OBSERVATIONS ON THE BIONOMICS AND PHYSIOLOGY OF *TREBIUS CAUDATUS* AND *LERNAEOCERA BRANCHIALIS* (COPEPODA)

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(Text-figs. 1–5)

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THE HABITAT AND DISTRIBUTION OF *TREBIUS CAUDATUS*

Trebius caudatus Krøyer is a parasitic copepod belonging to the family Caligidae: a remarkably uniform group which is among the least modified by the parasitic habit. The body form is similar to that of *Caligus* and *Lepeophtheirus*, but unlike the former it lacks the pair of frontal suckers, and unlike both of these common genera the fourth legs are biramous in both sexes. The most obvious adaptation to the parasitic habit in this family is the roundish flattened carapace, which has a sucker-like action and prevents the animal from being washed off the surface of the fish on which it lives. This action is easily seen when caligids are transferred to a glass vessel: if an attempt is made to remove them, the previously swimming animal comes to rest and applies its carapace to the smooth surface with surprising tenacity. Another adaptation is the presence of strongly chitinized hooks on various cephalothoracic appendages.

All those who have worked with caligids remark on their peculiar habit of swimming to the edge of the sea water when placed in vessels in the laboratory. If left for a time they will swim out of the water and perish by becoming dry. We have seen this in several species and in no instance did they attempt to return to the water. This peculiar taxis is difficult to explain in relation to their normal habits.

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The life cycle of all caligids is a simple one, involving only one host. For the most part the species are host-specific; but some are found on hosts of closely related genera, and these parasites are notably those which are not confined to a particular habitat on the host, being found in various locations and on both surfaces in flat fish. The strictly host-specific ones, such as *Lepeophtheirus pollachii*, found under the tongue of the pollack, are usually confined to a special habitat. Even those showing host specificity to a less degree, such as *L. pectoralis* on various pleuronectids, very rarely migrate to fish of other species in a crowded aquarium. Fish heavily infected with caligids have been brought to the laboratory from the quay packed together in baskets, and in no instance have we found parasites characteristic of one species transferred to the adjacent fish of other species, though the parasites were alive and active and conditions were moist enough for them to move from fish to fish had there been any tendency to do so. An example of an exceptional degree of freedom is *Caligus rapax*. This very common parasite is found most frequently on gadoids, but it is also found on a large variety of other teleosts and even on elasmobranchs; moreover, it is not uncommonly met with in the plankton (Lebour, 1931, p. 173). *Trebius caudatus* has an intermediate degree of freedom: it is confined to elasmobranchs and is most common on Rajidae. Scott & Scott (1913, p. 82) mention that it is found '...on skates, rays, dog-fishes, etc.', but they do not give any specific names. It appears from the records that *T. caudatus* is confined to European waters, from which it is the only species of the genus recorded. Three other species have been found in the western hemisphere, also on elasmobranchs (Wilson, 1907, 1921). We have been able to add four new hosts to the records for this parasite, and three new hosts for the Plymouth district; the complete host list is given below.

Summary of Distribution of Trebius caudatus *according to Hosts*

Raja clavata Linn.
   Plymouth: Hartley, December 1934 (vide infra).
   Roscoff: Sproston, June 1937, on the upper and lower surfaces of the head, and
      rather more numerous (young, paler forms) in the gill cavities, spiracles and a few
      in the mouth.
R. maculata Mont.
   Plymouth: Oakley (in Leigh-Sharpe, 1933), 'on the dorsal surface'. Hartley,
      December 1934 (vide infra).
   North Sea area: cited by Lint & Stekhoven (1936).
R. microcellata Mont.
   Plymouth: Hartley, December 1934 (vide infra).
R. blanda Holt & Calderwood.
   Plymouth: Hartley, December 1934 (vide infra).
   Irish Sea: Great Orme to New Quay Head (Scott, 1929); Red Wharf Bay, N. Wales.
      Scott (1929) found seventeen females and three males on one fish.
   North Sea area: cited by Lint & Stekhoven (1936).
R. fullonica Linn.
   North Sea area: cited by Lint & Stekhoven (1936).

R. batis Linn.

> Polperro, Cornwall: Norman (1859) (in Norman & T. Scott, 1906).
>
> Plymouth: Bassett-Smith (1896), on the dorsal surface of the head and in the nasal cavities.
>
> Irish Sea: Belfast Bay, W. Thompson, September 1838 (in Baird, 1850). Great Orme to New Quay Head (Scott, 1929).
>
> North Sea area: cited by Lint & Stekhoven (1936), 'head and nasal cavities'.

R. marginata Lacepède.

> Roscoff: Sproston, June 1937, three medium-sized fish all had a few of these parasites, mostly on the underside of the head. One large fish had 18 adults on the upper and lower surfaces of the head, 10 young (pale) forms in the spiracles and 5 in the nasal cavities. None was found on medium and small fish examined in September–October 1938 at the same place.

Galeus vulgaris Fleming.

> Cited by Gerstaecker (in Bronn, 1866).

Acanthias vulgaris Risso.

> Roscoff: Sproston, September 1938, on the gills.

> *Note.* The nomenclature of these fish is that used in the *Plymouth Marine Fauna*, 1931.

It is unfortunate that those studying parasitic copepods have seldom investigated their ecology, so that we have few records of the exact location of these animals on their hosts or other data concerning the host-parasite relationship. MacCallum (1916, p. 23) was one of the first to stress the importance of such observations when he drew attention to the nasal cavities of elasmobranchs as favourite habitats for ectoparasites—both for copepods and monogenetic trematodes—which habitat, he says, seems to have been overlooked. For instance, it was not until 1918 that Leigh-Sharpe first discovered *Lernaeopoda globosa* in the nasal cavities of *Scylliorhinus caniculus* (L.) Blainville, 1816; this parasite has since been found very frequently at Plymouth and at Roscoff, invariably in the same situation. Considering the large numbers of dog-fish examined annually in laboratories it is remarkable that it escaped notice until so recently.

Of the species of *Raja* examined by one of us (N. G. S.) at Roscoff in 1937 and 1938, it was noticed that most of the large fish were infested with *Trebius caudatus*, while only a few of the medium-sized fish and none of the small fish had them. They occurred on both surfaces of the head near the anterior end, and when immature forms were found they were invariably in the mucus of the nostrils, gill cavities and spiracles, and on two occasions a few in the mouth near the internal aperture of the spiracle. These immature forms were always pale in colour in contrast to the rather darkly pigmented adults. They were often associated in the mucus with the filamented eggs of *Rajonchocotyle* sp., a monogenetic trematode not uncommon on the gills. Of the twenty fish examined in detail at Roscoff, four, or 20 % (large to medium fish), were infected; this is about the same degree of infection as that found at Plymouth (see below).

During December 1934 one of us (P.H.T.H.) had the opportunity of examining several trawled species of *Raja* from the Mewstone Grounds and from Cawsand Bay, Plymouth. Special attention was given to the exact location on the host of the *Trebius caudatus* found, and other ecological data were noted. The distribution of these copepods on the different hosts from the two habitats is set out in Table I, and their distribution on the host is shown in Fig. 1.

TABLE I. THE DISTRIBUTION OF *TREBIUS CAUDATUS* ON *RAJA* FROM TWO LOCALITIES NEAR PLYMOUTH IN DECEMBER 1934

	R. blanda	R. clavata	R. maculata	R. microcellata	All species
Cawsand Bay					
No. of fish examined	28	13	20	9	70
No. of infected fish	2	1	5	2	10
Percentage infected	7·2	7·7	25	(22)	14·3
Mewstone Grounds					
No. of fish examined	0	14	7	1	22
No. of infected fish	0	5	3	0	8
Percentage infected	—	35·7	(43)	—	36·36
Both localities					
Total fish examined:					
Number	28	27	27	10	92
Length range: cm.	25–35	5–70	10–55	20–60	5–70
Mean length: cm.	23·0	30·3	29·1	37·5	28·5
Infected fish:					
Number	2	6	8	2	18
Percentage	7·2	22·2	29·6	20·0	19·6
Mean length: cm.	20·0	52·5	42·2	52·5	44·4

In spite of the small size of the samples, it may be permissible to point out certain items of interest in these observations at Plymouth in 1934.

