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A COMPARISON OF BEATING PARAMETERS IN LARVAL AND POST-LARVAL LOCOMOTOR SYSTEMS OF THE LOBSTER *HOMARUS GAMMARUS* (L.)

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A study has been made of the interrelations between rhythmical exopodite beating in different larval stages and swimmeret beating in poast-larval stages of the lobster *Homarus gammarus*. Data on exopodite beat cycle durations have been used for statistical comparisons of exopodite performance within one larva, and also between different stages of larval development. Inter-exopodite comparisons reveal clear bilateral differences (table 1), although there is no consistently favoured relationship (tables 2 and 3). There are significant differences in cycle duration between the first three developmental stages, with a slight increase at the first moult, and a marked decrease at the second (table 4). However, within each stage the repeat frequency exhibits little change (table 5). Therefore it appears that changes in swimming behaviour occur discontinuously in development, and are associated with the larval moults. It is suggested that changes in beat frequency, and especially the faster beating in stage III, may represent responses to changed loading conditions (table 7).

Measurements of swimmeret beating in post-larval lobsters have been analysed in terms of cycle durations, and inter- and intra-segmental phase relations. Swimmeret beating patterns are very regular (figure 1), but not restricted to a narrow range of frequencies (table 6a). Intersegmental phase lag remains constant around 0.2 (figure 3) independent of beat frequency (figure 4). Similarly the powerstroke/returnstroke ratio of approximately 0.5 (figure 5) shows no significant correlation with cycle

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duration (figure 6). Differences emerge in the performance of larval exopodites and post-larval swimmerets (table 6*b*), although the possibility cannot be excluded that the larval exopodite oscillator in some way influences the developing action of the post-larval swimmeret system.

INTRODUCTION

In the first two papers of this series we discussed the rationale behind the current interest in rhythmic systems for behavioural analysis and have presented a descriptive account of some aspects of lobster larval development (Neil, Macmillan, Robertson & Laverack 1976) and a quantitative analysis of some key parameters of exopodite beating in each developmental stage (Macmillan, Neil & Laverack 1976). As more and more rhythmic systems are described in different adult animals, interesting interrelations between oscillators become apparent. This report presents findings which bear on the question of the interrelations between oscillator systems during development through several pre-adult stages.

Some of the putative oscillator relations which have been described in adult animals are as follows. An oscillator may act on one set of motoneurones but be involved in different ways with other oscillators during different behavioural activity. Such a situation has been described in the grasshopper *Stenobothrus rubicundus* in which bifunctional thoracic muscles are driven by the flight oscillator to produce both leg and wing stridulation patterns (Elsner 1974). Oscillators may also be linked together within a system to produce a coordinated multi-oscillator output, such as that seen in the macruran swimmeret system (Hughes & Wiersma 1960; Stein 1971; Wiersma & Ikeda 1964). There is also evidence indicating that a variety of oscillators may be loosely linked even though they operate onto entirely separate motoneurone pools so that the individual frequencies and their common basal frequency are related (Kutsch 1969). Two oscillators which are capable of separate operation may also feed onto one set of motoneurones simultaneously to produce other complex behavioural outputs. This mode of interaction occurs in the control of abdominal movements in the locust by the ventilatory and flight oscillators (Camhi & Hinkle 1974) and in the generation of some cricket songs (Kutsch 1969).

In the developing lobster the possibility of combination of these different types of relations together with interactions of oscillators throughout the developmental stages makes this a particularly interesting system for study of both oscillators and development. In the first three stages the animal locomotes utilizing the exopodite rami of the thoracic appendages. In these stages the swimmerets of the abdominal segments develop sequentially but do not move (Herrick 1895). There is, however, evidence which suggests that the driving oscillators are present and active even though no output is apparent at the limbs (Davis 1973; Davis & Davis 1973). In the fourth stage of development, not only do the swimmerets start to function but the exopodites cease beating and become vestigial, whilst the endopodite rami of the same segments (pereiopods) begin to operate in walking. This switch in modes of locomotion introduces the possibility of oscillators being present which either start or terminate their activity at a moult, as well as the possibility of segmental oscillators which change or modify the direction of their output from one set of motoneurones to another as a result of moult rearrangements of limb muscles and the required movement.

Materials and methods

A detailed description of the methods used to maintain larvae and to record the development of successive stages together with an account of the filming procedures is given in the first paper of this series (Neil *et al.* 1976). The methods used to analyse and process the filmed records are described in the second paper of the series (Macmillan *et al.* 1976). The statistical comparisons made in this paper were conducted by using a computer program for the Behrens-Fisher *t*-test for samples of unequal size (Snedecor 1973). This is adequate for the simple developmental comparisons made here and a complete analysis of variance of all the data identifying all components of variation will be reported separately.

