
A Quantitative Analysis of Exopodite Beating in the Larvae of the Lobster *Homarus gammarus* (L.)

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A QUANTITATIVE ANALYSIS OF EXOPODITE BEATING IN THE LARVAE OF THE LOBSTER *HOMARUS GAMMARUS* (L.)

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CONTENTS	PAGE
INTRODUCTION	70
MATERIALS AND METHODS	71
RESULTS	73
Cycle duration and beating pattern	73
Ipsilateral phase relations	75
Bilateral phase relations	77
Powerstroke/returnstroke ratio	78
DISCUSSION	81
REFERENCES	84

Raw data on exopodite beating in the first three developmental stages of the lobster *Homarus gammarus* were collected and analysed for key beating parameters. The analysis was computer assisted and the main procedures used are described. Beating patterns are the same in all three stages and are usually very regular although perturbations do occur (figures 1, 2). When beating stops the deceleration and subsequent re-acceleration is very rapid (figure 1) and limb movement sequences usually start posteriorly and move forwards (figures 1, 2*d*). Ipsilateral phase relations are generally maintained at 0.4–0.6 (figures 3, 4) and while the coupling between adjacent exopodites is usually stronger than for those further apart various deviations from this are occasionally seen (figure 5). No significant correlation between the ipsilateral phase relations of adjacent exopodites and base cycle duration was detected for any of the stages (figure 6). Contralateral phase relations undergo a constant progression (figures 7, 9) and this was found to be due to a heterodyne effect (figure 8) also described as gliding coordination. The powerstroke/returnstroke ratio for all stages was approximately 0.5 (figure 10) and no significant correlation was found with cycle duration (figure 11). The only substantial difference between the three larval stages which was noted was that of cycle duration, the cycles of stage III being shorter than those of the first two stages. The exopodite beating pattern was discussed in context with other metachronously cycling systems in arthropods and the implications of the present study discussed.

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INTRODUCTION

Control mechanisms of rhythmic activities such as locomotion, flight, respiration and feeding are currently being investigated in some detail by behavioural-neurobiologists. This is because they demonstrate features which permit the study of a wide variety of related neurobiological problems. In general, they can be evoked easily, repeatedly and reliably without complex sensory stimuli. In many cases it is possible to manipulate parameters such as cycle frequency, amplitude and duration by applying normal sensory stimuli. The repetitive nature of the activity generates large samples which permit statistical analyses and quantitative descriptions and, if the environmental conditions are controlled, large samples can often be collected with a low probability of major changes in the endogenous state of the animal.

There are now a large number of studies of rhythmic systems in many phyla that investigate a wide variety of physiological and behavioural problems, and no attempt will be made to review them here (for reviews with sections relevant to the broader aspects of the topic see Bizzi & Everts 1972; Bullock 1970; De Long 1972; Evoy & Cohen 1971; Hinde 1970; Hoyle 1970; Kennedy & Davis 1976). Among the better-known examples the decapod crustacea have proved very useful as experimental subjects. There have been studies of respiration and scaphognathite beating (Mendelson 1971; Pasztor 1968), of swimming in adult animals (Hartnoll 1971; Paul 1971*a, b, c*), of cheliped flexion (Field 1974*a, b*), of antennular flicking (Snow 1973*a, b*), of maxilliped exopodite beating (Burrows & Willows 1969), of gastric mill rhythms (Morris & Maynard 1970; Powers 1973), of walking (Barnes, Spirito & Evoy 1972; Macmillan 1975; Spirito, Evoy & Barnes 1972) and of swimmeret beating (Davis 1968*a, b*, 1969).

In the lobster, *Homarus*, it has also proved possible to examine swimmeret beating activity in the early developmental stages (Davis 1974), and Davis and his colleagues have produced evidence that the motor patterning responsible for swimmeret beating, which appears first in stage IV of development, is present in the central abdominal ganglia in the absence of prior sensory input from the swimmerets (Davis 1973; Davis & Davis 1973). Although swimmeret beating does not start until stage IV, it is not the first rhythmic activity of the larva. The first three stages display rhythmic beating of the exopodite branches of the thoracic appendages leading to swimming (Herrick 1895, 1909; Neil, Macmillan, Robertson & Laverack 1976). We felt that it was important to make a detailed study of exopodite beating in the developing lobster larva not only because it would provide another description of a rhythmic system in a rather specialized case but also because it was necessary for further understanding of Davis's results.

In the first of this series of three papers (Neil *et al.* 1976) we give a description of the development and anatomy of the early stages of *Homarus gammarus* together with a general, illustrated, qualitative description of the overall behaviour and, in particular, of the modes of exopodite beating. In this, the second paper, we provide a quantitative description of exopodite beating and in the third paper (Laverack, Macmillan & Neil 1976) we give a quantitative description of swimmeret beating and make statistical comparisons between the parameters of beating in each stage.

MATERIALS AND METHODS

A detailed description of the methods used to hatch and rear the larvae of *Homarus gammarus*, together with the methods for filming and recording other data, is given in the first paper of the series (Neil *et al.* 1976). Swimming behaviour, and the appendage movements responsible for providing motive power were analysed from filmed records. A Bolex camera was used throughout. The films, taken at a film speed of 64 frames/s, were later analysed by means of a 'Specto' motion analysis projector equipped with a single-frame advance/reverse mechanism coupled to a film-frame counter. Frame-by-frame examination of swimming was carried out but, because of the continually changing orientation of the animals during filming, it was not always possible to observe all exopodites at once. None the less as far as possible the beating of the five posterior exopodites on each side was followed, and in a few cases it was possible to observe six ipsilateral appendages. For each exopodite, the film-frame numbers corresponding to the start of successive powerstroke or returnstroke movements were recorded in separate columns of ascending film-frame number, and hence of progressive time. The number of measurements for any given exopodite in a continuous behavioural sequence varied from a complete record for all limbs through a series with small and large gaps to series with no information for some exopodites.

The results from this type of frame-count were entered in a matrix of 20 columns (powerstroke and returnstroke columns for five exopodites per side) with gaps in the data indicated by a zero entry. Although some other beating parameters are described qualitatively in the first paper (Neil *et al.* 1976) no attempt has yet been made to quantify all of these. The quantitative description given here is restricted to intra- and inter-exopodite time relations.

The matrices of film-frame numbers were entered on disk for subsequent manipulation and processing by computer programs written in FORTRAN IV and executed on an I.B.M. 360/44 computer.

Some of the programs used were designed to produce general statistical parameters of cycle durations of individual exopodites, of pooled results from all exopodites in a single animal, and of pooled results from all animals within a developmental stage. These programs not only provide the basis for the description of beating frequency but were also used for statistical comparisons between developmental stages, which is the subject of the third paper in this series (Laverack *et al.* 1976). These programs dealing with cycle duration were also planned to allow the data matrices to be presented in graphical form, thus providing a complete pictorial description of the beating pattern for all the film sequences analysed.

Other programs were designed to take selected pairs of columns (i.e. the beating of specific limbs) and consider the phase relations between events recorded in the two columns. Use of the term 'phase' in behavioural descriptions is subject to some variation but we have adhered to the definition of Wilson (1966*b*) as follows: 'The phase of an event is the fraction of some cycle which has elapsed at the time of the event's occurrence.' The fraction is usually expressed in degrees (0–360°) or as percentages in decimal form (0–1.0). The frame-count column selected in each case to provide the 'cycle' we term the *base* column (or cycle) and the column selected to provide the 'event' we term the *test* column (or cycle).

