The propulsion and use of water currents for swimming and feeding in larval and adult *Artemia*

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Abstract

Propulsion of water by *Artemia* has been studied using high speed cinemicrography. Nauplii use one pair of limbs for swimming and in later stages also for feeding ; this system is inefficient compared to that found in copepod nauplii and may be a compromise dictated by environmental and developmental factors.

Pairs of thoracic limbs develop at successive moults. Older larval stages and adults use a metachronally beating system of thoracic limbs to produce water currents for both swimming and feeding. Antennae and thoracic limbs function together in mid-development stages. The metachronal system of the adult is of a type that occurs widely in branchiopods especially in the Anostraca.

Introduction

Interest in the swimming and feeding mechanisms of the Branchiopoda seems to have declined over the last 40 years, if one can judge from the number of publications. Recent descriptions of the limbs and mouthparts of *Branchinecta* (Fryer, 1966) relate more to the taxonomic significance of the structures than to their functional operation. Earlier work on the Branchiopoda was aimed at understanding feeding mechanisms in various component groups, notably on *Apus* (now *Triops*) (Lankester, 1881), *Estheria* (Cannon, 1924), *Chirocephalus* (Cannon, 1928), *Sida* (Storch, 1929) and various anostracans, conchostracans and notostracans (Lundblad, 1920). Storch (1929) was the only one of this group to use high speed cinemicrography. The detailed work by Cannon (1928) on *Chirocephalus* included descriptions of the water currents created by the adult. This was followed by a discussion of feeding mechanisms in all orders of the Branchiopoda, including a brief comment on the nauplii of *Estheria* and *Chirocephalus* (Cannon, 1933). The relationship between the limb beat and the production of various water currents concerned with feeding of adult *Chirocephalus* was discussed by Lowndes (1933). The structure and movement of the limbs of *Balanus* (Cirripedia) nauplii and the water currents they produce was described by Lochhead (1936), and Gauld (1959) has more recently compared the feeding of nauplii of *Balanus*, *Artemia* and copepods.

In the account which follows the changes in activity of the limbs of *Artemia* during development from first stage nauplius to adult are described and related with the way in which the water currents created are used in swimming and feeding.

Materials and methods

Artemia cysts purchased from Interpet Ltd. (Dorking, Surrey, England) were hatched at $20\,°C \pm 2\,°C$ in the laboratory in normal seawater (s.g. 1.030). Cultures were reared in crystallising dishes of 19 cm diameter and 10 cm depth. Animals fed on microscopic algae growing in the dishes, which were kept by a well lit window, but this was supplemented by brewers yeast and added phytoflagellates. Cultures were aerated and the water was changed whenever it became cloudy. Cultures, once established, were self sustaining for many months with several generations completing their life cycles. This gave rise to a mixed culture with all developmental stages present.

Animals were examined either in the free-swimming state or else tethered to fine drawn glass needles. Individuals were glued to the needles using a butyl ester cyano-acrylate adhesive from Avdel Ltd. (Eastleigh, Hampshire, England). For successful attachment animals were anaesthetized by placing them in CO_2 saturated seawater until all movements ceased. Specimens were allowed to recover for at least 2 hr in fresh seawater before being used. Survival of animals tethered in such a way varied with development. Stage 1 nauplii (Anderson, 1967) would swim actively for 3-8 hr after the operation, older stages would survive for progressively longer times. Adults were sometimes kept attached to needles for weeks, being very rarely killed by the process but often managing to free themselves. Survival time for early stages probably depends on how much time there is before the next moult, which may be prevented by the presence of the adhesive.

Animals were filmed under low power ($\times 10$ to $\times 40$) bright field optics on a Reichert Zetopan microscope. To record limb and particle movements, a Mitchell high speed camera was used driving a Chadwick-Helmuth strobe flash at frame rates up to 400 fps.

Results and discussion

Staging of animals is based on the descriptions of Heath (1924) and Anderson (1967). Anderson (1967) describes three moults as occurring within Heath's stage 1 and we have found diagnostic differences in antennal setation to correspond with Anderson's staging. Anderson's stage 4 corresponds with Heath's stage 2. Since Heath's stage 1 represents the true nauplius, whilst stage 2 larvae are metanauplii, we have designated the first 3 naupliar stages as stages 1a, 1b and 1c so as to maintain compatibility with Heath's staging for subsequent development. Propulsive antennae persist as thoracic limbs develop during metanaupliar stages 2 and 3 and later larval stages 4-7, but the antennae of post-larval stages 8-12 and adults serve other functions.

