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EFFECTS OF BODY LENGTH ON THE SWIMMING BEHAVIOUR OF *BAETIS TRICAUDATUS* DODDS (EPHEMEROPTERA: BAETIDAE)

By

Tracy N. Kutash ©

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA
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FRONTISPIECE

Baetis tricaudatus Dodds nymphs swimming in an experimental tank. (Photo by Simon D. Pollard)

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EFFECTS OF BODY LENGTH ON THE SWIMMING BEHAVIOUR OF *BAETIS TRICAUDATUS* DODDS (EPHEMEROPTERA: BAETIDAE) submitted by TRACY N. KUTASH in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Dr. D.A. Craig

Dr. H.F. Clifford

Dr. B.S. Heming

Dr. B.K. Mitchell

Date: 04-10-24

DEDICATION

I dedicate this thesis to my parents, George and Lillian Kutash, for their love, encouragement and support.

ABSTRACT

The swimming method used by small nymphs was different from that used by large nymphs. Small nymphs (≤ 3.0 mm) combined dorso-ventral oscillations of the abdomen with rowing movements of the legs to swim while large nymphs (≥ 4.0 mm) used only abdominal oscillations for propulsion. Transition from rowing to non-rowing swimming behaviours occurred when the nymphs were 3.5 ± 0.2 mm long.

Change in swimming behaviour took place between Reynolds numbers $20 \leq Re \leq 200$, which is within the range where transition from predominately viscous to inertial forces occurs. When viscous forces predominate, friction based methods of locomotion, such as paddling or rowing, are most efficient. Propulsive methods are more effective when inertial forces are more prevalent then viscous. It is likely that small *B. tricaudatus* row because viscous forces account for a larger proportion of the total drag experienced. Use of legs minimizes the drag of the recovery stroke relative to that of the power stroke which facilitates locomotion at low Re .

In *B. tricaudatus*. average swimming speed increased with growth. Average swimming speed increased linearly with body length in small nymphs, but exponentially in large nymphs. Transition from linear to exponential increases in swimming speed occurred in the same range of body lengths as changes in swimming behaviour. Changes in swimming speed and behaviour could prove to be a mechanism for other size-dependent behaviours observed in *Baetis* spp.

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1. INTRODUCTION

Mayflies are ubiquitous inhabitants of temperate streams. Most nymphs are either herbivores or detritivores and are regularly preyed upon by both vertebrates (*e.g.*, trout) and invertebrates (*e.g.*, stoneflies). Many studies have investigated the dynamics of predator-prey interactions involving ephemeropteran species (*e.g.*, Peckarsky 1980, 1987; Allan *et al.* 1987a, 1987b; Allan & Flecker 1988; Peckarsky & Penton 1989a; Soluk & Collins 1988). These studies have emphasized mechanisms of prey selection (*e.g.*, Allan *et al.* 1987a, 1987b; Molles & Pietruszka 1983; Peckarsky & Penton 1989a; Peckarsky & Wilcox 1989; Peckarsky *et al.* 1994; Siegfried & Knight 1976; Soluk and Collins 1988) predator avoidance (Peckarsky 1987; Peckarsky & Penton 1989b; Scrimgeour & Culp 1994; Scrimgeour *et al.* 1994).

Important components of predator-prey interactions are the defensive mechanisms used by prey species. Primary defenses, such as cryptic colouration, operate even if a predator is not present (Edmunds 1974). Secondary defenses, such as escape maneuvers or defensive posturing, are used only during an encounter with a predator (Edmunds 1974).

Mayfly nymphs use a variety of primary and secondary defenses to avoid or escape predation (Peckarsky 1980). The types of defensive mechanisms deployed by a nymph can be predicted by its external morphology. Numerous studies have focused on defensive or escape mechanisms in relation to three general mayfly body shapes: dorso-ventrally flattened, 'bulky' and streamlined (*e.g.*, Peckarsky 1980, 1987; Molles & Pietruszka 1983).

Dorso-ventrally flattened nymphs (*e.g.*, Heptageniidae) are anachoretic and can be found in crevasses or under rocks. The most frequent response to predators by heptageniids is crawling although other locomotory responses, such as drifting, have been observed (Peckarsky 1980).

Unlike the dorso-ventrally flattened heptageniids, the more robust or bulky ephemerellid mayflies inhabit exposed wood or rock substrates (Edmunds 1984). These mayflies have thick, spiny cuticles that may increase handling time and therefore require greater energy investment by potential predators (Molles & Pietruszka 1983). This is thought to reduce the selection of these nymphs as prey by some stoneflies (Molles & Pietruszka 1983). In response to a stonefly predator, ephemerellids either decrease movement to avoid detection, crawl away, or assume a 'scorpion' posture with the abdomen flexed forward over the longitudinal axis of the head and thorax (Peckarsky & Penton 1988).

Streamlined baetid nymphs frequently respond to a predator by swimming, although their initial response is to decrease activity (Peckarsky 1980). *Baetis bicaudatus* Dodds (Ephemeroptera: Baetidae) may detect stoneflies approaching from downstream by laterally flexing their cerci towards them as they pass (Peckarsky 1987). Following predator detection, the mayflies first respond passively with a reduction in movement (Peckarsky 1987). If a foraging predator comes within < 2 cm, *B. bicaudatus* will attempt to escape by swimming or drifting, with increasing probability as the stonefly approaches (Peckarsky & Penton 1989a). Hydrodynamically conspicuous behaviours, such as swimming, are usually not initiated before this proximity is breached (Peckarsky & Penton 1989a; Peckarsky & Wilcox 1989). Some stoneflies can discriminate between *Baetis* and other mayfly nymphs by using hydrodynamic cues (Peckarsky *et al.* 1994). They exhibit an "if it swims pursue it" response to potential prey (Peckarsky *et al.* 1994). The authors suggested this method of prey selection may have evolved in predaceous stoneflies because of the high frequency of encounters with *Baetis* spp. which are excellent swimmers, in comparison to other mayfly species that are generally less abundant and display less active types of escape responses. If mayfly evolution follows the Red Queen hypothesis (Van Valen 1973), they should have evolved numerous behaviours to counter the selective pressures placed on them by foraging stoneflies. This repertoire of adaptive behaviours should include various aspects of locomotion, particularly since some predators prefer to attack swimming prey (Peckarsky & Wilcox 1989; Peckarsky *et al.* 1994). In theory, for an active escape response to be successful, swimming mayflies should be capable of rapid acceleration from rest.

Despite frequent use of streamlined mayfly nymphs in laboratory and field studies, literature on their swimming behaviour and performance is limited (but see Craig 1990; Craig & Weihs unpubl. manuscript), although it is generally accepted that streamlined nymphs are capable of rapid swimming (*e.g.*, Needham & Lloyd 1916; Hynes 1970; Nachtigall 1974). Understanding the locomotory performance of an organism is important because the outcome of predator-prey interactions is influenced by the physical capabilities of the participants (Webb 1986).

The locomotory performance of an aquatic organism depends on the nature of the flow around it. It is affected by both the abiotic conditions (*i.e.*, temperature, flow velocity, viscosity) and the morphology of the animal (*i.e.*, size, shape, muscle arrangement). A general indicator of how a fluid will flow upon encountering a solid is given by the Reynolds number (*Re*), which broadly defines the ratio of viscous to inertial forces acting on the organism ($Re = lU/\nu$ where l = length of an immersed object, U = the relative velocity and ν = the kinematic viscosity of the fluid). At low *Re*, viscous forces, which are the fluid equivalent of friction, predominate whereas inertial forces constitute a higher percentage of the total drag acting on a body at high *Re*.

The interaction between form and flow creates drag. Drag is commonly described as the rate of removal of momentum from a flowing fluid, and therefore acts opposite to the direction of motion. It is dependent on both speed and body morphology. The total drag on an organism has two components: skin friction and pressure drag. Skin friction varies with the amount of surface area exposed and is most important at low *Re* where viscous forces predominate. As the surface area exposed to the fluid increases, so does the skin friction. To decrease total drag at low *Re*, a bluff or rounded body that minimizes the surface area for any given volume, is most suitable. At high *Re,* inertial forces predominate and minimizing pressure drag, which is proportional to the square of the velocity, becomes more important than reducing skin friction. At high *Re*, a streamlined form delays separation of the boundary layer which diminishes the wake at the trailing edge and serves to decrease pressure drag (Vogel 1981).

Based on the definition of *Re*, an increase in length, or a change in body shape, will alter the nature of the flow, and consequently the drag forces acting on an organism. Insects with hemimetabolous development, such as mayflies, experience punctuated increases in size with each molt while the general body morphology is conserved. Statzner (1988) concluded that "evolution compromises between a life at low and at high *Re*" and therefore "the shape of a benthic macroinvertebrate is not adapted in such a way that drag is minimized at a certain *Re*". Consequently, nymphs may not display optimal drag-minimizing morphologies, nor will they experience equal flow conditions across all instars, providing that all instars occupy the same microhabitat. Smaller nymphs will experience relatively more skin friction than larger ones since their surface area to volume ratio is higher and larger nymphs will be more intensely affected by inertial forces.

Sufficiently large increases in size, speed, or body shape may result in a change in the hydrodynamic regime an animal occupies. For example, because of their size, larval fishes occupy a hydrodynamic environment very different from that of adults (*e.g.*, Batty 1981, 1984; Webb & Weihs 1986). A change in the hydrodynamic regime also occurs as a consequence of increasing swimming speeds which, in fish, is characterized by the transition from labriform to carangiform swimming modes (Archer & Johnston 1989). Labriform swimming is achieved through the paddling of pectoral fins and is used during slow swimming and maneuvering (Batty 1981). A gradual change in an animals' hydrodynamic regime occurs when *Re* is between 20 and 200 (Webb & Weihs 1986). This range defines the transition zone from one where viscous forces dominate to one where inertial forces are responsible for most of the drag sustained. When viscous forces predominate, friction based methods of locomotion are used. In contrast, propulsive mechanisms are used when inertial forces are more prevalent.

To adjust to the change in its hydrodynamic environment, an animal may go through ontogenic changes in behaviour by using friction based swimming methods, such as rowing, at lower *Re* and propulsive mechanisms at high *Re* (*e.g.*, Hunter 1972; Batty 1981, 1984). Many aquatic insects rely exclusively on either rowing or walking movements to swim through the water (*e.g.*, Nachtigall 1974; Blake 1986). Although the hydrodynamics of several insects have been described in considerable detail, locomotion of swimming mayflies, which are cosmopolitan in both lentic and lotic habitats, have received little attention (but see Craig 1990; Craig & Weihs unpubl. manuscript; Saita 1979).

In southern Alberta, *B. tricaudatus* nymphs commonly have two overlapping generations with two visually distinguishable size classes occurring concurrently within similar microhabitats (Culp & Scrimgeour 1993). Since small and large nymphs occupy the same microhabitat, I hypothesize a change in the swimming behaviour and locomotory performance between these two size classes of nymphs based on principles of fluid dynamics.

The following study was conducted to analyze the swimming behaviour of *Baetis tricaudatus* Dodds (Ephemeroptera: Baetidae) nymphs. The objectives were to determine the swimming methods used, to study aspects of swimming performance and to interpret the relationship between the two with emphasis on the physical restraints placed on nymphal behaviour by the environment. I will show that swimming behaviour in small nymphs is highly dependent on their hydrodynamic environment and discuss the underlying consequences of a change in swimming behaviour and locomotory performance in relation to predator-prey interactions.

2. METHODS

2.1 Collection of Study Organisms

Baetis tricaudatus nymphs were collected from Stauffer Creek, about 10 km north of Caroline in south central Alberta. Nymphs were brought back to the laboratory and placed in aquaria in a room with controlled ambient temperature of 15° ± 2° C. Photoperiod corresponded to the natural light regime at time of collection. Large stones were positioned in the centre of aquaria and air stones were placed in one corner to generate a current. Mortality in the tanks was high, so all experiments were conducted within one month of collecting.

2.2 Filming

A still water system was used to simplify experiments so that the counteractive effects of water flow would not have to be subtracted from the results. Furthermore, nymphs in a flowing system would have been carried downstream as they entered the water column. An experimental tank constructed of 1 mm thick Plexiglas® with interior dimensions 65 mm H x 25 mm W x 75 mm L was filled with 100 ml of water taken from the rearing tanks and cooled to 13°C. A light diffuser was placed behind the tank and was back-lit with two high intensity lights (Wild Heerbrugg, Switzerland MTr20, output 0-12V, 10A max.) positioned to illuminate the entire area of the tank (Fig. 1). Swimming sequences were recorded using either high-speed cinematography or high-speed video.

Prior to recording swimming sequences, approximately 10 nymphs of various size classes were placed in the experimental tanks and allowed to acclimate for at least 10 minutes. For high-speed cinematography, an 8 mm high-speed camera (Cine-8 Model V, Mekel Engineering Co., Covina, Calif.) fitted with a Nikon® 55 mm lens was used to record nymphs at 250 frames per second (fps) (= 0.004 s between frames) using Kodak® Tri-X reversal film (7278 cat. # 502 9046). A ruler placed in the experimental tank was filmed for calibration before swimming sequences were recorded. Nymphs were allowed to swim spontaneously, but occasionally were stimulated with a metal probe to induce swimming.

A high-speed video camera (Kodak EktaPro® 1000 Motion Analyzer) recording at 1000 fps was also used to record some swimming sequences. Data was then downloaded at 30 fps to a Panasonic® VCR. (Model AG6200 video recorder) and measurements were taken from images on a Sony® Trinatron super fine pitch monitor (model # CVM - 1270).

2.3 Swimming Behaviour

For each filming session approximately 10 nymphs of various sizes were placed in the experimental tank and allowed to acclimate for approximately 10 minutes, after which time the swimming sequences were recorded using either high-speed cinematography or high-speed video. The type of swimming behaviour used by each nymph was recorded. Nymphal lengths were measured from the projected images.

2.4 Average Swimming Speed

Results obtained from both high-speed cinematography and high-speed video were pooled. Specifications to determine average swimming speed of nymphs were not as rigid as those needed for instantaneous analysis. Many nymphs did not maintain a lateral swimming position, but instead turned so the orientation of the nymph changed. For analysis, it was required that the animal maintain the thorax in focus, which ensured the swimming path was perpendicular to the camera. The first frame of any chosen sequence was always one where the front of the head (either lateral, dorsal, or ventral view) was in focus. A reference mark was placed on the image at the base of the antennae and the film advanced until the head was again in focus. Thus, a path depicting the average displacement of the animal resulted. If the path swum was not linear, marks were placed on suitable images when a change in direction occurred. Elapsed time was monitored using the frame counter on the projector or video screen. Displacement was measured using Image Analysis 1.41 (Freeware, Wayne Rasband, NIH, Research Services Branch, NIMH, Bethseda, ML).

Displacement data were used to calculate the average speed (Uav) using the equation:

$$Uav = \frac{\Delta d}{\Delta t}$$

where d is the distance swum and t the time elapsed.

2.5 Instantaneous Swimming

2.5.1 Swimming Speed

Observations recorded on high-speed cine film were projected using a stop motion projector (Lafayette Analyzer model 00927, Lafayette Instrument Co. Lafayette, Indiana). Only nymphs that remained in the plane of focus were selected for sequential frame analysis. A reference mark placed at the centre of mass (CM *ca.* 0.4 the length of nymph from the head, cerci not included) was traced on each image in a sequence to determine the path of movement. Nymphal length was measured from the front of the head to the tip of the abdomen. Distances between consecutive CM points on the drawings were measured using "Images 1.41" on a Macintosh IIfx computer connected to a video camera (Hitachi® VK-C350 fitted with a Nikon® 55 mm lens). The drawing was aligned so that the path the nymph had swum was horizontal to the camera (Fig. 2).

