Behavioural hydrodynamics of *Cloeon dipterum* larvae (Ephemeroptera:Baetidae)

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Abstract. Relationship of aquatic benthic macroinvertebrate body form to habitat has been questioned for more than 80 years, without satisfactory explanations. Physical determinants of locomotion can provide more definitive answers. *Cloeon dipterum* (Linn.) larvae live in still and slowly moving water, but have highly streamlined cylindrical (width : length 1:8) bodies. Because of a low density ratio the larvae walk slowly. At 1.2 mm/s, the 95% boundary layer extends beyond 3.0 mm. Gill size and orientation fall close to permissible height of projections for the boundary layer while swimming. Reynolds number ($\sim$1.2 × 10³) of a swimming larva is sufficiently low that the streamlined shape will do little to reduce drag. However, the streamlined shape will be important during accelerative escape motion when velocities >200.0 mm/s within 0.04 s are achieved, giving accelerations of the order of 6.5 m/s², because the streamlined shape confers a low coefficient of added-mass. This reduces virtual mass during initial acceleration. Highly streamlined cylindrical macroinvertebrates could be expected to have accelerative motions in their behavioural repertoire.

Key words: Ephemeroptera, Baetidae, *Cloeon dipterum*, behavioural hydrodynamics, body form, locomotion, accelerative escape motion.

Anatomical adaptation of animals inhabiting lotic environments has been much discussed since Steinmann (1907) theorized that dorso-ventral flattening of the body of torrenticolous animals minimized area of body exposed to flow, thus helping the animal maintain its hold on the substrate. Many workers (e.g., Needham and Lloyd 1916, Dodds and Hisaw 1924, Welch 1935) discussed efficiency of streamlined body form in terms of force of water against the body, and/or reduction in eddy formation and its retarding effect. Hora (1930) noted that torrenticolous organisms have shapes similar to those of aeroplane struts; however, he was unaware that reduction of drag by shape is size related.

Ambühl (1959) is generally considered to be the first to apply hydrodynamic factors to the shape of benthic organisms, illustrating for the first time for biologists that lotic organisms might make use of the velocity profile of the boundary layer. However, Stuart (1958) had investigated the lifting effect of current on ephemeropteran larvae and concluded that the flattened body was not designed to withstand currents, but enabled larvae to inhabit crevices and avoid current. Hynes (1970) discussed adaptations, especially behavioural ones, of insects to running water, noting that some flattened insects which live under stones during the day may be found on the top of them at night, exposed to the full force of the current.

Statzner (1981) and Statzner and Holm (1982) began a recent trend of using hydrodynamic principles to reexamine the problems of morphological adaptations to flow. Statzner (1981) referred to the Principle of Critical Phases (Schwerdtfeger 1977): exposure to forces of flow for only minutes a day may determine whether an animal will be present in a particular hydrodynamical regime. Statzner and Holm (1982) repeated some of the work of Ambühl, using Laser Doppler Anemometry. They showed that a dorsoventrally flattened streamlined body is more likely to produce maximum lift directly over the legs than to allow the animal to live in reduced velocity in the boundary layer. That work, although it dealt only with dead insects, provides the best insight to date on the flattened streamlined shape of some insect larvae.

More recently Statzner (1988) examined the relationship between growth of lotic organisms and Reynolds number (as an expression of drag), concluding that shape of benthic macroinvertebrates in flow is a compromise between life at low and high Reynolds number and is not adapted to minimize drag at any particular Reynolds number. While this conclusion may apply to some situations, reduction of drag may

not always be the main requirement for rapidly accelerating macroinvertebrates. He also called for reexamination of the basic tenets of the debate surrounding morphological adaptations of aquatic benthic macroinvertebrates. Statzner and Holme (1989) continuing their earlier work (Statzner and Holme 1982) concluded that the physical significance of morphological adaptations of lotic macroinvertebrates depends on the Reynolds number of the organism and is mainly affected by flow separation which is related to the ratio of body length to height and to slope of the posterior body.

Although such studies and those of others (e.g., Bournaud 1975, Chance and Craig 1986, Soluk and Craig 1988) show that shape and behaviour of lotic benthos affect responses to flow, the presence of cylindrical streamlined insects in lentic environments has still not been adequately explained. However, a common point made by almost all who have dealt with body form of aquatic insects is that cylindrical streamlined insects have darting movements and swim fast.

Swimming in aquatic insects that use legs as propulsive devices has been examined in detail by Nachtigall (1985), as has locomotion of dipteran larvae, which use curling motions of the abdomen. Jet-propulsive locomotion, used by odonate larvae, is also well documented (Mill and Pickard 1975). But undulative motions of the abdomen for linear forward motion, examined in great detail for fish (e.g., Webb 1976), has not been examined in insects, although Saita (1979), who used high speed cinephotography to observe movements of gills of ephemeropteran larvae, made superficial observations on larvae swimming.

Also much discussed has been shape and size of aquatic insect gills. Dodds and Hisaw (1924), and others (see Hynes 1970), thought that insects in running water, being well supplied with oxygen, would have a smaller gill surface area than those in lentic habitats. But Hynes (1970) commented that this suggestion does not bear close examination and that adaptations for respiration are much more complex.