Phase programs were used not only to compare ipsi- and contralateral phase relations between exopodites (by selecting ipsilateral and contralateral pairs of columns respectively)

but also to examine powerstroke–returnstroke relations (by selecting powerstroke and returnstroke entries for the same exopodite).

The relation between phase and duration was readily obtained by combining output from the two different types of program and all results from whatever source were transferred to output operations which could be either numerical (tabular or algebraic), graphical (histogram, graph or sequential plot) or both.

TABLE 1. EXAMPLES OF DURATIONS OF EXOPODITE BEATING CYCLES
IN DIFFERENT DEVELOPMENTAL STAGES

	number of cycles	\bar{x} /ms	s.d.
stage I			
steady beating	1670	120.06	12.56
considerable starting and stopping	1591	113.67	16.92
stage II			
steady beating	828	117.62	12.69
stage III			
steady beating	1158	88.18	10.57

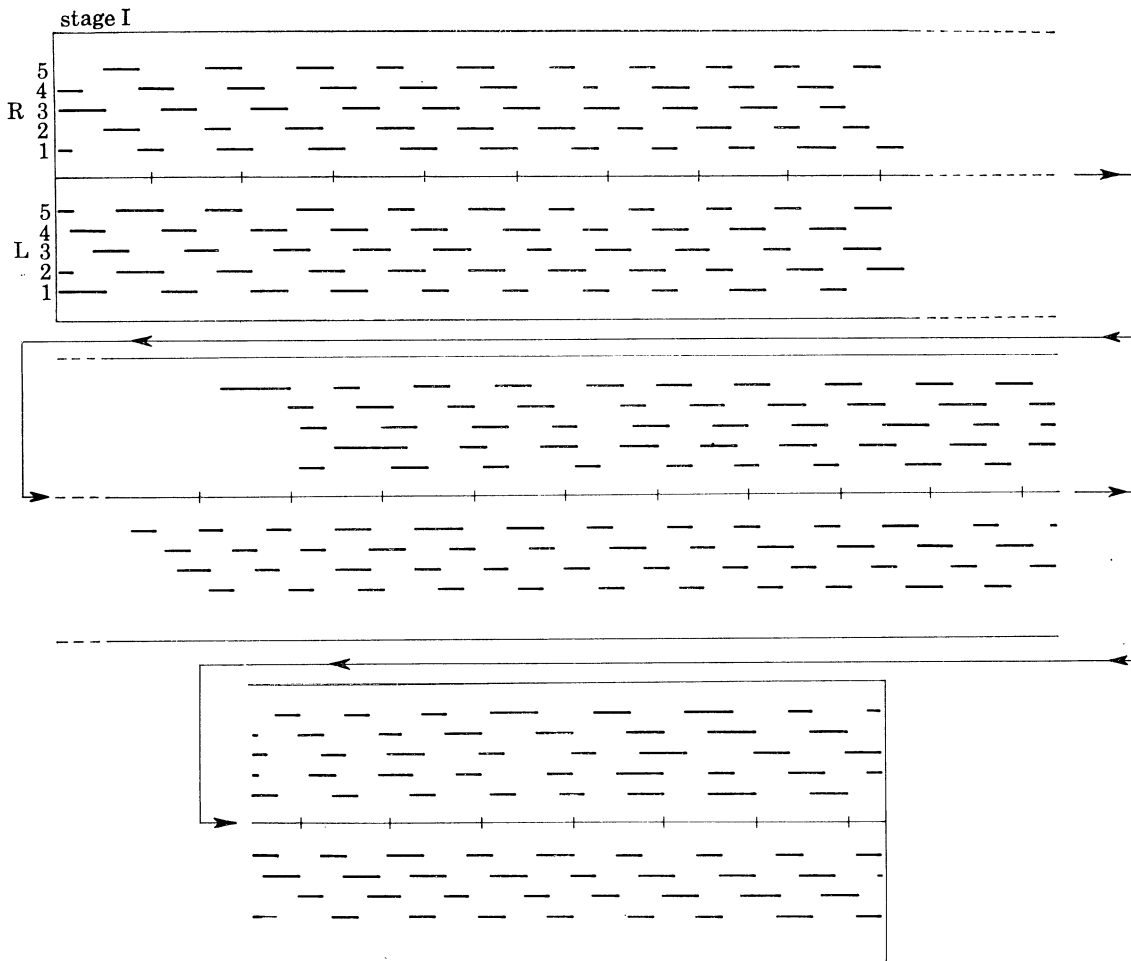


FIGURE 1. Example of the bilateral beating pattern from a stage 1 larva illustrating a sequence in which the animal stopped beating and restarted after a short time interval. Note the rapid acceleration and deceleration and that the most caudal exopodites (i.e. 5) beat first upon restarting of beating. R, right, L, left; 1, 2, 3, 4, 5 are exopodites 1–5 of pereopods. Black bars show duration of powerstroke. Time marks 125 ms.

EXOPODITE BEATING IN LOBSTER LARVAE

73

RESULTS

Cycle duration and beating pattern

A detailed analysis of differences in frequency of exopodite beating between individual animals and also between successive development stages is made in the third paper of the series which deals with developmental changes (Laverack *et al.* 1976). The coverage of this aspect in this paper will, therefore, be limited to a general outline of the characteristics of beating frequency sufficient to allow an understanding of the subsequent analysis of other parameters of beating.