The *Raja* caught on the Mewstone Grounds are between two and three times more heavily infected than those caught at the same time in Cawsand Bay. The depths of water in these two localities are respectively 10–15 and 3–5 fathoms, so that other things being equal, deep water appears to be more favourable to *Trebius caudatus* than shallow. One possible factor is that the parasite is less disturbed by currents in deeper waters. The fish themselves move but little, so that we feel justified in regarding the two habitats separately (see Steven, 1936).

On the whole, the larger the fish the more likely is it to be infected. No fish below 10 cm. long was found infected. The length distribution in three arbitrary groups in relation to the infection rates is given below (Table II). The arithmetic mean length of all the fish examined in 1934 was 28·5 cm. and that of the infected fish was 44·4 cm.

TABLE II. LENGTH DISTRIBUTION OF *RAJA* SPP.

Length group cm.	No. of fish examined	Infected fish No.	%
5–25	48	2	4·15
25–50	34	11	29·5
50–70	9	6	66·6

The mean rate of infection of the species of *Raja* both at Roscoff and at Plymouth was about 20 %. The mean intensity of infection per fish at Plymouth was only 1·45 parasites per fish, but at Roscoff it was 6·0. The latter figure includes only the adult forms on the skin; the immature forms from the head cavities were not included. Unfortunately, these cavities and their contained mucus were not examined in the Plymouth samples, and no immature forms were found.

At Plymouth both sexes of fish were about equally parasitized: ten females and eight males.
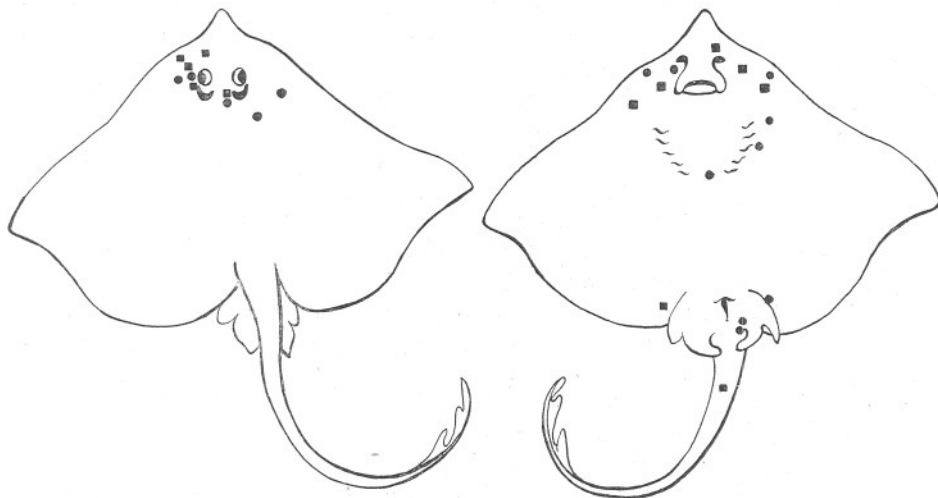

Fig. 1. Generalized diagram of *Raja* showing the location of each individual *Trebius caudatus* found in Dec. 1934. The black disks indicate males and the black squares females.

From Fig. 1 it is seen that the parasites tend to collect near the orifices on both surfaces of the body—ten on the upper side and sixteen on the under side—and that this distribution is also that of greatest concentration of mucus glands on the skin. It is understandable that this secretion would attract the parasites, for it is a necessary lubricant on so rough a surface and also is believed to form a large part of their food.

Of the *Trebius caudatus* collected at Plymouth, twelve were females and fourteen were males; the Roscoff records are not quite complete, but the proportion of the sexes was nearly equal, with a slight preponderance of females among the adults. This nearly equal distribution of the sexes is most unusual in caligids, in which the males are as a rule far less common than the females.

INTESTINAL RESPIRATION IN *TREBIUS CAUDATUS*

The cuticle of free-living copepods such as *Calanus* and *Cyclops* is very thin, and it is generally assumed to permit gaseous exchange, not only through the thin appendages but also over the whole surface of the body. In the

larger copepods, however, the specific surface (i.e. surface per unit volume) decreases significantly and the cuticle becomes thicker to withstand the stress of stronger musculature, so that superficial respiration alone is evidently inadequate.

The term 'anal respiration' is generally applied to that phenomenon in various invertebrates whereby a respiratory current is taken in by the anus. In Copepoda it includes peristalsis of the gut (which is only partly concerned with respiration), various movements of the hind body as a whole and the actual gaseous exchange through the gut wall; at the same time these movements are transmitted to adjacent organs and the body fluid between them, so that they serve as the motive power for a two-way circulation. We prefer to use the term 'intestinal respiration', because it does not exclude the homologous phenomena in those parasitic copepods in which there is no anal current.

Various authors have described rhythmic gut movements (peristalsis and 'anti-peristalsis') in copepods, and in those lacking a heart such movements have been considered as supplying the motive power for general circulation of the body fluids. Claus was strongly opposed to Weismann's interpretation of these movements as respiratory in function, in spite of numerous authors' observations of a current of water entering and leaving by way of the anus, in copepods, and in other crustacea of the same order of size. According to Hartog (1888, p. 26), Claus's chief difficulty in accepting anal respiration as a normal function lay in his conception of the function of the rectal dilator muscles as solely concerned in defaecation. Hartog, in his monographic account of the morphology of *Cyclops* (1888), shows that it is these muscles which are primarily concerned in admitting and ejecting the respiratory current through the anus. He shows that their action, in series with those of the higher reaches of the gut on the one hand, and that of the circulatory disposed muscle fibres in the walls on the other, have the combined action necessary to effect anal respiration. The events are thus described by Hartog (p. 25): the anus is dilated when the gut is stretched to its maximum extent, which allows free ingress of water, the anal valves then close and the rectum is pulled forward: the stomach meanwhile begins to expand and becomes strongly arched so that the anterior region of the gut assumes a marked sigmoid curve in the antero-dorsal direction, which causes a forward movement of the water recently taken in. With the immediate flattening of the sigmoid curve the stream of water is reversed and flows again into the hind gut as this, in turn, straightens out, and makes its exit as soon as the anal valves open. A fresh stream of water enters at the recommencement of the cycle, just as the rectum is being drawn forward and immediately before the anal valves close.

Probably the fine teeth or coarse setae described by Hartog (1888, p. 24, Pl. 3, fig. 2) as occurring on each anal valve, serve to filter the respiratory current, though he does not offer this as an explanation. Apparently the valves

in the intestine (also figured and described by Hartog) are too fine to allow the passage of food with the current, but he states (p. 26) that the rhythmic cycle is interrupted when a bolus of faeces collects in the rectum, but immediately on its expulsion movements are resumed with an extraordinary vigour.

This author claims to have observed a similar regular rhythmic anal respiratory current in three groups of free-living copepods and also in *Caligus* and in *Argulus* (as well as in cladocerans, gammarids, *Asellus*, larvae of *Apus* and *Zoea*). Wilson (1905, pp. 516–17) states that he has observed movements associated with anal respiration in *Lepeophtheirus edwardsi*, *Caligus rapax* and *C. bonito*, and that it was '...exactly like that described by Hartog for *Cyclops*, save that it was not as regular'. He does not, however, give any details of his observations. Scott (1901, p. 20) describes an intermittent two-way peristalsis in *Lepeophtheirus pectoralis* and a concomitant jerky two-way circulation of the blood; but though he describes anal dilator muscles in this species he remains sceptical of anal respiration. This scepticism is maintained by Scott & Scott (1913, p. 14).

We have both observed this phenomenon in various species of caligids from time to time, and we find that the underlying mechanism seems to be substantially the same as that described by Hartog for *Cyclops*, the action of the longitudinal muscles attached to the gut working in harmonic sequence, superimposed on the peristaltic movements of the gut itself. Here, however, the agreement ceases. Some years ago, one of us (P.H.T.H.), working at Plymouth, made an attempt to investigate the rhythmic nature of respiration in *Trebius caudatus*. It appeared far more complicated than that described by Hartog, and at first sight it seemed that the welter of pulsations was entirely arhythmic. The irregularity was apparent not only in numerous individuals on different occasions but in the same individual when examined over periods of 6–9 minutes. The main results of these observations on *Trebius* are summarized below:

(1) Peristaltic waves proceed along the entire length of the gut in both the forward and backward direction.

