

THE STRUCTURE AND FUNCTION OF
THORACIC EXOPODITES IN THE LARVAE OF
THE LOBSTER *HOMARUS GAMMARUS* (L.)

BY D. M. NEIL,† D. L. MACMILLAN,‡ R. M. ROBERTSON
AND M. S. LAVERACK

*Gatty Marine Laboratory and Department of Natural History,
The University, St Andrews, Fife KY16 8LB, Scotland*

(Communicated by H. G. Callan, F.R.S. – Received 24 September 1975)

	CONTENTS	PAGE
INTRODUCTION		54
MATERIALS AND METHODS		54
Rearing of larvae		54
Anatomy		55
Photography		55
RESULTS		56
General features of larval development		56
Anatomy of larval swimming appendages		58
External structure		59
Internal anatomy		60
Swimming behaviour in larval lobsters		60
Exopodite swimming movements		62
The metachronous wave		65
DISCUSSION		65
REFERENCES		67

The first three larval stages of the lobster *Homarus gammarus* are pelagic swimming animals. A description is given of the exopodite apparatus of the thoracic appendages that provide lift and propulsive power in these stages. Setal arrangement and display provides greater surface area during power strokes. Musculature is peculiar to the exopodites and concerned with rotational movements of the appendage. Metachronal beating takes place with the segmental appendages moving in a variable sequence.

† Present address: Department of Zoology, University of Glasgow, G12 8QQ, Scotland.

‡ Present address: Department of Zoology, University of Melbourne, Parkville, Vic. 3052, Australia.

INTRODUCTION

The study of rhythmical activities has proved profitable in advancing our understanding of the mechanisms underlying centrally generated patterns of behaviour (see De Long 1972 for a review). In particular, quantitative approaches to the study of cyclical systems in various arthropod groups have yielded much information about the nature of limb coordination (Barnes, Spirito & Evoy 1972; Davis 1968, 1969; Delcomyn 1971*a, b*; Macmillan 1975; Pearson 1972; Wendler 1966; Wilson 1966, 1968). In the crustacea most attention has been paid to swimmeret beating (Davis 1968, 1969; Ikeda & Wiessma 1964), respiration (Burrows & Willows 1969; Pasztor 1968; Wilkens & McMahon 1972; Young 1973), walking (Barnes 1975; Barnes *et al.* 1972; Macmillan 1975), and certain specialized swimming actions (Paul 1971; Spirito 1972) but relatively little is known about the cyclical organization of the various metachronous swimming systems (see Lochhead 1961 for a review). Previous studies of these swimming systems were devoted to general descriptions of limb movements (Manton 1930; Storch 1929), and especially to considerations of the various locomotory, respiratory and feeding currents produced by limb movements (Cannon & Manton 1927; Lowndes 1935). The present study of swimming in larval lobsters attempts to analyse a system of metachronous limb beating by applying the more precise techniques of physiological analysis.

Exopodite beating is the major means of locomotion in the larval stages of *Homarus*, involving the continuous action of a relatively small number of specialized swimming appendages (Herrick 1895). It is a particularly suitable system for the study of limb coordination because the exopodites project laterally, and the simultaneous movements of all limbs are clearly visible on filmed records. The thoracic exopodites provide data for quantitative analysis of both intrasegment relations, and intersegmental coordination. Choice of a larval locomotory system also provides an opportunity to study the development of rhythmical activities in successive stages. A study of the life-history of *Homarus* is especially appropriate for this purpose because not only are there three morphologically distinct larval stages which swim using thoracic exopodites, but also the first post-larval stage signals the cessation of exopodite beating and the simultaneous onset of walking and swimmeret beating. Comparison between these different rhythmical systems which operate sequentially during development provides a new approach to the study of the relationships between central nervous oscillators.

In this paper we describe the anatomy of the thoracic exopodites in larvae of *Homarus gammarus* (L.) and present a qualitative description of limb coordination during swimming. The following paper (Macmillan, Neil & Laverack 1976) is concerned with a quantitative description of various beating parameters at different stages of larval development, and in a third paper (Laverack, Macmillan & Neil 1976) we compare the characteristics of the larval swimming rhythm with those of post-larval locomotory systems.

MATERIALS AND METHODS

Rearing of larvae

Berried female lobsters, caught locally, were kept individually in small circulation tanks (60 cm × 60 cm × 10 cm) and fed with raw fish twice weekly. Each morning during the hatching period (mid-June until late August) hatchlings were collected and transferred into a large circulation tank (250 cm × 100 cm × 80 cm). Twenty larvae from the daily hatch of

each female were kept in labelled containers (10 l capacity) and, following a moult, each larva was isolated in a glass jar (1 l capacity). The water in these containers was aerated each day and renewed every second day, being maintained at a temperature of 14 ± 2 °C throughout the course of the rearing programme. All larvae were fed daily with newly hatched *Artemia* nauplii. (Among the lobster larvae maintained under conditions of overcrowding in the large holding tank, feeding was supplemented by cannibalism.)

The breeding records of the labelled stock not only provided data on rates of development throughout the three larval, and several post-larval stages which were studied, but also facilitated accurate prediction of the moults, so that it became possible to obtain records of swimming behaviour of an individual immediately before, as well as immediately after a moult.

Anatomy

The external structure of the thoracic exopodites was studied by light microscopy and scanning electron microscopy of preserved material. The disposition of the various muscles involved in swimming was determined from histological paraffin sections cut in various planes and stained with Heidenhain's Azan, and from whole-mounts of legs stained with Borax Carmine.

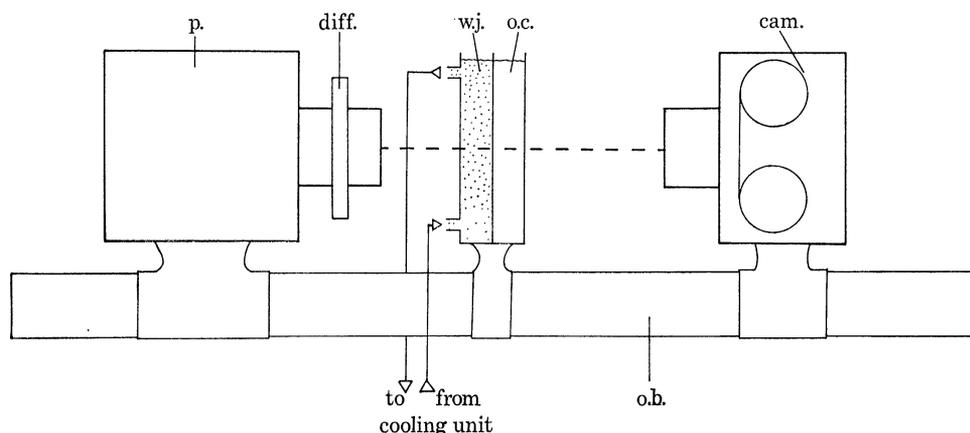


FIGURE 1. Diagram of the apparatus used to film swimming behaviour of lobster larvae. o.b., Optical bench; p., projector; w.j., water jacket; o.c., observation chamber (containing seawater); cam., Cine camera; diff., diffusing screen. Arrows indicate flow of water to and from cooling unit.

Photography

Larvae were placed in a 'Perspex' chamber of seawater, maintained at the temperature of the holding tanks by a water jacket of water cooled by a Churchill cooler. Illumination was provided by a projector mounted behind the chamber (figure 1). The larvae were allowed to move freely, and swimming behaviour was filmed with a Bolex 16 mm cine camera operating at 64 frames/s, choosing sequences in which the larvae were so orientated that all exopodites were visible. Some film was also taken of larvae beating their exopodites while lying on the bottom of the chamber. Sequences of beating lasting 20 cycles or more were analysed from the filmed records by single frame projection ('Specto' analytical projector).