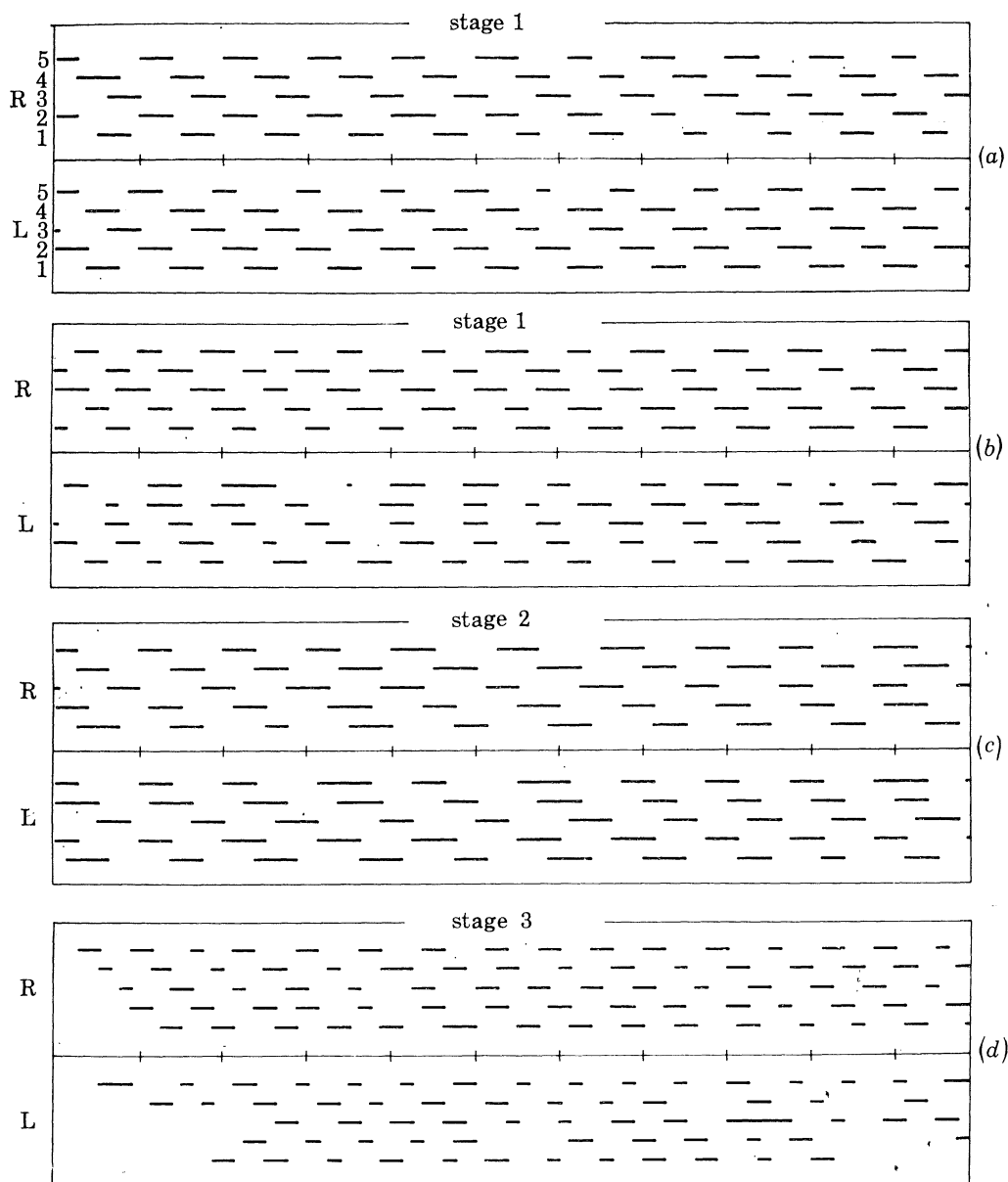


FIGURE 2. Examples of bilateral beating patterns from larvae in the first three developmental stages. (a) Stage 1 larva beating steadily. (b) Stage 1 larva. Sequence with a perturbation in the beating rhythm. (c) Stage 2 larva beating steadily. (d) Stage 3 larva initiating beating and beating steadily with some perturbations on the left side. Lettering as in figure 1.

In general there appeared to be quite a narrow range of preferred frequencies of beating for animals of a given developmental stage, as can be seen from the mean cycle durations and standard deviations of pooled results from several animals (table 1). Many of the sequences of beating that were analysed had periods in which the beating slowed to a stop and, after a pause of variable duration, started up again. The variation in cycle duration was nevertheless very small in such samples because the frequency of beat usually decelerated from the preferred range to zero and accelerated from zero to the preferred range in only a few cycles (table 1, figure 1).

Examination of the beating patterns over all exopodites showed that beating occurred in the very regular fashion typical of metachronous waves of activity. We did not attempt to quantify the preferred direction of initiation of movement for the waves, but qualitative

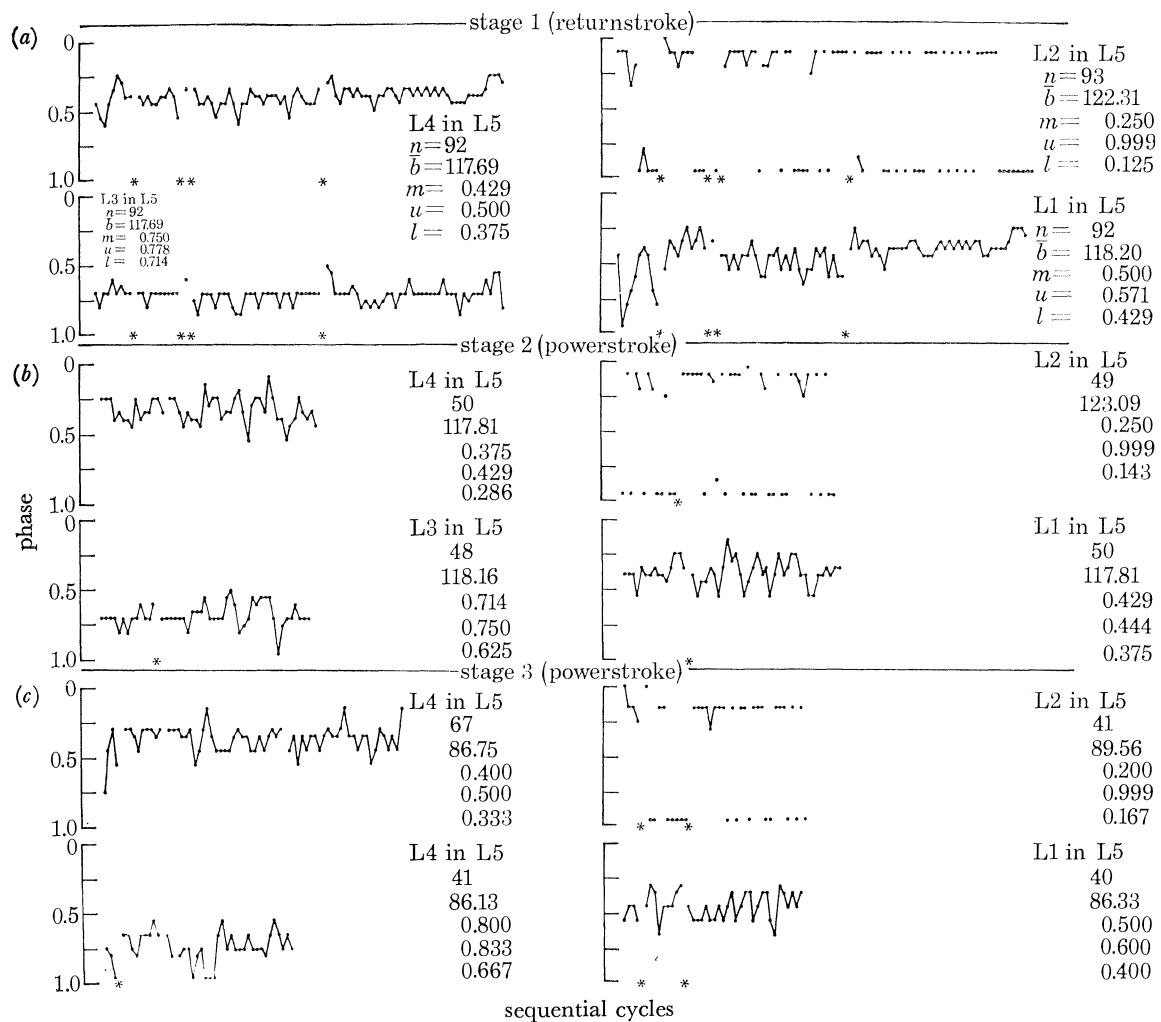


FIGURE 3. Examples of phase plots showing relative phase position of the *test* appendage in the *base* (see text) appendage cycle in sequential cycles. Illustration for each stage shows phase position of each ipsilateral exopodite (*test*) in the most posterior exopodite (*base*). The same sequence is illustrated for each animal although owing to some cycles being absent in some plots vertical alignment of the sequences is only approximate. Breaks in sequences are shown by stars. n , Total number of cycles in the plot; b , mean duration of base cycle; m , median phase value; u , upper quartile phase value; l , lower quartile phase value. (a) Stage 1. (b) Stage 2. (c) Stage 3.

observations suggest that movements start caudally and move rostrally (Neil *et al.* 1976); where the beating pattern shown in figure 1 slows to a stop and then restarts, the typical caudorostral initiation of movement is seen. Another example of initiation of beating can be seen in figure 2*d*.

