

KINEMATICS OF SWIMMING IN TWO SPECIES OF *IDOTEA* (ISOPODA: VALVIFERA)

By DAVID E. ALEXANDER*

*Department of Biology, Bellarmine College, Newburg Road, Louisville,
KY 40205, USA*

Accepted 29 February 1988

Summary

Individuals of *Idotea resicata* and *I. wosnesenskii* were videotaped at 200 frames s^{-1} while swimming freely. Propulsion is provided by the first three pairs of abdominal appendages (pleopods), which may also function as gills. Unlike typical crustacean metachronal beating, in *Idotea* all three pairs of propulsive pleopods begin their recovery strokes simultaneously. Each pair then carries out its power stroke in sequence: third pleopods have a short power stroke, then second pleopods have an intermediate power stroke, finally first pleopods have a long power stroke. After these power strokes, there is a pause before the next recovery stroke begins. The duration of the power stroke of any pair of pleopods, as well as the overlap with other pleopods' power stroke, is variable and is not directly related to swimming speed. Stroke amplitude is approximately constant, but stroke frequency is significantly correlated with swimming speed. Other stroke variables which could affect swimming speed are also loosely correlated with frequency, but it appears that frequency is the most important determinant of swimming speed. The unusual stroke pattern in *Idotea* may be related to the respiratory function of the pleopods.

Introduction

Crustaceans typically propel themselves with their appendages when swimming (Lochhead, 1961, 1977), in contrast to the undulatory locomotion used by most fish (e.g. Videler & Hess, 1984; Webb *et al.* 1984), or jet propulsion used by many invertebrates (e.g. Packard, 1969; Daniel, 1983). Several different patterns of appendage movement are used by different crustaceans, including both lift- and drag-based mechanisms. For example, the propeller-like propulsion used by portunid crabs is probably lift-based (Lochhead, 1977). The most common, and perhaps most primitive, drag-based mechanism is metachronal beating by many similar appendages in series (Cannon, 1933; Davis, 1968; Barlow & Sleight, 1980;

*Present address: Department of Physiology and Cell Biology, University of Kansas, Lawrence, KS 66045, USA.

Key words: *Idotea*, isopod, kinematics, locomotion, propulsion, pleopods, swimming.

Macmillan *et al.* 1981). Metachronal swimming is found in generalized crustaceans such as syncarids (Macmillan *et al.* 1981) and brine shrimp (Barlow & Sleigh, 1980), as well as in such specialized groups as lobsters and crayfish (Hughes & Wiersma, 1960; Davis, 1968). Other crustacean swimming modes include antennal propulsion by many planktonic forms (Lochhead, 1961, 1977) and the rapid flip of the tail fan seen in many decapods (Webb, 1979).

Many marine isopods swim using a 'rowing' motion of the abdominal appendages (pleopods) that are also used for gas exchange (Richardson, 1904; Schram, 1986). The swimming stroke that these isopods use with their multiple pleopods is very different from the basic metachronal pattern. In the latter, all the appendages go through a stroke cycle of the same period with identical power and recovery strokes, but each appendage slightly lags the phase of its posterior neighbour, giving the appearance of a wave of movement moving anteriorly along the appendages (Cannon, 1933; Davis, 1968). In idoteid isopods (and probably most other swimming isopods), the swimming stroke pattern is very different: only three pairs of pleopods are used for swimming, and the bases of the pleopods are very close together, so the metachronal phase pattern would be physically difficult to achieve.

In this study, I used high-speed video photography to describe the kinematics of swimming in two species of marine isopod in the genus *Idotea*. My objectives were (1) to describe the swimming movements in *Idotea* and relate them to swimming speed, (2) to contrast these movements with the metachronal pattern and with movements used by other swimming animals, and (3) to use these comparisons to discuss the possible evolutionary significance of the combined locomotory and respiratory functions of the pleopods.

Materials and methods

Study organism

A brief description of the external anatomy of *Idotea* will facilitate description of its swimming kinematics. In common with other valviferan isopods, those in the genus *Idotea* have uropods modified to form trap-door-like 'operculae'. When closed, these operculae cover the ventral surface of the abdomen and the pleopods, forming a gill chamber (Naylor, 1972; personal observation). The bases of the five pairs of pleopods are concentrated near the anterior of the abdomen. When the operculae are closed, the pleopods form two flat stacks, somewhat like book pages, between the ventral surface of the abdomen and the operculae. Each pleopod is biramous, consisting of two very similar, flat, paddle-like blades; each pair works as a functional unit, so that a pair of pleopods forms a fan of four blades. By convention, pleopods are numbered from anterior to posterior, with the first being the most anterior. In this study I will refer to the most anterior pleopods as P-1, the next pleopods posteriorly as P-2, and so on.