The shape and size of gills, plus the body shape of aquatic insects, can be reconsidered using principles of locomotion. Work by Daniel (1984) and Daniel and Webb (1987) shows that the problems associated with achieving rapid acceleration in a fluid medium are different from

those of dorsoventral flattening to resist forces due to flow.

Physical principles of locomotion

Daniel and Webb (1987) examined physical mechanisms underlying various modes of locomotion, identifying where possible the limits of use of each mechanism for animals of different size in different environments. They identified density ratio, ρ_a/ρ_e (ρ_a = density of the animal; ρ_e = density of surrounding medium) as the single most important factor determining the feasibility of using various propulsion mechanisms in different environments. A high density ratio allows more effective use of the substrate. In water, where density ratio may approach unity, effective weight tends towards zero and use of the substrate becomes increasingly difficult. Any vertical component of walking removes the animal from the substrate, to which it returns only slowly. Because of a low density ratio, benthic insects will walk more slowly than their terrestrial counterparts. Because of decrease in effective weight, components of forces involved in walking change from predominantly vertical to horizontal. The shift to a predominantly horizontal force may also help overcome the greater drag resisting forward motion in water.

Propulsion involving rapid acceleration is affected by size. For all organisms moving in a fluid medium, forces resisting their motion can be considered as having three components: resistance = drag + acceleration reaction + body inertia. Drag depends only upon absolute speed of the animal, while the latter two terms depend upon changes in the animal's velocity and thus resist acceleration or deceleration. The acceleration reaction depends on size, shape and acceleration of the body and has the same effect as an increase in mass (added-mass) of the body. Daniel (1984) expresses the acceleration reaction as:

$$G = -\alpha\rho V(dU/dt) \qquad \text{(Equ. A)}.$$

where α is the added-mass coefficient, ρ is the density of the medium, V is the volume of the body and (dU/dt) is the acceleration of the body relative to the medium far away. Added-mass ($\alpha\rho V$) is the additional mass of fluid that can be considered as accelerated with the accelerating body in a fluid medium (Daniel 1984). The

sum of mass of the body plus added-mass is virtual-mass. Size dependence of the acceleration reaction is given by the volume factor: larger bodies will experience a greater force. Shape dependence of the acceleration reaction is given by the size independent added-mass coefficient (α). For spheres, the added-mass coefficient is 0.5 and for a prolate spheroid (fish-shaped) of fineness of 1:8 (width : length) it is 0.029 (Lamb 1945). Thus streamlined animals are clearly better suited than those unstreamlined for rapid acceleration in a dense medium. Equation A will apply to animals in both lentic and lotic situations. The function dealing with acceleration will be larger for acceleration upstream and less for that downstream.

The acceleration reaction overwhelms the effects of drag in animals swimming with large-amplitude undulations, but the relative importance of this reaction decreases rapidly with time when acceleration is high (Daniel 1984). Drag, then, is not a major initial consideration for an animal undergoing rapid acceleration. Thus the shape of an animal having rapid acceleration as part of its behavioural repertoire relates more to reduction of virtual mass (i.e., mass of body plus added-mass) than to reduction of drag. Streamlining and elongation of an animal serve this purpose (Daniel 1984).

Accelerative escape motion (AEM)

Rapid acceleration may relate to the "critical phase" (Statzner 1981) of behaviour of the animal under consideration. Daniel and Webb (1987) argued that maximum speed and acceleration are likely to be important during escape manoeuvres from predators and they proposed the term "accelerative escape motion" (AEM). Although it may be used only rarely, this critical phase may determine to a large extent the success or failure of predator-prey interaction, i.e., the rarely used event may have great selective advantage. If selection for high performance in AEM is particularly strong, the shape of animals will be optimal, not for the common, steady-state mode of movement, but for the infrequently used, unsteady accelerational mode (Daniel and Meyhofer 1989).

In this work I apply the physical determinants of locomotion as outlined above, together with other hydrodynamical principles (Vogel 1981), to observations on body shape, walking, and acceleration and swimming behaviours of

Cloeon dipterum (Linn.) larvae to establish whether this highly streamlined animal fits the general constraints on moving rapidly in water and to give some insights to why some lentic insect larvae are highly streamlined. I do this in the context of what I term "behavioural hydrodynamics", i.e., the complex feedback interactions between the fluid, body shape and, in particular, the behaviour of the organism (sensu Bournaud 1975, Chance and Craig 1986, Soluk and Craig 1988, Lacoursière and Craig 1990). I hypothesize that cylindrical streamlined aquatic insects are more capable of rapid acceleration and swimming than those less streamlined.