Examination of records taken from sequences of steady, sustained beating within the preferred frequency range showed that the basic pattern was remarkably stable. While small perturbations do occur they do not cause reordering of the overall pattern but are instead resolved within the continuing framework of the pattern (figure 2*b*). Comparisons of beating patterns from all three exopodite stages showed that the basic pattern was similar in structure even when the preferred frequency was different (figure 2*a, c, d*).

Ipsilateral phase relations

The ipsilateral phase relations were studied by considering the phase of the start of the powerstroke movement and the start of the returnstroke movement of each ipsilateral exopodite (test) in relation to the cycle of all the other ipsilateral exopodites (base). A series of graphs expressing the phase position of the powerstroke movement of the test exopodite within each successive base exopodite cycle for each of the other ipsilateral exopodites during the same sequence of beating, shows clearly the variation in the coupling between each two exopodites as a function of time (or more precisely as a function of consecutive base cycles as time progresses). Examples of this type of sequential phase plot for animals in the first three

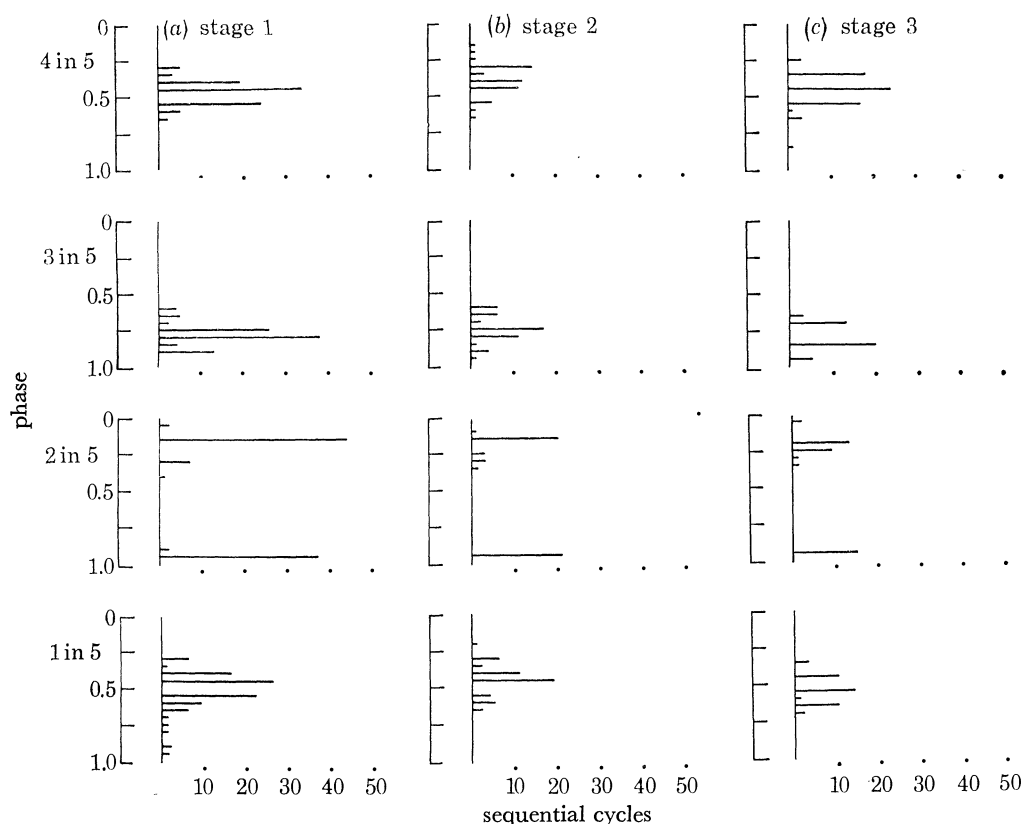


FIGURE 4. The data which were presented in figure 3 as sequential phase plots are here presented as the more conventional phase histogram.

developmental stages are given in figure 3 (examples of plots based on both powerstroke and returnstroke data).

Although some variation in the ipsilateral phase relationships was seen, a mean phase position was maintained, as was more clearly seen when the same relations were expressed as phase histograms (figure 4).

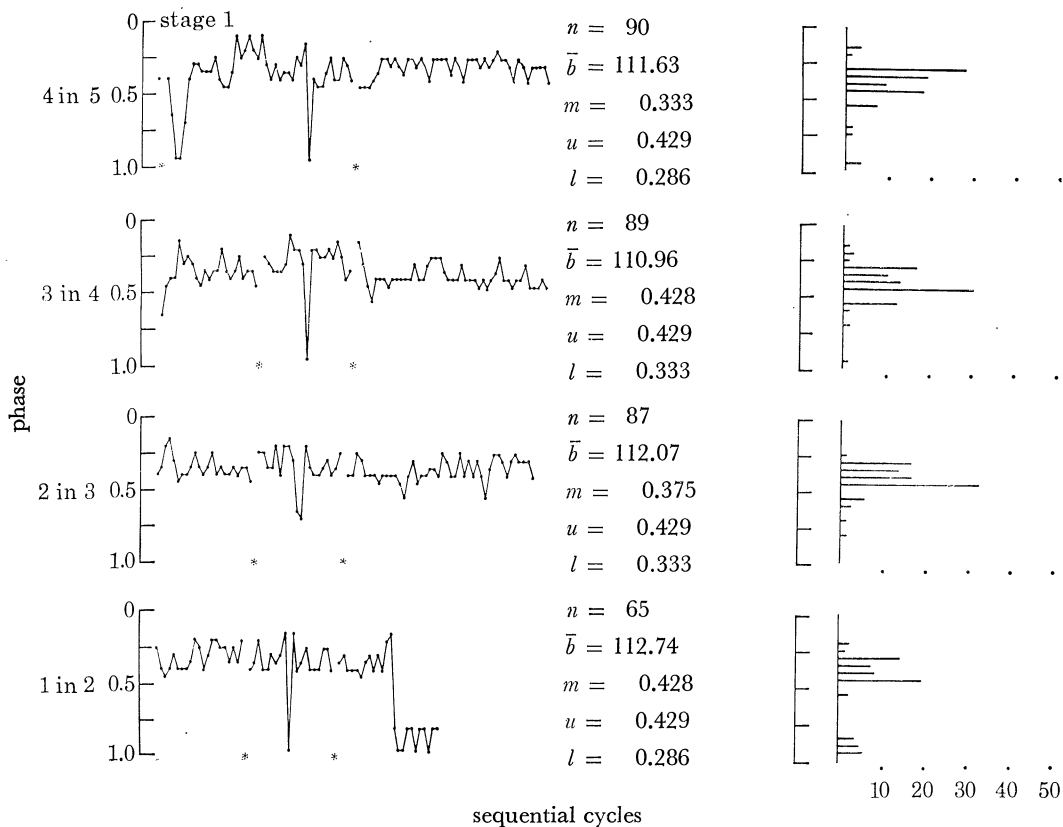


FIGURE 5. Examples of phase plots and corresponding phase histograms for adjacent segments in a stage 1 larva. This segment of data was chosen because it illustrates both the more usual tight coupling seen between adjacent exopodites (last half of sequence) and also less common perturbations in the relationship (first half of sequence). In the 1 in 2 relation a small unusual complete phase change is also seen. Owing to some cycles being absent in some plots the vertical alignment of the sequences is only approximate. Breaks in sequences are shown by stars. n , Total number of cycles in the plot; \bar{b} , mean duration of base cycle; m , median phase value; u , upper quartile phase value; l , lower quartile phase value.