RESULTS

General features of larval development

Under our holding conditions larvae were released from each female over periods of 3 weeks beginning in mid-June, with maximum nightly numbers in the middle of these periods (figure 2). The hatchlings emerged as free-swimming pelagic stage I larvae, approximately 1 cm long from the tip of the rostrum to the end of the telson (figure 3a). They differ from adult lobsters both in general body proportions, and in the possession of rudimentary antennae and an undivided telson. Major distinguishing features are the exopodite branches on the thoracic limbs, which are the functional swimming appendages of larval lobsters. The abdominal pleopods or swimmerets, which assist locomotion in post-larval stages of *Homarus*, are visible in stage I only as rudimentary outgrowths of the ventral body wall.

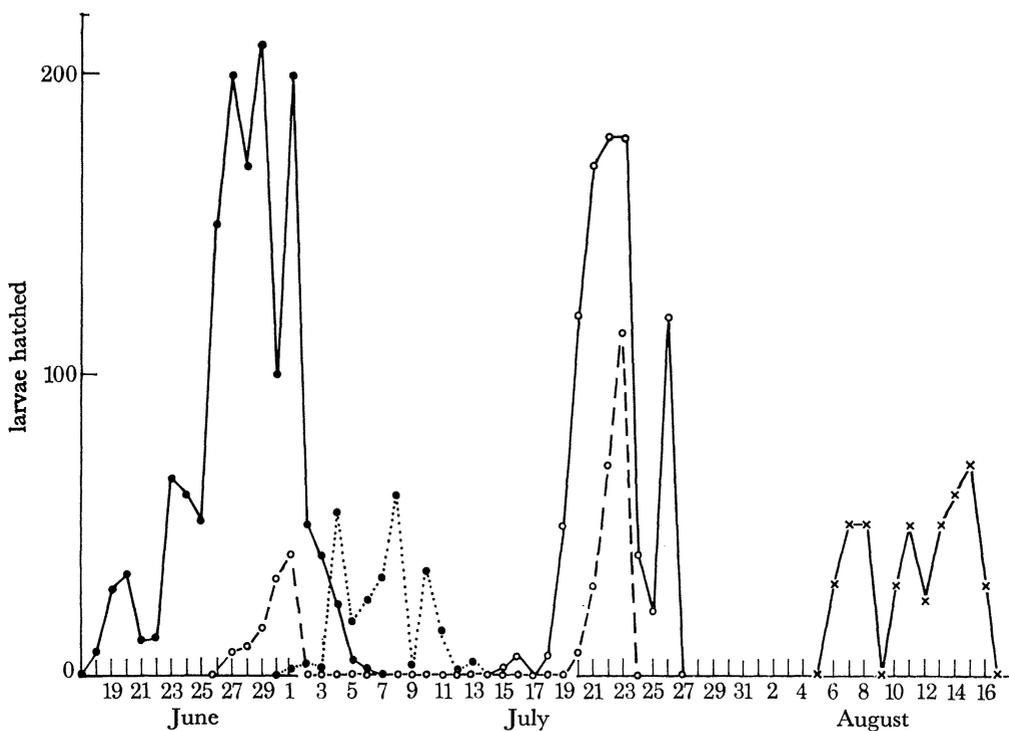


FIGURE 2. The number of larvae hatched from each of the five ovigerous female lobsters which supplied the stock for the present study. —●—, ♀ A; - -○- - , ♀ B; ····, ♀ C; —○—, ♀ F; —x—, ♀ G.

Under the rearing conditions we employed the duration of stage I was 8–9 days before the moult to stage II occurred (table 1). The second instar is little different in appearance from the first, except for a 10–15% increment in body length, and an increase in size of the swimmeret rudiments (figure 3c). Larvae remained in stage II for an average of 11 days (table 1). The third and final larval stage is marked by the appearance of uropods and prominent swimmerets, by a 20–25% increase in body length, and by changes in the proportions of the two rami of the thoracic appendages. While the endopodites, especially those of the chelipeds, lengthen considerably, the exopodites show only a small increase in absolute size, and become smaller in relation to other body dimensions (figure 3b).

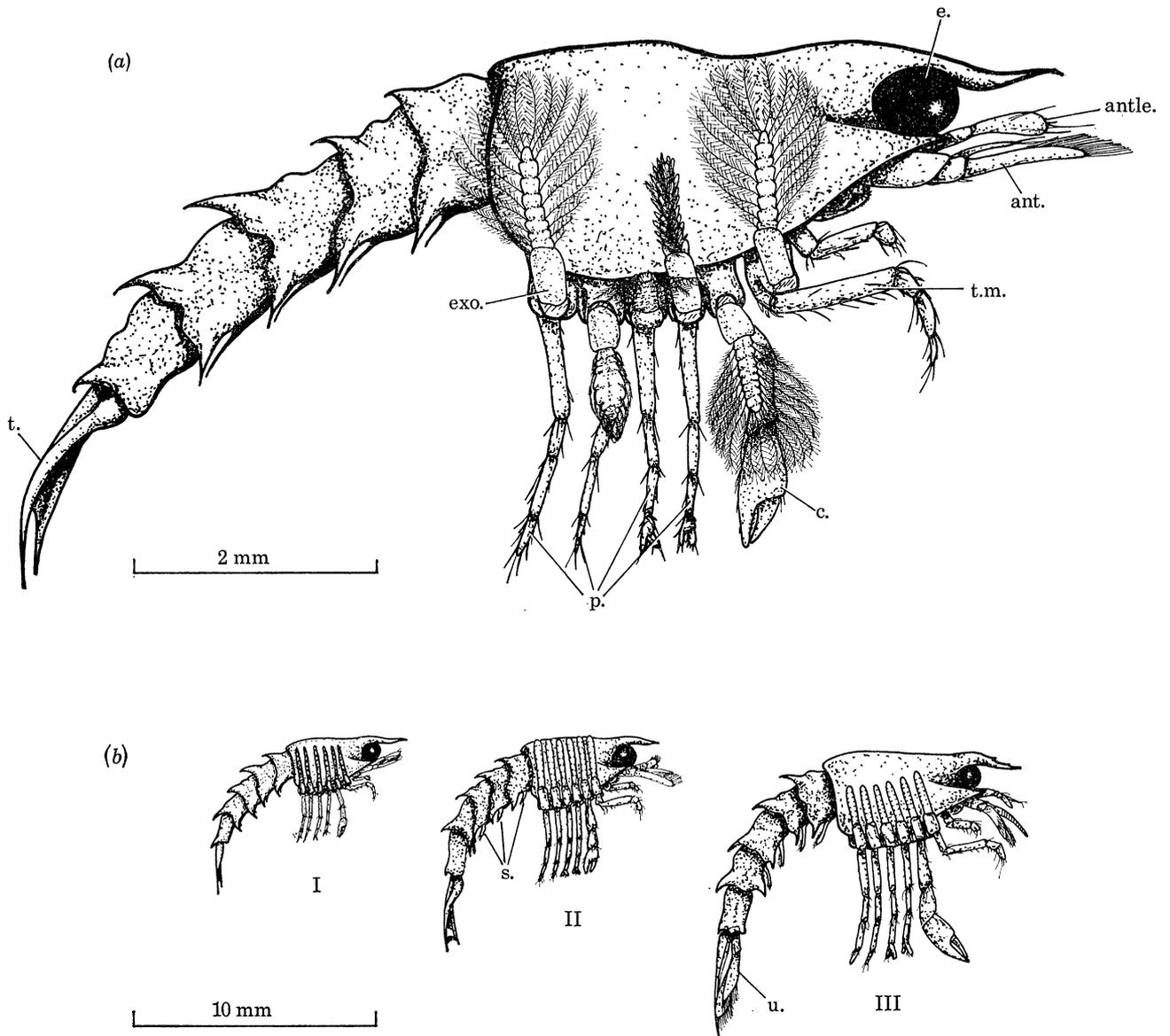


FIGURE 3. (a) Stage I larva in normal swimming posture, with the exopodites shown in their correct phase relations to one another. ant., Antenna; antle., antennule; e., eye; t.m., third maxilliped; c., cheliped; p., pereopods; exo., exopodite of fourth pereopod; t., undivided telson. (b) Scale representations of larvae in stages I, II and III to show the increase in body size during development, and the changes in the relative dimensions of the exopodite and endopodite branches of the thoracic appendages. Note also the appearance of swimmeret buds in stage II, and the uropods in stage III. s., Swimmerets; u., uropod.