By measuring the angles between consecutive points, the horizontal (x) and vertical (y) components of distance were obtained using the following trigonometric functions:

$$y = \text{Sin}\ \beta\ (\Delta d)$$

and

$$x = \text{Cos}\ \beta\ (\Delta d)$$

where Δd is the distance between two consecutive points and β the angle created through these points and the horizontal path the nymph had swum. Speed (U) was calculated using the equation:

$$U = \frac{\Delta d}{\Delta t}$$

where Δd is the distance traveled between consecutive frames and Δt the time elapsed between frames. This formula was used to find the x and y components of velocity by substituting y or x for d in the previous equation that resulted in the following:

$$U_x = \frac{\Delta x}{\Delta t} \qquad \text{and} \qquad U_y = \frac{\Delta y}{\Delta t}$$

Speed data was then used to determine actual acceleration (a) between consecutive frames using the equation:

$$a = \frac{\Delta U}{\Delta t}$$

2.5.2 Abdominal Angles

Nymphal images were traced in sequence. Five reference points were placed on each tracing: (1) centre of the thorax, (2) the junction between the thorax and abdomen (this point is near the centre of mass), (3) 1/3 the length of the abdomen from the thorax, (4) 2/3 the length of the abdomen from the thorax and (5) the tip of the abdomen (Fig. 3). All reference points were positioned mid-way through the depth of the nymph. The line through the thorax to the junction of the thorax and abdomen (segment through points 1-2) was chosen to represent the long axis of the body since there was little flexion in this area. The points along the abdomen were selected because most of the articulation occurred around segments. The following angles were measured in the analysis: (Ta) the angle created through the intersection of lines 1 - 2 and 2 - 3, (A1) the angle at the intersection of lines 2 - 3 and 3 - 4 and (A2) the angle at the intersection of lines 3 - 4 and 4 - 5 (Fig. 3). Another angle created through the intersection of point Ta by the segments 1-2 and 2-4 was used to describe the abdominal position during a swimming cycle. Resulting angles were measured using Images 1.41.

Using these angles, the angular velocity (ω) of the abdomen and the various abdominal sections was determined using the equation:

$$\omega = \frac{\theta}{\Delta t}$$

where θ is the angle through which a segment has rotated and Δt the time elapsed. The data calculated from this equation was then used to determine linear quantities of velocity using the formula:

$$v = l\omega$$

where l is the length of the rotating segment (the segment created between points 2-3, 3-4 or 4-5).

Instantaneous angular acceleration (α) was calculated using the formula:

$$\alpha = \frac{\Delta v}{\Delta t}$$

Using this equation, the tangential linear acceleration (a_t) is defined by:

$$a_t = l\,\alpha$$

2.5.3 Leg Angles

Tracings of the nymphs showing leg positions were made for each image in a sequence. A line drawn through the centre of the thorax and the junction between the thorax and abdomen represented the long axis of the body. Points were placed at the distal end of the femur of each leg. A line was drawn through the long axis of the femur and the angle of leg rotation was taken between the femoral and the body axis (Fig. 3). These angles were measured and analyzed following the methods used above for abdominal angles. Because of the poor resolution of the film, the proximal leg segments could not be seen, therefore, leg length was measured from the point at which they began to project from the body to the distal end of the tibia. Also, the meso- and metathoracic pairs of legs, though somewhat flexed during swimming, were treated as straight and rigid structures.

2.6 Hydrodynamic Equations

Reynolds numbers (*Re*) were calculated for all sequences analyzed. The Reynolds number describes the ratio of inertial to viscous forces. It is defined as:

$$Re = \frac{l\,U}{\nu}$$

where l is the greatest length of a body parallel to the flow (in this case the length of the nymph, not including cerci), U the relative speed at the fluid-solid interface (in a still water system it is the speed of the organism), and ν the kinematic viscosity ($\nu = 0.01204$ cm/s^2, freshwater at 13°C), which is constant for a particular fluid at a given temperature.

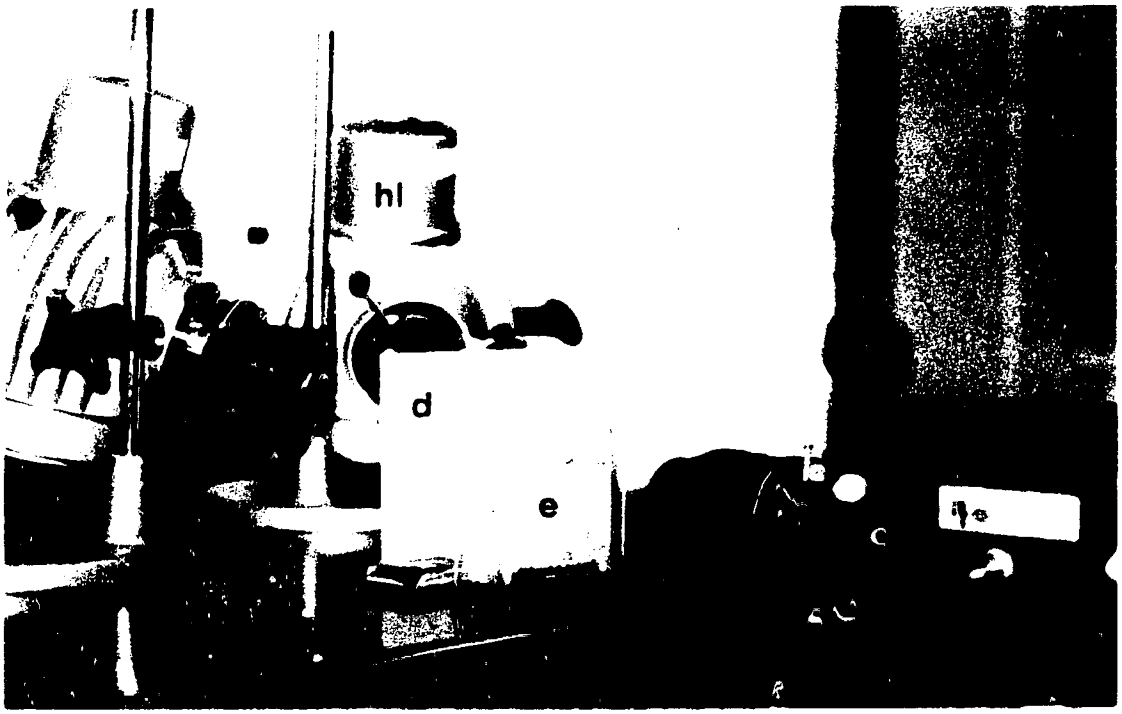


Figure 1. Still water system used in high speed filming, **hl**, high intensity lights; **d**, light diffuser: **e**, experimental tank; **c**, 8 mm high speed camera.

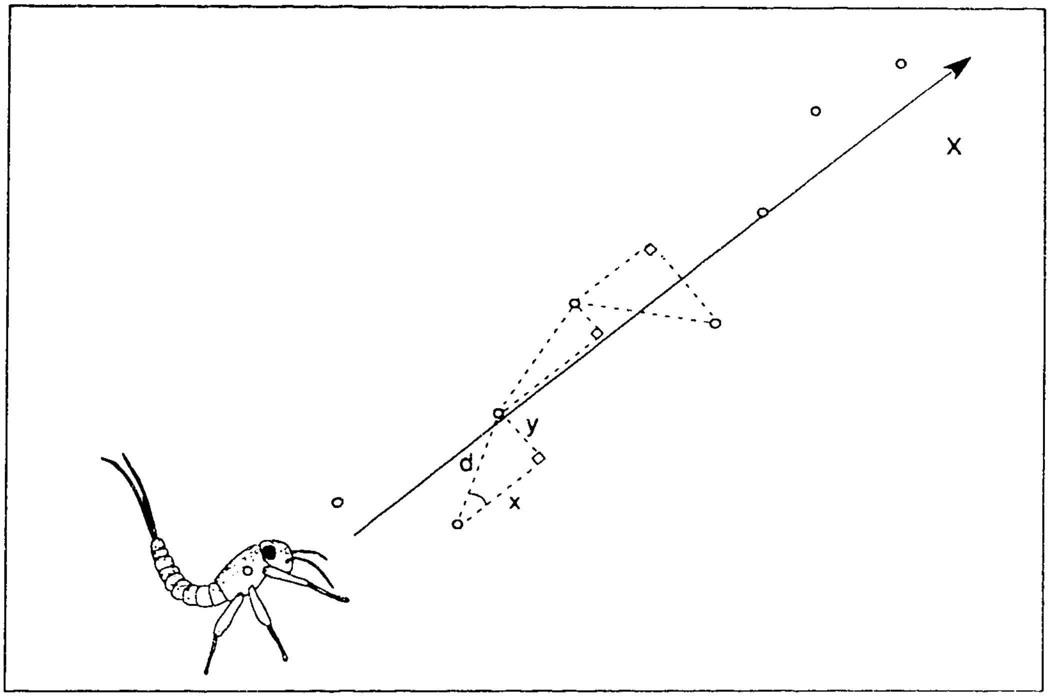


Figure 2. Depiction of a swimming sequence of a small *B. tricaudatus* nymph in the experimental tank. Reference marks were positioned at the centre of mass. A line (X) was drawn to represent the average displacement of the nymph. The tracing was aligned so that X was horizontal and the horizontal (x), vertical (y) and total (d) components of the distance swum between consecutive reference points could be determined.

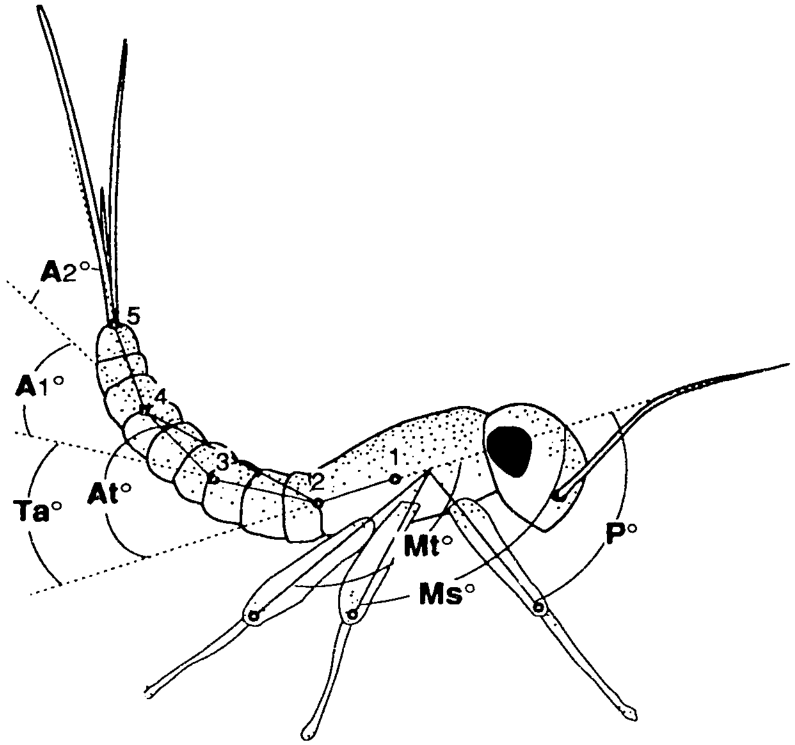


Figure 3. Lateral view of a *B. tricaudatus* nymph illustrating average abdominal flexion (**At**), the five reference points used in determining degrees of abdminal flexion and the three angles measured (**Ta**, thoracic-abdominal; **A**1, 1/3 length of the abdomen from the thorax; **A**2, 2/3 the length of the abdomen from the thorax). Also shown are the reference points used to determine leg position during a swimming sequence and the leg angles measured (**P**, prothoracic leg; **Ms**, mesothoracic leg; **Mt**, metathoracic leg).

3. RESULTS

3.1 Swimming Behaviour and Performance in Small *Baetis tricaudatus* Nymphs (≤ 3.00 mm)

3.1.1 Behavioural Observations

Small *B. tricaudatus* nymphs swam by oscillating the abdomen in a dorso-ventral plane using motions similar to those used by cetaceans. As the abdomen oscillated, the head and thorax also rotated in a dorso-ventral plane, and this movement was dependent on abdominal position (Fig. 4 & 5). In conjunction with abdominal oscillations, small nymphs also used synchronized rowing of their legs when swimming. This manner of swimming was consistent for all nymphs < 3.0 mm. None of the observed nymphs displayed piscean swimming patterns where oscillations occur laterally in relation to the rest of the body.

For a nymph that measured 2.0 mm, the power stroke began with the abdomen maximally flexed (dorsal) and the legs extended ventrally and somewhat laterally away from the body with approximately a 60° angle between the pro- and metathoracic legs (Fig. 4a). When the abdomen was thrust downwards, the prothoracic legs continued to be brought forward while the meso- and metathoracic ones were brought backwards which increased the angle between the pro- and metathoracic legs (Fig. 4a-d). The greatest angle between the pro- and metathoracic legs occurred about halfway through the deflexion of the abdomen as it approached its most linear position (Fig. 4e). After this time, the prothoracic legs were retracting and the meso- and metathoracic legs started to move towards the anterior. As the legs were drawn closer together, the abdomen was deflected ventral to the rest of the body (Fig. 4f-j). At the same time the head and thorax were also tilted ventrally. Power strokes were completed when the abdomen was fully deflexed. With the onset of abdominal recovery, all leg pairs were synchronously carried anterior in a slightly flexed position (Fig. 5k-m) and continued to be drawn closer together. When the abdomen started to flex dorsally from the linear axis of the body, the legs began to extend outwards and the angle between them increased (Fig. 5n-r).

The legs also extended laterally from the body during rowing. The meso- and metathoracic legs were the first to move posteriorly during the power stroke (Fig. 6a-c). When the body was in the most linear configuration (body alignment was determined by observing the length of the projected image), the prothoracic pair of legs was drawn posteriorly (Fig. 6d). As the abdomen approached maximum deflexion, the legs were brought close to the body (Fig. 6e-h). As a result, the lateral projection of the legs was minimized. At the onset of the recovery stroke, all legs were synchronously transferred anterior until the body assumed a linear configuration, at which time they simultaneously began to extend laterally (Fig. 7i-l). When the abdomen began to flex dorsally in relation to the rest of the body, the legs were extended outwards (Fig. 7m-p). Movement of the thoracic legs resembled the arm motions of a swimmer during the breast stroke where the arms are first extended anterior and then drawn back postero-laterally for the power stroke, but are kept close to the body with virtually no lateral projection upon recovery.

A typical swimming sequence consisted of short burst of activity (usually fewer than 5 cycles) into the water column. Once in the column, nymphs generally ceased swimming and assumed a 'splayed' position with their legs extended ventro-laterally with the abdomen flexed. This position was maintained until the nymphs either sank to the bottom of the tank, or resumed swimming.

3.1.2 Average Swimming Performance

Nymphs showed a linear increase in average velocity with increasing length. Average swimming velocities (U_x) were initially plotted against nymphal length (**L**) using ordinary least squares regression which gave the following equation:

$$\mathbf{U_x} = 2.9 + 6.4\mathbf{L}$$

Since the constant was not significantly different from zero (y-intercept = 2.9 ± 2.8, $p = 0.317$), it was deleted from the equation and the regression line was fitted so that it passed through the origin (Fig. 8). Passing a regression line through the origin is frequently done when analyzing biological data sets because it takes into consideration the naturally occurring limitations of these systems (Sokal & Rohlf 1981). In this case, for example, there will never be a 0 mm nymph swimming at any speed. The relationship between length and average swimming speed in small *B. tricaudatus* was thus described by the equation:

$$\mathbf{U_x} = 7.9\ \mathbf{L}$$

where **L** is the length of nymph measured from the front of the head to the apex of the abdomen ($R^2 = 0.442$, $p = 0.004$).

Since *Re* is dependent on velocity, the relationship between length and *Re* was also linear (Fig. 9). This relationship was defined by the equation:

$$\boldsymbol{Re} = -16.8 + 22.1\mathbf{L}$$

where L is nymphal length ($R^2 = 0.813$, $p = 0.0001$).

3.1.3 Instantaneous Swimming

3.1.3.1 Swimming Speed

A total of eight small nymphs met the criteria for instantaneous swimming analysis (nymphs chosen for discussion were those that had swum through the most cycles). Instantaneous speed fluctuated during the swimming cycle. These fluctuations were dependent on both abdominal and leg positions. Measurements taken from a 1.3 mm nymph show that minimum swimming speeds occurred when the abdomen was either maximally flexed or deflexed, at which time the nymph was nearing completion of either a power or recovery stroke (Fig. 10a & b). During a swimming cycle, there were two local maximums in speed. The highest swimming speed attained during a cycle was reached during the power stroke when the abdomen approached its most linear position and the angle between the pro- and meta-thoracic legs was largest (Fig. 10a-c). At this time the abdomen had reached the maximum angular velocity during the power stroke (Fig. 10d). Another local maximum occurred following the onset of the recovery stroke when the abdomen was approximately in its most linear position and the pro- and meta-thoracic legs were closest together. Maximum angular velocity for the recovery stroke was reached at this time. Instantaneous *Re* frequently fell to near 10 during a swimming cycle as the abdomen approached high degrees of flexion or deflexion and reached a maximum when the body was in the most linear configuration (Fig. 11). Although the net displacement was forward, backward movement occurred during the recovery stroke (Fig. 12).