(2) In regard to these movements the three sections of the gut, the cephalothoracic, that in the genital segment and that in the abdomen, appear more or less isolated, and each has its own set of peristalses. These may, or may not, be transmitted to the adjacent segments.

Fig. 2. *Trebius caudatus* (female) (diagrammatic), showing gut and the three centres controlling peristalsis.

(3) The peristaltic waves appear to be initiated from three centres which are situated towards the posterior end of each gut section: these are shown dia-
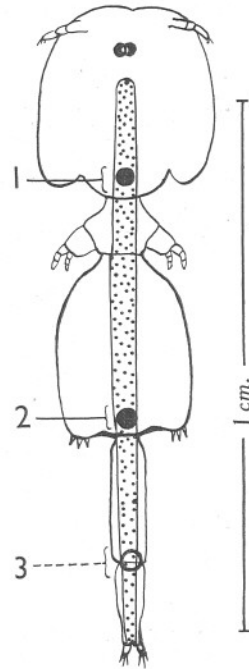
grammatically in Fig. 2. The exact situation of the abdominal centre was difficult to determine and its approximate position is indicated by an open circle.

(4) Each section of the gut is able to initiate contractions in either direction, but at times a wave of contraction started in one section may be continued into another. Forward peristalses in the abdominal gut, the only type of continuation observed with any frequency, were often continued into the genital gut. Backward peristalses of the genital gut were twice seen to be continued into the abdominal section. In one set of observations only, backward peristalses in the cephalothorax were seen to be continued into the genital section on three occasions during 6 minutes.
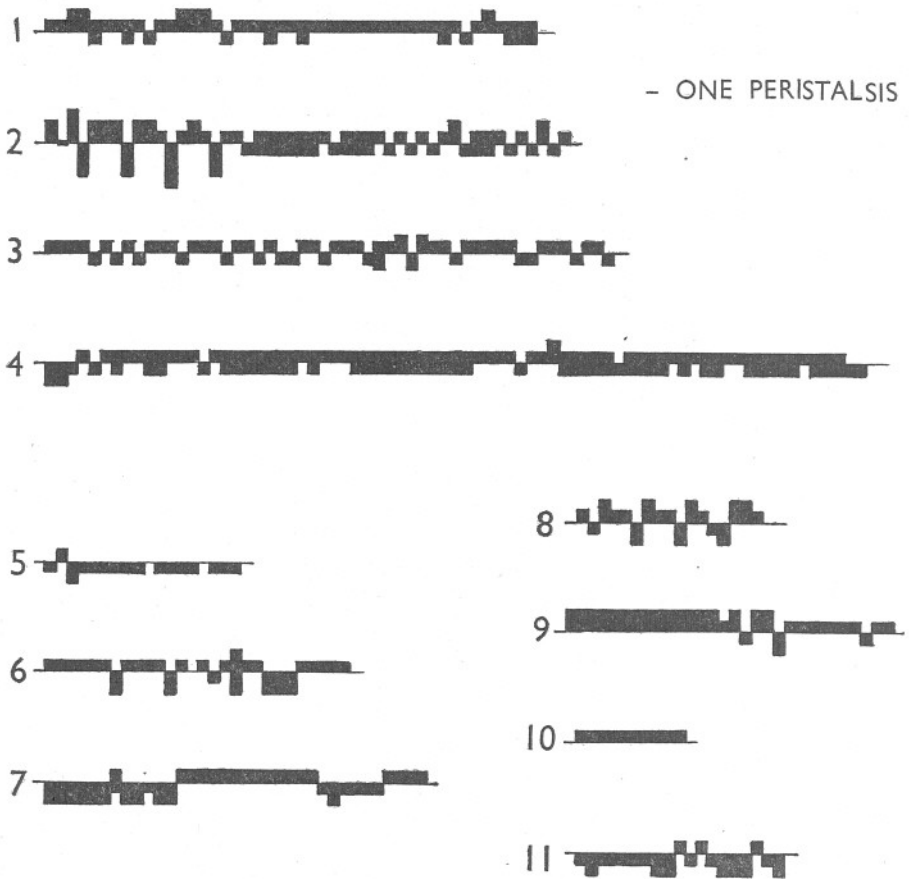

Fig. 3. Graphical representation of the direction and relative intensity of the peristalses in *Trebius*: 1–4 from the cephalothoracic section of the gut, 5–7 from the genital segment, and 8–11 from the abdominal gut. The records are of selected typical examples, and the blocks above and below the central line represent forward and backward peristalses respectively.

(5) Peristaltic contractions were more numerous per unit time in the cephalothoracic than in the other two sections.

(6) Simultaneous peristalses in both directions were characteristic of the cephalothoracic section. They were very infrequent in the genital section (1·5 % of the total observations only), and unknown in the abdominal section.

(7) The duration of peristalsis in either direction was extremely variable, as was the intensity (strength of beat) and the frequency of the waves of contraction.

(8) It is beyond doubt, however, that forward peristalses were the more numerous.

Fig. 3 illustrates the change of direction and the relative intensity of some selected typical series of peristalses in each section of the gut. The value of the time axis is not given. These particular examples show extreme irregularity in the maintenance of peristalsis in a given direction; the relative intensity of the beats is also apparently capricious. Table III gives the means of the frequencies of peristalses in the complete series of observations.

TABLE III. THE FREQUENCY OF PERISTALSES IN *TREBIUS CAUDATUS*
(PER MIN.)

	Total peristalses			Backward peristalses only		
	Cephalo-thorax	Genital segment	Abdomen	Cephalo-thorax	Genital segment	Abdomen
	6·85	1·40	5·00	1·57	0·80	0·5
	4·36	0·60	1·28	0·535	0·20	0
	4·84	1·00	1·66	0·526	1·00	0
	11·00	3·86	9·5	3·67	1·17	0
	12·00	1·50	0·50	2·33	3·00	0
	9·00	5·83	3·16	7·33	0	2·67
	12·16	2·33	—	4·00	—	—
	5·00	7·00	—	8·83	—	—
Arithmetic means	8·15	2·94	3·52	3·60	1·03	0·53
Means of forward peristalses				4·55	1·91	2·99
Ratio of forward/total peristalses (%)				55·8	65·0	85·0

These observations were made under approximately similar laboratory conditions, and though the temperature factor was not controlled (albeit highly important), the high degree of variation observed during the short periods of observation cannot be due to this variable: it is probably a normal attribute of the process. Owing to this high degree of scatter, the number of observations is insufficient for the results to be treated statistically, so the arithmetic means alone have been reproduced in the table.

It is instructive to note that the frequencies of the forward peristalses expressed as percentages of the frequencies of the total peristalses (when the means are employed) increase rapidly from anterior to posterior ends of the gut. This—the increasing residuum of forward over backward peristalses, from head to tail—is one of the most significant features of that type of intestinal respiration which involves an anal current, for it ensures that the

contents of the gut are retained. It would seem that there is a necessary fall in the pressure gradient along the gut towards the anterior end, and that this prevents too great a movement in the middle region of the intestine where digestion is believed to take place; it would also reduce the chances of regurgitation through the mouth to a minimum. Much of the irregularity of the gut movements may be due to the impedance caused by the presence of more or less bulky food and faecal matter.

It was not possible at the time to make simultaneous observations on the relation of the peristaltic movements as a whole to the actual intake of water by the anus. A gaping of the anal lips followed by a closure strongly suggestive of the intake of water was seen repeatedly in *Trebius*; and in *Paracalanus* sp. the uptake of beads of water was seen distinctly on several occasions. In *Trebius* there was also a definite rubbing together of the anal lips: they showed, immediately after the intake of water, a differential up and down movement—along the antero-posterior axis—as if one side contracted and then the other. Lastly, it may be mentioned that the intake of water was always accompanied by a brisk wagging of the abdomen as a whole, a movement so violent that often it affected the whole body. This up and down beating of the hind body is especially characteristic of the chalimus stages of parasitic copepods, and is always very obvious in the 'cyclopoid' and 'pupal' stages of *Lernaeocera branchialis* on the gills of the flounder: this species is dealt with below.