NAUPLIAR LOCOMOTION

Although all three pairs of naupliar limbs, the antennules, antennae and mandibles, show a co-ordinated action during swimming, only the antennae contribute significantly to

swimming in *Artemia* nauplii. Copepod nauplii derive a certain amount of propulsion from all three pairs of naupliar appendages (unpublished observation).
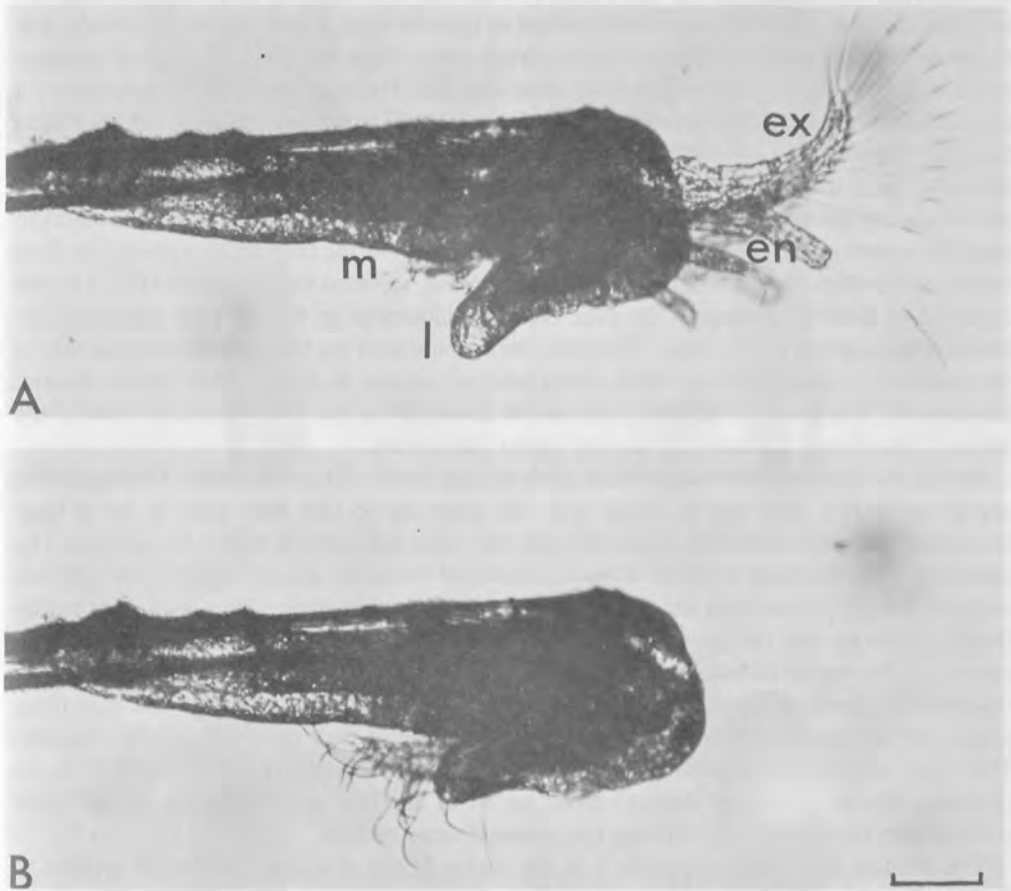

FIG. 1. Profile view of a stage 1b animal tethered with its ventral side down. The needle is visible on its dorsal surface. A) The start of the effective stroke. The setae of the exopodite (ex) and endopodite (en) are spread in a fan. The labrum (l) is starting to open and the mandibles (m) are just visible. B) The end of the effective stroke. The antennal setae are passing between the body and labrum. Scale bar: 0.1 mm.

In *Artemia* nauplii the antennal exopodite usually carries eight or nine setae at stage 1a increasing to nine or ten by stage 1b. The endopodite starts with two well formed plus one rudimentary seta in stage 1a. These develop a so called 'hinge' by stage 1b and by stage 1c the endopodite possesses three full setae and a fourth rudimentary one. By stage 2 the last has grown to give four large setae on the endopodite. The exopodite and endopodite setae together with their endites form a large propulsive fan.

The beat cycle of the antennae of excysted nauplii starts with both limbs directed anteriorly. The exopodites and endopodites and their setae are actively spread into fans (Fig. 1a) and the

two limbs move in phase through about 180° in the propulsive or effective stroke. After approximately 150° the straight limbs start to move inwards towards the body. Once the limb tips have passed the 180° mark the effective stroke has finished, but in at least the stage 1c nauplius the limb tips continue to curve round so that the setae project across the ventral side of the body and under the labrum which drops away from the body during the effective stroke and then closes over the antennal setae (Fig. 1b). The setal tips come to a halt having travelled through about 260° from the start of the stroke. The limbs recover flexed with setae bunched and trailing and initially with the endopodite leading the exopodite, but by the time the limbs reach their most anterior position the exopodite is leading. Thus the limb probably rotates slightly towards the end of the effective stroke to bring the exopodite under the labrum from the spread position seen during the effective stroke. During the recovery stroke the limb rotates in the opposite direction. A similar effect was reported by Lochhead (1936) in the antennae of *Balanus*. Stages of the beat cycle are illustrated in Fig. 2. This represents the maximum excursion of the limbs. However, the amplitude of the beat of each antenna can be independantly varied although both limbs always remain in phase. This allows turning movements. The plane of the limb beat lies at about 20° to the anteroposterior axis of the animal ; this allows the limb tips to pass under the labrum.