Values taken from a 2.0 mm nymph show that the amplitudes of abdominal oscillations were fairly constant, averaging 166.33° ± 3.51 (mean ± SE). Though the amplitude remained constant, the mean angle of flexion was 89.80° whereas the mean angle of deflection was consistently lower, averaging 68.21°. Frequency of oscillation gradually decreased with time, from 27.78 Hz in the first cycle to 15.63 Hz in the last cycle (21.00 ± 2.70, mean ± SE). This decrease in frequency was highly correlated with a reduction in average swimming speed and is defined by the following equation:

$$\mathbf{Uav} = 10.156 + 0.73247\, f$$

where f is the frequency of abdominal oscillation ($R^2 = 0.885$)

3.1.3.2 Abdominal Oscillations

The flexion around the points Ta, A1 and A2 varied depending on the length of nymph. For a nymph 2.0 mm long the flexion around point A1 (the middle third of the abdomen) was the highest, followed by that about the distal third and the flexion about the segment nearest the thorax was the lowest (Fig. 13). The greatest angle of deflexion occurred at the distal third of the abdomen and the deflexion around points Ta and A1 were about equal. Amplitude of oscillation about points A1 and A2 were 74.68 ± 2.47 and 75.9 ± 2.82 respectively (mean ± SE) whereas the amplitude about the thoracic point was 47.58 ± 1.66 (mean ± SE). The period of oscillation of the three abdominal segments was slightly asynchronous; the segment oscillating around point Ta was always the first to compete a cycle, followed closely by the middle segment, and finally the distal segment.

Oscillation of the abdomen was different in smaller nymphs. For a nymph measuring 1.3 mm, the greatest angle of flexion occurred around point Ta measuring 60.20 ± 2.95, followed by A1 then A2, which measured 40.08 ± 3.22 and 19.20 ± 5.16 respectively (Fig. 14). Deflexion was greatest around point A2 with A1 showing a slightly greater angle of deflexion than Ta. Amplitude of oscillation was highest around Ta (74.85 ± 4.24, mean ± SE), followed by A2 (63.83 ± 3.31, mean ± SE) and lowest around point A1 (52.58 ± 1.63, mean ± SE). Contrary to the movement of abdominal segments displayed by a 2.0 mm nymph, the oscillations of the abdominal segments in this nymph were essentially synchronous.

3.1.3.3 Leg Rotation

Rowing in *B. tricaudatus* followed a 3, 2, 1 metachronal pattern, although at most points during the cycle the prothoracic pair of legs traveled in a direction opposite that of the meso and metathoracic pairs of legs, which tended to move together (Fig. 15). When the angle between the prothoracic legs and the long axis of the body (measured from the anterior) was smallest, the angles between the meso and metathoracic legs and the long axis were at the highest degree of rotation from the anterior. This position occurred just after the abdomen was thrust downwards upon the initiation of the power stroke (Fig. 16). Of the three leg pairs, the prothoracic legs traveled through the largest angle (62.18 ± 3.52, mean ± SE), followed by the metathoracic legs (50.53 ± 4.76, mean ± SE) and finally the mesothoracic legs (39.33 ± 4.29, mean ± SE).

3.2 Transition of Swimming Behaviour

Swimming behaviour changed when nymphs were between 3.3 - 3.7 mm in length (Fig. 17). Nymphs within this range exhibited either rowing or non-rowing swimming patterns, but the behaviour used by a particular individual was consistent. Three nymphs displayed an 'intermediate' behaviour where the legs appeared to assume rowing-like motions, although their movement appeared more passive in nature than the rowing motions used by smaller nymphs observed. A G-test for homogeneity of percentages led to rejection of the null hypothesis that body length does not influence swimming behaviour ($G_{adj} = 53.52$, $X^2 = 13.8$, $p<0.001$).

Measurements show that *B. tricaudatus* assumed an exponential increase in average speed with length (Fig. 18). This relationship is best defined by the following equation:

$$U_{av} = 7.3519 \times 10^{(0.16824\ L)}$$

where L is the length of the nymph ($R^2 = 0.582$, $p < 0.004$)

The corresponding *Re*av (Fig. 19) associated with length are described by the equation:

$$Re = 4.75 \times 10^{(0.34\ L)}$$

where L is the length of the nymph ($R^2 = 0.896$, $p < 0.0001$).

The change in behaviour occurred between *Re* 60 and 90. This range also corresponded to the transition from linear to exponential increases in speed.

3.3 Swimming Behaviour and Performance in Large *Baetis tricaudatus* Nymphs (≥ 4.00 mm)

3.3.1 Behavioural Observations:

Large nymphs (≥ 4.0 mm) swam by oscillating the abdomen in a dorsoventral plane. None of the nymphs incorporated leg rowing into their swimming sequences.

The power stroke of a 4.4 mm nymph was initiated when the abdomen was in the most highly flexed position (Fig. 20a). Prior to the onset of the power stroke, the speed was at a minimum (Fig. 22a). As the abdomen was thrust downward, the speed of the nymph increased and reached a maximum when the body alignment was most linear (Figs. 20d, 22a & b). The abdomen then continued ventrad and the speed gradually declined (Figs. 20e & f, 22a & b), stopping when the abdomen reached the most deflexed posture. The power stroke for this nymph, which swam at an average speed of 49.77 mm/s, was completed in approximately 0.020s. Recovery was initiated as the abdomen was thrust upward from the most ventrad position (Fig. 21a). Maximum velocity for the stroke was reached when the angle between the abdomen and the body approached 180° (Fig. 22a & b). The recovery stroke was completed in approximately 0.020s. For most of the cycles in this swimming sequence, the duration of the power and recovery strokes were roughly equivalent.

3.3.2 Average Swimming Performance:

Nymphal length was not a good predictor of the average swimming velocity (Fig. 23). The relationship between average velocity and nymphal length was best described by the equation:

$$\mathbf{U} = 27.0 + 5.1\mathbf{L}$$

where L is the length of the nymph. ($R^2 = 0.016$, $p = 0.617$)

The corresponding *Re* calculated from the previous average velocity data and the relationship with nymphal length (Fig. 24) was best described by the following equation:

$$\boldsymbol{Re} = 94.1 + 62.0\mathbf{L}$$

where L is the length of the nymph ($R^2 = 0.149$, $p = 0.113$). The average *Re* for large nymphs was 197.71 ± 89.69.

3.3.3 Instantaneous Swimming

3.3.3.1 Swimming Speed

Analysis of instantaneous swimming was conducted on four large nymphs that met the criteria described in Chapter 2. Instantaneous speed was affected by abdominal position and angular velocity. Minimum swimming speeds were observed as the nymphs were nearing completion of either a power or recovery stroke and the abdomen was either maximally flexed or deflexed (Fig. 22a & b). At this time the angular velocity of the abdomen was also at a minimum (Fig. 22c). The highest swimming speed was attained during the first cycle. Local maximums in speed were reached when the abdomen approached its most linear position during the power and recovery strokes. The highest angular velocities and hence, swimming speeds reached for each cycle occurred during the power stroke (Fig. 22a - c). Instantaneous *Re* was highest when the body approached maximum deflexion during the power stroke (Fig. 25). Low *Re*'s were observed as the nymph was nearing completion of the recovery stroke.

3.3.3.2 Abdominal Oscillations

For a nymph 4.4 mm long, the flexion around point A2 (the distal third of the abdomen) averaged the highest, followed by that about the middle third and the flexion about the segment nearest the thorax was the lowest (Fig. 26), although no particular segment consistently had the highest flexion for all cycles in a sequence. The greatest angle of deflexion was about equal for all segments. Amplitude of oscillation about point Ta was 65.54 ± 7.36, about A1 was 72.86 ± 5.33 and at A2 was 66.87 ± 3.39. The period of oscillation of the three abdominal segments was somewhat asynchronous. The segment oscillating around point Ta was always the first to compete a cycle, which was then followed by the middle and distal segments. Maximum abdominal flexion (measured about point Ab) was about double that of deflexion for a power stroke and the corresponding recovery stroke in the swimming sequences.

The frequency (f)of the cycle was highly correlated with swimming speed as was described by the following equation:

$$\mathbf{U} = 5.0 + 2.4\boldsymbol{f}$$

($R^2 = 0.902$)

Amplitude of oscillation (A) also affected swimming speed. This relationship was described by the following:

$$\mathbf{U} = 30.0 + 0.5\mathbf{A}$$

($R^2 = 0.747$)

Although both the frequency and amplitude of abdominal oscillation appear to affect swimming speed, these results are not statistically significant because of the limited number of observations in this sample. Further observations are required before the relationship between frequency, amplitude and swimming speed can be described.

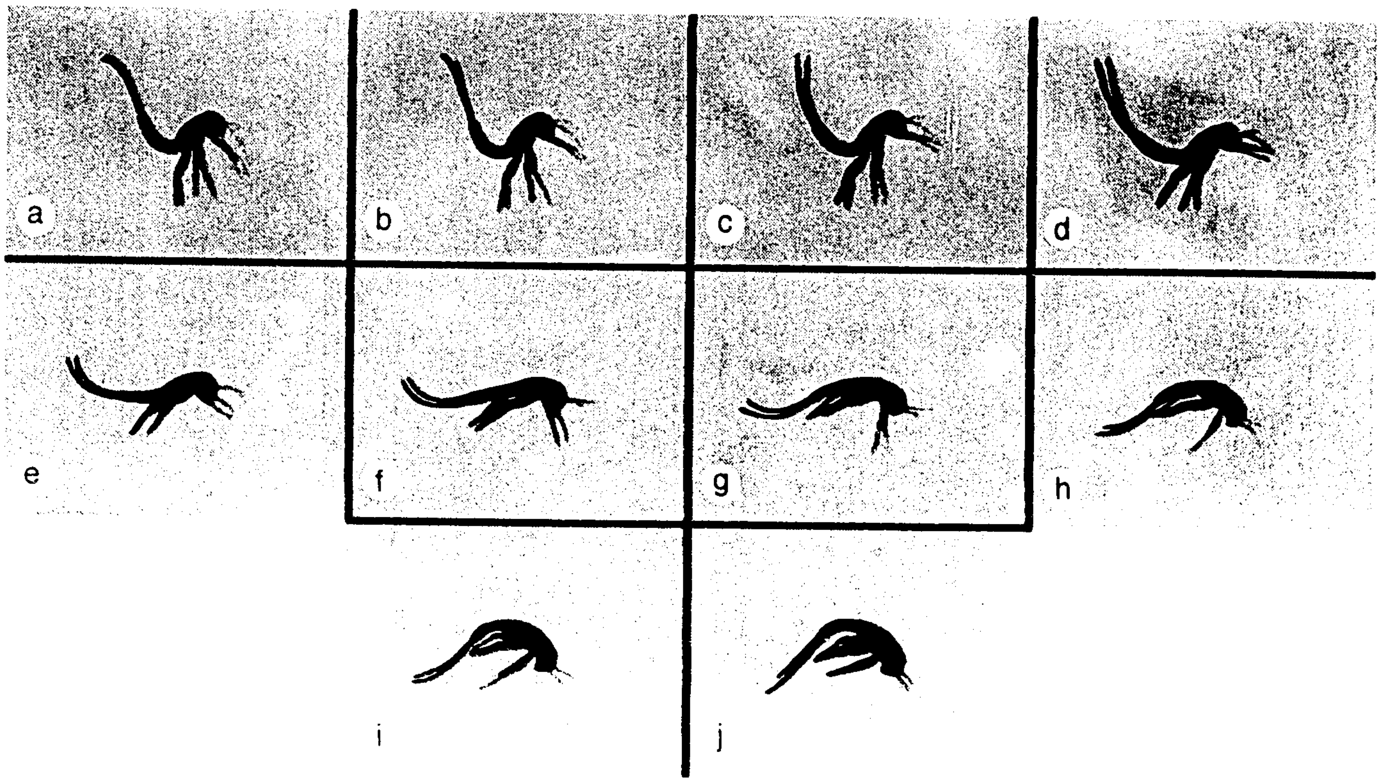


Figure 4. Lateral view depicting the sequence of events during the power stroke of a 1.3 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

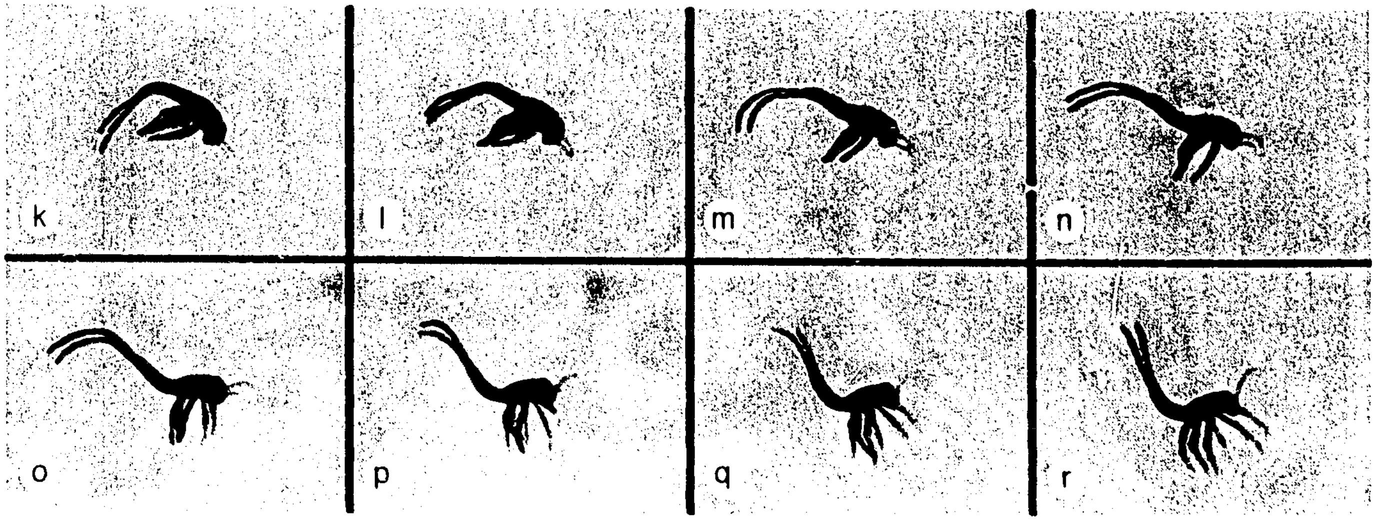


Figure 5. Lateral view depicting the sequence of events during the recovery stroke of a 1.3 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

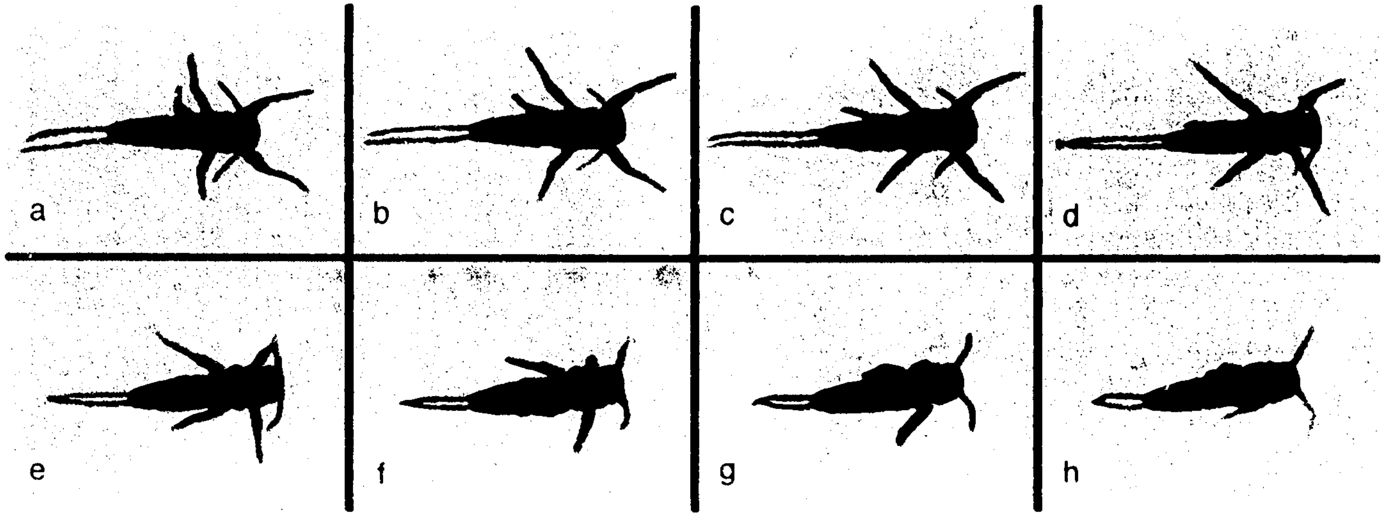


Figure 6. Ventral view depicting the sequence of events during the power stroke of a 3.4 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