Study Organism

Cloeon dipterum larvae live among vegetation in ponds and sluggish rivers in Europe and Central United States (Edmunds et al. 1976). The larvae are cylindrical and highly streamlined, of a prolate ovoid shape (Fig. 1) with a fineness ratio of approximately 1:8 (maximum diameter of thorax : total body length, exclusive of terminal filaments). The head, viewed laterally, is hemispherically-shaped and the thorax is smoothly tapered towards the abdomen. The antennae are long and hairless. The abdomen is flattened dorsoventrally and tapered smoothly laterally to the long terminal filaments. Eastham (1958) considered the larvae to be pelagic, noting that they swim rapidly, initially in a cetacean (dorsoventral movements) fashion, then with lateral rhythmical movements of the abdomen in a piscine fashion. Nachtigall (1985) stated that these larvae are jet swimmers, drawing water into the hind gut and expelling it suddenly. But he gave no source for that information and I have found no evidence in the literature on *Cloeon*, or from this study, that such locomotion is used.

Methods

Cloeon dipterum larvae (4–7 mm body length) were collected from ponds near Åsbo, Gästrikland, north of Uppsala, Sweden and kept in the laboratory at 10°C in an 8:16 hr L:D light regime.

To determine body density of larvae, five preserved larvae 6–7 mm long were placed in a previously filled 10-ml Gay-Lussac specific gravity bottle. Water displaced though the capillary ground-glass stopper was weighed on a balance accurate to 0.0001 g. Average volume
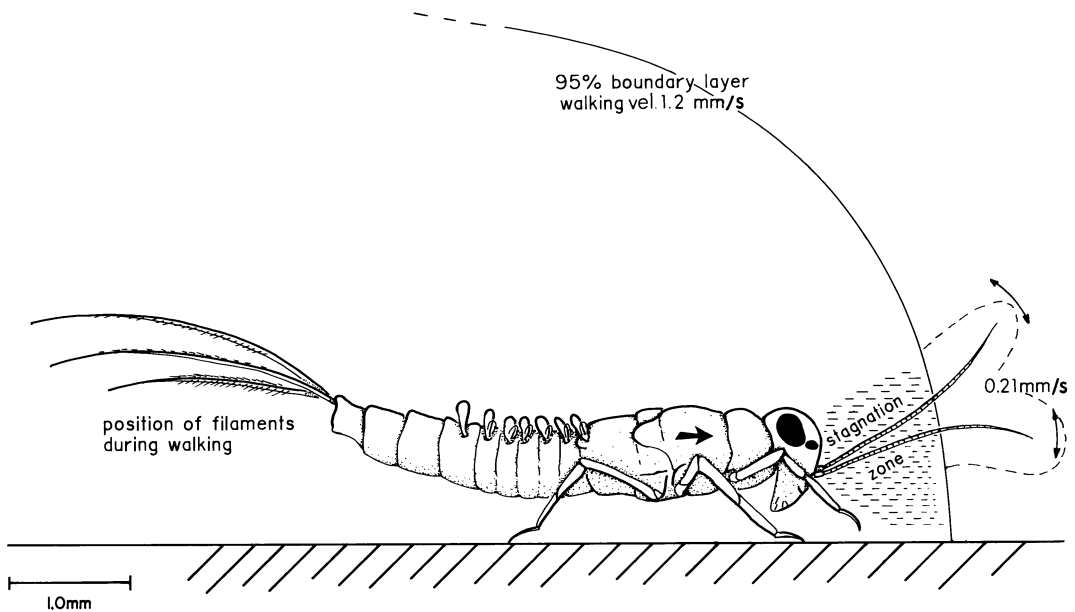
FIG. 1. Lateral habitus drawing (from video monitor) of a *Cloeon dipterum* larva walking at 1.2 mm/s showing observed thicknesses of the anterior stagnation zone and boundary layers around the body and antennae. Arrows indicate direction of movement.

was 1.20 mm³. Mass was determined by blotting the larvae to dampness and weighing. Average mass was 0.0015 g, giving an average density of 1.25 g/ml.

Observations of larval walking behaviour and AEM were made with larvae in a flat-bottomed 50-ml (2 × 5 × 5 cm) spectrophotometer cuvette containing pond water. Larvae were placed, either individually or in groups of four, into the cuvette and allowed to acclimate to room temperature (18°C) overnight. A suspension of either Day-glo® powder (Chance and Craig 1986) or microcrystalline cellulose (Avicel®, FMC Corporation, Philadelphia, USA) in water was used to make flow visible. Each suspension was allowed to equalize to the temperature of the water in the cuvette before being added, otherwise density differences induced bulk flow in the cuvette. Illumination was provided by a fibre optics light. Back lighting and lateral lighting provided adequate contrast between particles and background. Observations of larvae in the cuvette were made laterally. Observations on swimming behaviour were made from above on larvae that swam across the centre of a culture dish (15 cm diameter; water depth 5 cm). To elicit AEMs, terminal filaments of larvae were touched with a firm bristle.