Results

Exopodite cycle duration

Tests for the homogeneity of data on exopodite cycle durations in individual samples revealed, in accordance with the analysis of phase relations (Macmillan *et al.* 1976), both a strong correlation between the values for ipsilateral legs, and in many cases a tendency for differences bilaterally (table 1). The phase progressions which result from this latter

TABLE 1. CYCLE DURATIONS FOR INDIVIDUAL EXOPODITES OF A LARVA
WHICH SHOWS CLEAR BILATERAL DIFFERENCES $(1C2(10))$

	exopodite	left side			right side		
		N	$\bar{X}$/ms	s.d.	N	$\bar{X}$/ms	s.d.
1	powerstroke	100	118.12	16.88	95	122.70	9.87
	returnstroke	98	117.03	12.07	97	122.42	9.16
2	powerstroke	101	118.19	11.30	95	122.37	9.53
	returnstroke	98	117.98	10.26	96	122.40	10.50
3	powerstroke	99	117.90	10.00	97	122.26	8.98
	returnstroke	100	118.12	10.20	95	122.53	9.70
4	powerstroke	96	118.16	9.25	91	122.94	9.33
	returnstroke	99	118.21	9.20	94	125.33	12.73
5	powerstroke	72	118.27	10.36	45	122.92	10.73
	returnstroke	92	117.70	11.39	46	122.96	10.10
	totals	955	117.96	11.33	851	122.87	10.31

difference of means (right − left) = 4.91.
standard error of difference = 0.51.

$$t = \frac{\text{difference}}{\text{s.e.}} = 9.64 \ (> 2.58), \text{ therefore the difference is significant at the 1 \% level.}$$

effect may be in either direction, but, once initiated, they tend to be maintained throughout a particular bout of swimming. Thus, where data have been obtained from a long sequence of continuous beating, clear bilateral differences in cycle duration emerge. However, where data on one animal have been obtained from a series of shorter swimming bouts, involving different phase trends, the pooled measurements yield no significant differences between the beating frequencies on the two sides. All these possible bilateral relationships have been found in the data for each developmental stage (table 2), and thus pooled values within stages show no significant bilateral differences (table 3).

Despite bilateral differences within individual sequences, and sources of variation between individuals in one developmental stage (arising both from a selective component in data collection, and from real differences in performance) (table 2), comparisons between stages based on pooled data nevertheless reveal significant differences both between stage I and stage II (with a slightly increased cycle duration after the moult) and between stage II and stage III (with a greatly decreased cycle duration after the moult) (table 4). A check on the validity of the result based on pooled data was provided by using the data extracted from only one leg in all samples (table 3) as a basis for comparison, with the same result.

TABLE 2. CYCLE DURATIONS POOLED FROM ALL EXOPODITES IN
EACH LARVA AND FROM ALL LARVAE IN EACH STAGE

	N	mean, $\bar{X}$/ms	s.d.	bilateral differences significant at the 1 % level
stage I				
1A19(13)	1101	112.38	21.44	L = R
2A19(16)	115	109.92	19.98	L < R
1A20(11)	1591	113.67	16.92	L < R
4A22(10)	294	144.98	18.88	L = R
2A24(10)	411	108.88	11.60	
1C2(10)	1806	120.28	10.94	L < R
1C11(17)	597	108.07	13.26	L < R
2C11(17)	665	119.74	12.86	L < R
2G7(15)	436	99.05	21.76	L > R
3G7(15)	509	102.90	18.47	L = R
1G14(15)	544	113.83	14.29	L > R
totals	8025	114.28	18.10	
stage II				
A422(21)	828	117.62	12.69	L = R
2A25(20)	281	113.16	18.54	
1B3(20)	293	122.55	13.69	L = R
2B3(20)	151	111.13	9.77	L = R
C16(20)	528	121.09	19.51	L = R
1C6(212)	610	124.00	23.01	L = R
C14(212)	860	107.54	11.90	L > R
G114(20)	694	124.80	17.48	L = R
totals	4235	117.92	17.71	
stage III				
1A26(37)	758	97.40	12.01	L = R
B15(311)	1018	86.78	11.63	L < R
1C4(32)	1229	92.48	9.60	L = R
C17(313)	731	90.82	11.97	L > R
1C10(37)	584	88.08	10.53	L = R
2C10(36)	1158	85.15	11.80	L > R
1F19(35)	811	91.01	8.63	L > R
totals	6278	90.02	11.57	

Exopodite cycle duration in bridge pairs

Details were kept of the development of each larva, and in a few cases we were able to film the beating behaviour of an individual not only at the beginning and again at the end of a developmental stage, but also at the beginning of the following stage, thus obtaining a complete sequence of records before and after a moult from the same animal. We term these complementary sequences 'bridge pairs' (table 5). While the variation in the results for bridge pairs was relatively greater than for the pooled data because of the smaller sample sizes, the results support the conclusions of that data, in that animals maintain a narrow range of preferred beating frequencies when swimming.