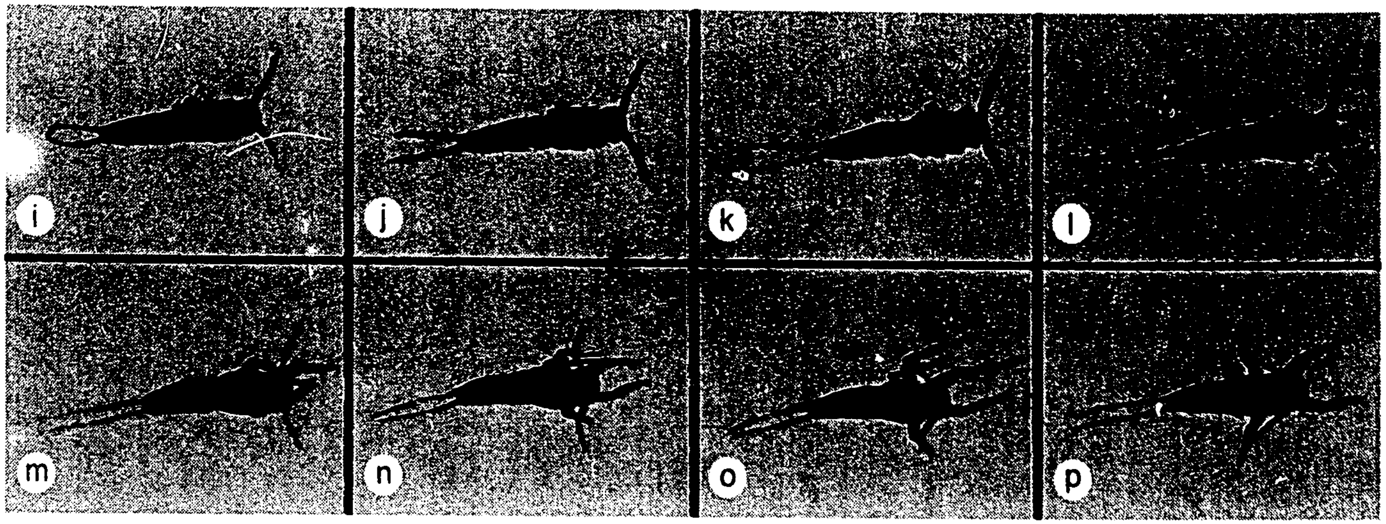


Figure 7. Ventral view depicting the sequence of events during the recovery stroke of a 3.4 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

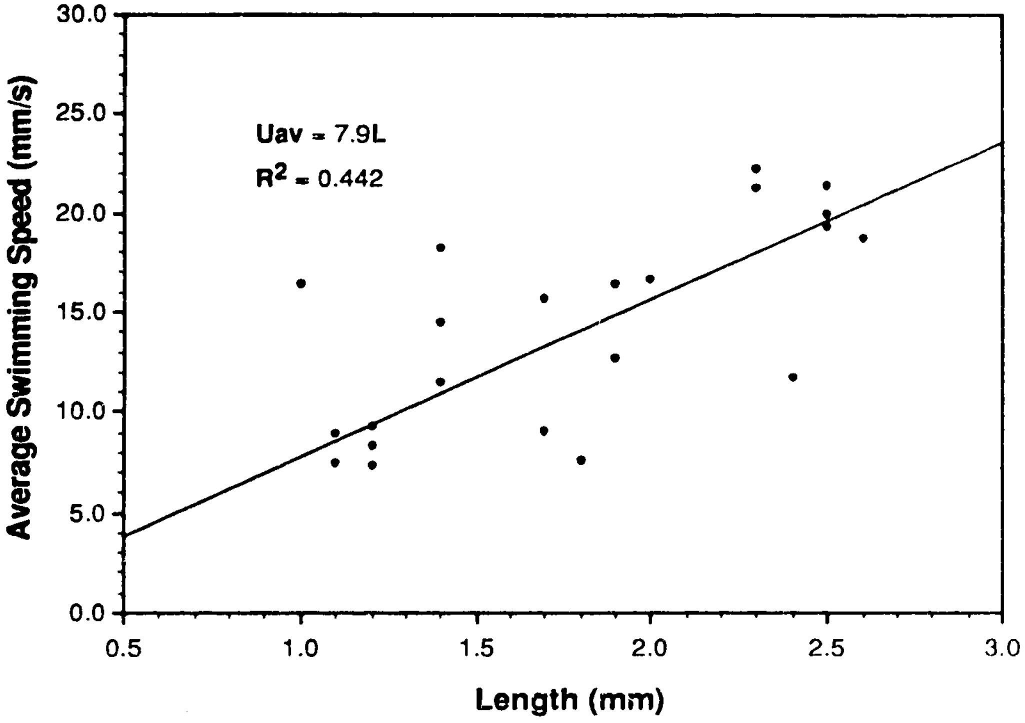


Figure 8. Effects of body length on average swimming speed in small (≤ 3.0 mm) *B. tricaudatus* nymphs.

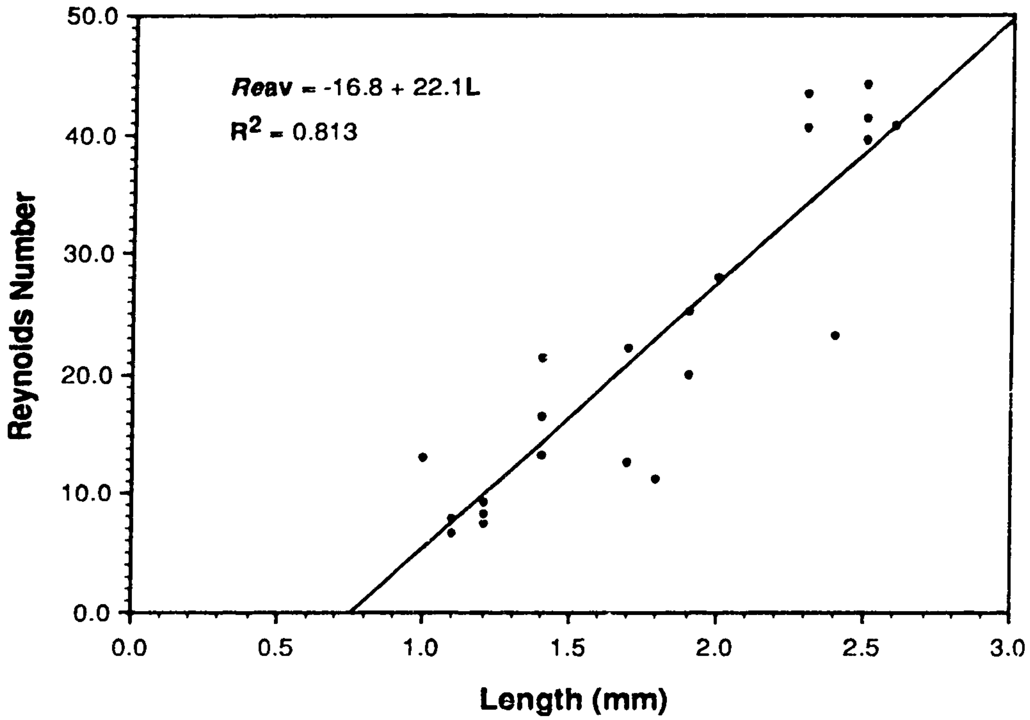


Figure 9. Effects of body length on Reynolds number in small (≤3.0 mm) *B. tricaudatus* nymphs swimming in freshwater at 13 °C.

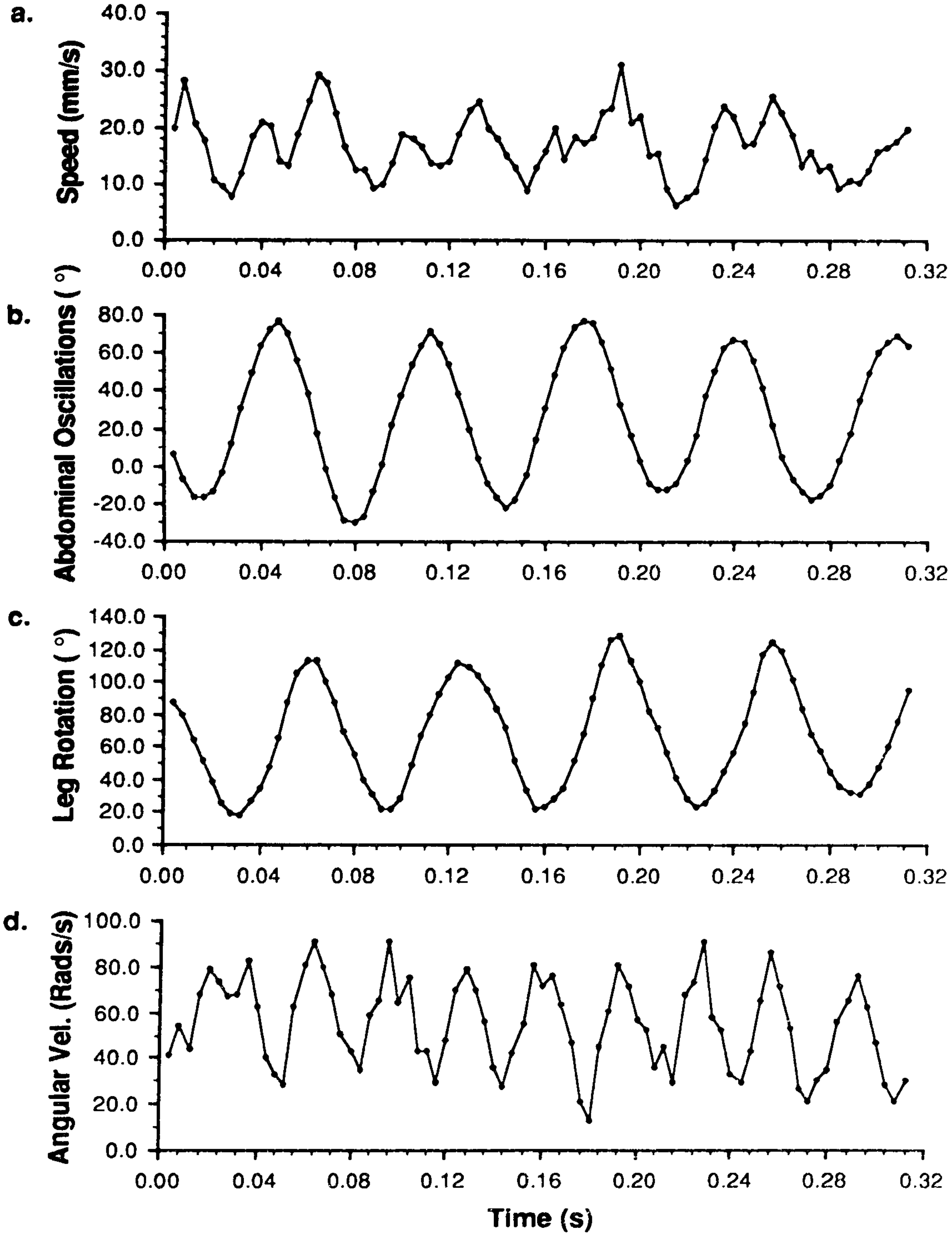


Figure 10. Relationship between swimming speed (a), abdominal oscillations (b), leg rotation (c), and angular velocity of the abdomen (d).

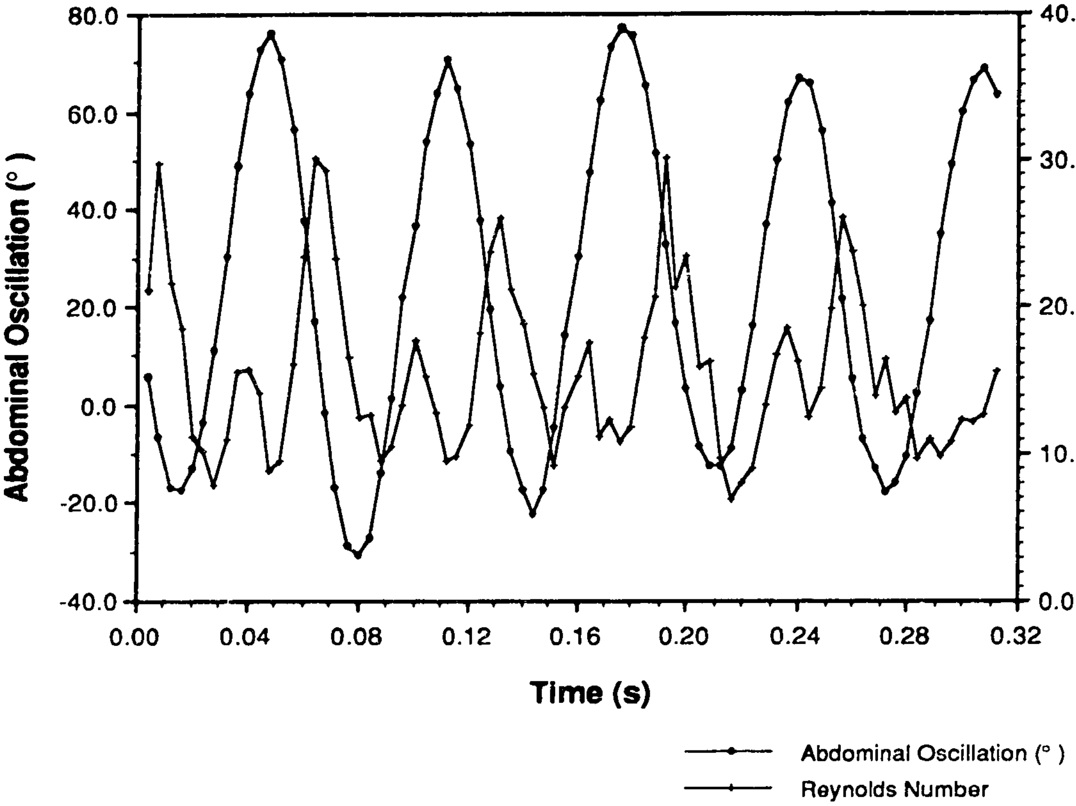


Figure 11. Relationship between abdominal oscillations and Reynolds number during a swimming sequence of a 1.3 mm *B. tricaudatus* nymph.

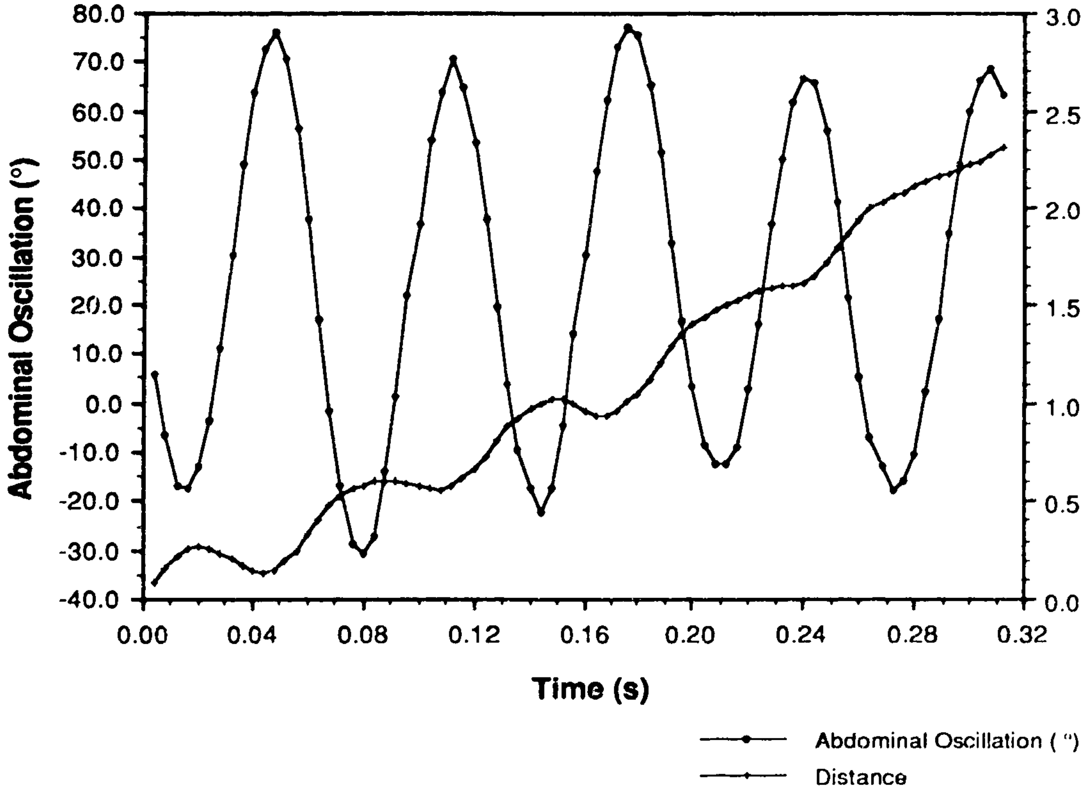


Figure 12. Relationship between abdominal oscillation and cumulative distance swum by a 1.3 mm *B. tricaudatus* nymph.