Observations were recorded with a European PAL Standard (25 frames/s) Panasonic WVP 100E video camera, NV-100 video cassette recorder (VCR), and TC-2633UR monitor. The camera was attached to a Wild M5 dissection microscope mounted either horizontally or vertically on a heavy base. A timing interval of 0.10 s was also recorded onto the videotape. For determination of dimensions and velocities, the TV monitor was calibrated by recording an accurate millimetre rule. As far as possible, measurements were made from the centre of the screen. Velocities were determined by measuring frame-by-frame the distance moved by either particles or larvae. Because of the lower resolution (noise and jitter) of the system in the VCR's "frame-by-frame" mode, movements readily detectable in "real" time could not always be resolved. For this reason, velocities <0.05 mm/s could not be detected. Because the PAL TV Standard uses 25 frames/s (i.e., one frame = 0.04 s), extremely rapid movements could not always be measured because they took place in a period shorter than the time for one frame, resulting in blurred images. Observations of AEM suffered from this problem.

Observations of distance swum by larvae were made at 2.5× magnification (video monitor);

TABLE 1. Velocities of movements of *Cloeon dipterum* larvae

Movement	Velocity (mm/s)			
	Mean	Range	n	SE
Walking	2.15	1.2–3.5	17	0.018
Sinking				
Legs retracted	13.6	11.7–15.0	6	0.53
Legs protracted	5.3	4.3–6.0	3	0.50
Antennal movements				
1 larva	0.25	0.21–0.29	5	0.014
4 larvae	2.12	1.04–3.04	6	0.028
Filament raising				
Stationary	1.83	1.52–2.20	14	0.056
Pre-AEM				
1 larva	1.34	1.02–1.56	9	0.07
4 larvae	0.69	0.40–1.08	7	0.10
Swimming	118.0	86.0–200.0	8	1.50

those of walking, jumping and acceleration behaviours at 24× magnification; and those of antennal movements and their boundary layer thickness at 90× and 268× magnification. When Harper and Blake (1989) evaluated errors in use of high-speed cinephotography for determination of fish acceleration, they showed that low film speeds (<100 frame/s) result in high error (underestimation) in determination of maximum acceleration. However, this is off-set by using higher magnification of the image for data extraction. They provide curves (their fig. 8) combining the effects of image size and film speed on percentage error of maximum acceleration. For the acceleration determinations of *C. dipterum* larvae using video recording at 25 frames/s at 24× magnification, the percentage error of the maximum accelerations recorded is <20%.

Measurements of the frontal area of larvae that were walking and swimming were made by holding the larvae in the orientation observed on the video tape and tracing the frontal area at a magnification of 25× onto paper. The area was then cut out and weighed, and the frontal area was determined from the weight of a known area of the same paper.

The hydrodynamic principles applied to this present study have been well explained by Vogel (1981) and applied to lotic freshwater in-

vertebrates by Statzner and Holm (1982), Chance and Craig (1986), Davis (1986), Craig and Galloway (1987) and Soluk and Craig (1988), so are not considered here.

Local Reynolds number of larvae were determined as $Re_x = UL/\nu$, where ν = the kinematic viscosity of water, 1.1 mm²/s, U = the forward velocity of the larva and L = length of the larval body, or diameter of antenna.

Observations

Velocities of *C. dipterum* movements are given in Table 1.

Walking behaviour

Larvae walked slowly along the smooth substrate, with Re's ranging from 4.4 to 22.3. Faster movements resulted in larvae losing contact with the smooth substrate. The legs were protracted and retracted slowly with the pretarsal claws describing a retraction arc in the same plane as the substrate i.e., horizontal. The mesothoracic femur was held at right angles to the body with protraction and retraction achieved mainly through movement of the tibia. These leg movements resulted in little vertical movement of the body.

While walking, the larvae either dragged the terminal filaments along the substrate (10 out of 14 larvae observed) or held them slightly above the horizontal (Fig. 1). When larvae stopped, filaments and abdomen were raised slowly to an angle of 30–35°. Prior to AEM, the abdomen and filaments were raised further to an angle of ~90° (Fig. 3). For single larvae, filament raising was significantly slower ($p < 0.001$, t-test) than when other larvae were nearby.