During the beat the antennules follow the antennae about 1/3 cycle behind. The mandibles appear to be 1/2 cycle out of phase with the antennae so that they seem to be at their maximum sideways extension when the antennal setae are curving under the labrum. The mandible setae interlock with the antennal ones and these are drawn between the coarsely setulated mandibule setae as the antennae begin the recovery stroke. This was observed by Gauld (1959) as was the grooming of the antennae by the mandibles when nauplii were placed in very heavy suspensions of particles. We found that if we glued the antennal setae together they became repeatedly entangled in the mandible setae. Although the mandibles appear to be co-ordinated with antennae, the amplitude of their beat seems to be variable. They can move through a fairly large angle, about 30° according to Gauld (1959) or on occasons we have observed them to move hardly at all. This would give the animal some control over the amount of combing the antennal setae receive.

The greatest acceleration of water is in the region of the setal fan, but the fan appears to 'leak' badly, at least in tethered animals, with the water reaching only some 40 % of the speed of the setae. This leakiness persists through development up to about stage 5. Gauld (1959) has said that the antennae act as a casting net drawing particles towards the mouth area. From stage 1c onwards, this is probably true, because the antennae of free swimming animals can be seen to travel through the water drawing particles under the labrum and catching them on the antennal setae themselves. In heavy particle suspensions many particles can be seen clogging the antennal and mandible setae. However, in stage 1a and 1b nauplii filmed in the free swimming situation we find that the setae of the antenna do not travel through the water but rather seem to anchor themselves within it and lever the animal through. Water movement at the limb tips of the animal is virtually zero during the effective stroke and so the limb merely moves away from and back towards the body of the animal. Combined with this the body of the animal appears to be surrounded by a thick boundary layer and drags a large amount of water forward with it during the effective stroke. During recovery the animal drags a good deal of water forward with the recovering limbs and this results in the whole body being pulled backwards.
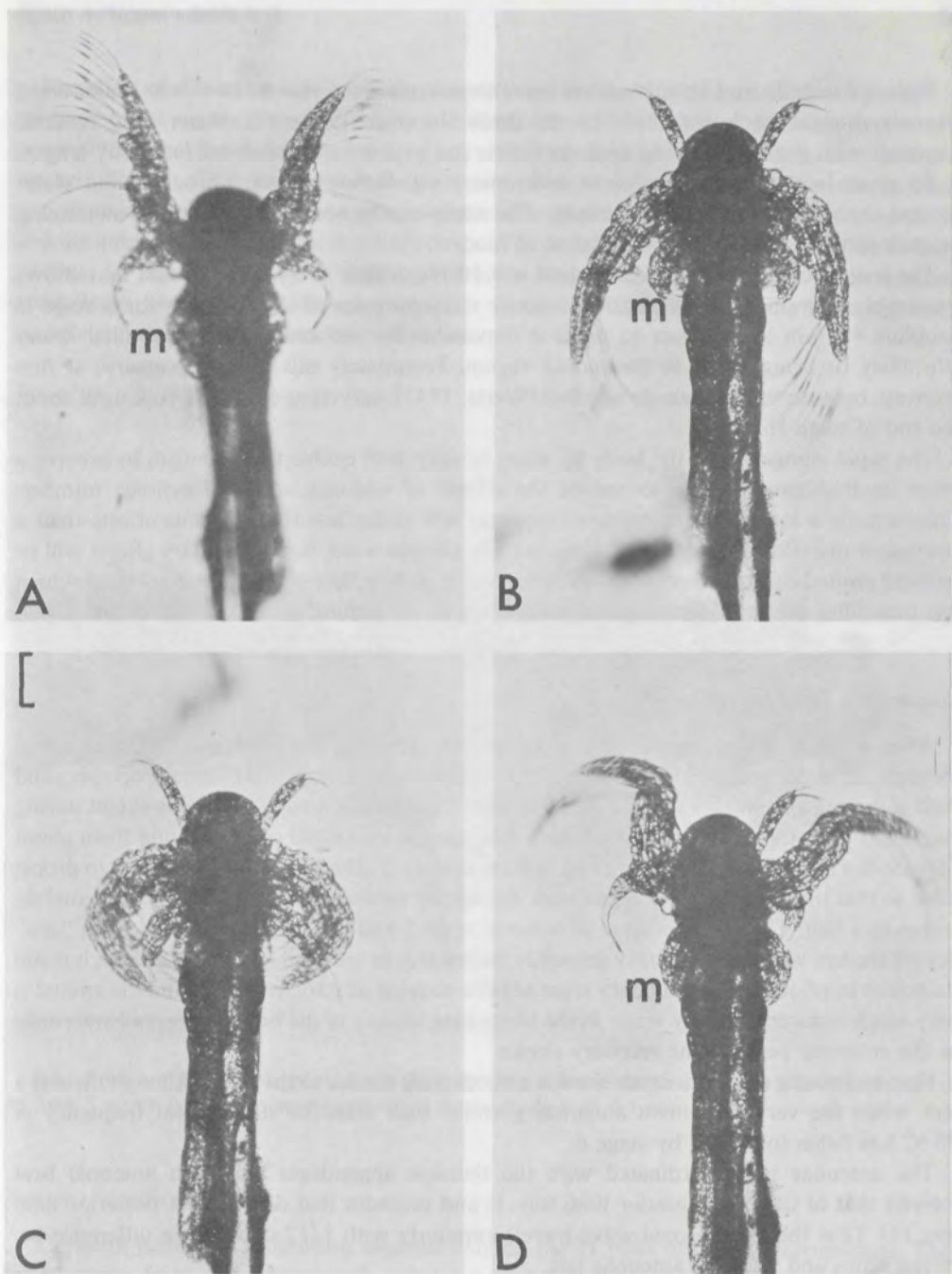
FIG. 2. The beat cycle in a stage 1c animal viewed from the dorsal aspect. A) The antennae are opening prior to the effective stroke. B) End of the effective stroke. C) Recovery stroke with setae under labrum. D) Flexed antennae and setae in mid recovery stroke. The right hand limb is prescribing a smaller amplitude recovery beat than the left. This will cause the animal to turn to the right with its next effective stroke. The mandibles (m) can be seen moving out to meet the antennae and then back under the labrum. Scale bar : 0.5 mm.