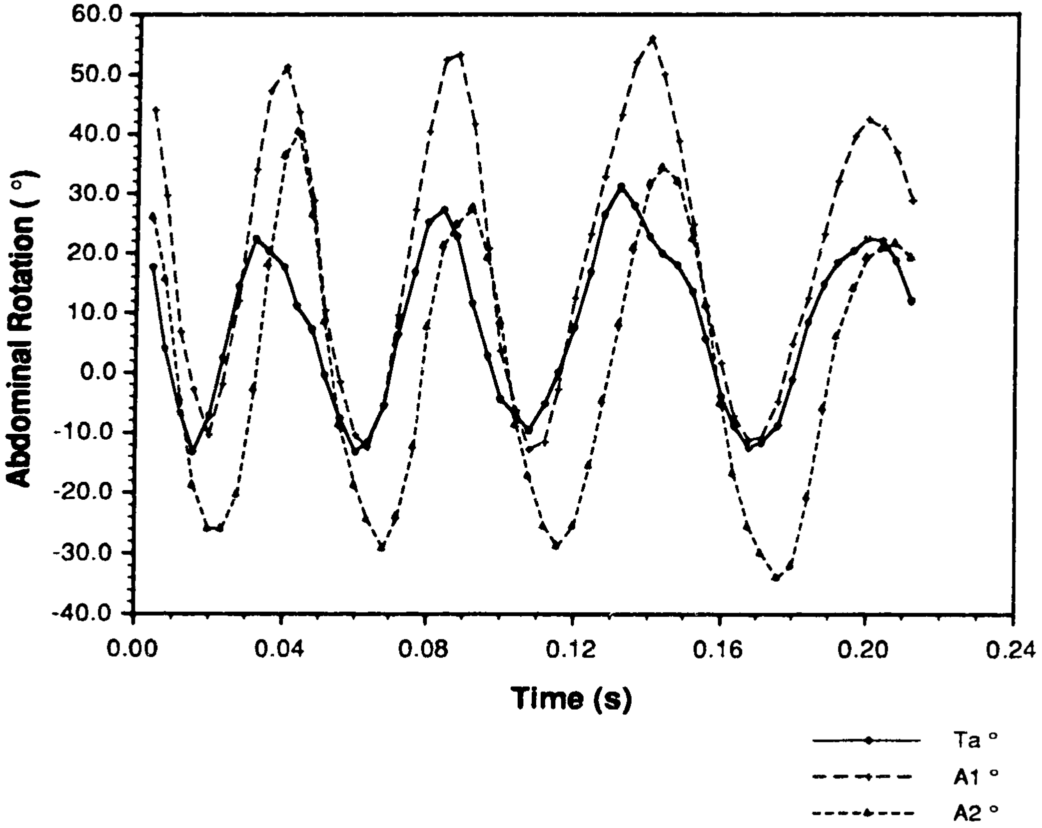


Figure 13. Rotation of abdominal segments created through points at the junction of the thorax and abdomen (Ta), the basal third of the abdomen (A1), and the distal third of the abdomen (A2) in a 2.0 mm *B. tricaudatus* nymph.

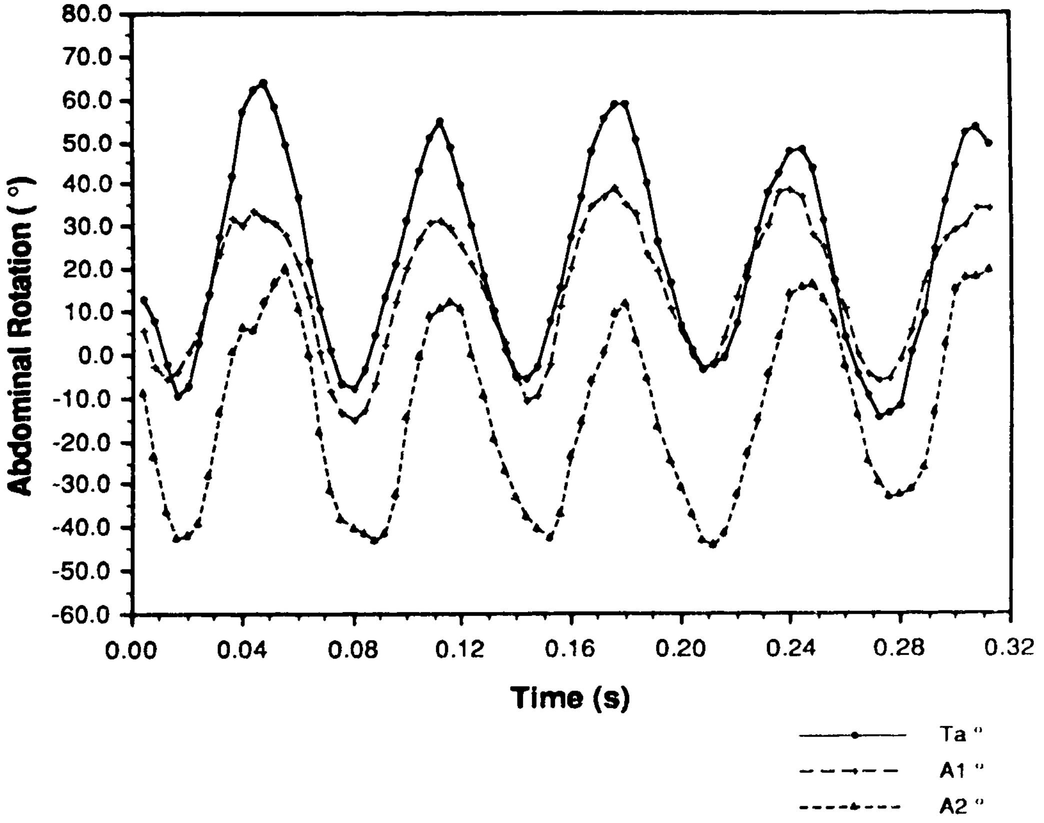


Figure 14. Rotation of abdominal segments created through points at the junction of the thorax and abdomen (Ta), the basal third of the abdomen(A1), and the distal third of the abdomen(A2) in a 1.3 mm *B. tricaudatus* nymph

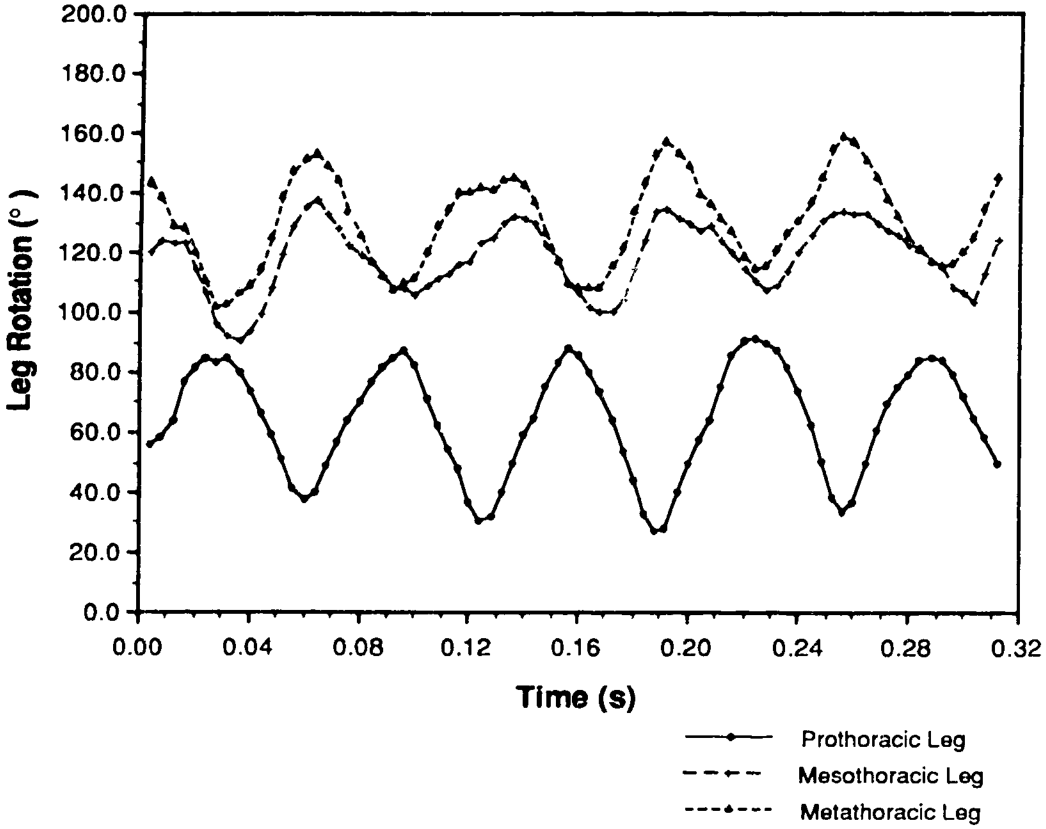


Figure 15. Rotation of the thoracic legs during swimming in a 1.3 mm *B. tricaudatus* nymph.

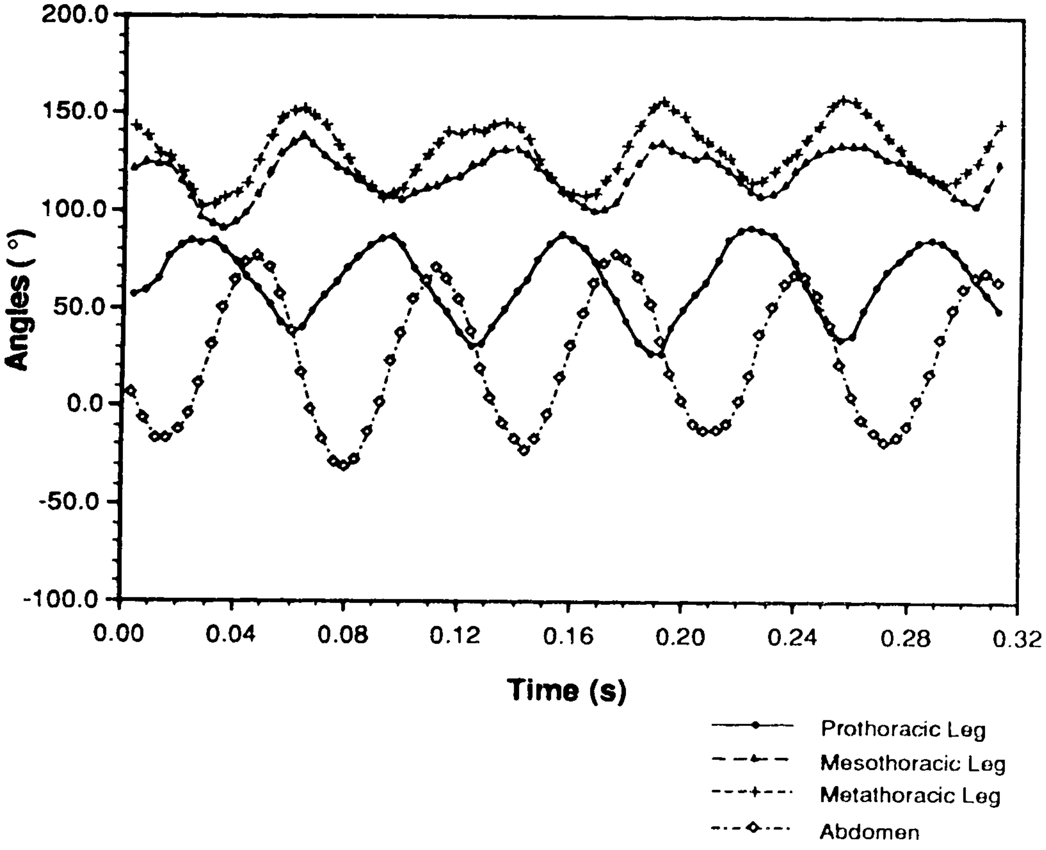


Figure 16. Oscillation of the abdomen and leg rotation during a swimming sequence of a 1.3 mm *B. tricaudatus* nymph.

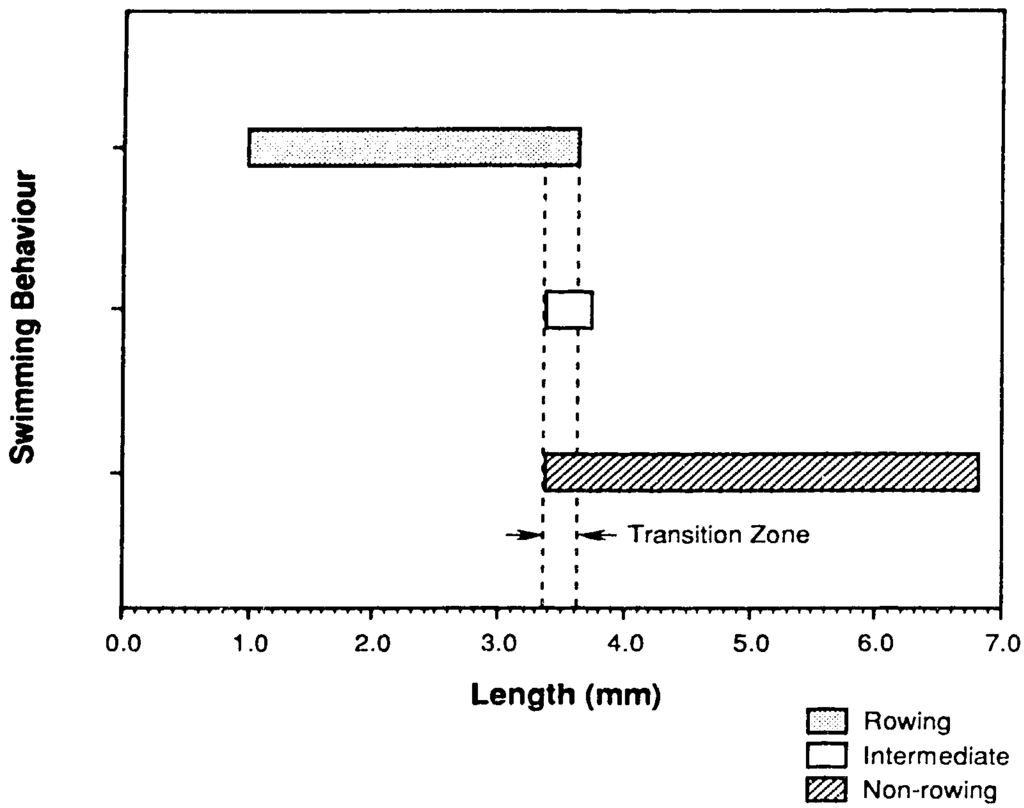


Figure 17. Changes in swimming behaviour that occur with increasing body length in *B. tricaudatus* nymphs.