TABLE 1. DURATION OF LARVAL STAGES

	stage I	stage II	stage III
mean, \bar{x} /day	8.55	11.07	12.10
standard deviation, s /day	2.01	2.77	1.32
number, n	162	39	12

The moult to stage IV, representing the end of the pelagic phase of development, occurred on average after 12 days in stage III (table 1). The stage IV megalopa approximates the adult lobster both in body structure (figure 4) and behaviour, and the stage III/stage IV moult may in fact be regarded as a metamorphosis between larval and juvenile phases of development. The major anatomical changes which occur are the loss of functional exopodites on the chelipeds and pereiopods, and a further increase in the size of the swimmerets. Concomitant changes in behaviour were observed: thoracic exopodite beating ceased (though the external rami persisted as small vestiges on the leg bases), the animal began to walk and climb rather than swim and, if presented with a sandy substrate, burrowed into it. These patterns of behaviour involve coordinated movements of the thoracic endopodites and meta-chronous beating of the swimmerets, two rhythmical activities which appear for the first time in the megalopa. Thus in stage IV there is a switch-over from a larval locomotory mechanism to one which persists throughout adult life.

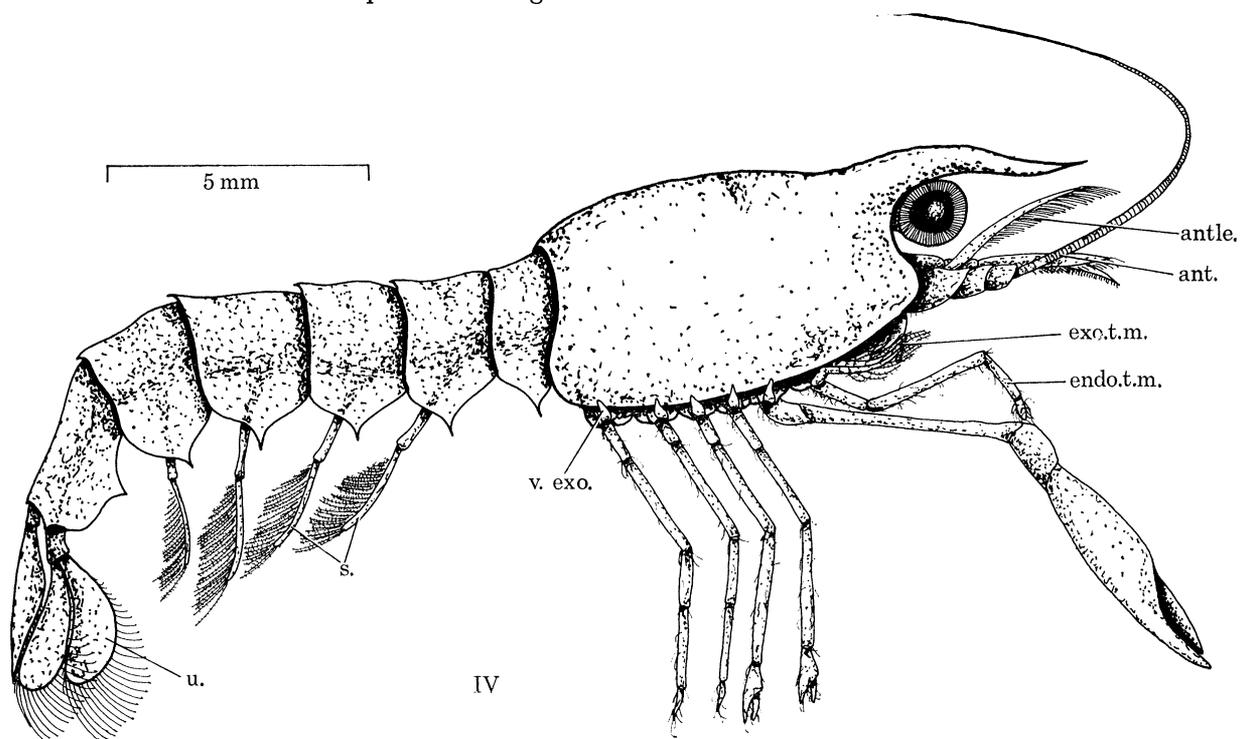


FIGURE 4. Stage IV megalopa. ant., Antenna; antle., antennule; exo.t.m., exopodite of third maxilliped; endo.t.m., endopodite of third maxilliped; v.exo., vestige of exopodite on fourth pereopod; s., swimmerets; u., uropods, bearing long setae. (Scale 5 mm.)

No systematic attempt was made to keep lobsters beyond stage IV, although a few individuals were brought through to stage V (the first juvenile stage) and stage VI. It was noted that the duration of each stage gradually increased, that the body increased in size and that all vestiges of the thoracic exopodites posterior to the third maxillipeds disappeared.

Anatomy of larval swimming appendages

The major swimming appendages of the pelagic larvae of *Homarus* are the exopodite branches of the third maxillipeds, chelipeds and four pairs of pereiopods. The more anterior

limbs are modified for the purposes of respiration and feeding, and those of the abdomen, although they emerge during larval development, do not contribute to larval locomotion. The biramous thoracic limbs are typical stenopodial appendages with an inner endopodite and outer exopodite (figure 5).