The highest frequency of total peristaltic beats occurs in the cephalothorax (Table III): this may well have a digestive rather than a respiratory significance, for simultaneous amphidirectional peristalsis was the general rule in this region, and would help the trituration process in the stomach. The amphidirectional peristalsis took place by a wave of contraction starting forwards from centre 1 (Fig. 2) which was balanced by a posterior wave starting, apparently at the same time, from the anterior limit of the gut: it had, in fact, the appearance of being reflected from the anterior wall. The observed effect was a regular wave, the wave-length of which was equal to the length of this section of the gut. If another initiation centre is present at the anterior limit of the gut, it is necessarily only concerned with backward peristalses.

The subdivision of the gut into three sections is a further aid to the retention of food in the respective regions for a sufficient time for digestion to be completed. Scott (1901, p. 16) has shown that there are no valves separating the sections, but Wilson (1905, p. 510) points out that there is a constriction at the junctions of these regions '...like the beginning of a sphincter muscle, but the opening cannot be closed'. Hartog has, however, demonstrated valves in *Cyclops*. Another safeguard against the premature passage of food from the stomach is the normal discontinuance of the cephalothoracic peristaltic waves into the genital segment. The rare instances in which this was seen may mark the passage of food through the sphincter-like constriction, and so be part of normal alimentation.

The continuation forwards of peristaltic waves from the abdominal into the genital gut, on the other hand, is part of the respiratory movements and is necessarily the rule in this section of the gut: handing on, as it were, the respiratory current from the rectum to the intestine.

The vigorous action of the longitudinal muscles moving the water current from stage to stage along the gut is doubtless the cause of the movements of the hind body as a whole. This is naturally more conspicuous in so light an animal as a chalimus, suspended as it is by its frontal filament: the muscular contractions cause it to swing through a considerable arc. The peristaltic movements serve to stir the water (oxygen vector) in each section of the gut and so effect maximum efficiency in the gaseous exchange through the walls. The generalized peristaltic movements are transmitted to the blood in the surrounding haemocoele and account for the discontinuity in blood circulation already referred to, and observed by Scott (1901, p. 20) and Wilson (1905, p. 515) as well as by many earlier authors.

The respiratory movements in caligid copepods show, therefore, an irregular regularity.

The Relation of the Internal and External Environment to the Feeding of *Lernaeocera branchialis*

Lernaeocera branchialis (Linn.) presents a complete contrast to the caligids in almost every respect: it is one of the most highly modified of the parasitic copepods. The adult female is permanently fixed to a gadoid with its head in the vascular tissue in the region of the heart; its food is almost entirely the blood of the host; its cuticle is relatively highly chitinized, so that it is more independent of its environment; and its life history is complicated by the interpolation of an intermediate host which the male never leaves. The first copepodid stage is free swimming as in *Trebius* and other caligids, and in general body form it is not unlike them. This stage finally settles on the gills of a flounder (*Pleuronectes flesus*) where it undergoes part of its metamorphosis (see Sproston, 1941), resulting in a free swimming cyclopoid male, and a female which is similar except for an elongated genital segment. Temporary attachment of these latter forms is effected by the chelate second antennae. After pairing, the male may return to the gill filaments, though it does not live for long; but the female becomes pelagic and seeks certain gadoid fish on which the metamorphosis is completed.

The following observations on *Lernaeocera branchialis* were undertaken by one of us (N. G. S.) at Plymouth during the period August 1939 to November 1940. It was mentioned above that respiratory movements were observed in the developmental forms on the flounder, and was accompanied by vigorous motion of the body as a whole which was visible to the naked eye. Detailed observations were only made on the adult female; although peristalsis in the thinner part of the hypertrophied genital segment could be seen while the

parasite was in situ, no details could be made out until it was excised and put in a strong transmitted light under a low power microscope. The parasites were accordingly carefully dissected away from the tissues of the host and placed for a time in circulating sea water, in which they remained apparently healthy for periods up to 9 days. The rate and vigour of the peristalsis did not appear to have diminished and it was assumed that the animal had not suffered any marked derangement in its functions by removal from the host. Important consequences of this, however, would include the gradual starvation and changes in osmotic equilibrium consequent on the change in internal environment, viz. the gradual substitution of sea water for gadoid blood in the intestine. These suppositions are supported by direct measurements of the osmotic pressure of the body fluid of the adult female *Lernaeocera* (Panikkar & Sproston, 1941).

It was found that the adult female *Lernaeocera*, unlike most marine invertebrates, is able to maintain a body fluid hypotonic to its external medium so long as it is attached to the host. It presents a complex osmotic system by virtue of its feeding on hypotonic blood, on the one hand (that of *Gadus pollachius* having an osmotic pressure equivalent to 1·443 % NaCl), and by being bathed externally by sea water on the other, the body fluid of *Lernaeocera* having an osmotic pressure equivalent to 2·0–2·8 % NaCl. When the parasite is removed from the host, however, isotonicity is established with the external medium owing to water being taken in through the mouth in place of the blood of the host. *Lernaeocera* was nevertheless still able to tolerate dilution of the external medium up to 2·243 % NaCl, which represents a salinity probably lower than that normally tolerated by the host.

Since the above paper was written other experiments have been conducted (by N. G. S.) which show that isolated *Lernaeocera* is unable to survive 50 % sea water for much longer than an hour. On three occasions perfectly healthy *Lernaeocera* were transferred to normal sea water after removal from the host, and when normal peristalsis had been verified they were subjected to a gradual dilution of the external medium and left in approximately 50 % sea water. They all became pale and peristalsis was increasingly disturbed and weakened, finally ceasing altogether; by this time the blood in the gut had been lost through the mouth (the actual stream of blood seen in one specimen only). Death, as judged by cessation of peristalsis, and complete pallor occurred in about an hour in two examples and in a little longer period in a third. The physiological effect was probably that of a violent endosmosis of the now hypotonic medium into the tissues of the parasite most probably via the alimentary canal—some vacuolation was seen in the body tissues of one specimen.

Since in the natural condition on the host a marked hypotonicity is maintained by the body fluid, any intake of water by the anus is precluded; indeed, the anus was carefully observed continuously for periods up to 20 min. (the period including several changes in direction of peristalsis), but no ejection

of fluid was seen or any movement in this region which could suggest that the anus was functional. To verify this, fine particles in suspension were watched in the neighbourhood of the anus but no movements occurred suggestive of an anal current.

The abdomen of this species has been figured in section by Scott (1901, Pl. V, fig. 4), in which the anus is shown as an aperture, but neither he nor subsequent authors actually mention that it is functional.[1] From the physiological considerations elaborated above we consider it non-functional, and examinations on the living animal do not disprove this. On microscopical examination of the whole parasite, a flattened funnel-like depression is seen at the posterior extremity, but it does not perforate the cuticle, and the rectum apparently ends blindly. It is not surprising that *Lernaeocera* has become aproctous in its final adult stage, for like many blood-feeding parasites the digestion is slow but complete.

No movement of fine particles in suspension in the neighbourhood of the mouth was observed in living (isolated) *Lernaeocera*, and it was assumed that this aperture was also closed during the period of observations. Though the mouth is morphologically of the suctorial type, we do not consider that it is functional, as such, in the adult female; for suction would certainly be superfluous against the pressure of the blood stream of the fish. Furthermore, the histological changes taking place as the result of traumatic injury by the parasite, as recently shown by Stekhoven (1936), consisting of a fibrotic thickening of the ventral aorta and bulbus arteriosus, produce a stenosis of the lumen in this region and a consequent increase in the blood pressure. The difficulty for the parasite, would, it seems, be the exclusion of an inrush of blood through its mouth. In view of these considerations it is not surprising to find that the mouth is normally closed, probably by valves, and that it opens only at well-spaced intervals to admit a meal of blood which is retained in the gut for a long period. In support of this it may be mentioned that the isolated specimen which survived 9 days in circulating sea water showed only a slight fading of the original red colour of the gut at the end of this time.