TABLE 3. BILATERAL COMPARISON OF DATA ON CYCLE DURATION
POOLED FOR INDIVIDUAL EXOPODITES IN ONE STAGE

(Data for the fourth pair of exopodites are shown.)

	exopodite L4 (powerstroke data)	exopodite R4 (powerstroke data)	all exopodites (combined data for power- and returnstrokes)
stage I			
N	470	491	8025
$\bar{X}$/ms	115.62	113.48	114.28
s.d.	18.33	17.77	18.10

$t = \dfrac{\text{difference (L4}-\text{R4)}}{\text{standard error}} = 1.83 \ (< 1.96)$, therefore the difference is not significant at the 5 % level

stage II			
N	222	254	4235
$\bar{X}$/ms	120.78	118.73	117.92
s.d.	19.33	16.53	17.71

$t = \dfrac{\text{difference (L4}-\text{R4)}}{\text{standard error}} = 1.53 \ (< 1.96)$, therefore the difference is not significant at the 5 % level

stage III			
N	340	277	6278
$\bar{X}$/ms	89.84	91.55	90.02
s.d.	11.36	12.44	11.57

$t = \dfrac{\text{difference (L4}-\text{R4)}}{\text{standard error}} = 1.76 \ (< 1.96)$, therefore the difference is not significant at the 5 % level

TABLE 4. t-TESTS FOR THE SIGNIFICANCE OF THE DIFFERENCE BETWEEN THE MEAN CYCLE
DURATIONS DERIVED FROM POOLING DATA WITHIN EACH DEVELOPMENTAL STAGE

	N	$\bar{X}$/ms	s.d./ms	
stage I	8025	114.28	18.10	
stage II	4235	117.92	17.71	$t = 10.74 \ (< 2.58)$

Difference significant at the 1 % level.

	N	$\bar{X}$/ms	s.d./ms	
stage II	4235	117.92	17.71	
stage III	6278	90.02	11.57	$t = 90.3 \ (< 2.58)$

Difference significant at the 1 % level.

TABLE 5. EXOPODITE CYCLE DURATIONS FOR COMPLEMENTARY DATA SEQUENCES ('BRIDGE PAIRS') FROM INDIVIDUAL LARVAE AT DIFFERENT STAGES OF DEVELOPMENT

(a) stage I – stage II bridge pair.

	N	$\bar{X}$/ms	s.d./ms	
1G14(15)	544	113.83	14.29	
G114(20)	694	124.80	17.48	$t = 12.15\ (> 2.58)$

Difference significant at the 1 % level.

(b) stage II – stage III bridge pair.

	N	$\bar{X}$/ms	s.d./ms	
C14(21)	860	107.54	11.90	
1C4(32)	1229	92.48	9.60	$t = 30.76\ (> 2.58)$

Difference significant at the 1 % level.

(c) bridge pair within stage II (measurements on the day of moult, and again 12 days later).

	N	$\bar{X}$/ms	s.d./ms	
C16(20)	528	121.09	19.51	
1C6(212)	610	124.00	23.01	$t = 2.31\ (> 1.96;\ < 2.58)$

Difference significant at the 5 % level but not significant at the 1 % level.

TABLE 6

(a) SWIMMERET CYCLE DURATIONS IN POST-LARVAL LOBSTERS.

	N	$\bar{X}$/ms	s.d./ms
stage IV			
1B5(40)	392	135.12	20.63
1C7(40)	410	164.21	24.65
C110(41)	690	114.74	18.19
FEA(40)	1073	152.22	24.54
totals	2565	141.44	28.46
stage V	55	138.5	—
stage VI	54	189.1	—

(b) EXOPODITE AND SWIMMERET CYCLE DURATIONS FOR BRIDGE PAIRS SPANNING STAGE III–STAGE IV.

	N	$\bar{X}$/ms	s.d./ms	
B15(311)	1018	86.78	11.63	
1B5(40)	392	135.12	16.62	$t = 52.8\ (> 2.58)$
C17(313)	731	90.82	11.97	
1C7(40)	410	164.21	24.65	$t = 56.6\ (> 2.58)$
1C10(37)	584	88.08	10.53	
C110(41)	690	114.74	18.19	$t = 32.6\ (> 2.58)$

In each case the difference is significant at the 1 % level.

From bridge pairs that span a moult the pattern again emerges of a slight increase in cycle duration between stage I and stage II (table 5 a), followed by a large decrease in cycle duration between stage II and stage III (table 5 b). However, results from a bridge pair within one stage suggest that there is no significant change in beating frequency from the beginning to the end of a stage (table 5 c). Therefore it appears that the observed changes in swimming behaviour take place discontinuously with developmental stage, rather than continuously with age.
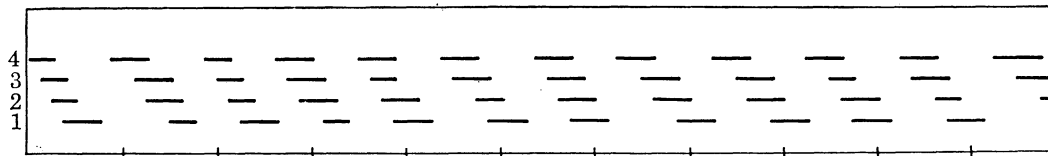
FIGURE 1. Example of the swimmeret beating pattern from a stage IV lobster. Note the regularity of the rhythm, and the interlude between whole-system cycles. 1, 2, 3, 4 are anterior to posterior swimmerets. Black bars show duration of the powerstroke. Time marks 125 ms.