Larvae remained stationary for periods of time varying from a few seconds to minutes. For example, a larvae by itself walked for 1.0–5.2 s ($n = 14$, $\bar{x} = 3.5$ s, SE = 0.39) and remained stationary for 1.0–60.0 s ($n = 14$, $\bar{x} = 12.5$ s, SE = 4.36). When nearby larvae were encountered, a larva would jump vertically off the substrate by downward protraction of the legs, maintain the body horizontal, and then sink passively back to the substrate. Sinking rate was much slower when the legs were protracted than when they were retracted (Table 1).
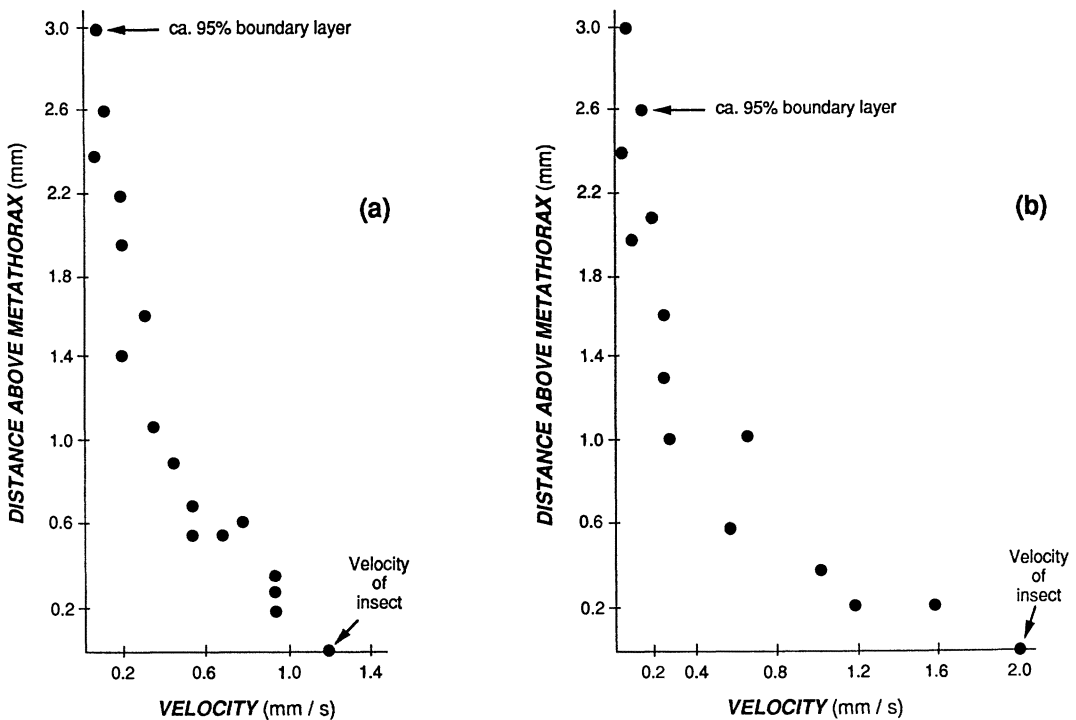
FIG. 2. Velocity profiles of boundary layers over the metathorax of walking larvae of *Cloeon dipterum* (a. walking velocity 1.2 mm/s; b. walking velocity 2.0 mm/s). Determined by measuring particle velocities from video monitor. Magnification 24×.

Boundary layer (and stagnation zone)

Because of viscous effects, a walking larva carried a stagnation zone extending anteriorly to ~1 mm (Fig. 1). The 95% boundary layer was ~3.0 mm thick for a walking velocity of 1.2 mm/s (Figs. 1, 2a) and ~2.6 mm thick at 2.0 mm/s (Fig. 2b). As expected, the velocity profile of the boundary layer for the slower larva had a steeper slope than that of the faster larva.

Antennae

As a larva walked, the distal one-third of its antennae extended through the stagnation zone in front of the head (Fig. 1). The antennae waved up and down, above the head to the substrate, in an arc of ~90°. For single larvae, walking or standing still, velocities for the distal one-third of a waving antenna were significantly slower ($p < 0.001$, t-test) than when other larvae were nearby (Table 1). The mean diameter (L) of the distal one third of the antenna, measured at 400× magnification, was 0.0186 mm ($n = 8$, SE = 0.0016), so Re was ~0.004 for the lower range of waving velocities and ~0.036 for the higher velocities. The observed 95% boundary layer thickness around an antenna moving at 0.21 mm/s was 0.34 mm (Fig. 1).

Body shape

Larvae held their heads at approximately right angles to the body while walking (Fig. 1), presenting a mean frontal area to the water of 0.61 mm² ($n = 6$, SE = 0.018). Prior to AEM and during swimming (Fig. 3), larvae retracted the head ventrally and arched the thorax dorsally, resulting in a more hemispherical shape with a mean frontal area of 0.58 mm² ($n = 7$, SE = 0.006), not significantly different ($p > 0.4$, t-test) from that when walking. During AEM and swimming, antennae and legs were held close to the ventral surface of the body forming a highly streamlined body shape. However, during swimming the gills protruded from the dor-

solateral surface of the abdomen. Projection height of the gills increased posteriorly from 0.29 mm to 0.33 mm.

Accelerative escape motion (AEM)

Determination of the initial velocity at which larvae moved during AEM was difficult because of limitations in the speed (frames/s) of the video recording system. However, immediately prior to the AEM, legs were retracted posteriorly against the body. This occurred in less than 0.02 s (one field) as indicated by the blurred image in the video frame prior to the one showing acceleration. It is possible that the gills moved too, because the image of the abdomen was also blurred.

A typical AEM is illustrated in Figure 3. From a stationary position, within 0.04 s, the body assumed a sinusoidal shape with the head and thorax highly arched as the posterior abdomen and terminal filaments moved downwards and touched the substrate. Within 0.08 s the abdomen and terminal filaments passed below the long axis of the body, a total angle of movement of ~80°, and maximum acceleration was reached (>962 mm/s^2). The head and thorax were now less arched. Within 0.12 s the body straightened out and acceleration was lower. By 0.16 s the body was essentially straight and the posterior abdomen had begun the reverse stroke. The larva was now decelerating.

