences the hinder segments, though the acts of proboscis extrusion and withdrawal concern only the more anterior ones (and can be carried out by these segments after the rest of the worm has been removed). By doing so, it could influence the water-movement tracings, since the latter are produced by the activity of the wave-carrying segments. I have not as yet been able to devise means of pursuing this question into further detail. As far as they go, the results are at least not inconsistent with the view that the oesophageal pacemaker determines periodic feeding when the worm is in sand.

DISCUSSION

To a large extent, the various activities of which a lugworm's behaviour cycles are made up are 'whole worm' activities, i.e. it cannot do more than one of them at any given moment. Vigorous tailward locomotion and vigorous head-

ward irrigation both depend on headward waves, but the attitude of the worm is different in the two cases. The facts described in the last section suggest that feeding, too, concerns more than the first few segments. Since the worm must do all of these things, and cannot do them all at once, its life must have a pattern; and because the worm's environment, once it has established itself in a favourably situated burrow, is exceedingly uniform, the pattern will result more from its own internal processes than from the impact of external events. A predator can only feed if it encounters suitable prey; *Arenicola* can eat whenever it feels so disposed, at least during the period of high tide. It already follows from these considerations, that the pattern of a lugworm's life will be pretty regularly cyclic, as long as it is comfortably settled in a burrow.

Such an integrated pattern could be achieved by means of a hierarchy of reflexes with appropriate responses to the worm's various needs—to an empty gullet, to a full rectum, and to oxygen lack or CO_2 excess. But all the evidence suggests that in *Arenicola* the organization is based quite differently, on spontaneously active 'clocks' in its oesophagus and nerve cord. This does not mean that the rhythms cannot be modified: we have seen that they can; but it means that the various activities can take place under conditions in which the corresponding needs can neither arise nor be satisfied. Defaecatory excursions may occur when the rectum is empty (Wells, 1949, fig. 5). Intermittent irrigation may occur when the worm is surrounded by well-aerated water (Wells, 1949, fig. 4). If the interpretation of the proboscis outbursts as feeding cycles is sound, then the feeding pattern occurs when the worm has been reduced to a shred of the oesophagus, all the rest of the body having been removed (Wells, 1937).

With regard to the adaptive significance of this type of organization, it has already been pointed out that under conditions which may arise from time to time in the field, intermittent irrigation cycles based on a 'clock' would have a greater survival value than those based on reflex responses to respiratory needs (Wells, 1949). The function of the presumed feeding cycle is not clear; perhaps it will come to light when the physiology of digestion in *Arenicola* is better understood.

With regard to the intimate mechanism of the cycles, it may be pointed out that both the feeding cycle and the irrigation-defaecation cycle consist of the periodic evocation—or perhaps the periodic suppression—of processes which are in themselves rhythmic. Proboscis activity, irrigation, creeping—in each of these there is a fairly rapid alternation of phases, as in a beating heart or a swimming dogfish. Such an alternation could be due to a spontaneous pace-maker, as in the heart, or to a reflex system in which each phase is the stimulus for the next, as in the dogfish (Lissmann, 1946). But the activity cycles of *Arenicola* involve bursts of rhythm separated by periods of rest; the latter, in the case of the irrigation cycles, may be of half an hour's duration; one can hardly suppose that a reflex chain is the determining factor. The same

argument holds for the oesophageal pacemaker, particularly when slowed up by magnesium excess (Wells & Ledingham, 1940). Here again, the outbursts may succeed each other very regularly, though separated by half an hour or so of complete quiescence. There must be a 'clock' mechanism, presumably of the nature of a relaxation oscillator. Occasionally, under abnormal conditions, an isolated vertebrate or crustacean heart shows grouped beats which greatly resemble the intermittent pattern of an isolated *Arenicola* extrovert (Wells, 1937); it may be that the behaviour of the lugworm's pacemakers represents a normalization of this condition.

SUMMARY

Worms were allowed to burrow in sand in the laboratory. The general form of their burrows resembled that found in the field. Their behaviour was studied by continuously recording the water movements through the burrows for periods up to 3 weeks.