(a) 3 in 4 (b)

$n = 100$
$\bar{b} = 152.61$
$m = 0.200$
$u = 0.222$
$l = 0.182$

$n = 133$

2 in 4

100
152.61
0.400
0.444
0.375

$n = 133$

1 in 4

100
152.61
0.607
0.625
0.571

$n = 131$
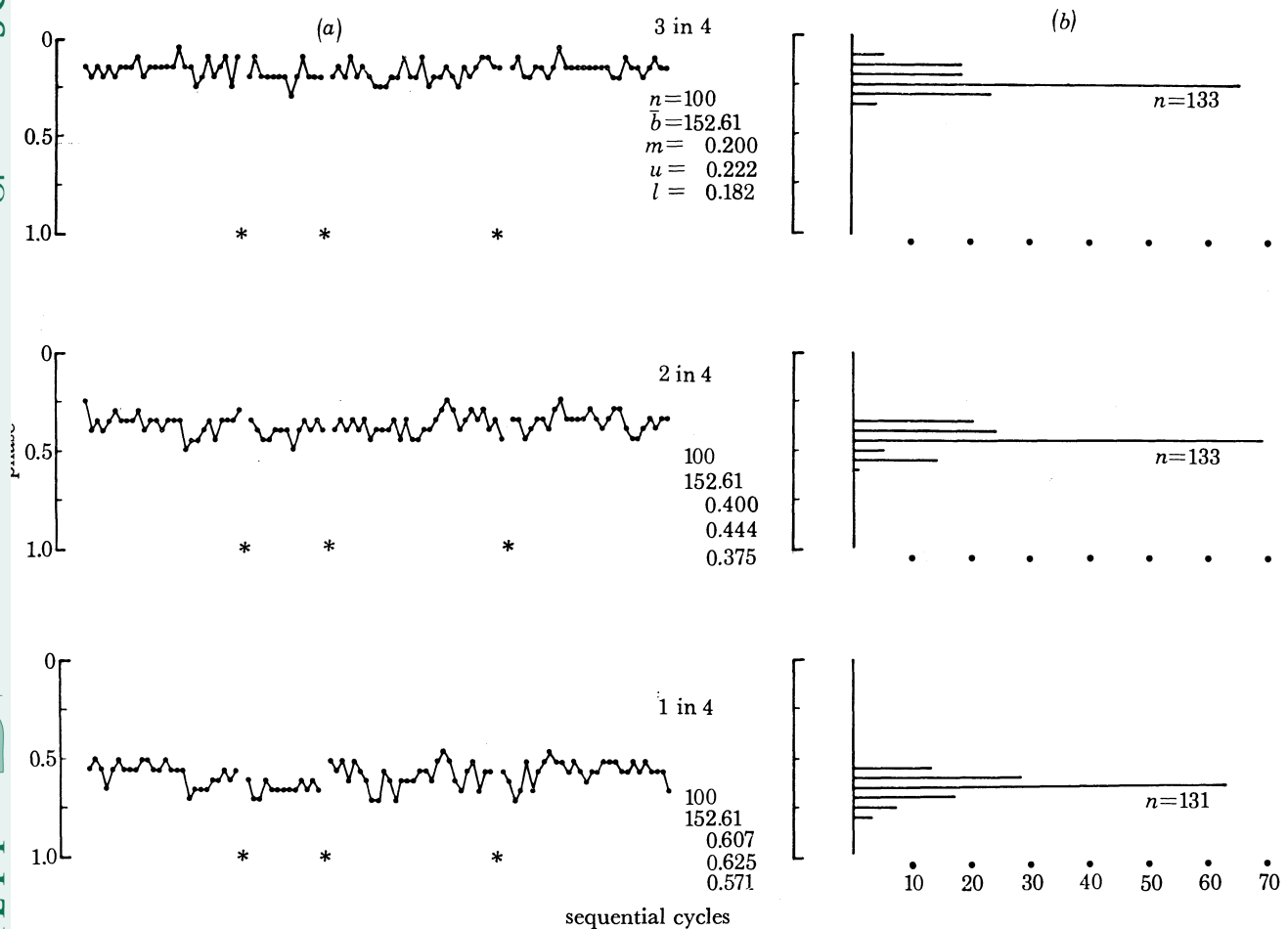
sequential cycles

FIGURE 2. (a) Examples of phase plots showing relative phase position of each swimmeret (test) in the most posterior swimmeret (base) in sequential cycles. Data from a stage IV lobster. Breaks in sequences are shown by stars. 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. (b) Same data presented as conventional phase histograms. n, Total number of cycles in plot.