Tethered stage 1a and 1b animals are also characterized by a viscous flow with water being strongly dragged back and forth by the limbs. In stage 1a nauplii, water flow reverses direction with the limbs during each half cycle out to a distance of about one body length.

By stage 1c the animal is able to make more satisfactory forward progress and water around the animal flows less viscously. The setae can be seen to 'leak' in free-swimming animals which is necessary for filtration of food.

The frequency at which the limbs beat is 8-10 Hz, which is about the lowest that allows reasonable movement. However, the viscosity characteristics of the situation for a stage 1a nauplius 450 μm long appear to make it impossible for the antennal setae to filter water effectively or bring water to the mouth region. Fortunately this is not necessary, at first anyway, because the animals do not feed (Weisz, 1947), surviving on stored yolk until about the end of stage 1b.

The rapid elongation of the body by stage 1c may well enable the organism to acheive a better hydrodynamic shape to reduce the effects of viscosity at low Reynolds number. Theoretically a longer, faster moving organism will suffer less from viscous effects than a short slow one (Blake and Sleigh, 1974). In a less viscous water flow, boundary effects will be reduced around the limbs and body, allowing water to flow between the antennal setae which can then filter out food particles and bring them to the mouth.

LOCOMOTION IN LATER LARVAL STAGES

After stage 2, when thoracic segmentation first appears, the movement of the animal through the water becomes less erratic. The antennae remain the only effective propulsive and food gathering appendages until stage 6. The antennae develop to a considerable extent during stages 2-5 with the setae becoming bigger ; the longest exopodite setae growing from about 150 μm in a stage 1a nauplius to around 500 μm at stage 5. The stage 2 animal is able to propel itself so that the body is not dragged back during the recovery phase of the limb but merely comes to a halt. The antennal setae of tethered stage 2 and 3 specimens still appear to 'leak', but off the tips water flow is fairly smoothly backwards in tethered specimens although it still fluctuates in velocity. The boundary layer of slow moving or static water around the animal is very much reduced and only water in the immediate vicinity of the limbs is dragged anteriorly as the antennae perform the recovery stroke.

Free-swimming stage 6 animals show a smooth glide similar to the adult although there is a jerk when the very prominent antennae perform their effective stroke. Beat frequency at 20 °C has fallen to 6-7 Hz by stage 6.

The antennae are co-ordinated with the thoracic appendages and each antennal beat follows that of the most anterior limb (no. 1) and precedes that of the most posterior limb (no. 11). Thus the metachronal wave travels anteriorly with 1/12 cycle phase difference between limbs and with the antennae last.