Measurements from artificially stimulated larvae gave velocities of 68.0–200.0 mm/s at the end of 0.04 s ($n = 9$; $\bar{x} = 122.0$ mm/s; SE = 12.6), giving accelerations of 1.7–5.0 m/s^2. However, larvae beginning an AEM naturally were capable of even faster acceleration, the fastest recorded being 6.5 m/s^2.

Swimming

During AEM, larvae reached a distance of 3.3 mm above the substrate (Fig. 3) but then swam closer (1.5–2.0 mm), so that the terminal filaments touched the substrate on each down stroke. Larvae sometimes swam as far as the full diameter (15 cm) of the observation chamber, but typically only shorter distances ($n = 15$, $\bar{x} = 7.3$ cm, SE = 0.72). Reynolds numbers for swimming larvae ranged from 312 to 1272. In all instances, only cetacean (dorsoventral) movement of the abdomen was observed. Ob-

servable particles near the larva swimming at 200 mm/s, and where the boundary layer was assumed to be fully established, showed that the 95% boundary layer over the position of the anterior gills was ~0.50 mm thick (Fig. 3; insert).

Discussion

Walking

With a body density (1.25 g/ml) close to that of water, the behaviour of a walking C. dipterum larva fits well constraints imposed on small walking organisms with a low density ratio (Daniel and Webb 1987). To maintain contact with the smooth substrate, larvae walk slowly. The retraction movement of the legs is in an arc mainly in the plane of the substrate, which means that most of the ground force of walking is in the horizontal forward direction and results in little vertical movement of the body. When disturbed and walking faster than 3.5 mm/s, larvae tend to lose contact with the substrate. Although a low density ratio may be a limiting factor for the upper walking velocity of such benthic insects, it is used to advantage by C. dipterum larvae which jump to avoid other larvae and then settle at a rate controlled by the spread of the legs.

The stagnation zone anterior to a walking larva, plus the boundary layer around the antennae and body (Fig. 1), constitute a barrier through which environmental stimuli and oxygen must diffuse to reach the animal. Only 3 of 14 larvae observed used their gills to produce respiratory currents. Perhaps walking and accelerative movements are used after stationary periods to carry the larva into more oxygenated water. It would be interesting to examine oxygen saturation profiles in water around a Cloeon larva prior to locomotory behaviour.

Antennae

It is not known if C. dipterum larvae use their antennae to detect chemical cues. If they do, antennae should be waved faster when such cues are detected. Higher velocity of movement would not only increase the sampling rate of water immediately in front of the larva but also decrease the thickness of boundary layer so that time taken for a chemical stimulus to reach sen-
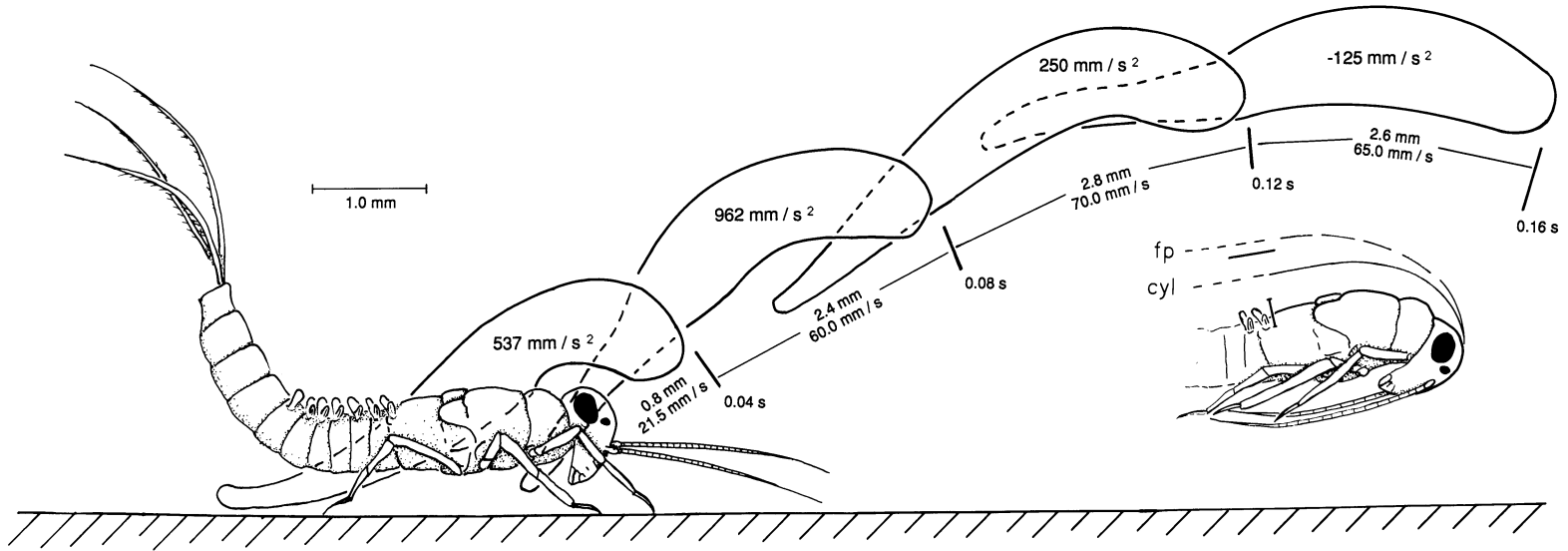
FIG. 3. Typical stance of *Cloeon dipterum* larva prior to accelerative escape motion (AEM). The position and shape of body during AEM from four consecutive video frames are superimposed. The distance (mm) moved between each frame (0.04 s) is given, as is the velocity at the end of each frame. The acceleration figures (mm/s²) given in each body outline is that achieved between each frame. Insert (to scale), is a composite drawing of the body shape and probable disposition of antennae and legs of a larva swimming at 200 mm/s. The broken line is the calculated 99% boundary layer assuming the larva were a flat plate (fp) (Vogel 1981). The solid continuous line is the calculated 99% boundary layer for a cylinder (cyl) with its long axis parallel to the flow (Silvester and Sleigh 1985): the varying radius of the body has been taken into consideration. No attempt to determine boundary layers along the ventral surface was made because of the complexity of that surface. The short solid bar between the two calculated boundary layers is the observed (~95%) boundary layer. The short vertical bar in front of the anterior gill is the height of permissible roughness for the "fp" boundary layer at that position (Vogel 1981).