When the phase relation of each exopodite to the one immediately rostral to it was considered it was found that there was an approximately constant phase interval of 0.4–0.6 between adjacent exopodites (figure 5). A comparison of the phase relations for non-adjacent exopodites (figures 3, 4) with the typical relation for adjacent exopodites (figure 5) showed that the strength of the phase coupling between two exopodites decreases as the number of segments separating them increases, although deviations can occur between adjacent exopodites (figure 5).

In order to determine whether there was some consistent relation between phase and beating frequency, at least within the normally narrow range of variation of the two parameters, the phase of adjacent pairs of exopodites was plotted as a function of the duration of the base cycle for a variety of animals. Figure 6 illustrates examples of such plots from animals in the

first three stages of development and no consistent relation was found for any of the animals examined.

Bilateral phase relations

The bilateral phase relations were studied by considering the phase of the start of the powerstroke movement and the start of the returnstroke movement of each exopodite on a side (test) in relation to the cycle of that contralateral to it in the same segment (base). Figure 7 shows examples of this type of representation based on some powerstroke and some returnstroke data from the five posterior thoracic exopodite pairs for each of the first three larval stages.

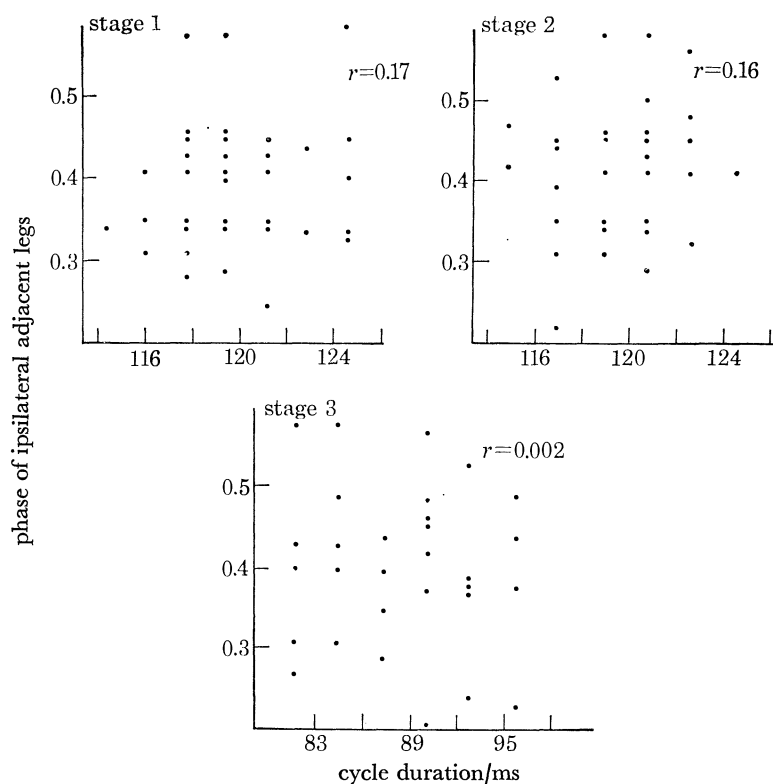


FIGURE 6. Examples of the ipsilateral phase values for adjacent exopodites plotted against the corresponding base cycle duration. One example from each of the first three developmental stages is shown. r , Coefficient of correlation.

The bilateral sequential plots were very different in appearance from the ipsilateral plots and were characterized by phase progressions in both directions. As the phase progressions approach 1 or 0 they undergo a sudden change to a new low or high value respectively so that the sequential plot often has the appearance of a sawtooth. This sawtooth result can be produced either by a double test event within a single base cycle whenever the test event approaches either phase limit (i.e. a restoring or relaxing effect) or by test and base cycles of stable but different frequencies (i.e. a heterodyne effect between two different frequencies). Reference to simultaneous print-out of actual film-frame numbers and the beating patterns generated from them showed that it is almost invariably the case that the two sides move at different frequencies so that the bilateral plots can also be represented as shown in figure 8. Presentation of the plots in this way drew attention to the fact that in many cases the phase

progression of one cycle through the other was not entirely smooth. Some phase relationships often appeared to be sustained for rather longer than a simple frequency beating would predict and appeared to be so sustained on most occasions when they occurred (figure 8). Examination of phase histograms of bilateral relationships (figure 9) confirmed that this was a real effect and that the favoured positions are usually just prior to or just following phase reversal.