The actual feeding depends, in our opinion, on the maintenance of a dynamic equilibrium of the osmotic system referred to above, and involves the following set of factors. A slow osmosis occurs through the body wall, i.e. water will pass out owing to the tendency for isotonicity to be established, and if salts enter they must do so far more slowly than water escapes. The gradual loss of water in this way would finally reduce the hydrostatic pressure in the gut of *Lernaeocera* to a limiting value which would determine the intake of a

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[1] Brady (1880) quotes Krøyer's observation that on touching the body of a mature female *Lernaeocera* a jet of liquid was forcibly ejected from the hind end of the abdomen. No one has been able to confirm this observation. We suggest that the animal was inadvertently punctured and that the contents, being under pressure, would, and do, escape in the form of a jet.

fresh supply of blood through the mouth: that is, the internal pressure in the gut gives way to the blood pressure of the host. This discontinuous feeding is supported by the findings of Panikkar & Sproston (1941, Table II) on the osmotic pressure of *Lernaeocera* in situ, where a considerable variation in values was observed for the body fluid: the low values would represent a comparatively recent meal of the hypotonic blood of the host, and the higher a corresponding degree of starvation—the body fluids having been concentrated by gradual loss of water through the cuticle.

Microscopical examinations made on the contents of the gut (by withdrawing it through fine glass cannulae as described in the paper cited) while the parasite was still attached to the host, and some 2 hr. after the death of the latter, showed a few fish erythrocytes which were quite normal in appearance and had no signs of crenation or other effects of digestion. The body fluid was examined in a similar way: it was reddish yellow in colour and contained even fewer cells; these were minute stellate cells which rapidly disintegrated, and were considered to be thigmocytes (proper to the blood of Crustacea). Stekhoven has made similar investigations (1936) and he found no fish erythrocytes in the body fluid; he considers that the red colour of the latter is due to a specific respiratory pigment which may, he thinks, be a 'reconstructed' pigment from the blood of the host, dissolved in the body fluid of the copepod, and acting as an oxygen carrier. He maintains that it is distinct from haemoglobin on the grounds of different colour; but he admits that he has not submitted it to micro-spectrographic tests. It is regrettable that our material was insufficient for such tests. In our opinion the different colour (reddish yellow) of the body fluid is due to its own intrinsic yellowish colour partly masking the haemoglobin, and that this yellowish tinge is partly the result of digestion, for fat droplets were frequently seen in suspension which were deep yellow in colour. We should expect to find that the reddish tinge was due to haemoglobin in solution, this having passed through the gut wall after the breakdown of the erythrocytes and accumulated in the body fluid as the parasite grew older. The more advanced the *Lernaeocera* the deeper we found its coloration to be: those females with partly spent egg strings were deep red, and those with spent egg strings were purplish red and the abdomen almost black. When the excised parasite was placed in circulating sea water the colour faded but little, except on two occasions when the specimens died prematurely. In these specimens the gut lost the red colour on the third day and on the succeeding day the body became increasingly pale until it died: the final colour on death was a brownish yellow.

Vanden Berghe (1933) made some investigations on the alimentary canal of *Lernaeocera*. In his discussion of the subject he rightly dismisses the remarks of Hesse (1863) on the subject of feeding in *Lernaeocera* as being confused and fantastic. Hesse also 'describes' (without figures) a heart and blood vessels which Vanden Berghe very justly denies, though his further remarks to the effect that both heart and blood vessels are unknown in

Copepoda are not accurate, for a saccular heart is present in Calanidae and Pontellidae and Ed. Van Beneden demonstrated blood vessels in *Lernan-thropus* (also in *Congericola* and *Hatschekia*), and proved that they contained haemoglobin in solution (see his claim to the priority for these discoveries, 1880); the complex vascular system in *Lernanthropus* was later described by Heider (1879) in his monograph on the subject, and, in American species, by Wilson (1922).

Vanden Berghe examined a large number of *Lernaeocera* from *Gadus morrhua* and *G. luscus* at Wimereux during the summers of 1931 and 1932, but his findings differ curiously from those of Scott (1901), Stekhoven, Punt (1936, 1937), and our own. He says that the red colour resides entirely in the haemocoele and that the gut of all his specimens was devoid of red colour. He examined the fluids by making an incision across one of the antlers and states that the haemocoele fluid which issued was of a bright red colour and labile; but on making a deeper incision into the body the liquid from the gut was liberated, which was viscous and yellow in colour. We can only assume that during the difficult process of dissecting out the parasite from the host tissues, some unnoticed injury occurred, perhaps to the proboscis, that the original contents of the gut escaped before the above examinations were made, and that the liquid he observed coming from the gut was merely the residuum of the original contents mixed with the tissue fluids. From the absence of all but traces of fish blood in the gut, and because he was unable to extract an anti-coagulant from any part of the alimentary system, he concluded that meals are taken at well-spaced intervals and rapidly digested. We, on the other hand, while agreeing that meals are rare, consider digestion to be a very slow process for, as explained above, by the micro-dissection methods employed we had no difficulty in extracting red liquid from the gut which was certainly no more viscous than the haemocoele liquid. It is difficult to see how Vanden Berghe reconciled these conclusions with his other findings on the rapid propagation of peristaltic waves in the intestine. In our experience the peristalses were conspicuous; for as the waves of compression and rarefaction travelled along the gut its red colour showed up as a band of colour of varying intensity against a background of a less intense red, which was tinged with yellow in the younger specimens.

INTESTINAL RESPIRATION IN *LERNAEOCERA BRANCHIALIS*

Observations were made on the peristaltic movements of *Lernaeocera branchialis* both from the whiting (*Gadus merlangus*) and from the pollack (*G. pollachius*); the length of continuous observations was between 20 and 40 min., but on two occasions it exceeded an hour. These two long records are reproduced in graphical form in Fig. 4 together with two others. Fig. 4 is in no way comparable with Fig. 3, for in it the abscissae represent the time in minutes during which the animal was observed and the ordinates, the number

of peristalses per minute passing through the mid-point of the genital segment; both forward and backward peristalses are recorded on either side of the abscissa passing through the origin. *a* is a recording from a freshly isolated parasite from the pollack: A–B was taken after the parasite had been in circulating sea water for only 2 hr., and C–D after the same specimen had remained in circulation for 48 hr., and it is seen that there is little difference in the type of recording. In both the backward wave was accompanied by a forward one
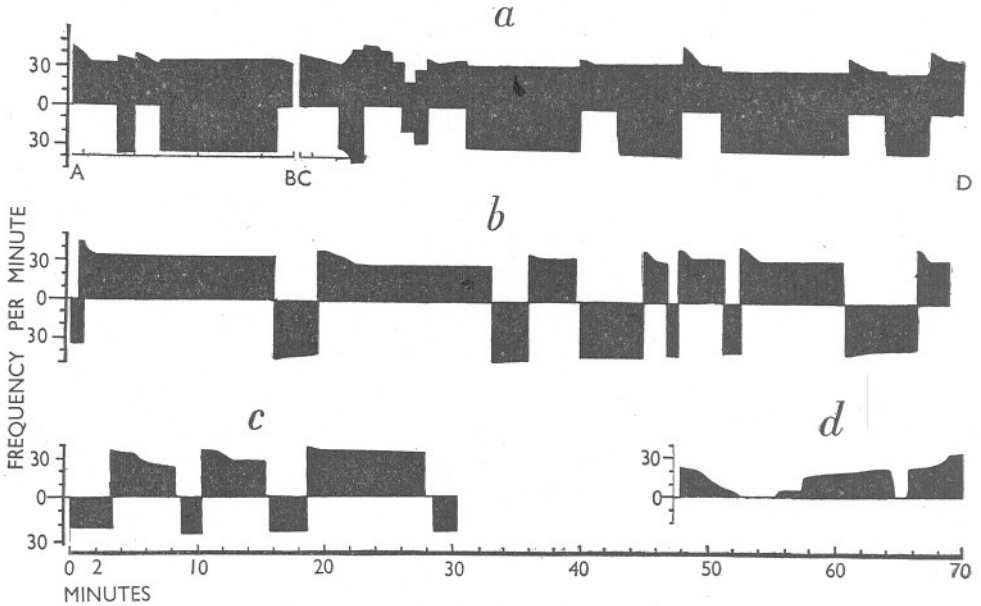

Fig. 4. Graphical records showing the frequency and direction of peristalsis in the genital segment of adult female *Lernaeocera branchialis*. Anterior and posterior peristalses shown respectively above and below the central line; frequency of waves per minute represented along ordinates and time in minutes on the abscissae. *a*, specimen from *Gadus pollachius*— A–B, 2 hr. after isolation of parasite from host; C–D, same specimen 48 hr. after isolation. *b*, specimen from *G. merlangus* 24 hr. after isolation. *c*, another specimen from same host 24 hr. after isolation. *d*, specimen from *G. pollachius* which had remained in situ on dead host for 7 days at 2° C.; recorded after specimen had been isolated and had remained in sea water for 3½ hr. at room temperature.

and these latter waves continued throughout the period of observation. This simultaneous, amphidirectional, peristalsis was rather unusual in our specimens. *b* is a record from a parasite removed from *Gadus merlangus* after it had remained in sea water for 24 hr., and *c* is one from another specimen from the same species of host on another occasion; in neither is there an amphidirectional peristalsis for more than a few beats at a time and this only occurred at the change-over from the backward to forward direction. In the change from forward to backward there was sometimes a slight pause (never more than half a minute, and usually less) at the actual change-over.