The major change in antennal beat, visible at this time, is that these limbs no longer curve over the ventral surface to bring water and filtered particles to the mouth. Instead, the setal tips come to rest after travelling through 180° and then recover with limbs flexed and setae bunched and trailing as in the nauplius. Exopodite and endopodite still appear to rotate during the beat cycle as described for the nauplius.

The effect of this is that water that previously went to the mouth is pushed down the side of the body to the region of limbs 2-3 which at this point are finishing their recovery strokes and proceed to propel the water posteriorly. The more posterior limbs are already in their effective strokes (Fig. 3). This is probably a good sign that from stage 6 onwards the thoracic appendages have developed enough to take over the adult functions of feeding and propulsion and the antennae have become auxiliary propulsion units. By stage 7 the antennae are already starting to regress and make little contribution to propulsion ; by stage 8 the thoracic appendages have fully taken over the adult function whilst the antennae have regressed completely and play no propulsive role.
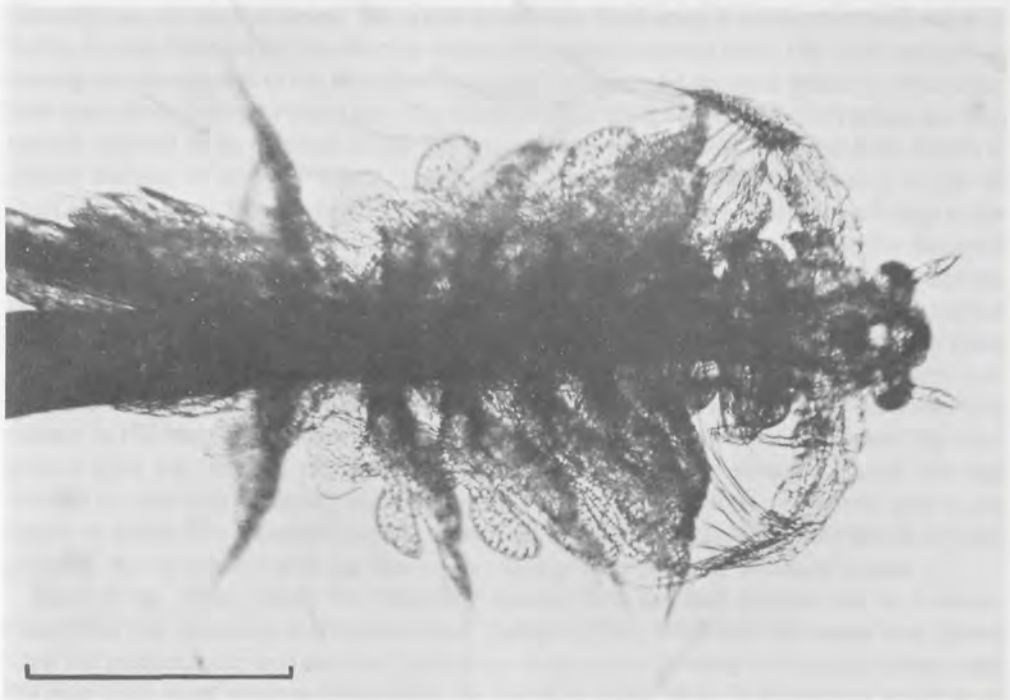

FIG. 3. Stage 6 larva. The antenna is at the end of the effective stroke and its tip is level with the tip of limb 3 which is about to start its effective stroke. Scale bar : 0.5 mm.

ADULT LOCOMOTION

The adult pattern of propulsion depends only on the 11 pairs of thoracic appendages. The larval stages from stage 5 onwards develop an adult pattern of water curents, due to the thoracic appendages, which soon dominates the flow around the animals. The description here is for adults of 9-11 mm in length, but seems to apply in general from stage 5 onwards.

In cruising adults the 11 pairs of thoracic limbs beat at an average of 3 Hz at 20 °C but the frequency can vary in the same individual from 2-4 Hz depending on conditions. The phase difference changes such that limbs 11 and 1 are beating in phase although the phase difference

can shorten slightly in faster beating individuals where 11 and 2 beat in phase. Thus there is an 1/10 to 1/9 cycle phase difference. The largest limbs travel through about 120° during the effective stroke.