$$n = 100$$
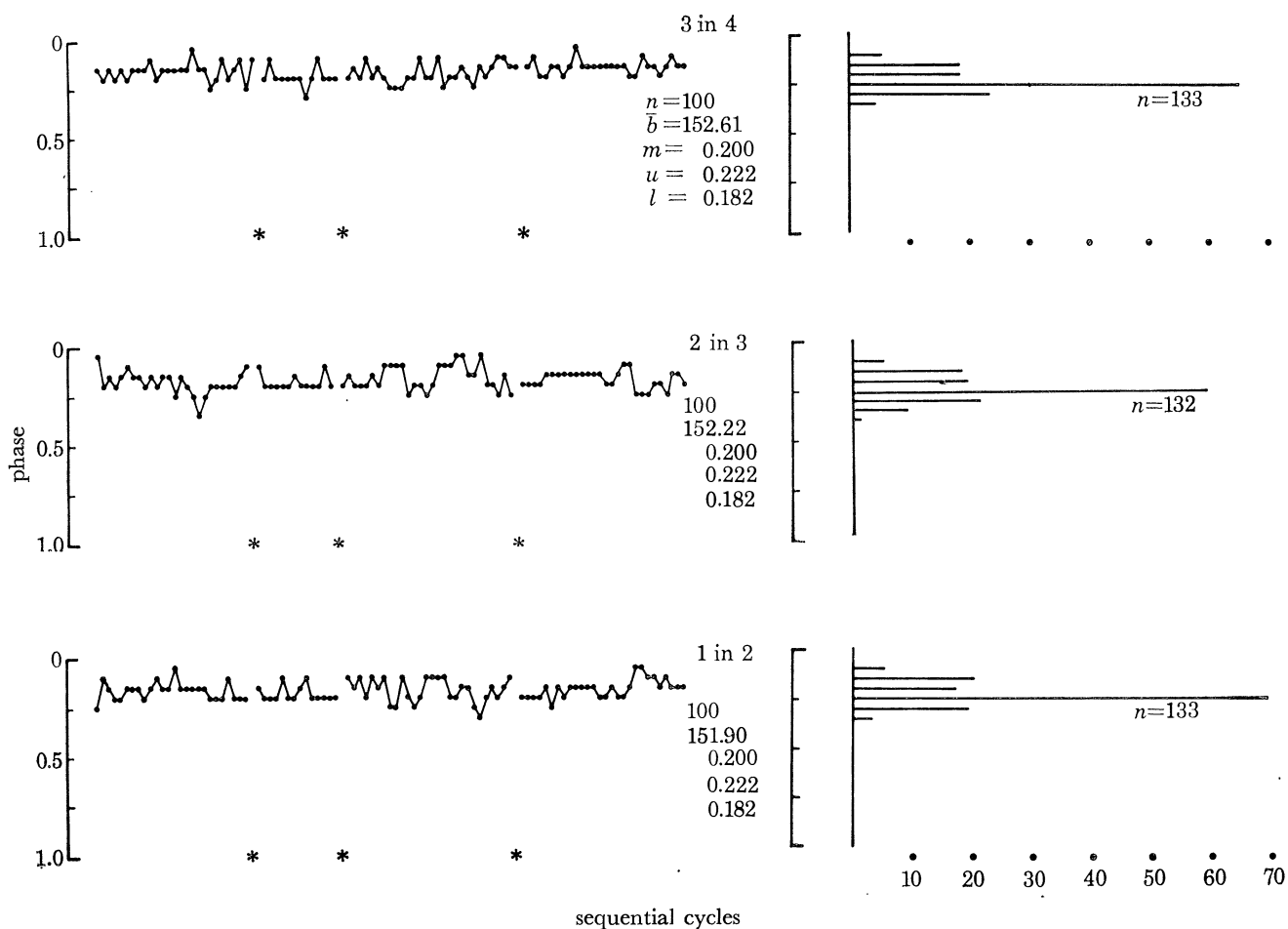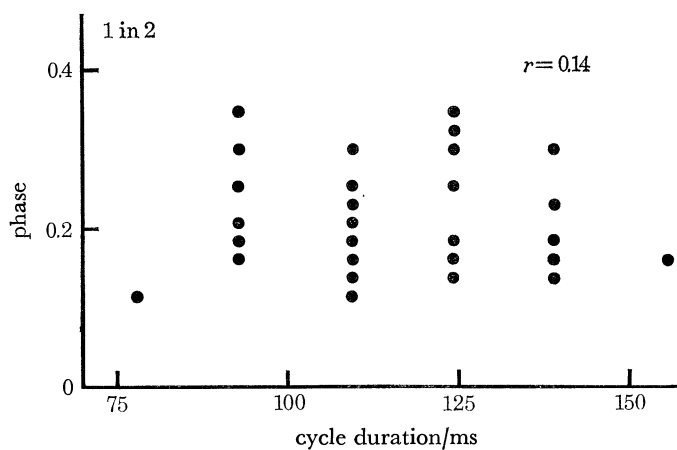$$\bar{b} = 152.61$$
$$m = 0.200$$
$$u = 0.222$$
$$l = 0.182$$

FIGURE 3. Examples of phase plots and corresponding phase histograms for adjacent swimmerets in a stage IV lobster. Breaks in sequences are shown by stars. 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.