silla would be less (Garvis 1976). Indeed, when a single larva was approached by another larva it significantly increased the velocity of its antennal movements.

The observed thickness of the 95% boundary layer round an antenna of diameter 0.0186 mm, moving at 0.21 mm/s was 0.34 mm (Fig. 1). The 99% boundary layer thickness (δ) around a filamentous shape normal to the flow, such as an antenna, can be approximated by the expression:

$$\delta = d / \sqrt{Re} \qquad \text{(Equ. B)}$$

where d = diameter of the fibre (Braimah 1987). For the antenna moving at 0.21 mm/s the theoretical thickness (0.31 mm) of the 99% boundary layer is in reasonable agreement with the observed thickness (0.34 mm) of the 95% boundary layer. Unfortunately, boundary layers around antennae moving faster were not observed, but it is to be expected that they would be thinner.

Body shape

Frontal area is one factor that determines drag, but the reorientation of the head of the larvae prior to AEM and swimming does not result in a significant change in frontal area, because more of the thorax is exposed. However, the shape change may serve two functions. Since drag is of minimal importance during AEM, the change in shape is probably to produce a more prolate-spheroid shape to reduce the added-mass coefficient. Further, the hemispherical shape of the head and thorax could be expected to reduce drag during swimming because it is known that such a shape has a lower coefficient of drag than a more bluff body (Vogel 1981).

Accelerative escape motion (AEM)

It is interesting that maximum larval acceleration occurs within the first body length of the distance travelled (Fig. 3). This is possibly the most important component of a successful escape manoeuvre and may explain why velocities achieved within 0.04 s by artifically stimulated larvae are within a close range. It would be interesting to know if giant axons, involved in initiation of muscle contractions in other arthropods with AEM (Webb 1979), are present in C. dipterum larvae.

According to Equation A, the force (G) nec-essary to accelerate a C. dipterum larva at the maximum acceleration recorded is G = -2.3×10^{-9} N (α = 0.029 for a fineness ratio of 1:8; ρ = 0.99 kg/m^3 @ 18°C; V = 12 × 10^{-9}/m^3; and (dU/dt) is 6.5 m/s^2). If the larva were of a fineness ratio of 1:4 where α = 0.082, but all other variables were equal, the force would be -6.3×10^{-9} N, a factor three times greater. Thus, if initial maximum acceleration is important, it is necessary for a larva to have a streamlined prolate ovoid shape with the lowest possible added-mass coefficient.

Equation A also shows that the force required to provide a large acceleration can only be minimized by reduction in added-mass coefficient and/or volume (Daniel 1984). Cloeon dipterum larvae are of a shape where any further streamlining would not provide further benefit by reduction of the added-mass coefficient. Further, Daniel (1984) suggested that reduction of volume can only be carried to a certain point because less volume would reduce muscle available for the propulsive force.

Eastham (1958) showed that, unlike more slowly swimming ephemeropterans, C. dipterum larvae have a cruciform arrangement of abdominal muscles, and hence these muscles can be considered to be slightly pennate. Alexander (1983) showed that pennate muscles can exert more force than a parallel-fibred muscle and that pennate muscles swell less at contraction, an advantage when in a confined space. Camatini and Saita (1972), Carnevali and Saita (1975), and Saita (1979) examined the ultrastructure of gill and abdominal muscles of fast swimming ephemeropteran larvae and showed that sarcomere length is 30% shorter than that for other skeletal muscles and that the ratio of actin to myosin fibrils is low, similar to that of flight muscle. Such short sarcomere length and arrangement of fibrils is known to be associated with rapid contraction (Aidley 1985). Given that the abdominal shape and volume of C. dipterum larvae are hydrodynamically optimal for AEM, it is highly probable that the larvae can achieve a more rapid power output than expected from the normal arrangement and structure of abdominal muscles.