Fig. 4 shows the major currents observed around a tethered male animal. However, it can be seen that little of the water flow shown in the ventral view (A) actually comes into contact with the limbs. The lateral view shows only a small flow of water past the dorsal side of the animal and a major flow on the ventral side travelling right into the limbs.
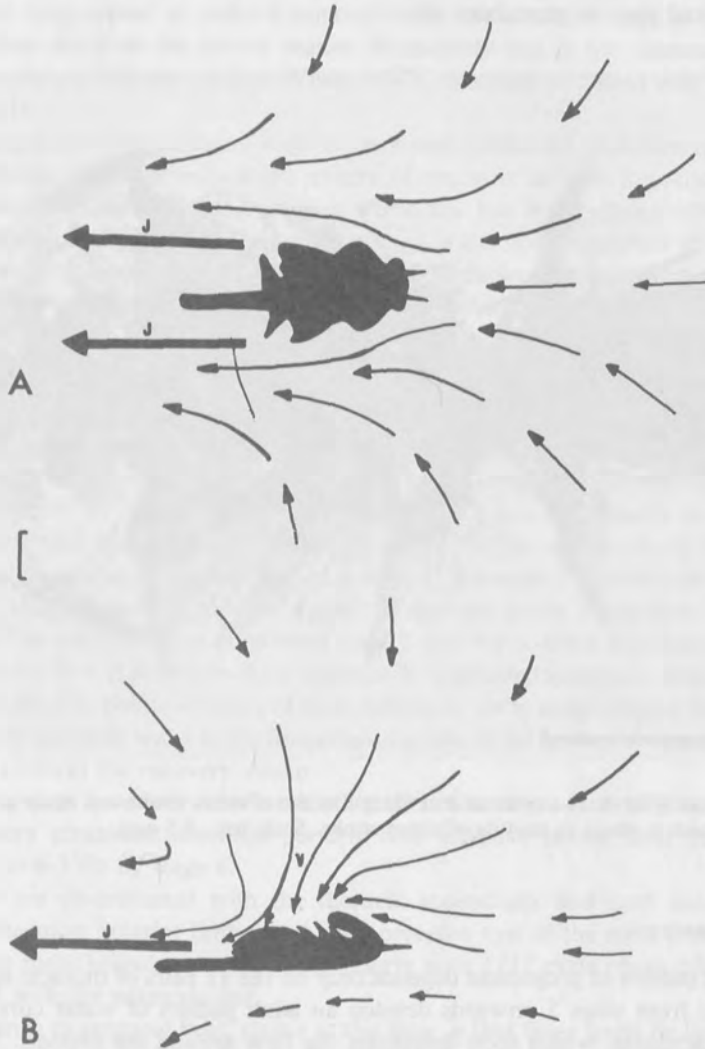

FIG. 4. A) Ventral view and B) lateral view of general water flow around a tethered adult male *Artemia*. Longer arrows represent areas of fastest flow. This occurs off the limb tips and in the two outflow jets (j). Little flow is generated on the dorsal side of the animal. The ventral current (v) can be detected over a body length away from the animal. Scale bar : 2 mm.

In free-swimming adults little water movement to the lateral and dorsal side of the animal is visible compared to the prominence of the ventrally directed current. There are two prominent jets of water leaving the posterior of the animal from the rows of limbs, one down each side. Fig. 5 shows in detail how the water is drawn through the limb system. The view is towards the side from the mid ventral line of the animal. During the recovery phase of the largest limbs water in the median space comes virtually to a halt, but as the limbs start to break away from the anteriorly directed recovery wave and perform their posteriorly directed effective stroke, the inter-limb space that forms anterior to each limb as it moves increases rapidly in volume. The result of this is for water to be accelerated laterally from the median space ; this gives rise to the ventral current (v in Fig. 5) which draws food particles perpendicularly into the median space. The water in the inter-limb space is accelerated backwards (a in Fig. 5) with the start of the effective stroke of the next anterior limb. The limb similarly is causing an enlargement of the inter-limb space anterior to it and drawing water into this inter-limb space from the mid ventral line. The third phase of the acceleration occurs when the limb reaches the end of its effective stroke and closes down on the next posterior limb which is already starting its recovery stroke. The water is jetted out of the closing space (j in Fig. 5). Thus all water used for propulsion travels from the v current to the a current and finally to the j current. The water undergoes a progressive acceleration as it travels through the sequence and is travelling at its fastest as it leaves the limbs in j. The two streams of ejected water are visible behind the animal in tethered and free-swimming animals. Water from the ventral current is filtered as it passes into the inter-limb space to be accelerated by the a current. Food particles caught on the filter setae appear to be caught up in an anteriorly directed current in the base of the food groove and carried to the mouthparts. Cannon (1928) described this current in *Chirocephalus*, believing it to be caused by water being blown back into the food groove from the bases of the limbs at the end of each effective stroke. Cannon said this resulted in anteriorly directed pulses of water. Our own observations on *Artemia* give us no reason to doubt that a similar system operates in *Artemia*. The rapid anterior travel of small particles, not in contact with the base of the food groove or setae, is clearly visible.