FIGURE 4. Example of the phase value for adjacent swimmerets in a stage IV lobster plotted against the corresponding base cycle duration. r, Coefficient of correlation.

Swimmeret cycle duration and beating pattern

Swimmerets (abdominal appendages) become active in stage IV, when exopodite beating ceases. The methods of analysis of swimmeret beating were the same as for exopodite beating (Macmillan *et al.* 1976), except that the complete synchrony between the two swimmerets in one segment made separate bilateral measurements unnecessary. Data were collected from several larvae in stage IV (table 6a), three of which had previously been filmed in
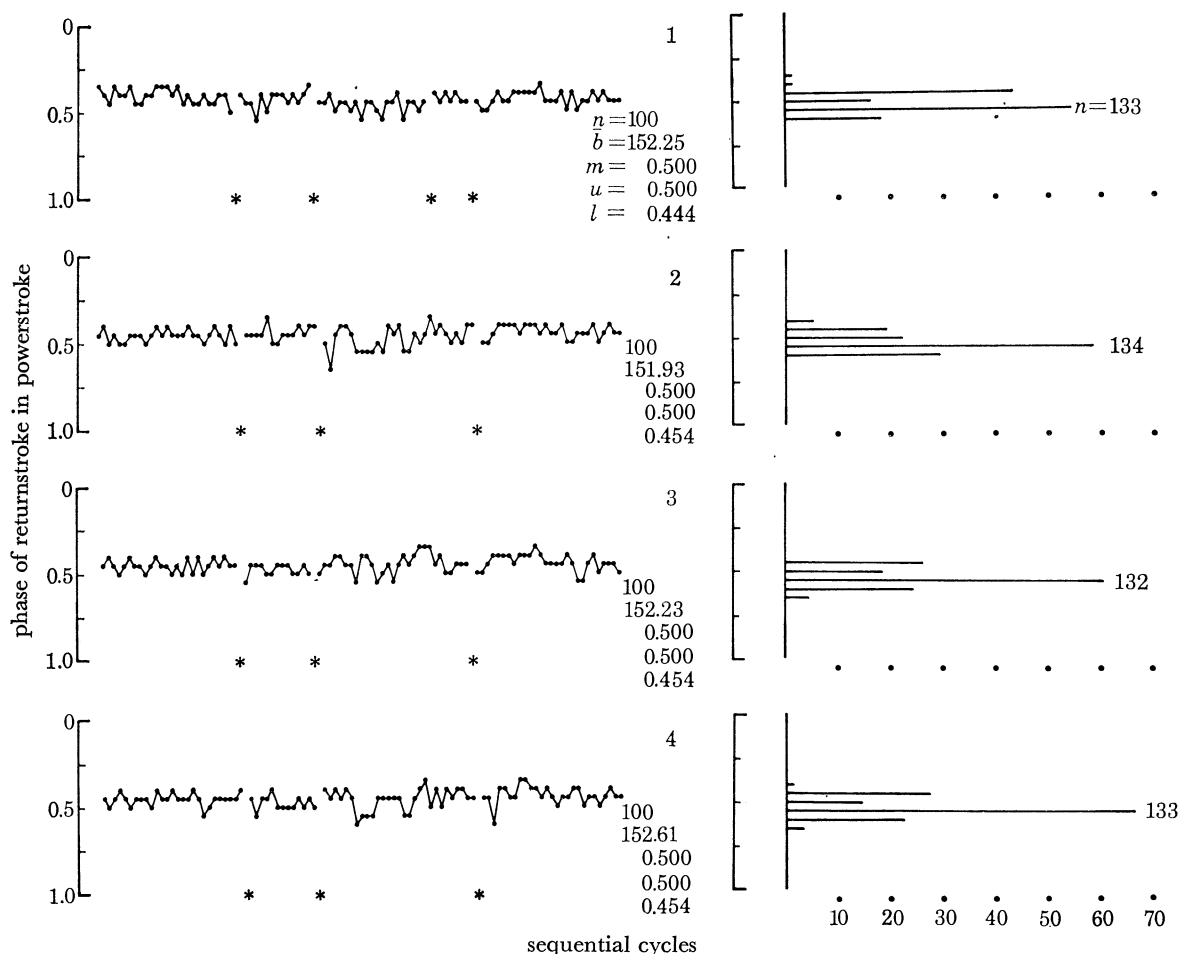

FIGURE 5. Example of phase plots and corresponding phase histograms for swimmeret beating in a stage IV lobster, showing the relative phase position of the returnstroke in the powerstroke. *n*, Total number of cycles in plot; $\bar{b}$, mean duration of base cycle; *m*, median phase value; *u*, upper quartile phase value; *l*, lower quartile phase value.

stage III so that complementary bridge pair sequences were available for cycle duration comparisons (table 6b). A limited amount of data were also collected from larvae in stage V and stage VI, and although we did not conduct as detailed an analysis for these later juvenile stages as for stages I–IV, the available data on beating cycle duration are included in table 6a for comparison. Table 6 shows that swimmeret beating in stage IV is slower by approximately 50% than exopodite beating in stage III, and that the range of beating frequencies is much larger. The available data also suggest that there is a trend towards further reduction in beating frequency through stages V and VI.