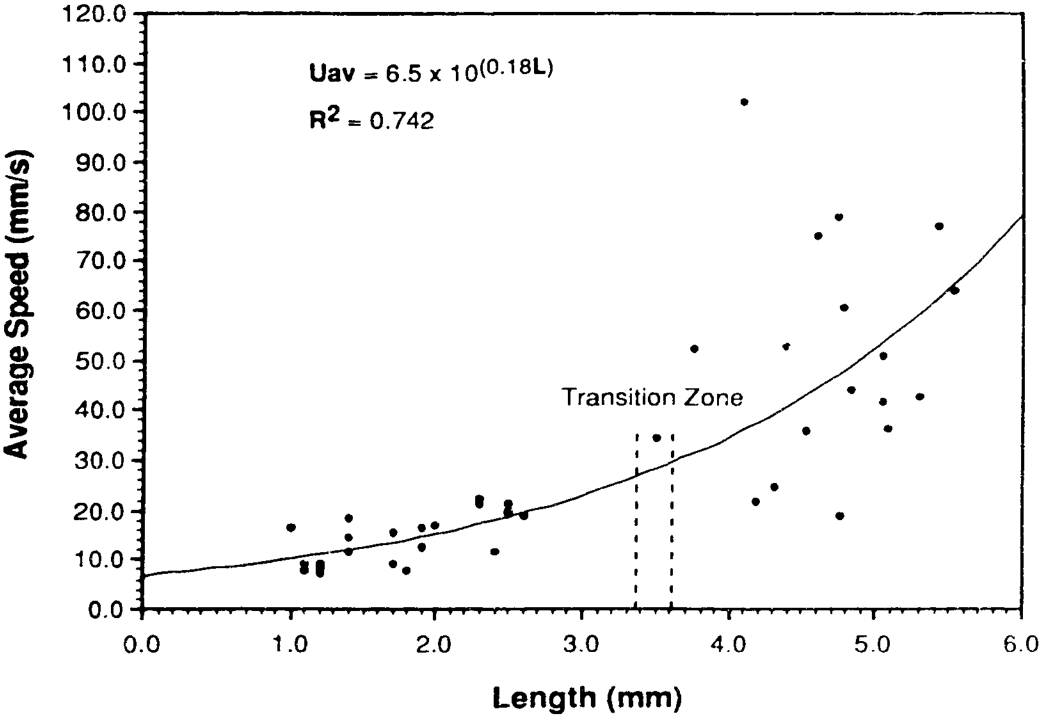


Figure 18. Effect of body length on average swimming speed in *B. tricaudatus* nymphs.

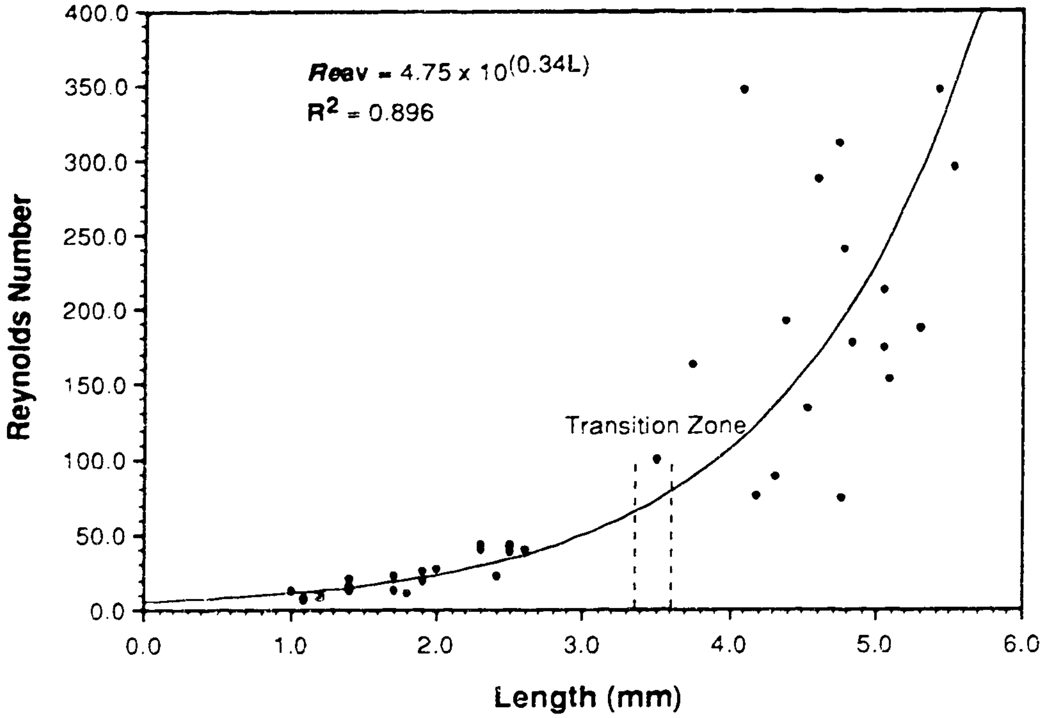


Figure 19. Effect of body length on Reynolds numbers in *B. tricaudatus* nymphs swimming in freshwater at 13°C.

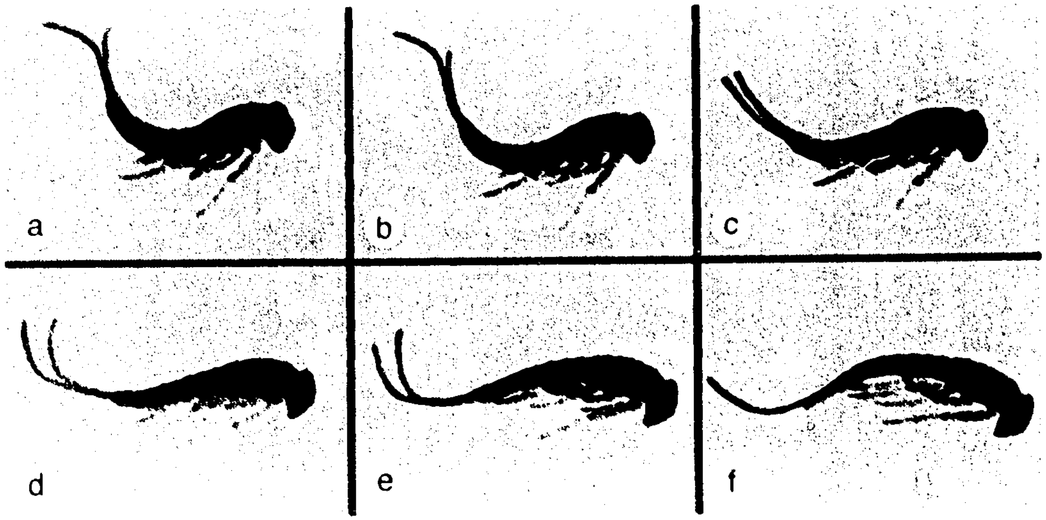


Figure 20. Lateral view depicting the sequence of events during the power stroke of a 4.4 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

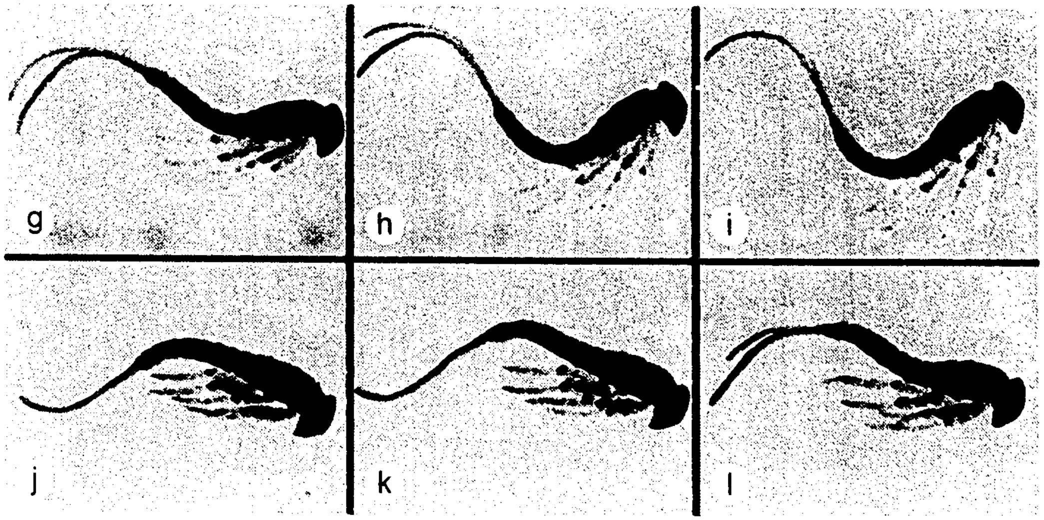


Figure 21. Lateral view depicting the sequence of events during the recovery stroke of a 4.4 mm *B. tricaudatus* nymph. Time elapsed between frames equals 0.004 s.

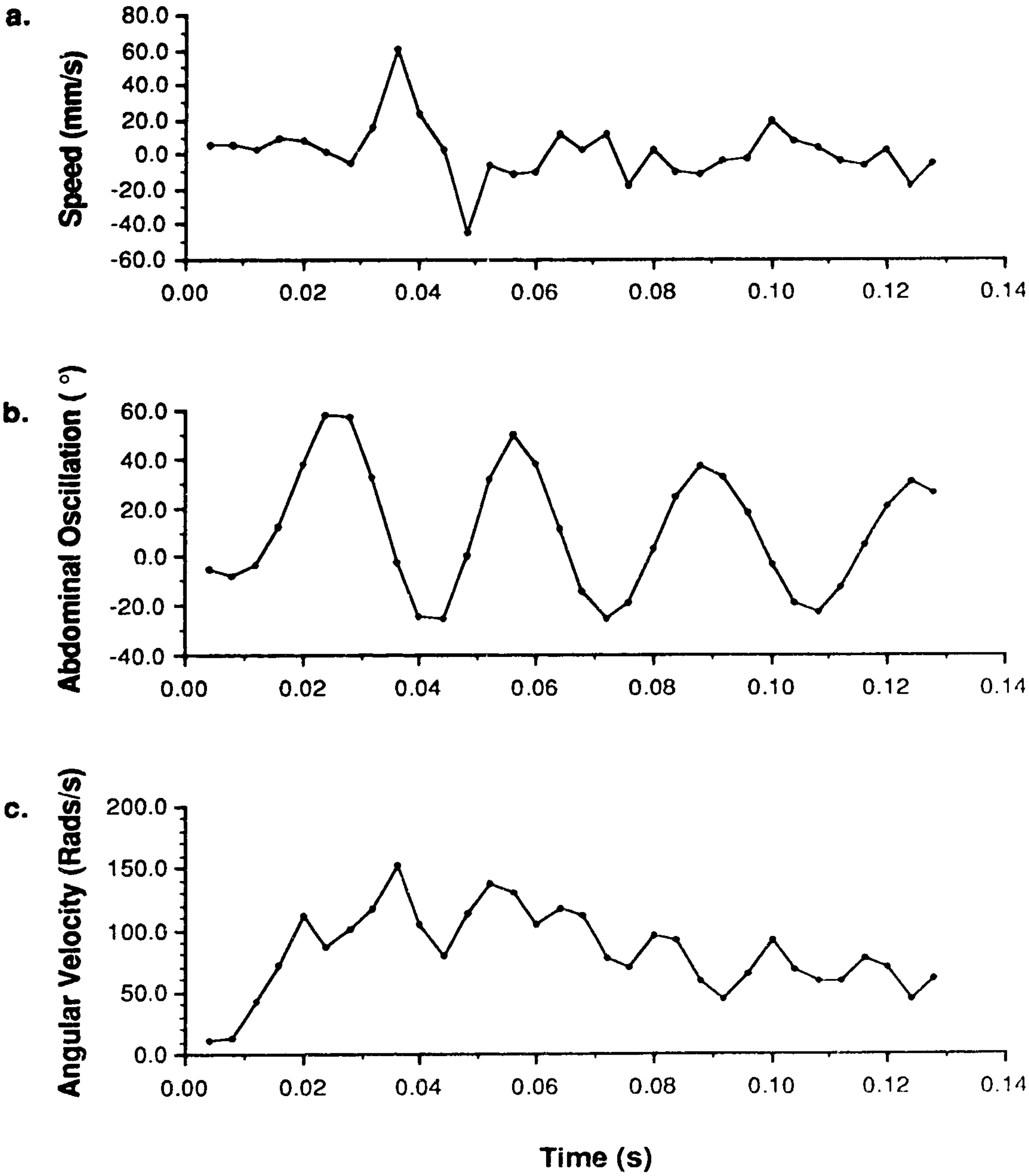


Figure 22. Relationship between swimming speed (a), abdominal oscillation (b), and angular velocity of the abdomen (c) in a 4.4 mm *B. tricaudatus* nymph.

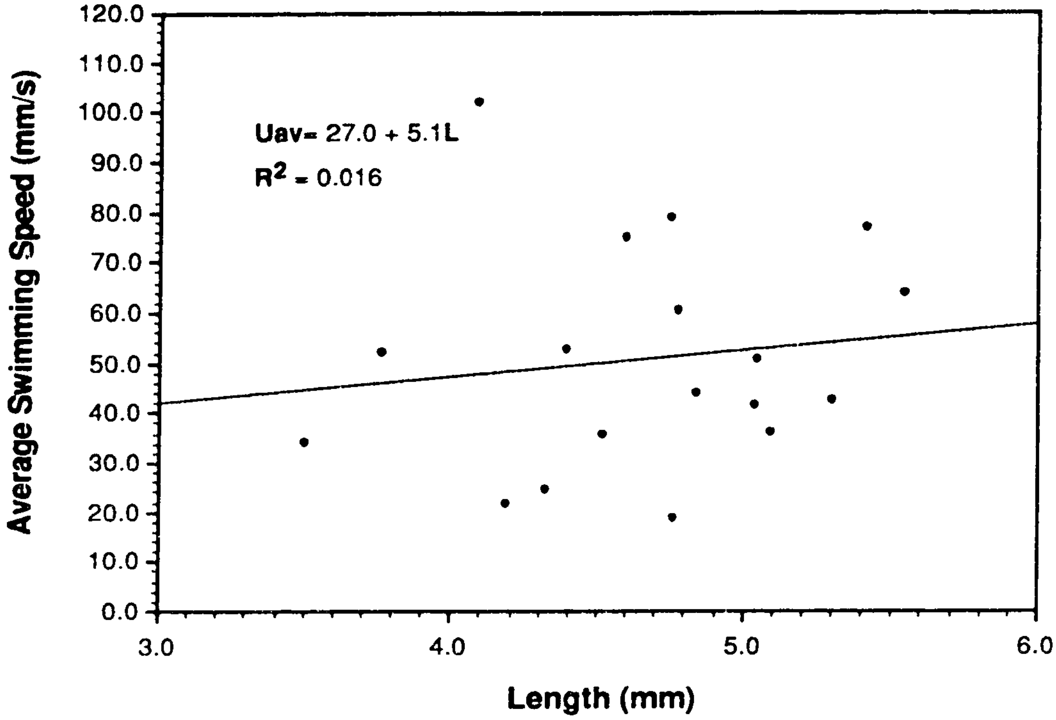


Figure 23. Effect of body length on average swimming speed in large (≥ 4.0 mm) *B. tricaudatus* nymphs.

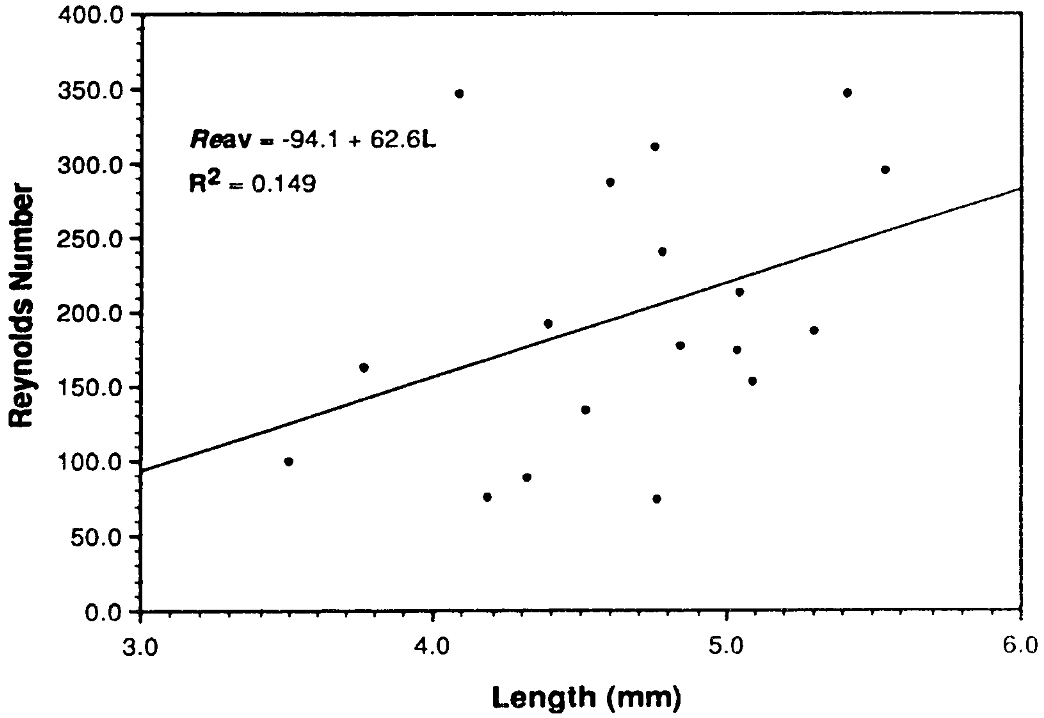


Figure 24. Effect of body length on Reynolds number in large (≥ 4.0 mm) *B. tricaudatus* nymphs swimming in freshwater at 13°C.