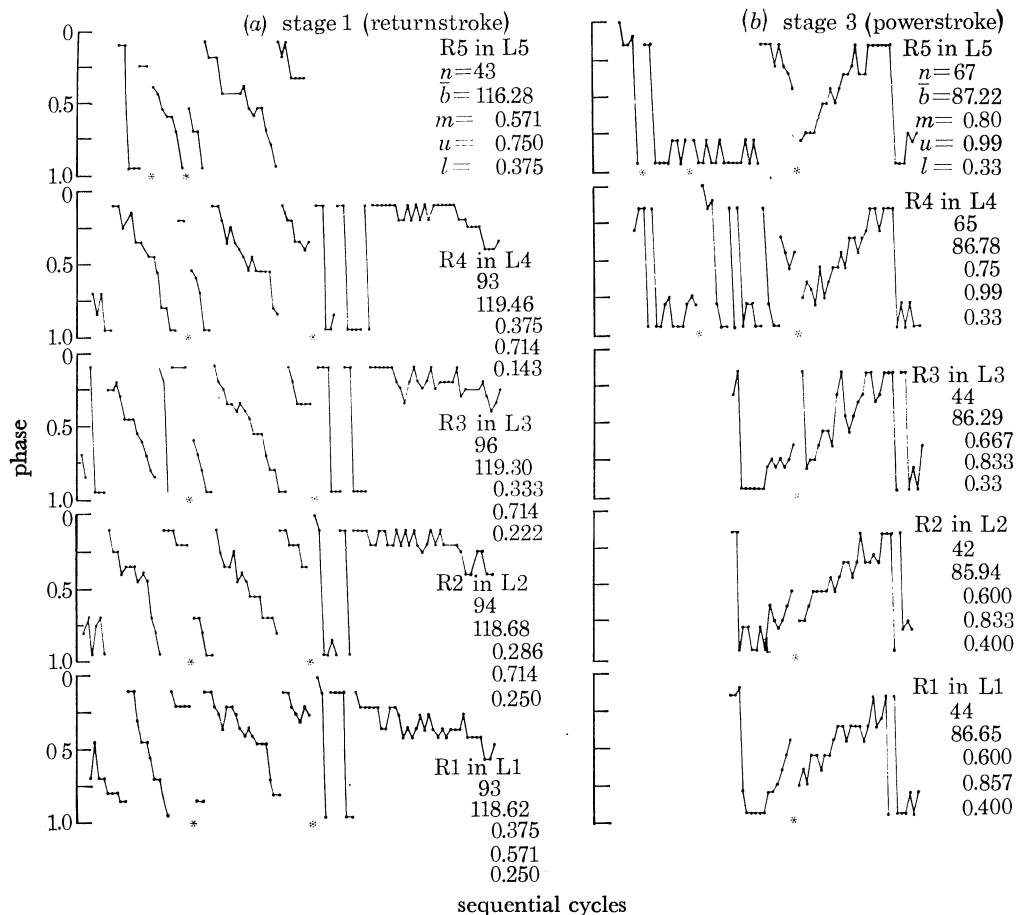


FIGURE 7. Examples of phase plots showing relative phase position of the *test* appendage in the *base* appendage cycle in sequential cycles. Illustration shows contralateral pairs from a stage 1 and a stage 3 animal. The same sequence is illustrated for each animal although owing to some cycles being absent in some plots vertical alignment is only approximate. Breaks in sequences are shown by stars. *n*, Total number of cycles in the plot; \bar{b} , mean duration of base cycle; *m*, median phase value; *u*, upper quartile phase value; *l*, lower quartile phase value. (a) Stage 1. (b) Stage 3.

Powerstroke/returnstroke ratio

Histograms of the phase relations of the start of the powerstroke in the concurrent returnstroke cycle (start of returnstroke to start of next returnstroke) and vice versa in the first three stages showed some scatter about a mean position of 0.4–0.6 (figure 10).

In order to determine whether there was some consistent relationship between the powerstroke/returnstroke ratio and beating frequency within the fairly narrow range of variation found for both, the phase of the powerstroke (*test*) in the returnstroke was plotted

EXOPODITE BEATING IN LOBSTER LARVAE

79

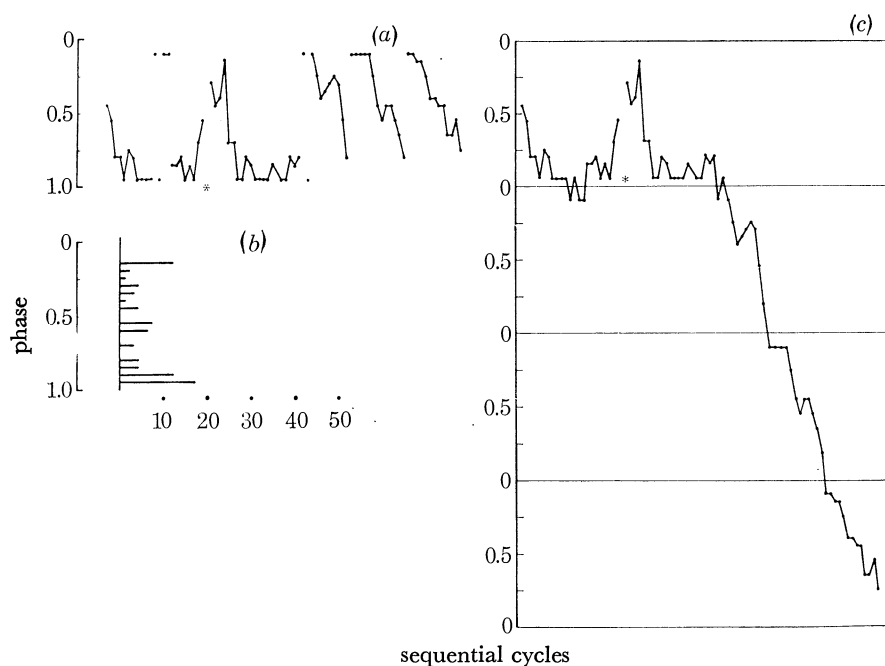


FIGURE 8. Contralateral phase plots such as those in figure 8 were examined to test whether the sawtooth appearance of the plots results from a 'relaxation' or a 'heterodyne' effect. Illustration here shows one such plot expressed as (a) sequential plot, (b) phase histogram and also (c) plotted out in continuing phase-reversal relation thus showing the 'gliding' coordination between contralateral pairs.

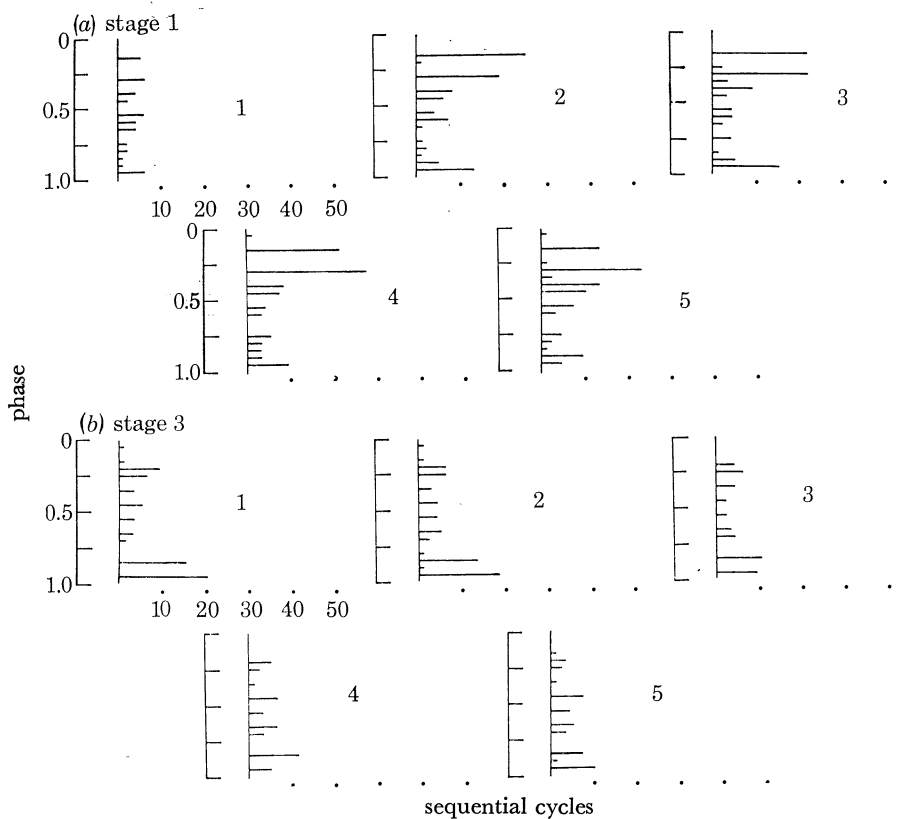


FIGURE 9. The data which were presented in figure 8 as sequential phase plots are here presented as the more conventional phase histogram. Note that phase values either side of phase reversal are slightly favoured. (a) Stage 1. (b) Stage 3.