Isopods were collected by hand from the intertidal zone in the vicinity of Friday

Harbor Laboratories (San Juan Islands, Washington State, USA). *Idotea resecata* Stimpson was collected from eel grass (*Zostera*) and *Idotea wosnesenskii* Brandt was collected from brown algae (*Fucus*). Animals were kept in individual containers in fresh, running sea water at 11–12°C, and fed *ad libitum* on *Zostera* and *Fucus*. The body length of each isopod was measured to the nearest 0.01 cm with Vernier callipers.

Kinematics of Idotea swimming

A high-speed video system (NAC HSV-200) was used to videotape swimming isopods at 200 frames s⁻¹, using a NAC synchronized strobe lighting system. Animals were filmed in a glass trough (46 cm × 8 cm, filled to 8 cm depth), either from the side or from the top using a mirror positioned at 45° over the tank. As the animals were swimming freely, it was not possible to videotape top and side views simultaneously. Approximately 200 sequences were filmed, ranging in duration from less than 1 to more than 30 s.

Frame-by-frame analysis was done on Ektachrome slides taken from the HSV-200 monitor or by playing the tapes back on a standard VHS videocassette recorder (Panasonic PV-6600). Nine swimming sequences that clearly showed the isopod and its pleopods from above were chosen for detailed analysis; the pleopods were partly hidden by the operculum in side view, which precluded accurate measurement of the positional angle (angle of the pleopods with respect to the long axis of the animal's body, Fig. 1C) at the end of the power stroke. For each frame, the phase (pause, recovery stroke, power stroke) of each pair of pleopods was recorded. To measure the animal's speed, a mark on the isopod was traced onto a transparent overlay, the distance between marks for successive frames on the overlays was measured with Vernier callipers, corrected for magnification using centimetre marks in the trough, and divided by the interval between frames to give a nearly instantaneous measure of the speed of the isopod. Three tracings were made from each sequence and averaged, to minimize tracing errors.

Eight other sequences were clear enough to measure the following general stroke parameters. Using two consecutive strokes, the time from the beginning of a recovery stroke to the beginning of the next recovery stroke, and the time from the end of a power stroke to the end of the next power stroke were measured and averaged to give the stroke period. The inverse of the period is the stroke frequency. The total power stroke duration was determined by measuring the time from the beginning of the power stroke of P-3 to the end of the power stroke of P-1 for both strokes and averaging them; this is the inverse of the 'corrected frequency' of Webb (1973). The time needed to travel between two or three centimetre markers was also measured to give the average speed over the analysed strokes. These stroke parameters (stroke period, stroke frequency, total power stroke duration and average speed) were also calculated for the nine strokes analysed in detail.

Results

General features of swimming behaviour

When not in contact with a surface, both species of *Idotea* assumed a characteristic 'swimming posture': ventral side up, anterior legs folded tightly against the body, the three (*I. ressecata*) or four (*I. wosnesenskii*) most posterior legs extended laterally and slightly caudally, probably as stabilizers (Fig. 1A). To swim, the operculae opened on their lateral hinges and the three anterior-most pairs of pleopods began their stroke. The stroke began with the recovery phase: the blades of the first three pairs of pleopods were compressed medially from two