Most of the water enters the inter-limb spaces from the mid ventral line in *Artemia*. Describing this operation in *Chirocephalus*, Cannon (1928, 1933) said the water was drawn from the median space into the inter-limb space throughout recovery of the major limbs since the inter-limb space enlarges throughout the recovery phase. (Fig. 5). Physically water must fill this space and is quite probably drawn from the median space. However, in *Artemia* at least, the quantity of water drawn into the inter-limb space during the passage of the recovery wave is small compared to the water drawn in at the start of the breaking away of the effective strokes from the posterior face of the recovery wave.

An observation which supports the idea that propulsive water comes from the ventral surface and median space is that animals cruising with the median space in very close contact with the meniscus at the water surface, so that no water can get into the median space, come to a standstill ; this effect is most noticeable in males where the presence of the claspers severely restricts the flow of water from ahead. Females can draw some water from ahead and thus move slowly forward even when very close to the surface.

This situation is the closest *Artemia* comes to hovering ; in midwater the animal will always swim forwards. Lowndes (1933) described how the anostracan *Chirocephalus* rotates the exopodite in a propellor action during the limb beat cycle and this allows this animal to
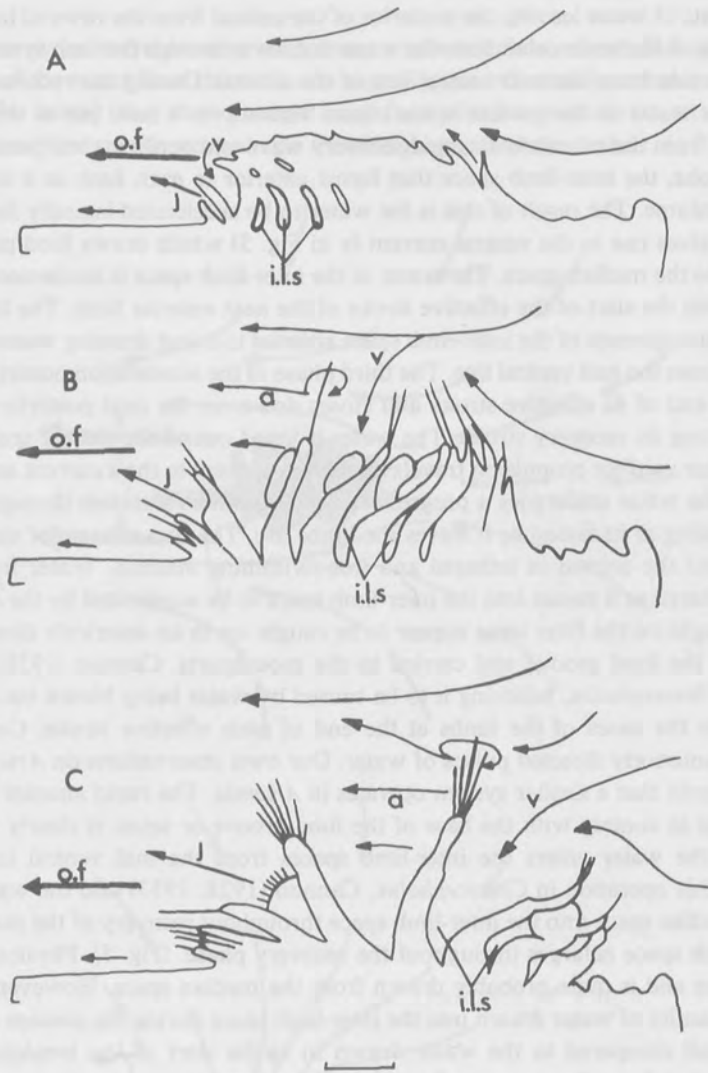
Fig. 5. Three stages, A–C, during the beat cycle of the adult limbs. The view is from the midline of the animal with ventral (v) acceleration (a) and jet (j) water flows marked. The inter-limb spaces (i.l.s.) can be seen enlarging as the limbs pass from the recovery to the effective phase (Cannon, 1928). Arrows represent direction of water flow, but not relative velocities, which are fastest in the j current. The j current marks the start of the outflow jet (o.f.) visible in Fig. 4. The ventral current has a component of flow into the plane of the diagram as well as the parallel component marked. Also note the counter-flow through the setal tips at the start of the effective stroke. Scale bar : 1 mm.

perform hovering manœuvres even in mid water. Such manœuvres do not occur in *Artemia* which does not seem to rotate its exopodite in the way described for *Chirocephalus*. To perform its normal manœuvres *Artemia* depends on bending its body and tail into a curve, thus using its tail as a rudder. The animal turns its body so that the propulsive jets of water point in the direction towards which it will turn. For left and right turns the amplitude of the limbs on the outside of the curve is increased and that of the limbs on the inside of the curve decreased. However, the pair of limbs on each segment always remain in phase. This results in a differential in the limb tip speeds of limbs on the same segment and in turn results in a relatively higher water speed in the propulsive stream on the outside of the curve of the body as compared to the inside, thus turning the animal.