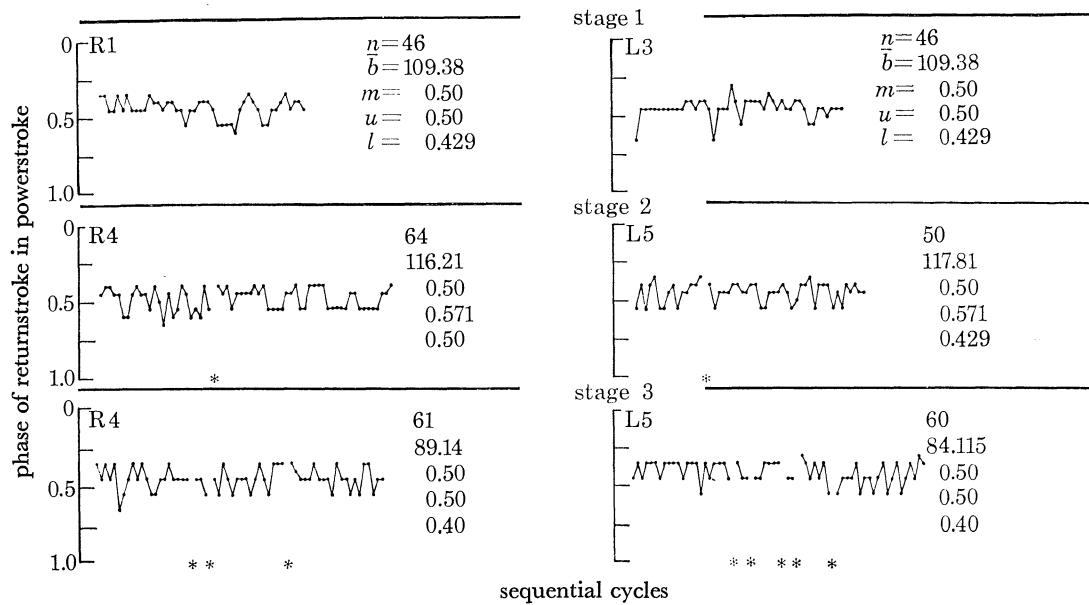


FIGURE 10. Examples of phase plots showing relative phase position of the returnstroke in the powerstroke. Illustration for each stage shows the powerstroke/returnstroke phase relation for sequential cycles in two representative exopodites. n , Total number of cycles in plot; \bar{b} , mean duration of base cycle; m , median phase value; u , upper quartile phase value; l , lower quartile phase value. R1, right 1; R4, right 4; L3, left 3; L5, left 5.

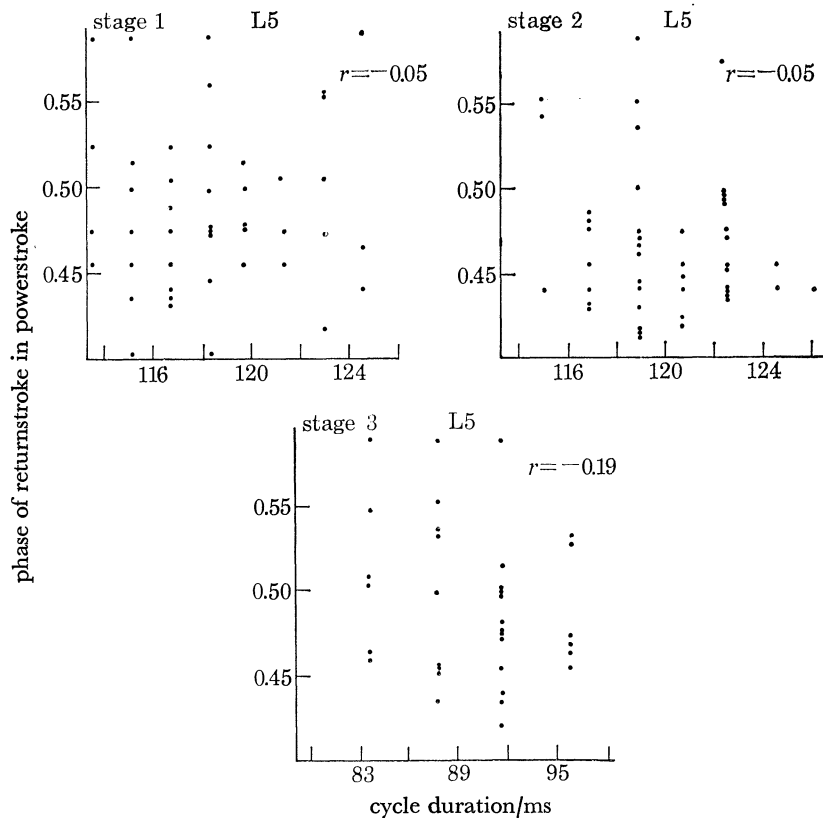


FIGURE 11. Examples of the powerstroke/returnstroke phase relations plotted against the corresponding base cycle duration. Representative examples from each of the first three developmental stages are shown. L5, left 5; r , coefficient of correlation.

as a function of returnstroke (base) cycle duration and vice versa for a variety of animals. Figure 11 illustrates examples of results from a number of animals (stages I–III), and no consistent relation was found in these or any other animals examined.

DISCUSSION

One of the interesting findings of the present study concerns the range of frequencies of exopodite beating observed in larval lobsters. Exopodite beating occurs over an extended range of low frequencies in some non-swimming situations (Neil *et al.* 1976) and yet, when the animals sustain locomotion, steady (i.e. regular) beating is usually restricted to a relatively narrow range of frequencies which we have defined as preferred frequencies. In this respect, the exopodite system of the larva of *H. gammarus* may resemble the walking system of the adult in the lobster *H. americanus*. There it has been reported that while a wide variety of lower stepping frequencies are seen in short, restricted walking sequences or when the animals turn or move sideways, when they walk directly forwards in a steady fashion the range of frequencies used is relatively restricted (Macmillan 1975). Both studies could be criticized on the grounds that a particular type of behaviour was selected, so that the selection occurs in the study and not in the animal. It is therefore necessary, when considering this type of result, to ask whether the experimental selection has a behavioural substrate. In the case of exopodite beating, there is a clear behavioural basis for the selection because, in general, the analysis was restricted to swimming animals and, as the animals have a density greater than sea water, they cannot remain off the bottom unless a certain frequency of beating is maintained to provide lift. In the study of lobster walking the position is not as clear. While the animals achieve a steady, sustained stepping only when walking forwards in a straight line, the selection of this segment of locomotory activity was made primarily because it presented a consistent behaviour for analysis (Macmillan 1975).

In general, other rhythmic systems described appear to cover the whole spectrum of frequency-range types from those with a very wide range such as cockroach walking (Delcomyn 1971) through more intermediate systems, as in lobster swimmeret beating (Davis 1969) to the restricted systems exemplified by the lobster pyloric filtering rhythm (Maynard 1965; Morris & Maynard 1970). This is not to imply basically different classes of systems, but whether a system is itself frequency selective or whether the analysis of the system has been frequency selective should be an important consideration when comparisons of function or cycle structure are made between different studies.