Whenever the worms were feeding from a gradually subsiding cone and piling up castings, as they do in the field, a characteristic cyclical pattern was traced. This was marked by conspicuous diphasic excursions at intervals of about 40 min. Defaecation occurs at the summit of the first phase. By comparison with records got from worms in glass tubes (Wells, 1949), it is inferred that the first phase consists of tailward locomotion to the sand surface, and the second to headward irrigation accompanied by gentle creeping back to the feeding point. The whole cycle is identical with the intermittent irrigation cycle shown in glass tubes.

In the intervals between the defaecation-irrigation outbursts, the tracing often shows a periodicity of smaller amplitude and period. This is probably due to intermittent feeding, under the influence of the oesophageal pacemaker (Wells, 1937). Experiments with dissected worms showed that an inhibitory influence of the oesophageal pacemaker can be detected in the segments responsible for creeping and irrigation.

The behaviour described above occupies about 45 % of the records (covering altogether 72 'worm-days'). Once having begun, it usually continues very regularly for many hours. For the rest of the time, other patterns were seen, which are described in the text.

The application of these results to the worm's life in the field, and the dependance of feeding, irrigation and defaecation on spontaneously rhythmic pacemakers, are discussed.

REFERENCES

CHAPMAN, G. & NEWELL, G. E., 1947. The role of the body fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola*. *Proc. Roy. Soc.* B, Vol. 134, pp. 431–55.

—— —— 1948. Burrowing of the Lugworm. *Nature*, Vol. 162, pp. 894–5.

DAM, L. VAN, 1937. Über die Atembewegungen und das Atemvolumen von *Phryganea*-Larven, *Arenicola marina*, und *Nereis virens*, sowie über die Sauerstoffausnutzung bei *Anodonta cygnea, Arenicola marina* und *Nereis virens. Zool. Anz.*, Bd. 118, p. 122–8.

DAM, L. VAN, 1938. *On the Utilisation of Oxygen and Regulation of Breathing in some Aquatic Animals*, 143 pp. Groningen.

HÄNTZSCHEL, W. 1938. Quer-Gliederung bei rezenten und fossilen Wurmröhren. *Senckenbergiana*, Bd. 20, pp. 145–54.

JUST, B., 1924. Über die Muskel- und Nervenphysiologie von *Arenicola marina. Z. vergl. Physio.*, Bd. 2, pp. 155–83.

LINKE, O., 1939. Die Biota des Jadebusenwattes. *Helgol. wiss. Meeresunters.*, Bd. 1, pp. 201–348.

LISSMANN, H. W. 1946. The Neurological Basis of the Locomotory Rhythm in the Spinal Dogfish (*Scyllium canicula, Acanthias vulgaris*). *Journ. Exp. Biol.*, Vol. 23, pp. 343–61; 162–76.

NEWELL, G. E., 1948. A Contribution to our Knowledge of the Life History of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 554–80.

OSLER, E., 1826. On burrowing and boring Marine Animals. *Phil. Trans. Roy. Soc.*, Part III, pp. 342–71.

THAMDRUP, H. M., 1935. Beiträge sur Ökologie der Wattenfauna auf experimenteller Grundlage. *Medd. Komm. Havundersøg., Kbh., Fiskeri*, Bd. X, no. 2, 125 pp.

WELLS, G. P., 1937. Studies on the Physiology of *Arenicola marina* L. I. The Pacemaker Role of the Oesophagus, and the Action of Adrenaline and Acetylcholine. *Journ. Exp. Biol.*, Vol. XIV, pp. 117–57.

—— 1945. The mode of life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 170–207.

—— 1948. Thixotropy and the Mechanics of Burrowing in the Lugworm (*Arenicola marina* L.). *Nature*, Vol. 162, pp. 652–3.

—— 1949. Respiratory movements of *Arenicola marina* L.: intermittent irrigation of the tube, and intermittent aerial respiration. *Journ. Mar. Biol. Assoc.*, Vol. XXVIII, pp. 447–64.

WELLS, G. P. & LEDINGHAM, I. C., 1940. Studies on the physiology of *Arenicola marina* L. II. Accommodation to magnesium concentration in the isolated extrovert. *Journ. Exp. Biol.*, Vol. XVII, pp. 353–62.