METACHRONISM AND ITS FUNCTIONAL SIGNIFICANCE

The metachronal beat of the limbs is vital to the maintenance of the type of water flow described here. The a current depends on one limb and this stage of acceleration on its own is of little use to the organism, as is illustrated by the naupliar stages. The v current, apart from providing the source of propulsive water for a and j, also provides the source of food for the filter mechanism. The j current produces the two streams of high velocity water on either side of the animal. The direction of these two jets can be controlled by means of bending the body and the power by the amplitude of the limb beat. The tail is also involved as a rudder being especially useful for dorsal or ventral turning. Thus the j current along with the tail enables the adult *Artemia* to effect manœuvres. Both v and j currents depend on the existence of phase differences between at least two limbs.

The existence of a metachronal beat may represent a real energy saving since no individual limb has to accelerate water from zero ; at any instant there will always be an energy input to keep the flow going. Energy losses between successive inputs are minimised and the speed of water flow can be maintained at the level of the limb-tip velocity, as is observed in adult *Artemia*.

The naupliar antennae manage to propel water to a mere 40% of the speed of the setal tips. It is interesting, therefore, to find that by stage 6 water flowing in similar regions around the antenna is reaching around 60% to 70% of the setal tip velocity. However by this time the antennae have become integrated members of a metachronal system and no longer function to filter particles from the flow.

Metachronism may also reduce the net forces acting on individual limbs, requiring lighter, less muscular appendages with a saving in weight and in the energy required to drive them. The thoracic appendages of *Artemia* are much more delicately built than antennae of a corresponding size.

The nauplius is extremely inefficient in terms of propulsion. The slow rate of beating of the limbs is just sufficient to allow enough movement for simple orientation responses but little else. This makes the nauplius completely defenceless and unable to feed until it grows. This may represent an adaptation to the temporary pond environment. Since the early nauplii do not feed but utilize yolk reserves they must save energy to grow and develop. Also a brine pond, especially a freshly flooded one, allows few organisms to survive and so *Artemia* nauplii possibly have fewer problems with predators than most animals. Thus a high rate of limb beat and high manœuvrability might well expend energy for no purpose. Freshwater

Anostraca all have similar slow moving nauplii and all survive in the temporary pond habitat. The nauplii hatch quickly after flooding and grow much faster than other potentially predatory crustaceans such as copepods. Insect predators also colonize temporary ponds and pose a similar threat. However, adult stages are well able to avoid such predators being much larger and more manœuvrable than *Artemia* nauplii. Copepod nauplii, on the other hand, survive in permanent bodies of water by moving fast with limbs beating at very high frequencies and they can move rapidly through the water to avoid predators. Although copepod nauplii are considerably smaller than nauplii of *Artemia* our observations show that they are able to swim and manœuvre with considerable agility.

The limited, low frequency, naupliar propulsion system may well be a compromise with other developmental factors which gives way to the multi-limbed metachronal mechanism of the adult as soon as possible. This endows the animal with greater manœuvrability and a more efficient energy expenditure which covers three major life functions; swimming, feeding and respiration.

Our continuing studies on propulsion are very much concerned with the question of the advantages in energy expenditure and hydrodynamic efficiency of metachronal systems in aquatic propulsion in crustacean limbs and protozoan cilia.

A full quantitative analysis of the movie films from which these descriptions are drawn is in progress.

Summary

1. Swimming movements of development stages of *Artemia* were filmed by high speed cinemicrography.

2. Animals were studied in the free-swimming state and also tethered to glass needles.

3. Naupliar locomotion utilises one pair of propulsive appendages, the antennae. These both propel the animal and filter food particles upon which it feeds. At the earliest stage viscous effects of the water prevent filtration of water in free-swimming animals and would thus prevent feeding until stage 1c.

4. The successive moults allow the development of thoracic appendages. The antennae appear to lose their feeding function by stage 6 and become incorporated into a metachronal propulsion system with the thoracic appendages.

5. The adult locomotion utilises 11 pairs of paddlelike limbs co-ordinated in a metachronal rhythm. These give rise to a continuous water flow which both draws food into the filter system and creates two propulsive water streams at the rear of the animal. These can be directed and independently controlled in power to enable manœuvres to be executed.

6. The relevance of metachronism is discussed, as is the possible importance of developmental and environmental factors in determining the form of naupliar locomotion in Anostraca.

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