Such considerations may account for some of the differences in the descriptions of the way in which different systems operate to meet changing output requirements, particularly with respect to inter- and intra-appendage phase relations and changes in beating frequency. It seems probable that problems of interpretation and comparison particularly in such areas as insect locomotion (Delcomyn 1971; Hughes 1965; Pearson & Iles 1970; Wendler 1966; Wilson 1965, 1966*a*) are partially due to frequency-range differences both intrinsic and imposed.

A comparison between the ipsilateral beating pattern in the larva of *Homarus gammarus* and the walking pattern described for the adult of *Homarus americanus* shows that while the two are generally similar there are some differences (figure 12). In the exopodites, if the most caudal appendage is considered first, waves of activity appear to pass rostrally in approximately

sequential fashion. The phase lag between all adjacent appendages is approximately the same at 0.4–0.6 so that appendages four segments apart are close to each other in phase and sometimes completely in phase. In the lobster walking system, if the most caudal leg is again considered first, similar waves of activity appear to pass rostrally although the sequencing is slightly altered because the phase lag is no longer the same between all adjacent pairs. There are again four segments between appendages which are approximately in phase. This produces a pattern rather similar to the alternating triangle seen in insects with the middle legs of a side alternating with the outside legs.

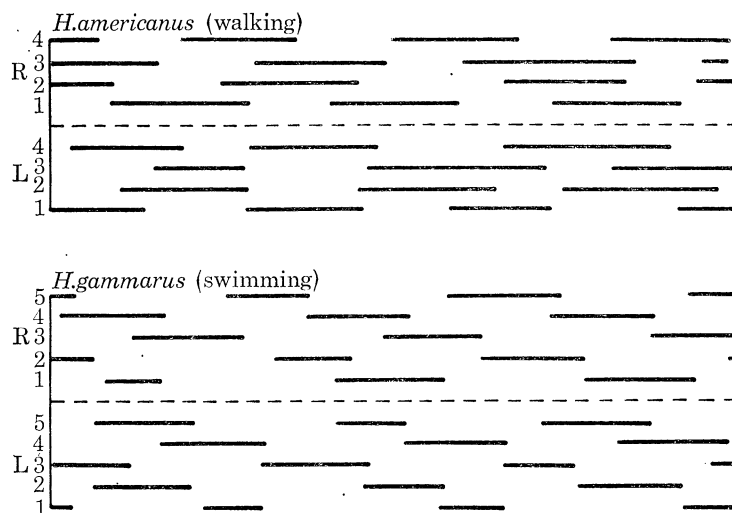


FIGURE 12. Comparison of the movement of limbs in walking of adult *H. americanus* (Macmillan 1975) where the chela plays no part, with use of exopodites in larval swimming of *H. gammarus*.

One of the striking features of the exopodite system is the very tight coupling between ipsilateral appendages and the loose coupling between contralateral exopodites. These two relations result in a system which is essentially bipartite since each side functions as a unit which is only loosely coupled with the other. This type of contralateral coordination has been termed gliding coordination (Wendler 1966) but the bilateral coupling of the present system appears to be weaker than that described for the stick insect *Carausius*. It would appear that it might be possible to place systems on a spectrum of coupling-types according to the strength of bilateral coupling which is normally seen. At one end of the range are the relatively rigid systems such as cockroach walking (Delcomyn 1971) in which both ipsi- and contralateral couplings are tight during forward walking (although it should be remembered that various degrees of uncoupling may occur during turning). Then there are systems such as lobster walking where there is a little gliding even in forwards walking (Macmillan 1975), and systems such as walking in *Carausius* where gliding is common during forwards walking but preferred phase positions are maintained between glides (Wendler 1966). Finally, at the other end of the spectrum is the present system in which continuous gliding occurs in either direction (phase +ve and phase -ve) with only slight favouring of some phase positions. It seems likely that the different types could be closely related to different functional situations such as the relative importance of the support input of each appendage, and the rate of movement and the frequency of cycling and hence the time available for error adjustment. Some of these concepts are discussed further below.

We do not have any evidence that the oscillator systems responsible for generating exopodite beating are the same as those involved in subsequent walking. The musculature of the two systems appears to coexist but never to function simultaneously in the same stage, and the exopodite musculature degenerates when the pereopod (endopodite) muscles start to operate (Neil *et al.* 1976). The differences between the modes of bilateral coupling of the two systems together with both the similarities and differences in beating patterns suggest the interesting possibility of a basic oscillator system loaded in different ways. The hypothesis would argue that the most efficient way for the larva to swim is by spreading the swimming load on each side equally over all appendages, i.e. equal inter-segmental phase lag. If an appendage deviates from its normal output or even fails for a cycle the stability of the animal is not threatened and indeed, in an animal with such loose contralateral coupling, stability can readily be regained by a bilateral gliding adjustment. Various amputation experiments in adult lobsters suggest that the walking pattern is very sensitive to the stability of the animal, which is threatened if one leg fails to meet its locomotory requirement. This factor also strictly limits the amount of bilateral compensation which can be made if normal locomotion is to be maintained. The patterns normally used, however, produce a situation in which failure of the function of each leg is optimally covered by the normal function or a slight extension of the normal function of other legs (Macmillan 1975). For the developmental hypothesis the pereopod walking pattern would thus be considered as the beating pattern of the four caudal exopodites with the two middle appendages of the four offset from their equal phase positions by the loading input compatible with the stability of the walking animal. Changes in patterning due to loading of a type similar to those which would be necessary have been described in both the lobster walking system (Macmillan 1975) and in the mandibular biting system (Wales, Macmillan & Laverack 1976*a, b*; Macmillan, Wales & Laverack 1976).

Although the argument presented is hypothetical and based on descriptive similarities which might well be fortuitous, it is worthy of consideration because of the changes found in larval development (Laverack *et al.* 1976) and also because of results suggesting that some lobster oscillators develop in the absence of sensory input but are subsequently modified by it (Davis 1973, 1974; Davis & Davis 1973).

Our results suggest that the ipsilateral exopodite beating pattern is phase constant for both intra-cycle (powerstroke–returnstroke) and intercycle (inter-appendage phase position) conditions. This result needs to be interpreted with caution, however, for several reasons. There is always the possibility of a correlation between cycle duration and phase parameters which is beyond the resolution of our film-frame speed. While such a correlation would not invalidate our findings and would only be a minor factor for pattern alteration at the level considered here, it might well be important in other contexts. In addition, there is the possibility that while an existing correlation was not found in the narrow range of preferred beating frequencies, pooled results from swimming and non-swimming animals (contributing various lower frequencies) would provide one. Again, such a finding would not detract from the present findings but would limit their applicability in some situations, such as consideration of central oscillator function; the same constraints were applied to the lobster walking analysis (Macmillan 1975).

Although the results given here have been descriptive rather than deductive they are nevertheless likely to be of importance in several areas. The study is intrinsically interesting as an analysis of a swimming behaviour in an animal with a relatively rigid body that locomotes

by beating appendages serially. Because the analysis was conducted on a developing system through several stages it provides new information about behavioural development and, in association with previous work (Davis 1973, 1974; Davis & Davis 1973), poses further questions in that area. The developmental aspect of the study is dealt with further in the third paper (Laverack *et al.* 1976).

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