Examination of the beating patterns reveals a regular metachronous pattern (figure 1). The phase relations between swimmerets were determined by considering the phase of the start of the powerstroke movement and the start of the returnstroke movement in the power-stroke or returnstroke cycle of each other swimmeret. Figure 2a shows a series of graphs expressing the phase position of each of the swimmerets in the cycle of the most posterior swimmeret as a function of time (or more precisely as a function of consecutive cycles as time
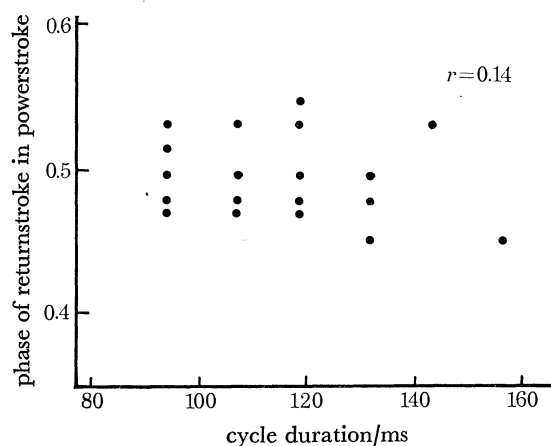
FIGURE 6. Example of the powerstroke/returnstroke phase relations for swimmerets in a stage IV lobster plotted against the corresponding base cycle duration. r, Coefficient of correlation.

progresses). When the same relations are displayed as phase histograms (figure 2b) the phase coupling can be seen to be quite tight although coupling is most precise between adjacent swimmerets (figure 3). The range of beating frequencies in any sample is often quite large (unlike the restricted range found in the exopodites) and yet there does not appear to be a significant relationship between cycle duration and intersegmental phase lag, which shows little variation about its mean position of 0.2 (figure 4). Examination of the beating pattern indicates that there is an interlude between the end of the cycle in the most rostral swimmeret and the start of the next cycle in the most caudal swimmeret. Quite large adjustments in overall swimmeret beating frequency can be made by variations in the duration of this temporary stoppage. The stability of the anteriorly moving wave over the range of frequencies examined was supported by the finding that the mean powerstroke/returnstroke ratio is 0.5 (figure 5) and that it does not appear to be related to cycle duration (figure 6).

DISCUSSION

The work described in these papers shows clearly that the manner in which the exopodites beat throughout the repeating cycles, and from stage to stage in development, is very similar, and that it is the preferred duration of each cycle that varies. The present paper demonstrates that this variation is statistically significant for stage II vis-à-vis stage I, with a small decrease in the rate of beating after the moult, and for stage III vis-à-vis stage II, when there is a noticeable increase in the rate of beat after the moult.

The possibility that the observed changes in exopodite beating reflect altered metabolic rates, brought about by temperature fluctuations during rearing, appears unlikely. Continuous

temperature records over the experimental period indicate no large fluctuations of mean temperature in the rearing chamber. Furthermore, larvae show a consistent pattern of changes in exopodite beating frequency during development despite a large spread in the times of larval hatch (Neil *et al.* 1976).

TABLE 7. INDICES OF GROWTH IN LARVAL LOBSTERS

(For each index data were obtained from five larvae in each stage. Normalized values, relative to stage I, are shown in parentheses.)

	stage I	stage II	stage III
dry mass/mg	1.70	2.20	3.65
	(1.0)	(1.29)	(2.15)
total surface area of expanded exopodites/mm²	7.93	10.11	13.48
	(1.0)	(1.27)	(1.70)