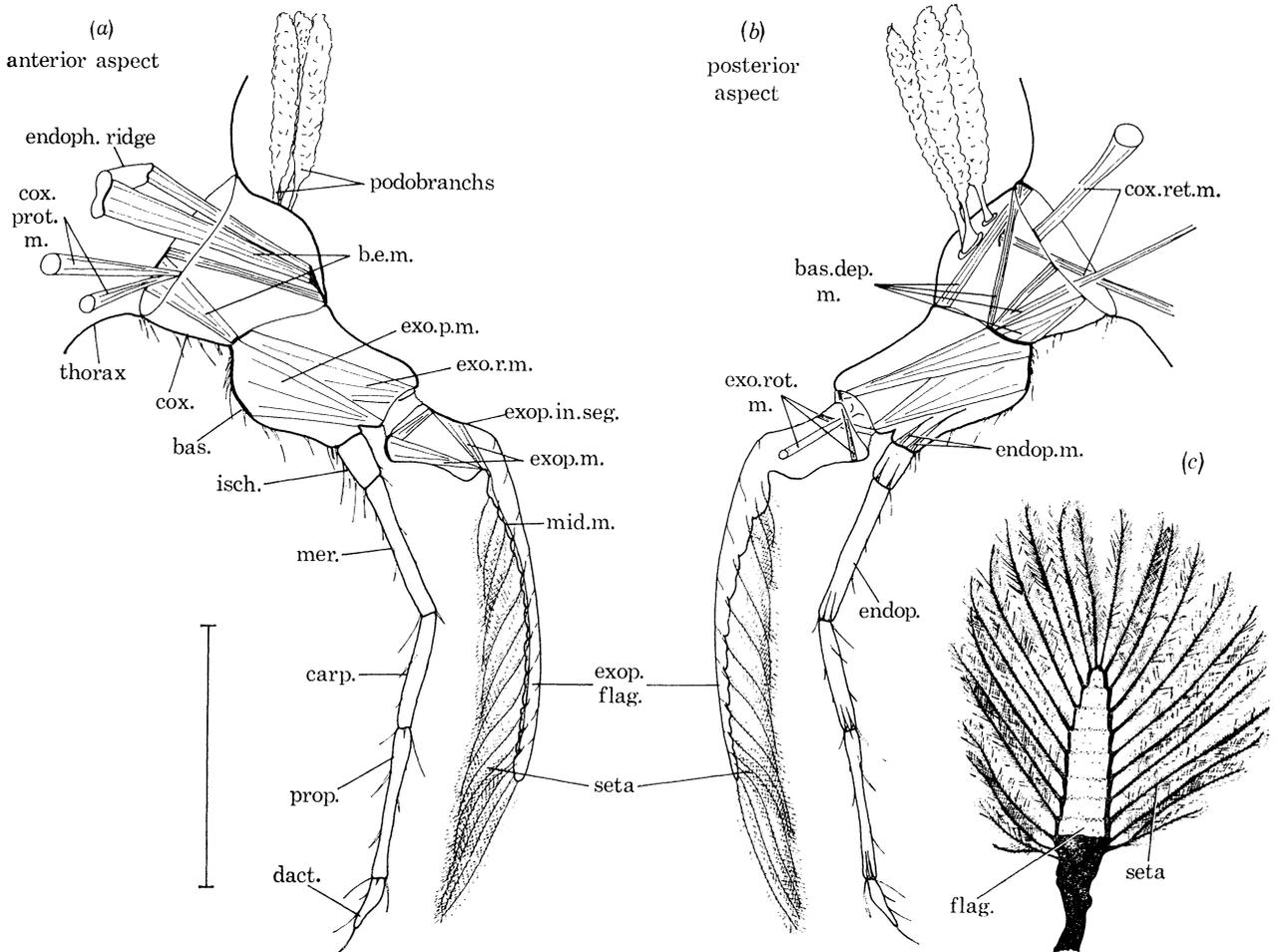


FIGURE 5. (a) Anterior view of the left third pereiopod. Abbreviations: b.e.m., basal elevator muscles; exo.p.m., exopodite powerstroke muscle; exo.r.m., exopodite returnstroke muscle; exop.in.seg., inner segment of exopodite; exop.m., exopodite muscles; mid.m., muscle fibres along midrib of flagellum; exop.flag., exopodite flagellum; dact., dactyl; prop., propus; carp., carpus; mer., merus; isch., ischium; bas., basis; cox., coxa; thorax., ventral thoracic wall; cox.prot.m., coxal protractor muscles; endoph. ridge, endophragmal ridge. (b) Posterior view of left third pereiopod. exop.rot.m., Exopodite rotator muscles; bas.dep.m., basal depressor muscles; cox.ret.m., coxal retractor muscles; endop.m., muscles of endopodite; endop., endopodite. (Scale 1 mm.) (c) Dried-down exopodite flagellum. The area enclosed by the tips of the setae is 10.5 times greater than the area of the flagellum blade alone. flag., Flagellum blade, annulated externally; seta, seta bearing setules.

External structure

The coxa, a short cylindriform segment, bears podobranchs laterally and articulates with the thorax in a simple hinge joint which allows movement in a sagittal plane. Distally, its articulation with the basipodite is oblique since the lateral hinge is distal to the medial hinge. As a result, movement at this joint carries the basis both anteriorly and dorsally.

The basis is a stout cylinder which subdivides distally to articulate medially with the endopodite and laterally with the exopodite. The inner ramus is made up of five segments distal to the basis, the dactyl being chelate on the cheliped and first two pereopods. The endopodite represents the adult walking leg, but in the larva it is much shorter in relation to the size of the body (figure 3*a*).

The outer ramus is composed of an inner tubular segment which connects to an outer flagellum through a region of flexible cuticle. The flagellum is a thin blade, segmented externally and grooved along its medial surface. Long branched setae emerge from its margins and articulate in such a way as to allow movement from a fully extended position during the powerstroke to a fully folded position during the returnstroke. When extended, the setae increase the surface area of the blade by ten times, enabling the limb to act as an effective paddle in swimming (figure 5*c*). The exopodite articulates with the basis through a flexible arthrodial membrane which completely surrounds the joint and permits rotation of the exopodite through a large angle. This facilitates changes in the direction of the propulsive stroke from directly forwards, through downwards, to directly backwards.

Internal anatomy

Movement at the joint between the thorax and the coxa is produced by two groups of muscles which arise on the lateral wall of the thorax and insert on the rim of the coxa (figure 5). The coxal protractor muscles insert anteriorly to the axis of the hinge, the coxal retractor muscle posteriorly.

The basis is moved by sets of elevator and depressor muscles, each set comprising an extrinsic muscle which originates on an endophragmal ridge in the thorax, and an intrinsic muscle which has its origin in the coxa (figure 5).

Muscles lying in the basis supply both the endopodite and the exopodite. Two small, thin muscles run from the posterior basipodite wall to insertions on the ischiopodite (figure 5*b*). They represent the first in a series of antagonist pairs which operate at the various joints of the endopodite, and appear as thin transparent sheets in the larval limb. Most of the basipodite cylinder is occupied by two large muscles supplying the exopodite. The powerstroke muscle originates in a large head medially and anteriorly on the proximal wall of the basis, and inserts on a cuticular extension of the antero-lateral exopodite wall (figure 5*a*). The returnstroke muscle, of slightly smaller diameter, arises alongside and posterior to the powerstroke muscle, and runs distally to a lateral insertion on the proximal exopodite rim. In addition, three small muscles span the joint from origins at the extreme distal end of the basis (figure 5*b*). They are disposed in such a way as to bring about different rotation movements of the exopodite about this mobile joint, and may also act to stabilize the joint, which has little mechanical rigidity.

Two muscles lying in the exopodite may also contribute to movements of the appendage. They originate on opposite sides of the inner segment, but insert together on the medial wall of the flagellum, just beyond the flexible region (figure 5*a*). A few muscle fibres continue up the midrib of the flagellum, and appear to insert near its tip.

Swimming behaviour in larval lobsters

In the pelagic stages swimming is accomplished by metachronous beating of the exopodites, which are in continuous motion during active locomotion. They were observed to slow to

rest on the occasions that the larvae sank to the bottom of the filming chamber. These quiescent periods were usually of short duration and were followed by renewed active beating. Most frequently larvae in stage I and stage II swam upwards and forwards, with the dorsal body surface pointing in the direction of movement, and the abdomen either slightly downcurved, or reflected under the body (figure 6*d*). Another commonly observed mode of swimming was a direct forward progression (figure 6*e*), and less frequently observed variants were vertical hovering (figure 6*c*) and swimming in an upward and backward direction (figure 6*b*). Third stage larvae are also capable of these different types of locomotion, but were most often seen swimming close to the bottom.