In each of these records (as in others not reproduced here) the initial forward contractions were stronger and more frequent in unit time than the subsequent ones: they started off at high speed which rapidly diminished, reaching a normal value within 1·5–2 min., and this frequency was then maintained steadily till the end of the phase. Only on two occasions did the backward peristalses start with a higher rate of contraction than the normal, and on a few they started at a lower rate which was soon brought up to normal.

As in *Trebius*, there appeared three initiation centres for the peristaltic waves in *Lernaeocera* (these were mapped out by Sproston before Hartley's observations were made known to her) and it is of great interest to note that their positions are homologous in two such widely differing copepods. Fig. 5 is a diagrammatic optical section of *L. branchialis* in which the approximate positions of these centres are indicated. Some attempt has been made to show the relative thickness of the cuticle in different regions of the body wall by the thickness of the outline: that of the antler-like outgrowths of the cephalothorax is very thick indeed, so that there is little space within them; elsewhere, particularly in the posterior two-thirds of the genital segment, there appeared a wide area of haemocoele (notably in advanced females) and at times some movement could be seen therein as a direct consequence of the peristalsis; but no movement, i.e. circulation, could be made out in the cephalo-thoracic region. The abdomen is also strongly chitinized and this made observations of peristalsis very difficult except in young females.

Fig. 5. *Lernaeocera branchialis* (adult female) (diagrammatic), showing the regions from which peristalses arise. These three 'centres' are homologous with those of Fig. 2.

The comparatively few observations we have on the abdominal peristalses agree in that they seldom coincide with those in the genital segment. Forward peristalses were less frequent in unit time than those in the genital segment so that they appeared out of phase, and they were never continued forwards past centre 2 into the genital segment; their frequency was fairly constant—from 16 to 20 per minute—but their intensity was feeble. Backward peristalses were also less frequent than the corresponding waves in the genital segment; they were fitful and sometimes the impulses failed to be transmitted; they appeared to originate from centre 2 and not be merely 'handed on' from those of the genital segment which originated from centre 1. Other instances of impedance were met with in the genital gut immediately on the cessation of a
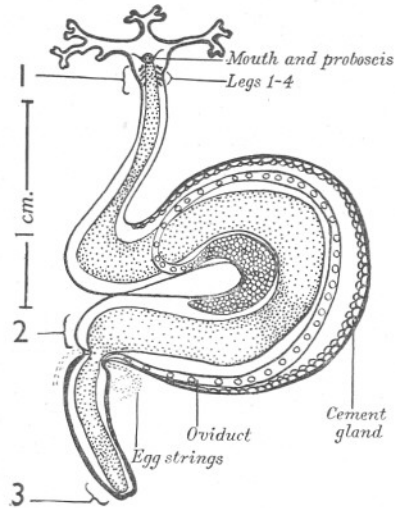
set of forward peristalses, when there was a pause before the impulses from centre 1, in the hind region of the cephalothorax, were manifested as backward waves (Fig. 4 *b, c*). On the other hand, immediately on the cessation of the impulses from centre 1, centre 2 appeared to be relieved of some depressor action and the forward impulses were abnormally strong and frequent (Fig. 4 *a, b, c*). On rare occasions the depressor action was insufficient to quell the normal impulses from centre 1, and they continued concurrently with those from centre 2, resulting in the amphidirectional peristalsis observed throughout this specimen (Fig. 4*a*).

A further demonstration of impedance in centre 1 was found when a specimen of *Lernaeocera branchialis* was kept in situ on a pollack in the refrigerator at 2° C. for 7 days. On removal at the end of this period the parasite was opaque and no movement was visible within it; it was dissected out and placed in circulating sea water at laboratory temperature, in which it became translucent and peristalsis was resumed—very fitfully at first, but after 3 hr. it became stronger and more or less continuous but in the forward direction only. The recording after $3\frac{1}{2}$ hr. is shown in Fig. 4 *d*. No backward waves were seen. After 24 hr. the forward peristalses were still in progress, with pauses of 1–5 minutes; the animal was then sacrificed for osmotic pressure determinations (Panikkar & Sproston, 1941, Table II (5)).

Stekhoven & Punt (1937) investigated the temperature effects on the peristalsis in *Lernaeocera branchialis* from the cod; they found that lowering the temperature reduced the frequency of the peristalsis, and also that the backward peristalses were almost completely inhibited by reducing the temperature to 5·5° C. for short periods (about 15 min. only in their experiments), but resumed their normal frequency when the temperature was raised again. They also determined the duration and frequency, under normal laboratory conditions, of the peristalses of seven specimens of *L. branchialis* and of two specimens of *L. lusci* (which gave substantially the same results). We have summarized their data and calculated the arithmetic means for comparison with our own (Table IV).

TABLE IV. THE DURATION AND FREQUENCY OF THE ANTERIOR AND POSTERIOR PERISTALSES IN THE GENITAL SEGMENT OF *LERNAEOCERA BRANCHIALIS*

Summary of Results obtained by Stekhoven (1936),
Stekhoven & Punt (1937) and Sproston (present paper)

	Forward		Backward	
	Duration min.	Frequency per min.	Duration min.	Frequency per min.
Stekhoven: Stekhoven and Punt				
Arithmetic means	2·75	44·0	2·12	37·5
Range	0·6–7·8	25·0–72·6	0·58–3·75	22·5–60·5
Sproston				
Arithmetic means	5·7	33·2	3·3	30·6
Range	2·0–15·4	19·0–48·0	1·0–15·0	19·0–48·0

From the preceding summary in Table IV and from Fig. 4 it is seen, without going into a statistical analysis, that our values vary over a wide range, but an approximate idea of the duration and frequency of peristalsis in both directions is given by the arithmetic means of our observations. The mean duration of backward peristalsis is just over half (58 %) that in the forward direction in our specimens, but the mean frequency per minute is only slightly less. The corresponding results obtained on the same species of parasite from the cod by Stekhoven (1936) and by Stekhoven & Punt (1937) show similar relative differences; but the durations of peristalses in a given direction were always much shorter than those obtained by us, i.e. about half, when the means of each set of observations are calculated. The frequencies of the peristalses in their specimens are, however, slightly higher than in ours. Considering the wide variations in both sets of results, we do not feel justified in analysing them further.

The conclusions arrived at by Stekhoven (1936) and Stekhoven & Punt (1937) are that there are two automatic centres controlling the gut movements of *Lernaeocera branchialis*: one associated with the circumoesophageal commissure and the other near the end of the mid-gut (also referred to as the caudal centre). The exact location of these centres is, of course, hypothetical; but it is curious that these authors do not refer to a centre in the abdomen, nor do they record the, admittedly weaker, series of peristalses in this region. In their analysis of the peristalses in the genital segment they state that the impulses from the hinder centre (centre 2 in our figure) have a greater frequency, are stronger and are also maintained for a longer time than those originating from the cephalic centre. Our observations also support this conclusion. Now in the change-over in peristalsis from one direction to another, Stekhoven mentions an overlap of waves; he implies that this normally takes place at each change-over, but that it is of a shorter duration in the backward-forward change-over. He did not record any pauses in peristalsis. On the other hand, we observed pauses occasionally, but they only occurred at the forward-backward change-over. Overlap of waves from both directions, i.e. amphidirectional peristalsis, was also occasionally seen by us, but only during the backward-forward change-over (Fig. 4). Though these details are slightly at variance with the results obtained by Stekhoven & Punt, their implication is the same: namely, that the forward impulses (those from centre 2) in the genital segment are in every way more effective, and that there is a lag or impedance imposed upon the backward impulses (coming from centre 1).