These changes in frequency may represent fundamental alterations in the underlying neuronal mechanisms operating and changing at each moult. On the other hand there is a striking parallel between the differential growth changes of the larva at successive moults (Gruffydd, Rieser & Machin 1975; Neil *et al.* 1976) and the changes in exopodite beat cycle duration (table 4). Data from dry-mass determinations indicate a 66 % increase in body mass between stage II and stage III (table 7). However, as previously described (Neil *et al.* 1976) there is no proportional increase in exopodite dimensions (table 7) and thus a greater load must be imposed upon the swimming apparatus. It is tempting to suggest that the heightened rate of beat in stage III is a response to this increased load, and is required to provide the extra lift necessary to enable the animal to remain clear of the substrate. Immediately following this enlarged swimming stage the subsequent stage is benthic in habit (Berrill 1974).
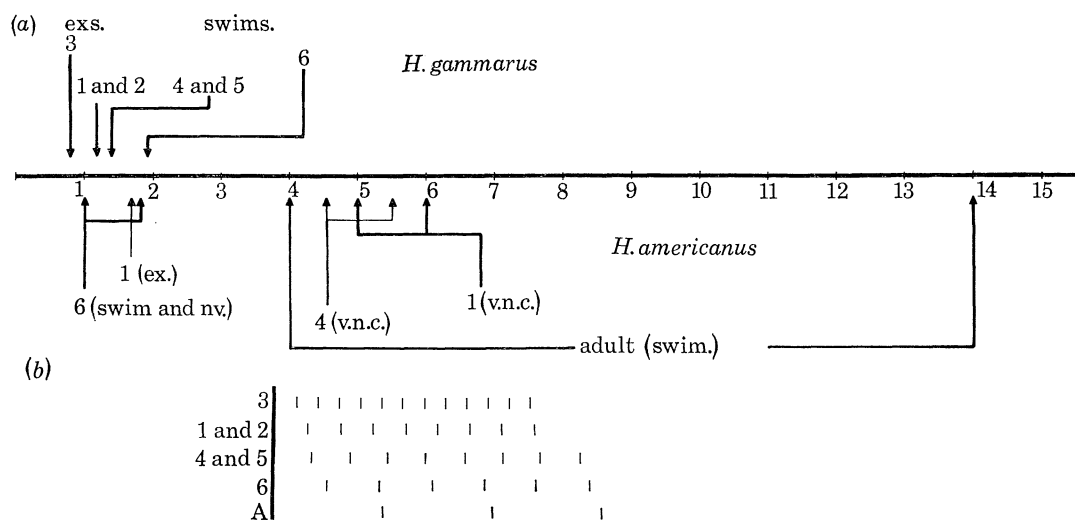

FIGURE 7. (*a*) Summary diagram of the exopodite and swimmeret beat cycle durations obtained for *Homarus gammarus* in the present study, and for *Homarus americanus* by Davis & Davis (1973) (as measured from their published figures of electrophysiological recordings). The time scale is marked in units of 100 ms. 1–6 are developmental stages I–VI; ex., exopodites; swim., swimmerets; n.v., v.n.c., ventral nerve records. (*b*) Frequency diagram of exopodite and swimmeret beating in developmental stages I–VI (1–6) and adult (A) lobsters. There is no clear interrelation between the different oscillators.

Kutsch (1969) found interrelations between oscillators based on cycle duration. We have examined our data for signs of similar relations but find none (figure 7 *b*). It is difficult to correlate our findings directly with those reported for abdominal swimmeret beating as the variation in frequency is very much greater. There is, however, no evidence from our results to support the notion that the different stages exhibit different harmonics of a basic frequency, although no Fourier analysis has been carried out to confirm this conclusion.

The anatomical study of endopodites in larvae of stages I–IV suggested that muscles are present, but small and non-functional (Neil *et al.* 1976). These are quite separate from those muscles associated with the exopodite and which are active in stages I–III, but which degenerate in stage IV. The similarities in the patterning of larval swimming and of adult walking (albeit in *H. americanus*, Macmillan 1975) and the way in which differences might be explained by load changes were examined by Macmillan *et al.* (1976). This circumstantial evidence suggests that this system might be a very suitable candidate for a study of an oscillator that switches output from one set of muscles to another at the critical moult, namely from stage III to stage IV.

In terms of both phase relations and beat cycle durations the pattern of larval exopodite beating is evidently different from that of subsequent post-larval swimmeret beating. These findings suggest that the oscillators within the nervous system responsible for the thoracic and abdominal rhythms are to a large degree independent in action. This is perhaps not surprising in view of their spatial and temporal separation, and of the different functional demands made upon the two limb systems. However, it seems probable that this condition has evolved from a more primitive one in which the abdominal and thoracic appendages performed as one unit. Such a situation, in which waves of activity appear to pass forward over both swimmerets and exopodites, has been described by Manton (1930) in the shrimp *Anaspides*.

Although the rhythmical activity of the larval exopodite oscillator does not appear to determine the precise output pattern of the swimmeret oscillator, the possibility nevertheless exists that more subtle interactions take place. This was not considered by Davis (1973) and Davis & Davis (1973) when they claimed, on the basis of extirpation experiments, that normal swimmeret motor output patterns arise from endogenous pacemakers, without the need for patterned sensory input. A more satisfactory proof of this hypothesis requires attention to the following questions: (1) Would exopodite beating rhythms develop naturally within the nervous system if the exopodites were removed? (2) Would this interference affect the development of normal abdominal swimmeret patterning in both the presence and absence of normal swimmeret afference?

Our findings suggest that Davis's conclusions are premature in the absence of further experimentation. Further support for this argument is provided by comparing the different electrophysiological measurements of exopodite and swimmeret cycle durations made by Davis (1973) and Davis & Davis (1973) (figure 7 *a*). The disparities suggest that experimental operations may alter the repetition rate, and thus there is no certainty that recordings in the ventral nerve cord are of swimmeret pacemaker output, rather than of exopodite pacemaker output conducted caudally to the abdomen by interneurones (cf. Stein 1971).

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