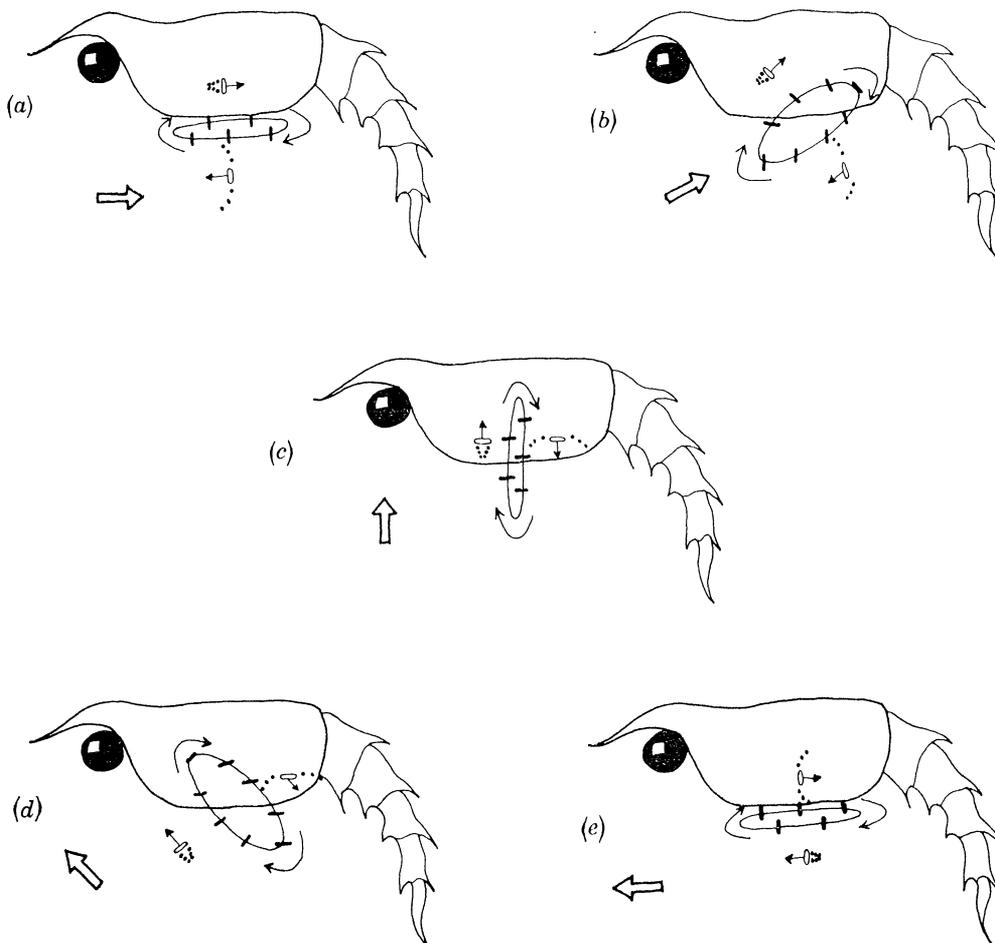


FIGURE 6. Diagrammatic representation of a lobster larva to show the different observed directions of exopodite beating. The movements of the flagellum are indicated by continuous ellipses, and its form is shown in transverse section during the powerstroke and returnstroke. The large arrows indicate the direction of movement of the animal. (a) Backwards swimming; (b) movement upwards and backwards; (c) vertical hovering; (d) progression forwards and upwards; (e) forward swimming.

As found by Hadley (1908) in the larval American lobster, light appears to be a major orientational cue for swimming in larvae of *H. gammarus*, although we made no systematic study of the phototactic reaction. On the other hand orientation to gravity is not well developed in pelagic larvae, which frequently somersault and pursue spiral swimming paths under conditions of strong illumination. A contributory factor to this disorientated behaviour may

be the absence of a functional statocyst in the larval stages. In histological sections no sign of a statocyst was observed in stage I, and in stage II and stage III there is only a simple cuticular intucking at the base of the antennule, with no associated sensory structures (figure 7*a*). A true statocyst sac, with an elevated sensory cushion bearing rows of cuticular hairs, appears for the first time in stage IV (figure 7*b*). It is probable that the improved equilibrium control displayed by the megalopa and benthic juveniles is in great part due to this development of functional statocysts.

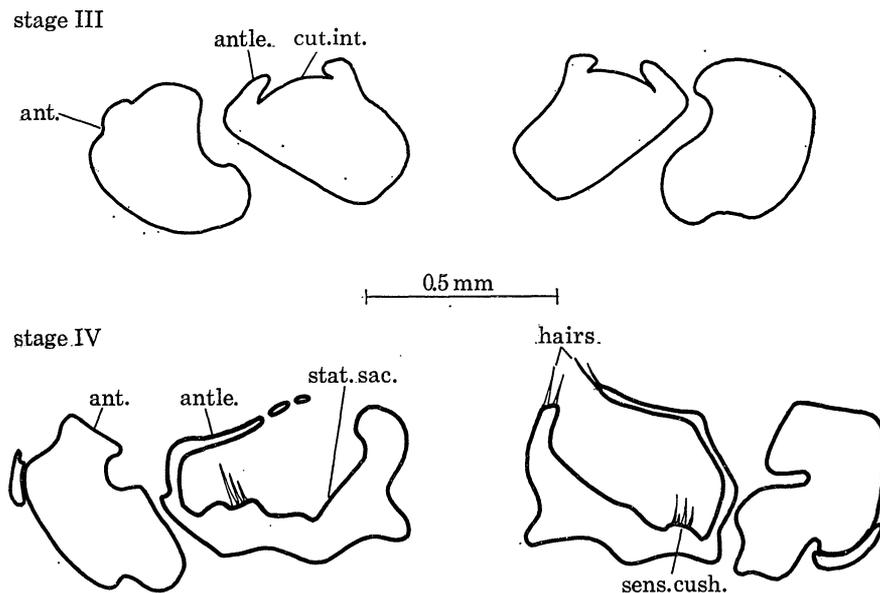


FIGURE 7. Transverse sections at the level of the base of the antennules in larval stage III and post-larval stage IV lobsters. ant., Antenna; antle., antennule; cut.int., cuticular intucking; stat.sac., statocyst sac, open to exterior; hairs, hairs over aperture of statocyst sac; sens.cush., elevated sensory cushion, bearing rows of cuticular sense hairs.

In addition to the propulsion provided by swimming appendages, *Homarus* larvae are also able to move by rapid tail-flicks. These abdominal flexions occur only when the animal contacts a solid object, such as the wall of the tank or another larva, and therefore constitute an escape response. As such, however, they are not very effective and produce 'jack-knifing' of the body with little actual backward movement (figure 8*a, c*). As the animal prepares to tail-flick the exopodites cease beating and are held out laterally from the body, while the endopodites hang ventrally. During the actual flexion, which occupies less than 60 ms, the limbs appear to be carried forward in a passive manner by the passage of water past them.

An interesting comparison can be made between the tail-flicks of larval and post-larval lobsters. The latter produce powerful flexions of the abdomen which propel the animal backwards for up to several body lengths (figure 8*b, d*). During this movement the legs are held forward, streamlining the outline of the body. The tail-flick of a post-larval lobster therefore resembles that of the adult, but contrasts with the less vigorous twitch of the larva.