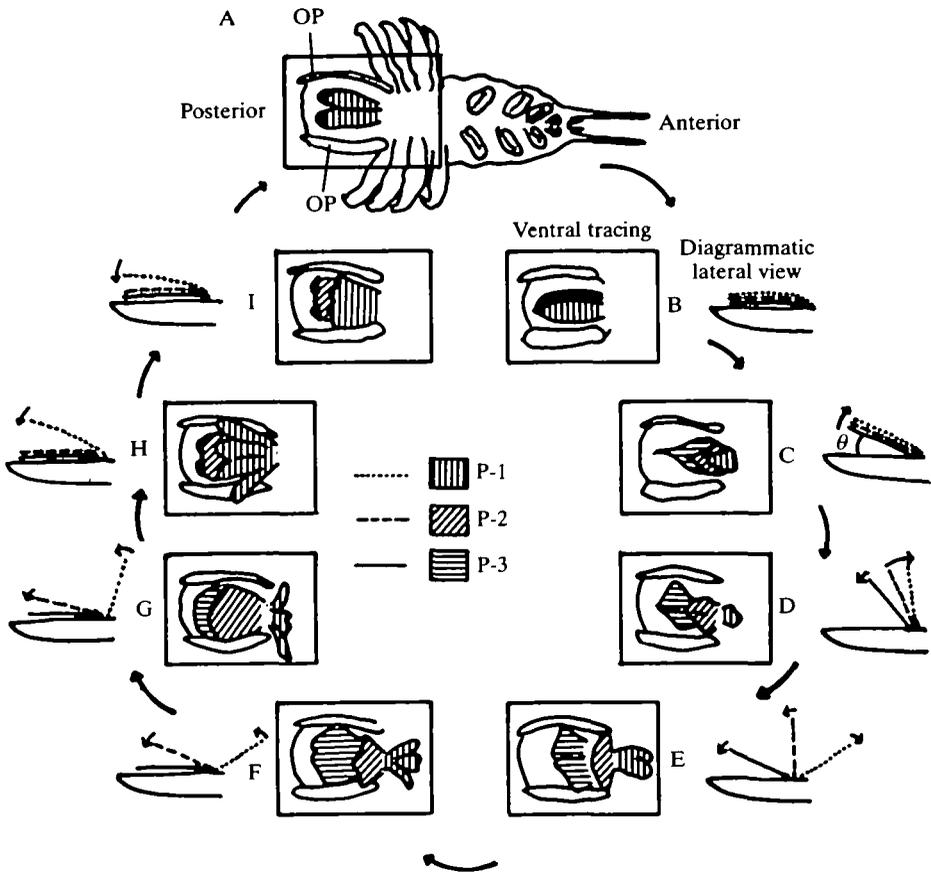


Fig. 1. Sequential tracings of a ventral view of *Idotea wosnesenskii* over the course of one stroke. (A) Ventral view of whole animal showing typical swimming posture, with antennae and posterior legs extended and anterior legs flexed. (B–I) Sequential tracings of ventral view of abdomen showing pleopods (boxed) and schematic lateral view showing pleopod angular positions in the associated tracing. (C) All pleopods in recovery phase. (D) Third pleopods (P-3) fanned out and beginning power stroke. (E) Second pleopods (P-2) fanned out and beginning power stroke. (G) First pleopods (P-1) fanned out and beginning power stroke. OP, operculum; θ , positional angle. Interval between tracings 0.01 s (except 0.02 s between G and H).

stacks into a single compact bundle and abducted ventrally and anteriorly (Fig. 1A–C, Fig. 2). As the bundle swung through its arc, each pair of pleopods fanned out and carried out its power stroke at a slightly different time (Fig. 2). When the bundle had moved through an angle of approximately 50° , the posterior-most pleopods in the bundle (P-3) were spread out, forming a nearly continuous fan of four blades, and adducted dorsally and posteriorly (Fig. 1D–E); when the bundle was at a positional angle of about 90° , the second pleopods (P-2) fanned out and began their power stroke (Fig. 1E–H). The remaining pair of pleopods (P-1) stayed compressed and continued their recovery stroke until they were very near the bases of the last pair of legs. They then also fanned out and began their power stroke (Fig. 1F–I). Thus, pleopods P-3 were the first to carry out their power stroke, and P-1 were the last to carry out their power stroke. As each pair of pleopods finished its power stroke, the blades of the pleopods on each side were overlapped and held in two stacks against the ventral surface of the abdomen. After the end of the power stroke of P-1, there was a pause phase (analogous to the ‘refractory phase’ of Webb, 1973), which was a period of no visible pleopod movement. At the end of the pause phase, all the swimming pleopods were again compressed and the next recovery phase began.

I will refer to the period when all three pairs of pleopods were in their recovery strokes as the ‘initial recovery phase’ to differentiate it from the recovery phase of any individual pair of pleopods (Fig. 2): within one stroke cycle, the recovery strokes and power strokes of the individual pairs of pleopods overlapped one another. Similarly, I will use ‘total power stroke duration’ to refer to the interval containing all three power strokes, i.e. the period from the beginning of the power

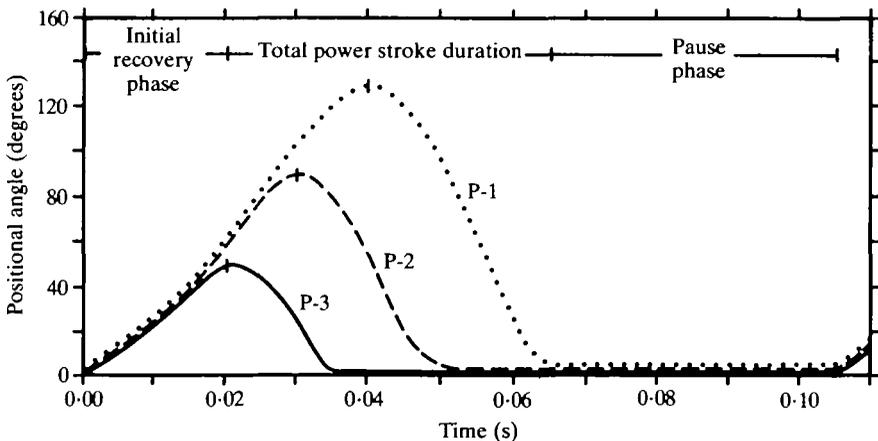


Fig. 2. Positional angle *versus* time, illustrating the time course of the phases for each pair of pleopods. Idealized curves are drawn through inflection points representing average positional angles and times. Positive slopes indicate recovery strokes; vertical bars indicate the time when a given pair of pleopods fans out and begins its power stroke. Power strokes are indicated by negative slopes. Horizontal segments of the curves represent pause phases.

stroke of P-3 to the end of the power stroke of P-1. Thus, the initial recovery phase ended, and the total power stroke duration began, with the beginning of the power stroke of P-3 (Fig. 2).