Swimming

I observed that C. dipterum larvae used only cetacean movements of the abdomen and terminal filaments. This is at variance with East-

ham (1958) and Saita (1979) who recorded that after the initial accelerative movement, which is cetacean, the larvae swam with piscine (lateral) undulations. Piscine movements would be unexpected because the abdomen is dorsoventrally flattened and side-to-side movements would be less effective. Swimming larvae complete one cycle of movement of terminal filaments and abdomen within 0.12 s. This is in close agreement with 0.15 s observed by Saita (1979) for the lateral abdominal movements. Alverdes (1925) showed that *C. dipterum* larvae rotated as they swam, which could give the appearance of piscine-type movement. Clearly, more observations of swimming are needed.

Webb (1981) has shown for benthic fishes that interaction of the body with the substrate produces important hydrodynamic ground effects for rapid starts. When the body works directly against the substrate rather than just against fluid, more muscle energy is converted into body motion. This likely occurs when the terminal filaments and posterior abdomen of *C. dipterum* larvae touch the substrate during the initial phase of AEM (Fig. 3), and also during swimming when the larva is close to the substrate. Eastham (1958) also observed that a swimming larva leaves a regular series of tail marks on the substrate.

Added-mass is of overwhelming importance during the initial period of AEM (Daniel and Webb 1987); in contrast, drag becomes more important when the boundary layer has developed fully. At $Re > 10^4$, streamlining reduces drag, but at $Re < 10^2$–10^4, streamlining is less important. Shapes of organisms with lower Re's tend to be more rotund because flow separation becomes less important than skin friction (Vogel 1981). Since Re for a swimming *C. dipterum* is $\sim 1.2 \times 10^3$ and intermediate in value among those considered by Vogel, there seems little need for the body to be as highly streamlined as it is. Therefore, streamlining of *C. dipterum* larvae probably confers an ability to accelerate rapidly, rather than a reduction of drag during swimming.

Boundary layer thickness and body roughness

When a larva is swimming, it can be assumed that the boundary layer around the body is fully developed. There will still be added-mass effects from acceleration due to movement of the terminal filaments and abdomen, but these will not be as severe as the initial effects, since the body has achieved a steadier state of movement.

Silvester and Sleigh (1985) calculated that thickness of the 99% boundary layer around a cylinder with the axis parallel to the flow would be slightly thinner than that over a flat plate. My observation (Fig. 3, insert) of 95% boundary layer thickness for a *C. dipterum* larva swimming at 200 mm/s is between the 99% boundary layer expected for cylinders and for flat plates.

If boundary layers are thick enough, rough surfaces will not interfere with flow in the boundary layer and cause appreciable increase in drag (Nachtigall 1983). The maximum allowable height of a projection that will not disturb boundary layer flow can be calculated if $Re > 100$ (Vogel 1981). Allowable height of a protuberance on an organism can increase with increasing distance downstream from the leading edge because boundary layer thickness increases. Vogel (1981) characterised this relationship as $E/x < 12.2\ Re_x^{-3/4}$ (where E = height of rounded projection, x = distance from edge of object, Re_x = local Reynolds number). Gills are the only major projections from the body of a swimming *C. dipterum* larva because the legs and antennae are retracted close against the ventral surface. Projection height of gills increases posteriorly, with the posterior pair of gills sticking out from the body at right angles.

The first pair of gills projects 0.29 mm from the body, which is close to the permissible height for a projection positioned 1.6 mm along the body of a larva moving at 200 mm/s when $E < 0.26$. At the position of the hind gills (3.0 mm along the body), $E < 0.32$ mm, again close to the projecting height (0.33 mm) of the gills (not shown). This close correlation between the theoretical length of gills as projections and the lengths actually measured suggests that projection length of gills is important for a swimming *C. dipterum* larva. Gills could be larger if larvae swam more slowly because the boundary layer would be thicker. But if velocity is important during swimming, then gills must be smaller so as not to disrupt the boundary layer. This is perhaps a better explanation of small gills than the assumption that they are reduced in the presence of readily available oxygen (see Hynes 1970). Furthermore, the shape and size could be adaptations to reduce added-mass during respiratory movements, rather than to plentiful oxygen. Gills of *C. dipterum* move very quickly during respiration (Saita 1979). The gills of my

study animals moved so fast they were not clearly observable with the video equipment (0.04 s/frame). It should not be difficult to determine if size of gill is related to the speed of ventilatory movement.

Concluding Statement

Daniel (1984) stated that where linear acceleration is important to survival of an organism, adaptations for a reduction of virtual mass may be expected, through streamlining and elongation of body shape. This may apply to ephemeropteran larva, but the converse, that possession of a streamlined body will allow rapid acceleration, can also be argued. A testable hypothesis is that highly streamlined cylindrical larvae will exhibit rapid acceleration and swimming, whereas those less streamlined will not do so to the same extent. Larvae could also be expected to actively reconfigure the body to produce a more prolate ovoid shape. Further, it could be expected that cylindrical, highly streamlined larvae exhibiting AEM will have specialized muscle organisation and structure. Morphological requirements for rapid acceleration and swimming should be similar for both lentic and lotic larvae.

Acknowledgements

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