Exopodite swimming movements

The best of a larval exopodite is essentially a rowing movement. During the powerstroke, which is most often directed ventro-posteriorly, the blade of the flagellum is straightened due to the elasticity of the cuticle at its base, the setal field is expanded passively (figure 9*a*), and

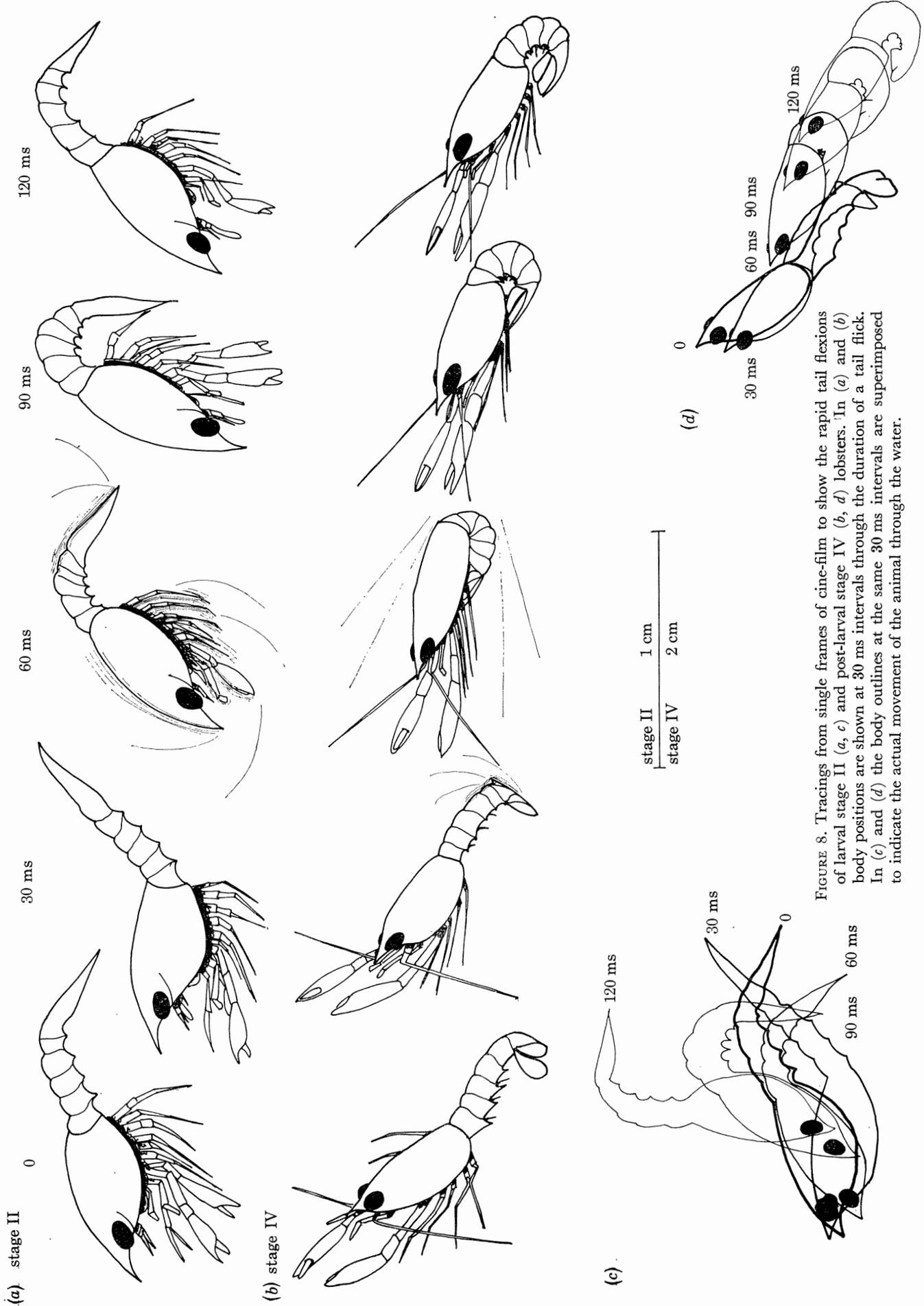


FIGURE 8. Tracings from single frames of cine-film to show the rapid tail flexions of larval stage II (a, c) and post-larval stage IV (b, d) lobsters. In (a) and (b) body positions are shown at 30 ms intervals through the duration of a tail flick. In (c) and (d) the body outlines at the same 30 ms intervals are superimposed to indicate the actual movement of the animal through the water.

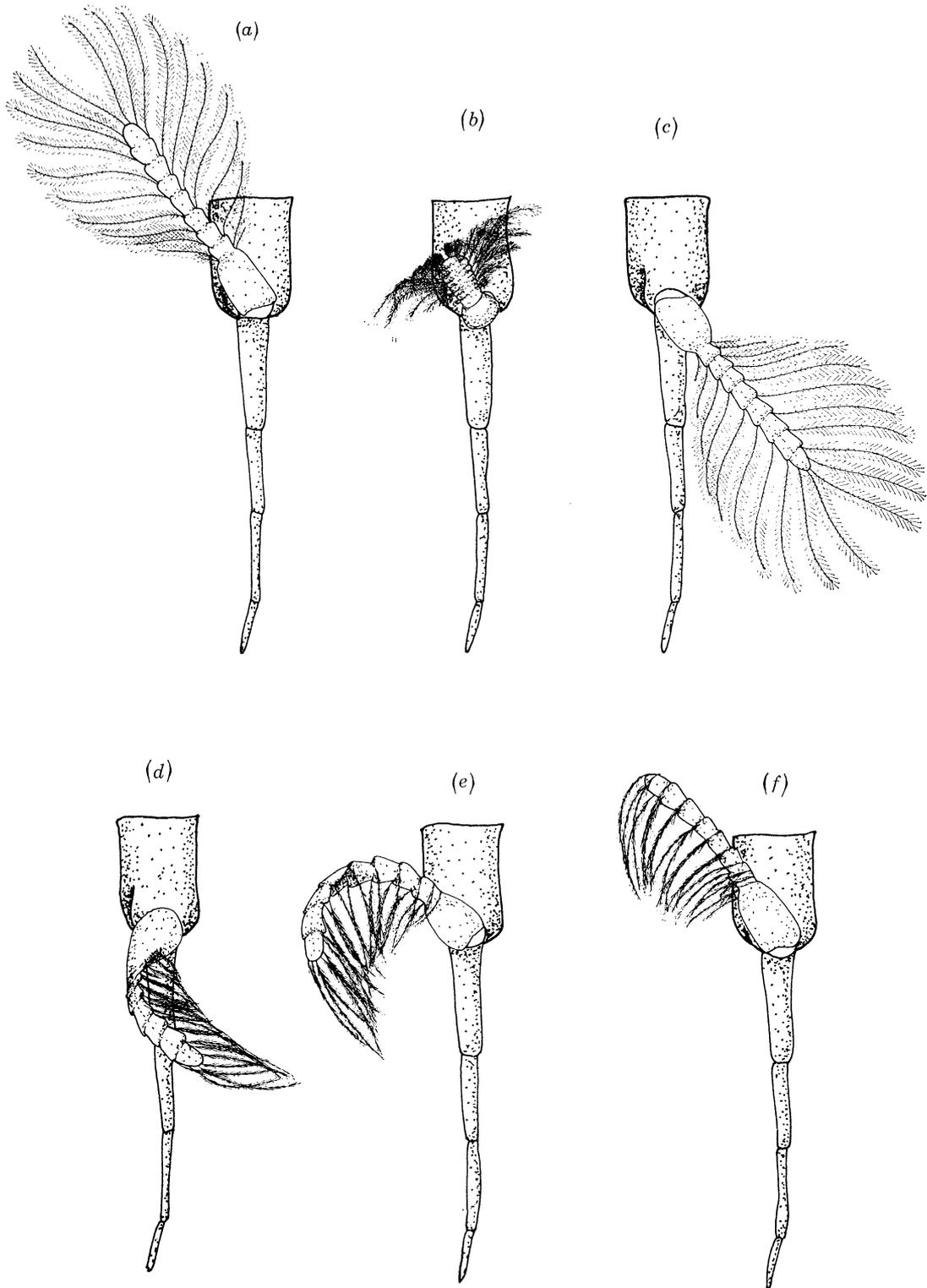


FIGURE 9. The appearance of the exopodite during a single cycle of movement. The powerstroke (*a-c*) extends the setal field passively thus presenting the largest surface area to the water. The exopodite is thrust ventro-posteriorly (*b*) and finally (*c*) there is a small flick of the flagellum. Upon recovery (*d-f*) the movement of the exopodite against the pressure of water flattens the setae (*d*) and decreases the surface area to that of the blade. The flagellum is folded actively towards the body (*e*) and at the same time rotates anticlockwise so that the return-stroke follows an anterior path relative to the powerstroke. The flagellum then again turns to face posteriorly and the next cycle begins.