Pattern of pleopod movements

In both species of *Idotea*, all the swimming pleopods began their recovery strokes together, but each pair carried out its power stroke at a different time. As P-3 began their power stroke, P-2 and P-1 were still in the recovery phase of their strokes; as P-2 began their power stroke, P-1 were still recovering (Fig. 2). Thus, the power strokes of P-2 and P-3 took place partly or completely during the recovery stroke of P-1. The time of overlap of the power strokes of the three pairs of swimming pleopods was variable (see Figs 3–5). There were obvious differences in the duration and overlap of the power strokes of the swimming pleopods, even between consecutive strokes by the same individual. For example, Fig. 3 shows that in the first full stroke, the power strokes of P-3 and P-2 were separated slightly, and the power strokes of P-2 and P-1 overlapped by 0.015 s. In the following stroke, the power strokes of P-3 and P-2 were not separated, and those of P-1 and P-2 only overlapped by 0.005 s. Fig. 4 indicates that the amount of variation in some individuals may change with speed: for the same individual, the duration and overlap of the power strokes of the swimming pleopods were much more uniform at very high speed (Fig. 4A) than at low speed (Fig. 4B). This may have been because the total power stroke duration also tended to be lower at high speeds. However, the power stroke of the swimming pleopods could display substantial variation over a wide speed range. Fig. 5 presents strokes from the

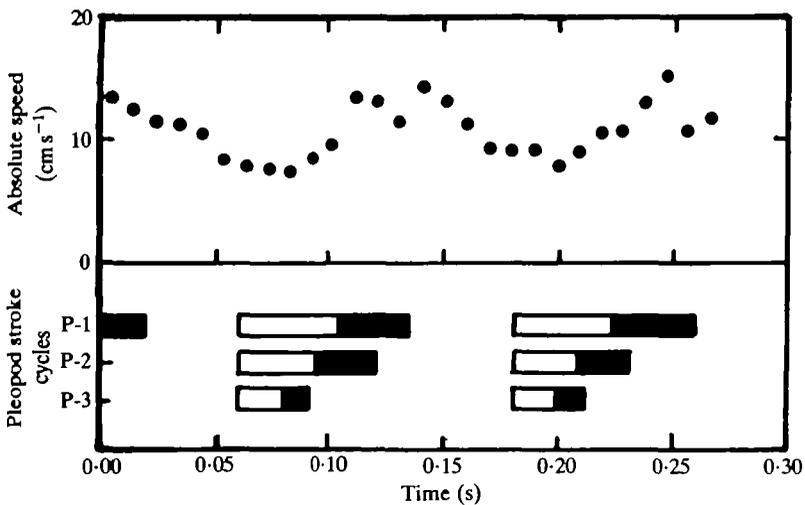


Fig. 3. Swimming speed and pleopod stroke patterns for individual M1 (body length = 3.52 cm, *Idotea ressecata*). Upper graph: swimming speed measured by displacement between frames. Lower graph: power stroke (filled box) and recovery stroke duration (open box) for each pleopod.

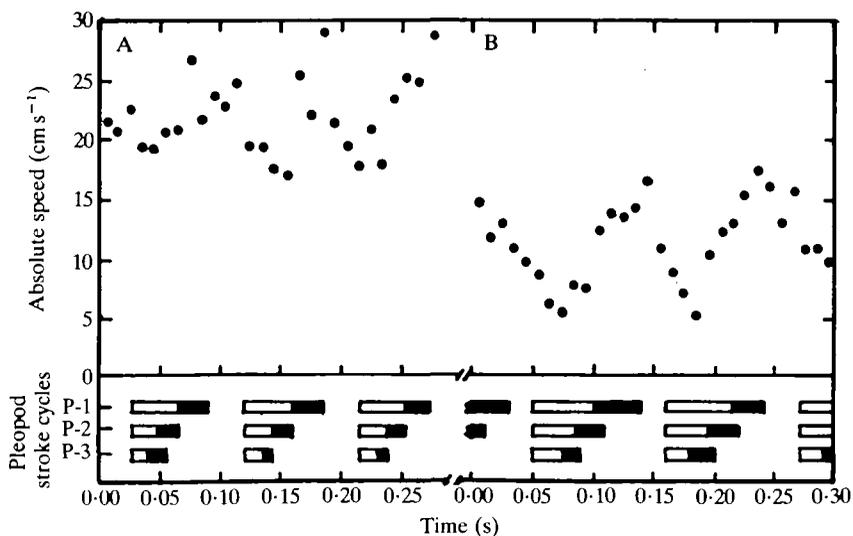


Fig. 4. Swimming speed and pleopod stroke patterns for individual C1 (BL = 3.14 cm, *Idotea wosnesenskii*). (A,B) Two different bouts of swimming. Upper and lower graphs as in Fig. 3.

beginning (Fig. 5A), middle (Fig. 5B) and end (Fig. 5C) of the same bout of swimming by one individual. In all three sequences, there was considerable difference (even between successive strokes) in duration of the initial recovery phase, power stroke duration, and overlap in power strokes.