As Stekhoven & Punt overlooked Vanden Berghe's paper it is necessary to review some of the interesting results obtained by this author on the peristaltic movements of *Lernaeocera*. Vanden Berghe finds that the initial contractions in each set of waves are stronger and more frequent than the succeeding ones (a point not mentioned by Stekhoven & Punt); they begin at about 44 per min. and gradually diminish, and the average duration for the backward phase is about 3 min., but that in the reverse direction it is about

twice as long. This agrees very well with our findings (Fig. 4). He also mentions amphidirectional waves—disordered surgings to and fro—lasting for 2 or 3 sec. occurring at the backward-forward change-over, though he does not state exactly what happens at the other change-over. Like Stekhoven, he does not record pauses between the phases. He publishes very few actual records, and those, only of the number of waves of an entire phase of peristalsis. The means of these ten observations are: backward phases 65 and forward phases 107; he emphasizes this marked dissimilarity but he has found that it is far less marked in the younger specimens which had periods of the order of 50 and 70 respectively. We have not yet been able to confirm this.

Like Stekhoven & Punt, Vanden Berghe only recognizes two initiation centres: one near the mouth and one at the other extremity of the body, but unfortunately his statements are not very clear in regard to them, and not once does he mention that he noticed waves originating from the hind end of the genital segment. This is to be regretted for he goes on to describe some very interesting experiments in which he ligatured the body of a young specimen, first in one place and then in two places along the body. In the absence of diagrams the value of these experiments is diminished, for we do not know the position of the ligature in relation to the centre 2 in our figure. When one ligature was used an alternating peristalsis was seen as before, but the waves 'originating' from the ligature in both directions were weak and markedly less numerous than those starting from either of the ends. When two ligatures were used the central region between the ligatures showed no sensible movement. After consultation with V. Willem, Vanden Berghe concludes that, on a myogenic theory, these movements need not involve a special nervous intervention; for as peristaltic contraction is an intrinsic property of the gut wall, the reversal is explicable on the basis of fatigue and that the return wave at the single ligature is a reflected one.

We cannot wholly subscribe to this explanation, for it does not account for the difference in character of the peristalses in the genital segment and in the abdomen, nor does it cover the initial 'kick' in the forward waves, nor again the reduced facility of propagation of the backward series and their final suppression when submitted to low temperatures. We therefore maintain that it is probable that the intrinsic contractility of the muscle fibres in the gut wall is controlled by at least three autonomic nerve centres in copepods, and that the depressor action of centre 1 is significant in retaining the contents of the gut in those forms which utilize an anal current in respiration.

THE EVOLUTION OF THE RESPIRATORY MECHANISM IN PARASITIC COPEPODS

It is of interest, in passing, to review briefly the evolution of the respiratory mechanism in parasitic Copepoda. In *Trebius* and other caligids as well as in the developmental stages of the Lernaeoceridae an anal current introduces the water of the external environment which acts as the oxygen vector.

Hartog (1879) considered respiration in *Cyclops* to be 'entirely anal'. The gut movements are subservient to the circulation of a colourless blood in the lacunar system of the haemocoele. In the Dichelesthiidae, in such forms as *Congericola*, *Hatschekia* and *Lernanthropus*, there is a peculiar development of vessels containing blood with haemoglobin in solution, and this oxygen carrier supplements the respiration which takes place by means of an anal current and a lacunar system in the haemocoele. In *Lernanthropus* there are foliose outgrowths of the cuticle along the margins of which the large vessels run, and these are connected by a network in the substance of these append-ages. The haemoglobin is probably obtained by diffusion through the gut wall in these blood-feeding forms. In the Lernaeoceridae an evolutionary series can be made out which shows a decreasing dependence on the anal current, or in other words, a tendency to become independent of the external environment. In *Lernaeenicus* the long thin body of the adult female hangs quite freely in the water and it is possible that cuticular respiration is of importance in this genus; it is probably not a blood feeder, but is nourished largely by the coelomic and tissue fluids of the clupeoid host. *Pennella*, though deeply imbedded in the skin of Cetacea, is not red in colour, and probably feeds on tissue fluids only. That it is still largely dependent on its external medium is shown by the presence of delicate feathery caudal append-ages which are thought to aid cuticular respiration; also it is well known that *Pennella* is killed when the whales migrate into the colder polar waters. In *Peroderma* the short body is largely imbedded in the muscles of the back of the sardine and the head bears a tuft of thin-walled digitiform 'rhizoids'. This parasite has been the subject of numerous papers by Monterosso (1921–30), who shows that though the alimentary canal is still functional (he does not state whether the genus is aproctous), the cephalic rhizoids serve as absorptive organs both of nutriment in solution and of oxygen from the blood of the host. The rhizoids, he maintains, are syncytial in structure as are all the other organs of the body (Caullery (1926, p. 19) doubts this, and thinks that the syncytial appearance may be due to defects in fixation) and their growth in the renal tissue of the fish causes vascular hypertrophy, so that the rhizoids are bathed in host blood in the lacunae in which they come to lie. The haemo-globin which either passes into the haemocoele via the rhizoids, or via the gut wall, or both, acts as an accessory vector of oxygen; there may or may not be an anal current, but active peristalsis is noted in the gut, especially in the median section, and waves are said to be initiated in the posterior region. He emphasizes the kinetic function of the gut in relation to the body fluids.

In *Lernaeocera* the cuticle has become particularly heavily chitinized and the cephalothoracic outgrowths are purely mechanical anchors; cuticular respiration is reduced to a minimum and both oxygen and food enter the animal through the mouth in the form of the blood of the gadoid. A vigorous two-way peristalsis keeps the ingested blood in circulation, so that absorption of solutes is facilitated, and at the same time a feeble circulation is transmitted

to the haemocoele fluid. Independence of the external environment has reached a high level as shown by the osmotic gradient and by the toleration of brackish water by this genus of parasites.

A comparison of the details of respiration in *Lernaeocera* and in *Trebius*, which represent the two extremes in the above series, is particularly instructive. The two-way respiratory current in the gut of *Trebius* is complicated by the muscular action of the relatively powerful mouth parts, the trituration of food in the stomach and its periodic expulsion as faeces by the rectum. In *Lernaeocera* digestion is apparently slow, and during this process the gut is closed at both ends, so that the two-way peristalsis is unimpeded by the exigencies imposed upon it in *Trebius*, and a higher frequency is observed. The freedom from extraneous movements enabled the characteristics of the peristalses of *Lernaeocera* to be studied in detail: whereas in *Trebius* the movements had to be analysed to show the preponderance of forward waves (which enables the food to be retained in the gut for a sufficient time for digestion to be effected), in *Lernaeocera* this emphasis on the forward peristalses is very obvious. In the latter type of parasite this inequality is clearly a relict from the earlier stages when peristalsis had to be controlled with a view to the retention of food in the gut in the face of a continuous current via the anus.

SUMMARY

A study of the distribution of *Trebius caudatus* from four species of *Raja* trawled from two localities of different depths at Plymouth shows that there is a higher infection rate in the deeper water.

Both at Roscoff (France) and at Plymouth the mean total rate of infection is about 20 %, and the larger fish are more often infected than the smaller. Both sexes are equally parasitized and the copepods tend to collect near orifices on both surfaces of the fish (regions where the mucus secretion is maximum). Immature forms were found at Roscoff in the mucus of the orifices themselves. The collections from both places contained about equal numbers of male and female parasites.

Intestinal respiration, a feature common to free living and parasitic copepods, includes the gaseous exchange through the gut wall, the associated movements stirring the oxygen vector (which is either the external medium taken in by the anus, or the food current when this is the blood of the host), and the circulation of the body fluid as a direct result of these movements. The significance of the gut movements, which include the peculiar two-way peristalsis, is examined in detail in *Trebius caudatus* and *Lernaeocera branchialis*:

the former has a functional anus which admits the external medium and the latter has a closed anus and employs the blood of the host as the oxygen vector.