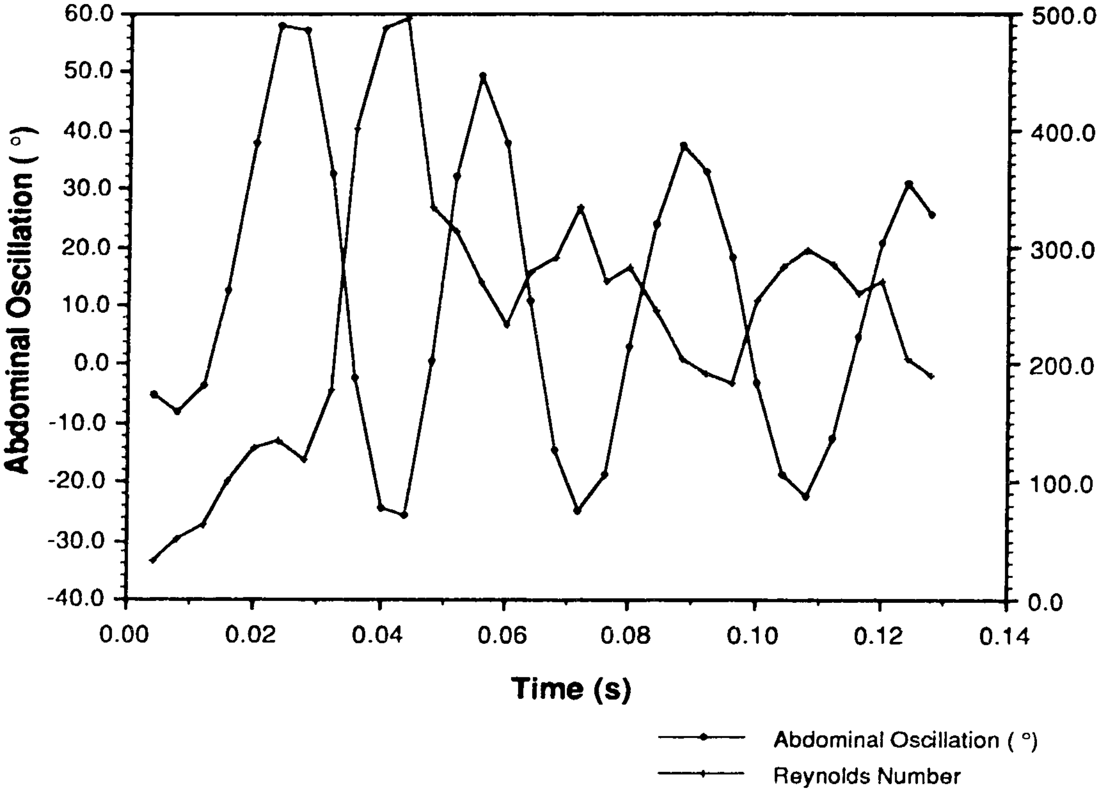


Figure 25. Relationship between abdominal position and Reynolds number during a swimming sequence of a 4.4 mm *B. tricaudatus* nymph.

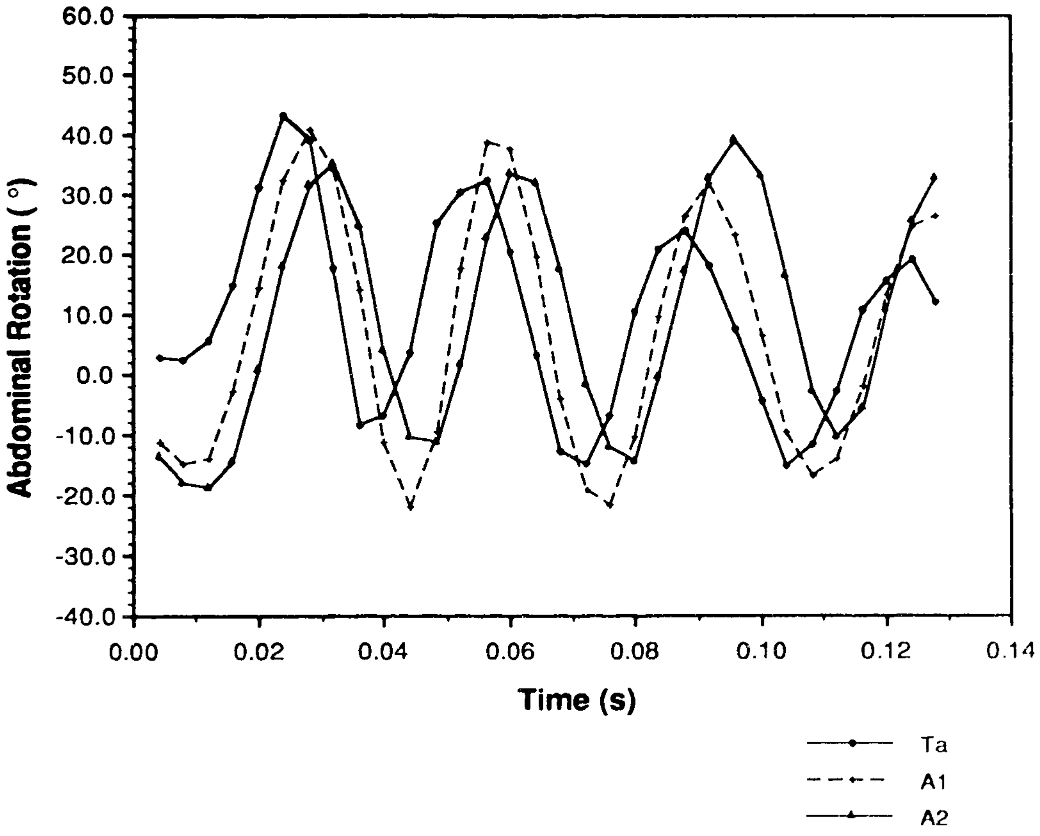


Figure 26. Rotation of abdominal segments created through points at the junction of the thorax and abdomen(Ta), the basal third of the abdomen (A1), and the distal third of the abdomen (A2) in a 4.4 mm *B. tricaudatus* nymph.

4. DISCUSSION

4.1 Swimming Behaviour and Performance of Small *B. tricaudatus* Nymphs (≤ 3.0 mm):

Aquatic insects exhibit a variety of swimming behaviours. Dragonfly nymphs (Odonata: Anisoptera) use jet propulsion to swim (Mill & Pickard 1975), mosquito larvae (Diptera: Culicidae) move by wriggling their abdomen (Natchigall, 1985), whereas adult diving beetles (Coleoptera: Dytiscidae) and water boatmen (Hemiptera: Corixidae) use their legs to row through the water (Nachtigall 1974; Blake 1986 respectively). Fusion of body segments can restrict the way an animal swims. For example, locomotion in adult dytiscids and corixids is confined to rowing because their abdominal segments are fused. In other insects, the methods used for locomotion are less restricted. Larvae of the aquatic beetle *Acilius sulcatus* (Coleoptera: Dytiscidae) crawl through the water whereas *Hydrophilus* (Coleoptera: Hydrophilidae) larvae use paired rowing of the appendages to swim (Nachtigall 1974). Although both species having a flexible abdomen, neither use it for propulsion.

Small *B. tricaudatus* nymphs use dorso-ventral oscillations of the abdomen in conjunction with rowing movements of the legs to swim. Contrary to observations made by Saita (1979), all abdominal oscillations occurred in the dorso-ventral plane as opposed to a lateral one. Dorso-ventral oscillation is theoretically a more efficient means of generating thrust in *B. tricaudatus* nymphs because of the arrangement of their abdominal musculature and the dorso-ventral flattening of the abdomen (Craig 1990). The function of the abdomen is similar to that of a paddle, which is more efficient when the broad side is used to push large amounts of water as opposed to using the narrower edge to cut through it.

Although the use of dorso-ventral abdominal oscillations in concert with leg rowing is a unique method of swimming within the Insecta, similar movements have been observed in *Cyclops* (Copepoda: Crustacea) and other copepods (*e.g.*, Strickler 1975; Morris *et al.* 1985). These crustaceans and small *B. tricaudatus* nymphs are similar in size, shape and in the flexibility of their corresponding abdominal sections. Therefore it is probably not coincidental that these animals exhibit comparable swimming behaviours. Morphological similarity places them in comparable hydrodynamic regimes that may in part influence swimming behaviour.

An animal's behaviour is influenced by the hydrodynamic environment in which it exists. Reynolds numbers provide a general guide to determining what hydrodynamic forces an animal may face in its environment. At low *Re* (<20), viscous forces prevail and drag is proportional to the viscosity of the medium and the relative velocity (Webb & Weihs 1986). An intermediate zone between $20<Re<200$ defines the range where a gradual transfer from primarily viscous to inertial forces occurs (Webb & Weihs 1986). Reynolds numbers taken from average velocities show that small *B. tricaudatus* nymphs are in a hydrodynamic environment where viscous forces predominate. Instantaneous *Re* frequently falls to 10 or lower as the abdomen approaches either the maximally flexed or deflexed position.

At very low *Re*, flows are reversible due to a lack of fluid circulating around an object. Circulation of fluid around an object takes time to develop, and the time taken is proportional to the relative velocity at the solid-fluid interface (Vogel 1981). Propulsive methods of locomotion, which are inertial based, are not possible at low *Re* (Webb & Weihs 1986). Instead, organisms at low *Re* must use friction based locomotion to maintain the drag of the recovery stroke at a level lower than that experienced during the power stroke. If a power stroke equaled the recovery stroke in all aspects, an organism would experience virtually no net forward movement (Purcell 1977).

Decreasing the effective area of the appendage during recovery, or moving the appendage along a path near the body where the flow is slower, are two frequently adopted methods of lowering drag at low *Re* (Vogel 1981). These methods decrease the amount of water displaced during a recove stroke, relative to that of the power stroke. During the power stroke of a rowi *B. tricaudatus* nymph, the abdomen is positioned dorsal to the head and thorax and the legs are positioned ventrally, whereas at the beginning recovery, both abdomen and legs are in the same plain, ventral to the rest of the body. This orientation decreases the total frontal area normal to the direction of motion during recovery. Since drag varies with the frontal area exposed to the flow ($D = \rho SU^2$ where ρ is the density of the medium and S the exposed area), the drag would be lowest when both the abdomen and the legs are in the same plane (Fig. 27). Nymphs extend their legs ventrally and laterally on the power stroke, but recover the legs in a somewhat flexed position extending only ventrally, which localizes the projected area to one plane. The ventral inclination of the head and thorax at the onset of the recovery stroke permits the legs to recover in the wake of the frontal portion of the body where the flow is slower (Strickler 1975) serving to minimize drag.

During the swimming cycle of a nymph, decreases in velocity occur twice. These can be attributed to the increase in exposed frontal area when the abdomen is in a flexed position and to the deceleration of the abdomen as it completes either a power or recovery stroke. The first is a result of a greater area projected in the direction of the flow which increases drag. As the surface area exposed increases, the forces countering forward movement also increase and the velocity decreases. The second component occurs as the abdomen changes its direction. When this occurs, the velocity of the abdomen is zero and therefore does not contribute to the propulsion of the nymph.

Two localized peaks in swimming velocity occur when the abdomen reaches its highest angular velocity and hence is moving the most water at any given time. The highest peak in swimming speed occurs during the power stroke, even though the angular velocities during the power and recovery stroke for any given cycle are comparable. What differs between the two cycles is the exposed frontal area caused by the orientation of the legs and the configuration of the abdomen in relation to the flow of the fluid. When in a linear configuration, the animal is subjected to the least amount of frontal drag. A lower peak occurs as the abdomen is about halfway through its recovery and has reached its maximum velocity. At this point, it is moving the most water and therefore offers the most propulsive force (Fig. 7a & b).

The oscillation of the abdomen changed as the nymphs grew larger. Rotation about points Ta, A1 and A2 were fairly synchronous in small nymphs, but slightly asynchronous in larger nymphs. This is a result of increasing flexibility as the abdomen becomes longer. As the abdomen increases in length it begins to undulate, starting from the point at which thrust is initially generated (the basal third) and gradually proceed along the length of the abdomen.

Frequently in nature, large organisms are faster than small ones (Vogel, 1981). The results of this study conform to this general principle, with the larger nymphs reaching higher swimming velocities and therefore higher *Re* than smaller nymphs. The high correlation between length and *Re* combined with the linearity of this relationship suggest a physical constraint on small *B*.

tricaudatus by the fluid environment. Speed is also directly dependent on the frequency and amplitude of the oscillating appendages of body segments (Bainbridge 1957). Though the results support this dependence, the relationship between speed, frequency, amplitude and length has not yet been adequately established for *B. tricaudatus.*

Baetis tricaudatus nymphs exhibit 'burst' swimming; they swim for a short time then stop and exhibit a 'splayed' position in the water column. Burst swimming is energetically profitable (Wiehs 1974) and is consistent with the field observations of swim-drift behaviours that are frequently adopted by streamlined mayflies (Peckarsky 1980). Upon entering the water column in a lotic environment, nymphs are swept downstream with the current, essentially negating any locomotory effort by the nymph. The 'splayed' position taken in the column is similar to that at the onset of the power stroke and it may be that this is a type of 'ready' position to pre-set the body in a configuration from which swimming could be immediately initiated if required. Alternatively, a splayed position also serves to increase the projected area which may allow a nymph to use the flow more effectively when initiating drift behaviour.

4.2 Transition of Swimming Behaviour

The transition from linear increases to exponential increases in swimming speed occurred at the same point at which the nymphs changed their swimming behaviour. Corresponding *Re* associated with these speeds show that the change in swimming behaviour occurs within the zone from one in which viscous forces predominate to one where inertial forces prevail.

Few of the nymphs observed were within the transition zone where the change in swimming behaviour took place. Since *B. tricaudatus* sometimes has two overlapping generations, summer and winter, the gap in the data likely represents the difference in age structure of this population. However, based on limited observations of nymphs exhibiting an intermediate swimming behaviour, the transition from rowing to non-rowing swimming appears quite gradual. As nymphs became capable of swimming at higher speeds, the movements of the legs became more passive and were gradually held closer to the body as the boundary layer thickness around the nymph decreases.

4.3 Swimming Behaviour and Performance of Large *B. tricaudatus* Nymphs (≥ 4.0 mm)

Large nymphs used only abdominal oscillations of their abdomens to swim. As the abdomen oscillated, the head and thorax rotated as well. This rotation likely contributes to momentum balance while swimming (Fish & Hui 1991).

Physical principles of locomotion dictate that at *Re* above 200, inertial based propulsors are efficient means of transportation (Webb & Weihs 1986). At *Re* higher than 200 a streamlined body form is desirable since this shape delays separation of the boundary layer and decreases the wake at the trailing end.

It is possible that use of legs in locomotion could detract from locomotory performance at high Re_{av}. This would occur as the legs project beyond the limits of the boundary layer where the flow is faster and serve to increase drag. Flow visualization of the 95% boundary layer of a *Cloeon dipterum* (Ephemeroptera: Baetidae) swimming at a velocity of 200 mm/s showed it to be ~0.50 mm over the anterior gills (Craig, 1990). This thickness is much less than that needed to encompass the rowing legs of a large *B. tricaudatus* nymph.

Alternatively, the musculature in the legs may not be well enough developed to row at the higher frequencies needed to match the oscillation of the abdomen.