In all figures showing details of the stroke pattern, the speed increased during the power stroke and decreased during the pause and initial recovery phases. At high average speeds, the variation was about 25–35% (see Figs 4A, 5B), whereas at low average speeds the variation was substantially higher (Fig. 4B). Additionally, Fig. 5A shows that when the animal started swimming from rest, no movement occurred until after the power stroke of P-2 began.

Relationships among stroke parameters

The maximum positional angle represents the amplitude in *Idotea*. The videotapes showed that P-1 generally swung about as far anteriorly as possible without touching the leg bases. The exact angle of this arc could not always be measured, as the open operculum partially blocked a side view of the pleopods during the stroke. I was able to measure the maximum positional angle for five strokes from different sequences of an individual *I. wosnesenskii* and nine strokes from different sequences of an individual *I. resicata*. These angles for each pair of pleopods were quite constant, and were essentially the same for the representatives of both species (Table 1).

The stroke frequency (number of complete stroke cycles per second) showed much more variation. There was a positive correlation between stroke frequency and speed (Fig. 6) with little difference between the two species. Linear

regressions for each species were not calculated as the multiple observations for each individual were not independent. Instead, I calculated the average speed and frequency for each individual and found a significant positive correlation between frequency and speed ($r = 0.956$, $N = 5$, $P < 0.025$); the small sample size made it impossible to test for differences between the species.

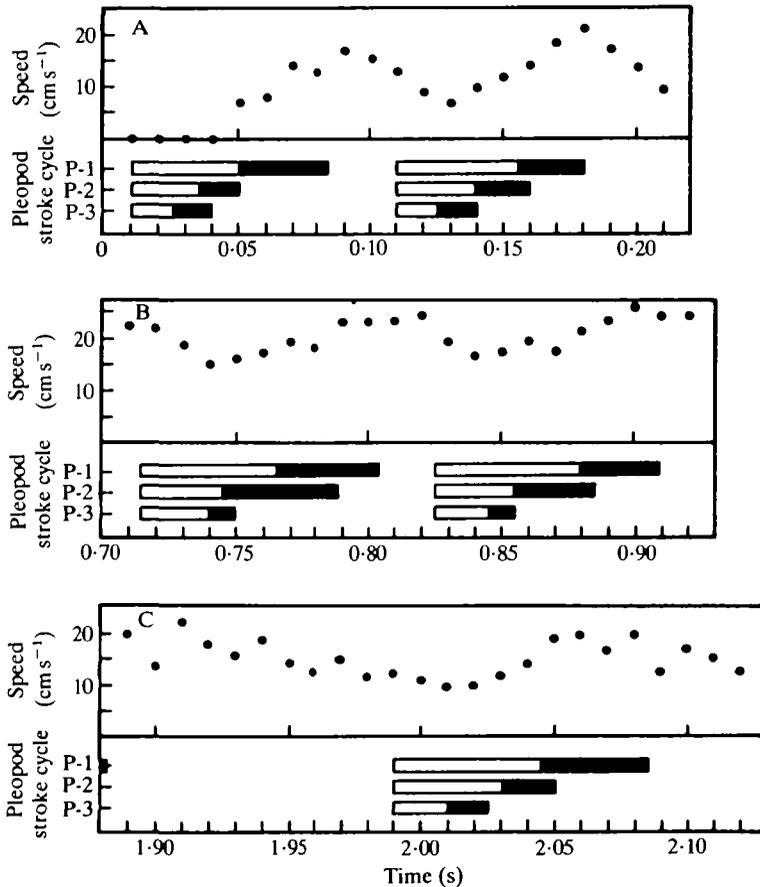


Fig. 5. Swimming speed and pleopod stroke patterns over the course of a sequence for individual J1 (BL = 4.78 cm, *Idotea resicata*). (A) Beginning to swim from rest; (B) middle of sequence; (C) deceleration, shortly before reaching end of tank. Upper and lower graphs as in Fig. 3.