the exopodite presents its largest profile to the water. At the end of the powerstroke there is a final flick of the flagellum (figure 9c), probably produced by contraction of muscles in the inner segment (figure 5a). As the returnstroke begins the setae are drawn passively inwards behind the blade, reducing the surface area of the exopodite by more than 90% (figure 9d). The reduction in drag is assisted by an active folding of the flagellum towards the body (figure 9e), probably brought about by the action of the muscle fibres which insert at the tip (figure 5a). At the same time the flagellum rotates anticlockwise through a small angle, so that the returnstroke follows a more anterior path than the powerstroke (figure 9d). Thus, during one cycle of beating the flagellum describes an ellipse whose major axis lies in the direction of propulsion (figure 6d).

This basic pattern of movement is common to all the various observed modes of beating, although the elliptical path of the flagellum is flattened when beating is directly anterior/posterior (figure 6a, e) or dorsal/ventral (figure 6c). In addition to those depicted in figure 5, all intermediate forms are possible and changes from one to another involve rotation of the whole exopodite relative to the basis. The various rotator muscles of the exopodite (figure 5b) are disposed appropriately to bring about these movements, as well as those which occur at the beginning of each returnstroke.

In addition to changes in the direction of the propulsive stroke, variations in both the amplitude of the stroke and the beating frequency have been observed. Coordinated control of these three parameters in all exopodites enables the larva to perform turning movements and other swimming manoeuvres.

A consistent observation in all larval stages was the absence of any contribution by the endopodite limb branch to locomotion. Slight twitching movements were ascribed to the mechanical connexion of the two rami through the basis, rather than to any active movement of the endopodite itself. In addition, larvae were never seen to be walking on the bottom, although it is possible that the chelipeds and perhaps other endopodites are involved in other activities, such as the manipulation of food.

The metachronous wave

Some indication of the nature of metachronous coordination of exopodites was provided by observing the initiation of beating from rest. On all occasions the rearmost limb was the first to move, followed in succession by the more anterior limbs. This anteriorly directed wave of initiation, which is common to all directions of exopodite beating, suggests that, as in the swimmeret system (Ikeda & Wiersma 1964), the metachronous wave also passes from posterior to anterior.

DISCUSSION

The specialized swimming system of the larvae of *Homarus gammarus* (L.) exemplifies the principle emphasized by Gurney (1939) that larval organization is determined to a great extent by locomotory requirements. The eggs hatch at an advanced state of development (Herrick 1895), the brief larval life represents only a small fraction of the potential life-span (Hewett 1974), yet the larvae display a mode of locomotion quite distinct from that of the adult lobster. The larval thoracic exopodites represent a large investment in terms of both muscular machinery and associated nervous apparatus, which perhaps reflects the importance of the pelagic dispersal phase in the life-history of the animal.

The well-developed exopodite muscles, which occupy most of the enlarged basipodite segment in the larval limb, are additional to the muscles of the future adult walking leg (Macmillan 1975). The adult complement is already present in the various endopodite segments of the larval limb, although it brings about little, if any, locomotory movement at that stage. Possible reasons for this are: (1) the muscles have not developed the ability to contract; (2) the appropriate motor innervation has not taken place; (3) the central connections to interneurons have not been made. Detailed physiological and anatomical studies are required to distinguish between these various possibilities.

The distinction between exopodite and endopodite muscles reflects a separation of their rôles in locomotion. After operating throughout larval life those of the exopodite degenerate at the post-larval moult, and simultaneously those of the endopodite become functional in walking. The accompanying changes in the nervous system which take place at this switch-over from swimming to walking are not known, but may involve a degeneration of the larval exopodite oscillator and initiation of activity in the walking oscillator. However, the possibility cannot be excluded that the same nervous oscillator underlies both swimming and walking, and that only a change in central connections occurs at stage IV. Further discussion of this possibility is presented in the accompanying paper (Macmillan *et al.* 1976) in the light of quantitative information regarding exopodite beating parameters.

Similar developmental questions are posed by the other behaviour patterns which appear for the first time in stage IV. The ontogeny of the swimmeret system has been studied by Davis (Davis 1973; Davis & Davis 1973), and its particular relation to larval exopodite beating is considered in the present study (Laverack *et al.* 1976). Also the form of the rapid tail-flick is strikingly different in larval and post-larval lobsters (figure 8) and it may be possible to interpret this difference in terms of the developing action of the various types of motor element which have been shown to control tail flexion in the adult *Macrura* (Bowerman & Larimer 1974; Larimer, Eggleston, Masukawa & Kennedy 1971; Schrameck 1970; Wiersma 1938; Wine & Krasne 1972). Successful recordings from giant fibres have recently been made in the early larval stages of the lobster (C. K. Govind, personal communication) and therefore it may be possible to demonstrate directly the nervous mechanisms involved in the different types of tail flexion.

The efficiency of the exopodite as a swimming appendage is largely due to the long branched setae, whose mode of articulation allows movement from a fully extended position during the powerstroke to a fully folded position during the returnstroke. Similar structural adaptations are found in the swimming appendages of other crustacea (Cannon & Manton 1927; Dennell 1933; Storch 1929). The exopodite beat is a rotatory action and, in addition to the main propulsive thrust, vortices will be produced along each limb. Such currents may provide a respiratory flow over the gills, but will generate only weak propulsive streams (Cannon & Manton 1927). In true rotary beating the limbs are inclined at an angle to the direction of motion (Lowndes 1935), but in lobster larvae the face of each exopodite flagellum points directly in the line of propulsion, and it seems appropriate to describe the exopodite beat as a modified oar-like action. All the observed changes in swimming direction from directly forwards to directly backwards can be accomplished by rotation of the flagellum, and thus there appears to be no need for a specific reversal mechanism.

The finding that laboratory reared larvae of *Homarus gammarus* tend to swim upwards in stage I, but stay near the bottom in stage III is in agreement with the field observations of

Ennis (1973). However, it is difficult to draw conclusions about the normal swimming behaviour of lobster larvae from laboratory observations since it involves a complex interaction of responses to hydrostatic pressure and light, with habituation effects and differences with age as well as stage (Ennis 1973; Rice 1967). In particular it is necessary to be cautious when making inferences about the behaviour of *H. gammarus* from studies on *H. americanus*, e.g. those of Hadley (1908) and Templeman (1937, 1939), since the larvae of the European lobster are rarely taken in plankton hauls (Jackson 1913), whereas those of the American lobster are regular members of the plankton (Scaratt 1964). These differences are probably a result of different responses to environmental stimuli, but it cannot be ruled out that there are also differences in the actual swimming mechanism in the two species.

We should like to thank Mr R. Hayward for his assistance in rearing the animals, Mr J. Watson for advice on photographic methods, Andrea Sylvester and Mr J. Stevenson for help with the illustrations, and Mrs D. Hunter for preparing the manuscript. D.M.N. was Research Fellow at the Gatty Marine Laboratory. D.L.M. was supported by S.R.C. grant B/RG/05857.