Amplitude of abdominal oscillations was lower in large nymphs compared to small nymphs. This likely reflects the transition from the action of predominately viscous to inertial drag forces. High degrees of abdominal flexion and deflexion would adversely affect swimming under these conditions. By minimizing dorsal and ventral projections of the abdomen, the fluid flows more smoothly over the trailing edge of the nymph and the formation of counteractive eddies is diminished.

The highest velocities were achieved when the nymphs were in the most linear position and parallel to the direction of motion. This corresponds to a point midway through either the power or recovery stroke. Maximum speeds occurred immediately following onset of the propulsive and recovery strokes with another local maximum reached when the animal assumed a linear configuration parallel to the direction of motion. These high speeds are likely the combined result of high acceleration and angular velocity of the abdomen at these times and because the projected frontal area was smallest. Unexpectedly, the highest *Re* experienced during a swimming cycle occurred when the abdomen was approaching maximum deflexion. This could be a result of the body assuming a more bluff configuration as the head is tucked ventrally which may allow the water to flow over the nymph more easily thereby decreasing the drag.

Body length was not a good predictor of velocity in large nymphs, which suggests that large nymphs are not rigidly confined by physical properties of their environment. Nymphs in this size class are capable of high accelerations and swimming velocities (Craig and Weihs unpubl. manuscript) and may use accelerative escape motions (AEM) to escape predation, although circumstances may not demand that nymphs always accelerate rapidly or swim at their maximum velocity. In some invertebrates, giant axons mediate escape behaviours with nature or intensity of a stimulus being the governing factor on whether these neurons are fired (Camhi 1984). Stronger stimuli, or certain types of stimuli, cause the giant nerve fibres to fire and elicit accelerative escape reactions. The stimulus eliciting the swimming behaviour, be it one spontaneously generated, for example, leaving poor foraging sites versus escape from a predator, may be the determining factor that regulates the magnitude of the swimming response.

4.4 Ecological Implications of Swimming Speed and Behaviour

If the outcome of a predator-prey interaction is dependent on the behaviour of the participants, which is in turn influenced by their physical capabilities (Webb, 1986), then it is possible that the ontogenic changes in swimming behaviour that occur in *B. tricaudatus* could have important ecological consequences, particularly in escape or avoidance strategies used by mayfly nymphs and prey selection by predators.

Scrimgeour *et al.* (1994) have shown that *B. tricaudatus* nymphs display risk adjustment strategies in predator prey interactions involving the longnose dace (*Rhinichthys cataractae*). Risk adjusting occurred in high and low food treatments and was dependent on the length of nymph involved in the interaction. Large nymphs delayed flight initiation upon predator detection in high food regimes whereas small nymphs fled once the dace was detected in both low or high food treatments.

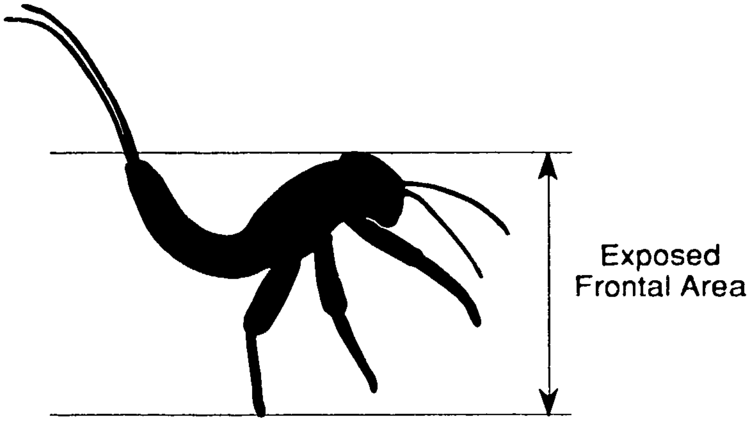
Although no mechanism for size dependent risk adjustment was determined, Scrimgeour *et al.* (1994) suggested that the speed at which mayfly nymphs swim away from an approaching predator might explain the size specific flexibility in drift initiation distances displayed by *Baetis*. The results from my study show that small nymphs display a linear increase in average speed with growth (see Chapter 2) and that the change in swimming behaviour coincided with exponential increases in velocity with growth that occurred once the nymph reached *ca.* 3.5 mm in length. Because swimming performance appears to be restricted by the hydrodynamic regime in which mayflies live, small nymphs likely have a somewhat limited flight initiation distance for which they can successfully escape predation. This strategy forms the basis of the perceptual limit hypothesis where foragers flee an approaching predator soon after detecting it (Ydenberg & Dill 1987, cited in Scrimgeour & Culp 1994). Once a predator is detected, small nymphs must flee into the water column as any subsequent delay could be fatal.

Conversely, large nymphs display a range of swimming speeds and are capable of high acceleration rates. Accelerative escape reactions have been found to occur in fish and have also been described for the baetid mayflies *Cloeon dipterum* (Linn.) (Craig 1990) and *B. tricaudatus* (Craig & Weihs unpubl. manuscript). Nymphs able to accelerate at high rates and swim at high speeds should theoretically be able to delay their flight response until a predator comes within a certain critical range. This type of behavioural plasticity would allow foraging nymphs to get maximum benefit from high food sites and provides a mechanism for risk adjustment. Peckarsky and Penton (1989b) have shown that *B. bicaudatus* Dodds nymphs permit a stonefly predator to get within 2 cm before attempting to escape; when a predator came within 1 cm, the probability of prey response by swimming was 90%. In optimal foraging sites, the increased swimming performance of large nymphs could provide them with the means to get maximal benefit from the foraging site and not risk changing this habitat by prematurely fleeing when unnecessary.

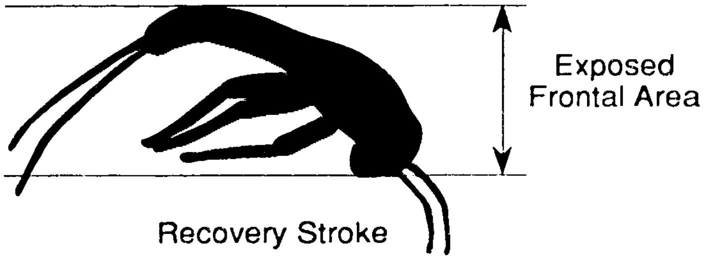
Locomotion may be important in the detection and selection of different size classes of prey by a predator. Some stoneflies display differential attack and consumption rates based both on predator and prey size (Allan *et al.* 1987). Small predators generally prefer small prey whereas amongst large predators there was almost no preference. It has been shown that predaceous stoneflies use hydrodynamic cues in locating possible prey items (Peckarsky & Penton 1989a). Further evidence suggests that stoneflies show preference for high frequencies generated by a swimming prey (Peckarsky & Wilcox 1989). This could in part explain why *Baetis* spp. are more frequently selected by stonefly predators over other mayfly nymphs. Furthermore, differences in frequency of abdominal oscillations between small and large nymphs could prove to be a means for differential prey selection.

Although *Baetis* spp. are able to use their lotic environment to some extent to escape a benthic predator by drifting, their relatively small size also permits them to hide in the boundary layer formed by the substrate, where the flow environment is much different from the mainstream. These nymphs are frequently found in patches of vascular hydrophytes (personal observation) which also serve to reduce the mainstream flow. For this reason, streamlined lotic nymphs ought to be good swimmers to facilitate successful escape in low velocity flows when drifting may not be advantageous.

Yet another reason why swimming may be important in escaping predation in lotic systems is that *Baetis* is a rheophilic animal and predaceous stoneflies frequently hunt downstream of their prey (Peckarsky & Penton 1989a). It is probable that if a nymph was to escape a predator approaching from downstream by merely drifting, it could be carried directly to the predator from which it was trying to escape. The direction from which a predator approaches *Baetis* spp. may influence the type of strategy, be it drifting, swim-drifting, or swimming, used by nymphs to escape benthic predators.



Power Stroke



Recovery Stroke

Figure 27. Exposed frontal area of the power and recovery strokes during a swimming sequence of a small *B. tricaudatus* nymph.

5. CONCLUSIONS

Of the many sub-disciplines in science, biology is one of the most complex and physics among the most fundamental. (Hazen &Trefil 1991). Behavioural hydrodynamics (*sensu* Craig 1990) incorporates the basic principles of fluid dynamics as they affect various aspects of an animals' behaviour. The swimming behaviours used by *Baetis tricaudatus* Dodds show a strong dependence on the nature of their environment. Although both small and large nymphs occupy the same habitat, the hydrodynamic environment they occupy changes as they develop and, as a result, so does the manner in which they swim.

Because of their size and relatively slow swimming speeds, small nymphs are more effected by the viscous effects of their fluid environment. In this hydrodynamic regime they must use friction based means of propulsion. This is achieved through rowing motions of the legs along with abdominal oscillations. *Re* of large swimming nymphs is about an order of magnitude higher than those of small nymphs. In this hydrodynamic environment, large nymphs are able to swim using inertial based abdominal oscillations.

The material presented here only begins to outline the hydrodynamics of *B. tricaudatus* locomotion. Few aspects of *B. tricaudatus* locomotion have been as extensively described as those for fish However, Craig and Weihs (unpubl. manuscript) are currently conducting a detailed analysis of large *B. tricaudatus* locomotion.

Apart from the physical aspects of *B. tricaudatus* locomotion, left to be described are the ecological implications of such findings. There can be no doubt the behaviour displayed by these nymphs is affected by their physical capabilities, and consequently, the behaviour of their predators is equally likely to be affected. The possibility that swimming speed is a mechanism for risk adjusting behaviour is one that requires further examination.

5.1 LITERATURE CITED

Allan, J. D., A. S. Flecker and N. L. McClintock. 1987a. Prey preference in stoneflies: sedentary vs. mobile prey. Oikos 49: 323 - 331.

Allan, J. D., A. S. Flecker and N. L. McClintock. 1987b. Prey size selection by carnivorous stoneflies. Limnol. Oceanogr. 32(4): 864 - 872.

Allan, J. D., and A. S. Flecker. 1988. Prey preference in stoneflies: a comparative analysis of prey vulnerability. Oecologia 76: 496 - 503.

Archer, S. D. and I. A. Johnston. 1989. Kinematics of labriform and subcarangiform swimming in the Antarctic fish *Notothenia neglecta*. J. exp. Biol. 143: 195-210.

Bainbridge, R. 1958a. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. exp. Biol. 35: 109-133.

Batty, R. S. 1981. Locomotion of plaice larvae. Symp. zool. Soc. Lond. 48: 53 - 69.

Batty, R. S. 1984. Development of swimming movements and musculature of larval herring (*Clupea harengus*). J. exp. Biol. 110: 217 - 229.

Blake, R. W. 1986. Hydrodynamics of swimming in the water boatman, *Cenocorixa bifida*. Can. J. Zool. 64(8): 1606-1613.

Camhi, J. M. 1984. Neuroethology: Nerve Cells and the Natural Behavior of Animals. Sinauer Associates Inc.

Craig, D. A. 1990. Behavioural hydrodynamics of *Cloeon dipterum* larvae (Ephemeroptera: Baetidae). J. N. Am. Benthol. Soc. 9: 346 - 357

Craig, D. A. and D. Weihs. unpubl. Accelerative escape motions and swimming in *Baetis tricaudatus* Dodds larvae (Baetidae; Ephemeroptera).

Culp, J. M. and G. J. Scrimgeour. 1993. Size-dependent diel foraging periodicity of a mayfly grazer in streams with and without fish. Oikos 68: 242 - 250.

Edmunds, G. F. Jr. 1984. Ephemeroptera. pp. 94 - 125 *in* R.W. Merritt and K.W. Cummins (editors). An Introduction to the Aquatic Insects of North America, 2nd Edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Edmunds, M. 1974. Defense in Animals: a survey of anti-predation defenses. Longman Inc. New York.

Fish, F. E. and C. A. Hui. 1991. Dolphin swimming - a review. Mammal Rev. 21: 181 - 195.

Hazen, R. M. & J. Trefil. 1991. "Science Matters: Achieving Scientific Literacy". Doubleday. New York, New York. 294 pp.

Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fishery Bulletin. 70(3): 821 - 838.

Hynes, H. B. N. 1970. Anatomical and behavioural adaptations of benthic invertebrates. In 'The Ecology of Running Waters'. University of Toronto Press. pp. 121-144.

Mill, P. J. & R. S. Pickard. 1975. Jet-propulsion in anisopteran dragonfly larvae. J. Comp. Physiol. 97: 329 - 338.

Molles, M. C. Jr. and R. D. Pietruszka. 1983. Mechanisms of prey selection by predaceous stoneflies: Roles of prey morphology, behavior and predator hunger. Oecologia 57: 25 - 31.

Morris, M. J., G. Gust and J. J. Torres. 1985. Propulsion efficiency and cost of transport for copepods: a hydromechnical model of crustacean swimming. Marine Biology 86: 283-295.

Nachtigall, W. 1974. Locomotion: mechanics and hydrodynamics of swimming in aquatic insects. pp. 381 - 432 *in* M.Rockstein (ed). The Physiology of Insecta, Vol. 3. 2nd ed. Academic Press, New York.

Nachtigall, W. 1985. Swimming in aquatic insects. pp. 467 - 490 *in* G.A. Kerkut and L.I. Gilbert (editors). Comprehensive Insect Physiology, Biochemistry and Pharmacology". Vol. 5. Pergamon Press, Oxford.

Needham, J. G. and J. T. Lloyd. 1916. The Life of Inland Waters. The Comstock Publishing Company. Ithaca, New York.

Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. Ecology 61: 932 - 943.

Peckarsky, B. L. 1987. Mayfly cerci as defense against stonefly predation: Deflection and detection. Oikos 48: 161 - 170.

Peckarsky, B. L. and M. A. Penton. 1988. Why do Ephemerella nymphs scorpion posture: A "ghost of predation past"? Oikos 53: 185 - 193.

Peckarsky, B. L., and M. A. Penton. 1989a. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology 70: 1203 - 1218.

Peckarsky, B. L., and M. A. Penton. 1989b. Early warning lowers risk of stonefly predation for a vulnerable mayfly. Oikos 54: 301 - 309.

Peckarsky, B. L. and R. S. Wilcox. 1989. Stonefly nymphs use hydrodynamic cues to discriminate between prey. Oecologia 79: 265 - 270.

Peckarsky, B. L., C. A. Cowan and C. R. Anderson 1994. Consequences and plasticity of the specialized predatory behavior of stream-dwelling stonefly larvae. Ecology 75(1): 166-181.

Purcell, E. M. 1977. Life at low Reynolds number. Am. J. Phys. 45(1): 3-11.

Saita, A. 1979. Analysis of abdominal movements in nymphal Ephemeroptera by means of high-speed cinematography. In 'Proceedings of the 2nd International Conference on Ephemeroptera (1975), Pánstwowe Wydawnictwo Nauukowe, Warsaw-Kraków. pp. 279 - 292.

Scrimgeour, G. J. and J. M. Culp. 1994. Foraging and evading predators: the effect of predator species on a behavioural trade-off by a lotic mayfly. Oikos 69: 71-79.

Scrimgeour, G. J., J. M. Culp and F. J. Wrona. 1994. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. J. N. Am. Benthol. Soc. 13(3): 368-378

Siegfried, C. A. and A. W. Knight. 1976. Prey selection by a Setipalapian stonefly nymph, *Acroneuria* (*Calaneuria*) *californica* Banks (Plecoptera: Perlidae). Ecology 57: 603-608.

Sokal, R. R. & S. J. Rohls. 1981. Biometry. W. H. Freeman & Company. New York. 859 pp.

Soluk, D. A. and N. C. Collins. 1988. Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. Oecologia 77: 370 - 374.

Statzner. B. 1988. Growth and Reynolds number of lotic macroinvertebrates: A problem for adaptation of shape to drag. Oikos 51: 84 - 87.

Strickler, J. R. 1975. Swimming of planktonic *Cyclops* species (Copepoda, Crustacea): pattern, movements and their control. In 'Swimming and Flying in Nature. Vol. 2. Edited by T. Y-T. Wu, C.J. Brokaw, and C Brennen. Plenum Press, New York and London. pp. 599 - 613.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory. 1: 1-30.

Vogel, S. 1981. Life in Moving Fluids: the physical biology of flow. Princeton University Press. Princeton, New Jersey.

Webb, P. W. 1986. Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterous salmoides*). Can J. Fish. Aquat. Sci. 43: 763 - 771.

Webb, P. W., and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Trans. Am. Fish. Soc. 115: 115 - 127.

Weihs, D. 1974. Energetic advantages of burst swimming of fish. J. theor. Biol. 48: 215 - 229.