Table 1. Amplitudes (maximum positional angles) in degrees for each pair of pleopods in both species

	<i>Idotea resicata</i> (N = 9) (degrees \pm s.e.)	<i>Idotea vosnesenskii</i> (N = 5) (degrees \pm s.e.)
P-3	50.7 \pm 3.1	49.0 \pm 5.8
P-2	92.3 \pm 2.8	90.8 \pm 5.3
P-1	129.8 \pm 2.1	131.0 \pm 4.0

There was a negative, but not statistically significant, correlation between the total power stroke duration and speed ($r = 0.865$, $N = 5$, $0.10 < P < 0.05$). The total power stroke duration had a more complex relationship with frequency. This relationship can best be expressed by comparing the inverse of frequency, stroke period, with total power stroke duration: the weak, statistically insignificant, correlation of period and total power stroke duration ($r = 0.878$, $N = 5$, $0.075 < P < 0.05$) indicated the loose inverse relationship between frequency and total power stroke duration.

Discussion

The kinematics of swimming in both *Idotea* species used in this study were strikingly similar, in spite of the fact that *I. resecata* preferred to swim faster than *I. vosnesenskii* (D. E. Alexander, in preparation). The movements of the swimming appendages in *Idotea* were very different from the usual crustacean metachronal pattern, such as pleopod (swimmeret) movement in lobsters (Davis, 1968) or thoracic appendage movement in mysids (Laverack *et al.* 1977). This difference may be due to the evolution of the locomotory appendages from purely respiratory ones in isopods (see below).

Kinematics of Idotea swimming

Because swimming was so similar in *Idotea resecata* and *I. vosnesenskii*, comments on general swimming behaviour apply to both species unless specified otherwise. The typical inverted swimming posture in *Idotea* was strongly preferred over swimming right-side-up, and appeared to be stable in the videotapes. This stability has been borne out by flow-tank measurements on preserved isopods (D. E. Alexander, in preparation); moreover, in the typical swimming posture, the body and legs generated lift comparable to the animal's submerged weight (D. E. Alexander, unpublished results). Although the extended legs seemed to contribute to stability, they did not play a noticeable role in manoeuvring: the high-speed videotapes showed that steering was accomplished by bending or twisting the anterior part of the body in the desired direction.

Owing to the nature of the stroke cycle, thrust was produced discontinuously in *Idotea*: it was produced during the power strokes of the three pleopods but not during the pause or initial recovery phases. This is clear from the variation in the speed over the course of the stroke cycle (e.g. Fig. 3). The videotapes did not directly show what proportion of the thrust was produced by each pair of pleopods. Given that P-1 tended to have a slightly longer power stroke than the other pairs, one might assume that P-1 produced the largest proportion of the thrust. Figs 3–5 indicate, however, that the acceleration may actually have been relatively low during the power stroke of P-1, which suggests that thrust may also be lower then. If so, lower thrust may have been due to the fact that body speed was highest during the power stroke of P-1, making the velocity of P-1 lower

relative to the water. A more detailed kinematic and mechanical analysis, analogous to that of Blake (1981), is necessary to resolve this ambiguity.

As well as thrust production by the pleopods, one might expect a significant amount of drag production during the initial recovery phase, when all three pairs of swimming pleopods are moving anteriorly. Such a drag increase would show up as greater deceleration than during the pause phase. Figs 3–5 show no noticeable evidence of such an increase; instead, Figs 3 and 5 show a fairly constant negative slope in velocity (indicating constant decelerations) as the animals change from pause to recovery. Top views of isopods videotaped during recovery showed that all four blades of each pair of pleopods were compressed and overlapped so that the whole bundle was only slightly wider than a single blade (Fig. 1B). The blades were also held so that the front ones (P-1) were perpendicular to their direction of movement, and the back ones (P-2 and P-3) formed a rough V-shape pointing away from the direction of movement, suggesting a crude approximation of a streamlined shape (Fig. 1C). The overlapping and streamlining of the pleopods are apparently sufficient to reduce the drag of the pleopods during recovery to negligible levels.

The speed at which an animal swims can be affected by several swimming stroke parameters. Studies of swimming kinematics in other animals typically focus on the relationship of stroke frequency and stroke amplitude with speed (e.g. Webb *et al.* 1984; Fish, 1984; Wassersug & Hoff, 1985; Hoff & Wassersug, 1986). In swimming *Idotea*, there is little or no variation in the amplitude (maximum positional angle) for a given pair of pleopods; this lack of variation indicates that amplitude has no role in speed regulation. There was essentially no difference in amplitude between the two species. The stroke parameter most closely correlated with swimming speed in *Idotea* was stroke frequency (Fig. 6), so variation in stroke frequency is the most likely candidate mechanism for controlling the speed. The role of variation of power stroke duration is unclear, and will require analysis of the stroke of one individual over a greater speed range than those available in this study. The probable use of 'frequency modulation' for speed control in *Idotea* should not be taken to imply mechanical similarity with other animals, particularly undulatory swimmers, which also use variation in frequency to control speed (e.g. Bainbridge, 1958; Hoff & Wassersug, 1986); swimming in *Idotea* is mechanically very different from that of such undulatory swimmers.