Peristalses in the three sections of the gut in *Trebius* are not synchronous and wide variations are found in the frequency and strength of the waves and also in the duration of the backward and forward phases of peristalsis. Much of the irregularity is due to the presence of food and faeces in the gut and to ancillary muscular activity.

In *Trebius* the maximum number of total peristalses per minute is in the cephalothoracic section of the gut, but the waves are never transmitted to and fro between this and the genital segment, though they are regularly passed forwards from the abdominal gut. The three sections of the gut are virtually separate in regard to peristalsis, which is controlled by three centres situated towards their distal ends. On analysis an increasing residuum of forward over backward waves is found from the fore to the hind end of the body; this is effective in retaining the food in the gut.

In *Lernaeocera* the cephalothoracic gut is practically absent and the peristalses in the abdomen are fitful and not synchronous with those in the large genital segment, where a two-way peristalsis is clearly seen. The peristalses in this species are unimpeded by the alimentary exigencies imposed upon them in *Trebius*, so that the superiority of the forward waves is obvious: they have greater strength, a higher frequency and a longer persistence than those in the backward direction, i.e. those originating from centre 1. This anterior centre has a depressor effect on the backward waves and is the most sensitive to temperature changes: complete inhibition is brought about by previously subjecting the animal to low temperatures.

Peristalsis in both species is controlled by three homologous autonomic nerve centres which have varying powers of stimulation and inhibition. The significance of the emphasis on the forward peristalses appears to be lost in *Lernaeocera*, for it is clearly a relict of the earlier stages when food had to be retained in the gut in the face of a continuous to and fro current through the anus.

The feeding of *Lernaeocera* takes place at rare intervals and digestion is slow. The intake of blood from the host is dependent on the same mechanism which maintains the dynamic osmotic equilibrium between the contents of the gut and the external medium.

The evolution of the modes of respiration in parasitic copepods is summarized.

REFERENCES

BAIRD, W., 1850. *The Natural History of British Entomostraca.* London: Ray Society.

BASSETT-SMITH, P. W., 1896. List of parasitic copepods of fish obtained at Plymouth. *Journ. Mar. Biol. Assoc.*, N.S., Vol. IV, pp. 153–63.

BRADY, G. S., 1880. *Monograph of the Free and Semi-parasitic Copepoda of the British Islands*, Vol. III. London: Ray Society.

CAULLERY, M., 1926. Review of Monterosso's paper in *Année Biologique*, 3me Sér. Vol. II, p. 19.

GERSTAECKER, A. D., 1866. In Bronn's *Klassen und Ordnungen des Thier-Reichs*, Vol. V.

HARTOG, M. M. 1879. On *Cyclops. Rep. Brit. Assoc.*, p. 374.

—— 1888. The morphology of *Cyclops* and the relations of the Copepoda. *Trans. Linn. Soc. Lond.*, Ser. 2, Vol. V, pp. 1–46, Plates 1–4.

HEIDER, C., 1879. Die Gattung *Lernanthropus. Arbeit. Zool. Inst. Wien u. Triest.*, Vol. II, pp. 269–368.

HESSE, E., 1863. Recherches sur quelques Crustacés rares ou nouveaux des côtes de France. *Ann. Sci. Nat.*, Sér. 4, 20, Vol. XX, p. 101.

LEBOUR, M. V., 1931. In *Plymouth Marine Fauna*, 2nd ed., p. 173.

LEIGH-SHARPE, W. H., 1918. *Lernaeopoda globosa* n.sp., a parasitic copepod of *Scyllium canicula. Parasitology*, Vol. XI, pp. 29–34.

—— 1933. A second list of parasitic Copepoda of Plymouth with a description of three new species. *Parasitology*, Vol. XXV, pp. 113–18.

LINT, G. M. VAN OORDE-de & STEKHOVEN jr., J. H. SCHUURMANS, 1936. Copepoda (Copepoda parasitica) in *Die Tierwelt der Nord- und Ostsee*, Vol. XXXI (Xc₂).

MACCALLUM, G. A., 1916. Some new species of parasitic trematodes of marine fishes. *Zoopathologica*, Vol. I, p. 23.

MONTEROSSO, B., 1921. Contributo allo studio di *Peroderma cylindricum* Heller, copepode parassiti *Clupea pilchardus. Atti Acc. Gioenia*, Ser. 5, Vol. XIII, Mem. 19, pp. 1–20.

—— 1926. Sulla prevalenza della struttura sinciziale nell' organizzazione di *Peroderma cylindricum* Heller. *Atti R. Accad. Lincei* (Ser. 6), Vol. III, pp. 278–81.

—— 1926. La Struttura del corpo di *Peroderma cylindricum* Heller in relazione alla Teoria cellulare. *Atti R. Accad. Lincei* (Ser. 6), Vol. III, pp. 507–10.

—— 1926. Studio anatomo-istologico sul più giovanno individuo finora rinvenuto di *Peroderma cylindricum* Heller. *Arch. Zool. Ital.*, Vol. XI, pp. 105–41.

—— 1926. Su un nuovo reperto contrario allo 'teoria cellulare'. *Boll. Soc. Biol. Sper.*, Vol. I, pp. 205–7.

—— 1926. Contributo alla conoscenza dei Copepodi parassiti. Le appendice risoidi cefaliche di *Peroderma cylindricum* Heller. *Arch. Biol.*, Vol. XXXVI, pp. 168–222.

—— 1930. Contributo alla conoscenza dei Copepodi parassiti. L'intestino di *Peroderma cylindricum* Heller. *Arch. Zool. Ital.*, Vol. XIV, pp. 169–225.

NORMAN, A. M. & SCOTT, T., 1906. *The Crustacea of Devon and Cornwall.* London.

PANIKKAR, N. K. & SPROSTON, N. G., 1941. Osmotic Relations of some metazoan parasites. *Parasitology*, Vol. XXXIII, pp. 214–23.

SCOTT, A., 1901. *Lepeophtheirus* and *Lernaea. L.M.B.C. Memoirs*, no. VI.

—— 1929. The copepod parasites of Irish Sea fishes. *Report Lanc. Sea Fish. Lab.* for 1928, pp. 81–118.

SCOTT, T. & SCOTT, A., 1913. *The British Parasitic Copepoda*, Vol. I. London: Ray Society.

SPROSTON, N. G., 1941. The developmental stages of *Lernaeocera branchialis* (L.). (Unpublished.)

STEKHOVEN jr., J. H. SCHUURMANS, 1936. Beobachtungen zur Morphologie und Physiologie der *Lernaeocera branchialis* L. und der *Lernaeocera lusci* Bassett-Smith (Crustacea parasitica). *Z. Parasitenk.*, Bd. VIII, Heft 6, pp. 659–96.

STEKHOVEN jr., J. H. SCHUURMANS & PUNT, A., 1937. Weitere Beiträge zur Morphologie und Physiologie der *Lernaeocera branchialis* L. *Z. Parasitenk.*, Bd. IX, Heft 5, pp. 648–68.

STEVEN, G. A., 1936. Migrations and growth of the Thornback Ray (*Raia clavata* L.). *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 605–14.

VAN BENEDEN, ED., 1880. De l'existence d'un appareil vasculaire à sang rouge dans quelques Crustacés. *Zool. Anz.*, Bd. III, pp. 35–9.

—— 1880. Idem. (continuation). *Zool. Anz.*, Bd. III, pp. 55–60.

VANDEN BERGHE, L., 1933. Observations sur le sang et le peristaltisme alternatif de l'intestine chez les Lernées. *Acad. Roy. Belg.* Cl. d. sci., Sér. 5, Vol. XIX, pp. 821–36.

WILSON, C. B., 1905. North American parasitic copepods belonging to the family Caligidae. Part 1. The Caliginae. *Proc. U.S. Nat. Mus.* (no. 1404), Vol. XXVIII, pp. 479–672.

—— 1907. Idem. Part 2. The Trebinae and Euryphorinae. *Proc. U.S. Nat. Mus.* (no. 1504), Vol. XXXI, pp. 669–720.

—— 1921. New species and a new genus of parasitic copepods. *Proc. U.S. Nat. Mus.* (no. 2354), Vol. LIX, pp. 1–17.

—— 1922. North American parasitic copepods belonging to the family Dichelesthiidae. *Proc. U.S. Nat. Mus.* (no. 2400), Vol. LX, pp. 1–100.