REFERENCES

- Barnes, W. J. P. 1975 Leg co-ordination during walking in the crab, *Uca pugnax*. *J. comp. Physiol.* **96**, 237–256.
- Barnes, W. J. P., Spirito, C. P. & Evoy, W. H. 1972 Nervous control of walking in the crab *Cardisoma guanhumi*. II. Role of resistance reflexes in walking. *Z. vergl. Physiol.* **76**, 16–31.
- Bowerman, R. F. & Larimer, J. L. 1974 Command fibres in the circumoesophageal connectives of crayfish. II. Phasic fibres. *J. exp. Biol.* **60**, 119–134.
- Burrows, M. & Willows, A. O. D. 1969 Neuronal co-ordination of rhythmic maxilliped beating in brachyuran and anomuran crustacea. *Comp. Biochem. Physiol.* **31**, 121–135.
- Cannon, H. G. & Manton, S. M. 1927 On the feeding mechanism of a mysid crustacean, *Hemimysis lamornae*. *Trans. R. Soc. Edinb.* **55**, 219–253.
- Davis, W. J. 1968 The neuromuscular basis of lobster swimmeret beating. *J. exp. Zool.* **168**, 363–378.
- Davis, W. J. 1969 The neural control of swimmeret beating in the lobster. *J. exp. Biol.* **59**, 99–117.
- Davis, W. J. 1973 Development of locomotor patterns in the absence of peripheral sense organs and muscles. *Proc. natn. Acad. Sci. U.S.A.* **70**, 954–958.
- Davis, W. J. & Davis, K. B. 1973 Ontogeny of a simple locomotor system: Role of the periphery in the development of central nervous circuitry. *Am. Zool.* **13**, 409–425.
- Delcomyn, F. 1971 *a* The locomotion of the cockroach *Periplaneta americana*. *J. exp. Biol.* **54**, 443–452.
- Delcomyn, F. 1971 *b* The effect of limb amputation on locomotion in the cockroach *Periplaneta americana*. *J. exp. Biol.* **54**, 453–469.
- De Long, M. 1972 Central patterning of movement. *Neurosci. Res. Prog. Bull.* **9**, 10–30.
- Dennell, R. 1933 The habits and feeding mechanism of the amphipod *Haustorius arenarius* Slabber. *J. Linn. Soc. Lond. Zool.* **38**, 363–388.
- Ennis, G. P. 1973 Behavioural responses to changes in hydrostatic pressure and light during larval development of the lobster *Homarus gammarus*. *J. Fish. Res. Bd Can.* **30**, 1349–1360.
- Gurney, R. 1939 *Larvae of decapod crustacea*. London: Ray Society.
- Hadley, P. B. 1908 The behaviour of the larval and adolescent stages of the American lobster (*Homarus americanus*). *J. comp. Neurol. Psychol.* **18**, 200–301.
- Herrick, F. H. 1895 The American lobster, a study of its habits and development. *Bull. U.S. Fish. Comm.* **15**, 1–252.
- Hewett, C. J. 1974 Growth and moulting in the common lobster (*Homarus vulgaris* Milne-Edwards) *J. mar. biol. Ass. U.K.* **54**, 379–391.
- Jackson, H. G. 1913 Decapod larvae in the Irish Sea. *Rep. Lanc. Sea-Fish Labs.* **21**, 254–259.
- Ikeda, K. & Wiersma, C. A. G. 1964 Autogenic rhythmicity in the abdominal ganglia of the crayfish: the control of swimmeret movements. *Comp. Biochem. Physiol.* **12**, 107–115.
- Larimer, J. L., Eggleston, A. C., Masukawa, L. M. & Kennedy, D. 1971 The different connections and motor outputs of lateral and medial giant fibres in the crayfish. *J. exp. Biol.* **54**, 391–402.
- Laverack, M. S., Macmillan, D. L. & Neil, D. M. 1976 A comparison of beating parameters in larval and post-larval locomotor systems of the lobster *Homarus gammarus* (L.). *Phil. Trans. R. Soc. Lond. B* **274**, 87–99.

- Lochhead, J. H. 1961 Locomotion. In *The physiology of crustacea*, vol. II (ed. T. H. Waterman). New York & London: Academic Press.
- Lowndes, A. G. 1935 The swimming and feeding of certain calanoid copepods. *Proc. zool. Soc. Lond.* **1935**, 687-715.
- Macmillan, D. L. 1975 A physiological analysis of walking in the American lobster (*Homarus americanus*). *Phil. Trans. R. Soc. Lond. B* **270**, 1-59.
- Macmillan, D. L., Neil, D. M. & Laverack, M. S. 1976 A quantitative analysis of exopodite beating in the larvae of the lobster *Homarus gammarus* (L.). *Phil. Trans. R. Soc. Lond. B* **274**, 69-85.
- Manton, S. M. 1930 Notes on the habits and feeding mechanisms of *Anaspides* and *Paranaspides*. *Proc. zool. Soc. Lond.* **1930**, 791-800.
- Pasztor, V. M. 1968 The neurophysiology of respiration in decapod crustacea. I. The motor system. *Can. J. Zool.* **46**, 585-596.
- Paul, D. H. 1971 Swimming behaviour of the sand crab *Emerita analoga* (Crustacea, Anomura). 1. Analysis of the uropod stroke. *Z. vergl. Physiol.* **75**, 233-258.
- Pearson, K. G. 1972 Central programming and reflex control of walking in the cockroach. *J. exp. Biol.* **56**, 173-193.
- Rice, A. L. 1967 The orientation of the pressure responses of some marine crustacea. *Proc. Symp. Crust. mar. biol. Ass. India*, part III, 1124-1131.
- Scaratt, D. J. 1964 Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. *J. Fish. Res. Bd Can.* **21**, 661-680.
- Schrameck, J. E. 1970 Crayfish swimming: alternating motor output and giant fibre activity. *Science, N.Y.* **169**, 698-700.
- Spirito, C. P. 1972 An analysis of swimming behaviour in the portunid crab *Callinectes sapidus*. *Mar. Behav. Physiol.* **1**, 261-276.
- Storch, O. 1929 Die Schwimmbewegung der Copepoden, auf Grund von Mikro-Zeitlupenaufnahmen analysiert. *Verhandl. deut. zool. Ges.* **33**, 118-129.
- Templeman, W. 1937 Habits and distribution of larval lobsters (*Homarus americanus*). *J. Biol. Bd Can.* **3**, 345-347.
- Templeman, W. 1939 Investigations into the life history of the lobster (*Homarus americanus*) on the west coast of Newfoundland 1938. *Nfld Dep. nat. Resour. Res. Bull. (Fish.)* **7**, 1-52.
- Wendler, G. 1966 The co-ordination of walking movements in arthropods. *Symp. Soc. exp. Biol.* **20**, 229-250.
- Wiersma, C. A. G. 1938 Function of the giant fibres of the central nervous system of the crayfish. *Proc. Soc. exp. Med.* **38**, 661-662.
- Wilkens, J. L. & McMahon, B. R. 1972 Aspects of branchial irrigation in the lobster *Homarus americanus*. I. Functional analysis of scaphognathite beat, water pressures and currents. *J. exp. Biol.* **56**, 469-480.
- Wilson, D. M. 1966 Insect walking. *Ann. Rev. Entomol.* **11**, 103-123.
- Wilson, D. M. 1968 The nervous control of insect flight and related behaviour. In *Recent advances in insect physiology* (ed. J. E. Treherne & J. W. L. Beament). New York: Academic Press.
- Wine, J. J. & Krasne, F. B. 1972 The organisation of escape behaviour in the crayfish. *J. exp. Biol.* **56**, 1-18.
- Young, R. E. 1973 Nervous control of ventilation in the shore crab *Carcinus maenas*. Ph.D Thesis, University of St Andrews.