Comparison of Idotea's stroke with the metachronal pattern

The stroke pattern in *Idotea* is quite different from the typical metachronal pattern seen in the swimming appendages of other crustaceans. In metachronal beating, all swimming appendages have a similar stroke cycle with the same period, but each appendage has a slightly different phase from neighbouring appendages (Cannon, 1933; Barlow & Sleight, 1980). In the stroke pattern of *Idotea*, all the swimming appendages begin in phase, but each pair has a power stroke that is of progressively greater duration and amplitude within one stroke period.

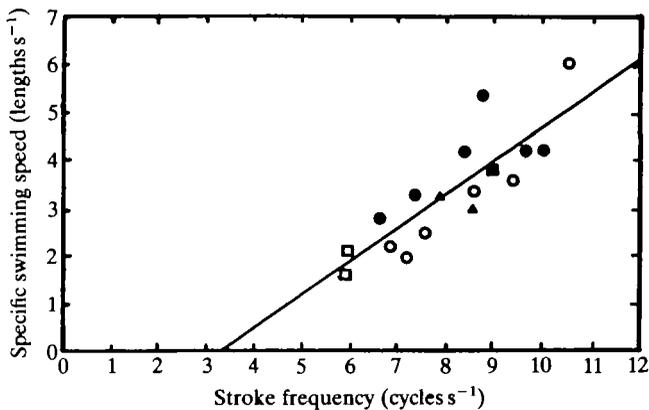


Fig. 6. Specific swimming speed (lengths s⁻¹) versus stroke frequency for both species. Each symbol represents one individual (\blacktriangle = Ab, body length = 3.55 cm; \bullet = J1, body length = 4.78 cm; \blacksquare = M1, body length = 3.52 cm; \circ = C1, body length = 3.14 cm; \square = D1, body length = 3.14 cm). Filled symbols, *Idotea resecata*; open symbols, *I. wosnesenskii*. Line is from linear regression of specific speed on frequency for the averages of each individual: $y = 0.719x - 2.41$, $r = 0.956$.

The metachronal stroke pattern appears to be primitively associated with simultaneous production of oppositely-directed feeding and propulsive currents (Cannon, 1933; Lochhead, 1961; Barlow & Sleight, 1980). It has been suggested that advanced crustaceans, which no longer use the feeding current, have retained the metachronal stroke pattern because it is more efficient when using large numbers of similar appendages (Barlow & Sleight, 1980), but no mechanical analysis has been made to support this suggestion.

In contrast, it is clear that the pleopods of isopods have a long history as exchange organs (Schram, 1982): isopods are the only major group of crustaceans that depend primarily on the pleopods for gas exchange (Wolvekamp & Waterman, 1960; Schram, 1986), and the pattern of abdominal blood circulation is heavily modified from the usual crustacean plan in order to support pleopodal exchange (Schram, 1986). The fact that several isopod groups have independently evolved protective covers over the pleopods may be evidence of the vital importance of these appendages. To function under such covers, the pleopods must pump water through the branchial chamber, and it is this pumping action which *Idotea* and other isopod groups appear to have modified to provide swimming locomotion. Observations with dye clearly show water being pumped through the branchial chamber in *Idotea*, and rapid sequential movements of the pleopods can be seen through the translucent operculae during this pumping (personal observation). The swimming movements of the pleopods are probably large exaggerations of the respiratory stroke. The variation in the timing of the power stroke, indicating a small amount of independence among the pleopods in *Idotea*, is more akin to the movement patterns associated with walking in crustaceans than the tightly phase-coupled metachronal swimming pattern

(W. J. P. Barnes, quoted in Laverack *et al.* 1977); this may be of interest to students of central pattern generators.

As only a subset of the pleopods are used for swimming (three of the five pairs in *Idotea*) in isopods (Schram, 1986), it has long been assumed that the swimming pleopods have lost their respiratory function (Richardson, 1904; Wolvekamp & Waterman, 1960; Schram, 1986), but this has not been tested. An anthurid isopod, *Cyathura carinata*, has enlarged and thickened outer branches of the pleopods (exopods) which are used as operculae and for respiratory pumping; the epithelium of the exopods has histological characteristics of gas transport tissue (Wägele, 1982). The smaller, more delicate, inner pleopod branches (endopods), which have been presumed to be gills, have histological characteristics of tissue for ion transport (Wägele, 1982). Thus, it is possible that the swimming pleopods of *Idotea* may indeed have retained their respiratory function, and that their stroke pattern may reflect this function. In contrast to both the typical metachronal pattern and the modified metachronal pattern of mysids, in *Idotea* each succeeding pair of pleopods sweeps out a larger arc. Thus, each pleopod initially passes through a volume of water that has not encountered another pleopod, and is potentially less oxygen-depleted; this may have a bearing on the striking similarity in amplitude for each pair of pleopods between the two species (Table 1). Further analysis of respiration in *Idotea* will be necessary to determine whether gas exchange is rapid enough for a pair of pleopods to remove a significant amount of oxygen during one power stroke. Studies of respiration of *Idotea* should prove particularly rewarding, especially in conjunction with analysis of swimming mechanics, in clarifying the extent of the combined respiratory and locomotory functions of the pleopods.

I would like to thank Helen M. Alexander, Paul W. Webb, and two anonymous reviewers for criticizing this work, and Robert W. Blake and Steven Vogel offered helpful comments on an earlier version of this manuscript. Special thanks go to Karel Liem for the loan of his high-speed video system. Dennis Willows and the staff of Friday Harbor Laboratories were, as always, generous with facilities and support. This research was supported by a Summer Stipend Award from Bellarmine College.

References

- BAINBRIDGE, R. (1958). The speed of swimming fish as related to size and to the frequency and amplitude of the tail beat. *J. exp. Biol.* **35**, 109–133.
- BARLOW, D. I. & SLEIGH, M. A. (1980). The propulsion and use of water currents for swimming and feeding in larval and adult *Artemia*. In *The Brine Shrimp Artemia*, vol. 1 (ed. G. Persoone, P. Sorgeloos, O. Roels & E. Jaspers), pp. 61–73. Wetteren, Belgium: Universa Press.
- BLAKE, R. W. (1981). Mechanics of drag-based mechanisms of propulsion in aquatic vertebrates. *Symp. zool. Soc. Lond.* **48**, 29–52.
- CANNON, H. G. (1933). On the feeding mechanism of the *Branchiopoda*. *Phil. Trans. R. Soc. Ser. B* **222**, 267–352.

- DANIEL, T. L. (1983). Mechanics and energetics of medusan jet propulsion. *Can. J. Zool.* **61**, 1406–1420.
- DAVIS, W. J. (1968). Quantitative analysis of swimmeret beating in the lobster. *J. exp. Biol.* **48**, 643–662.
- FISH, F. E. (1984). Kinematics of undulatory swimming in the American alligator. *Copeia* **1984**, 838–843.
- HOFF, K. & WASSERSUG, R. J. (1986). The kinematics of swimming in the clawed frog, *Xenopus laevis*. *J. exp. Biol.* **122**, 1–12.
- HUGHES, G. M. & WIERSMA, C. A. G. (1960). The co-ordination of swimmeret movements in the crayfish, *Procambarus clarkii* (Girard). *J. exp. Biol.* **37**, 656–670.
- LAVERACK, M. S., NEIL, D. M. & ROBERTSON, R. M. (1977). Metachronal exopodite beating in the mysid *Praunus flexuosus*: a quantitative analysis. *Proc. R. Soc. Ser. B* **198**, 139–154.
- LOCHHEAD, J. H. (1961). Locomotion. In *The Physiology of the Crustacea*, vol. 2 (ed. T. H. Waterman), pp. 313–364. New York: Academic Press.
- LOCHHEAD, J. H. (1977). Unsolved problems of interest in the locomotion of Crustacea. In *Scale Effects In Animal Locomotion* (ed. T. J. Pedley), pp. 257–268. New York: Academic Press.
- MACMILLAN, D. L., SILVEY, G. & WILSON, I. S. (1981). Coordination of the movement of the appendages in the Tasmanian mountain shrimp *Anaspides tasmaniae* (Crustacea: Malacostraca: Syncarida). *Proc. R. Soc. Ser. B* **212**, 213–231.
- NAYLOR, E. (1972). *British Marine Isopods*. New York: Academic Press.
- PACKARD, A. (1969). Jet propulsion and the giant fibre response of *Loligo*. *Nature, Lond.* **221**, 875–877.
- RICHARDSON, H. (1904). Contributions to the natural history of the Isopoda. *Proc. U.S. natn. Mus.* **27**, 657–681.
- SCHRAM, F. R. (1982). The fossil record and evolution of Crustacea. In *The Biology of the Crustacea*, vol. 1 (ed. L. G. Abele), pp. 92–148. New York: Academic Press.
- SCHRAM, F. R. (1986). *Crustacea*. New York, Oxford: Oxford University Press.
- VIDELER, J. J. & HESS, F. (1984). Fast continuous swimming of two pelagic predators, saithe (*Pollachius virens*) and mackerel (*Scomber scomber*): a kinematic analysis. *J. exp. Biol.* **109**, 209–228.
- WÄGELE, J.-W. (1982). Ultrastructure of the pleopods of the estuarine isopod *Cyathura carinata* (Crustacea: Isopoda: Anthuridae). *Zoomorphology* **101**, 215–226.
- WASSERSUG, R. J. & HOFF, K. (1985). The kinematics of swimming in anuran larvae. *J. exp. Biol.* **119**, 1–30.
- WEBB, P. W. (1973). Kinematics of pectoral fin propulsion in *Cymatogaster aggregata*. *J. exp. Biol.* **59**, 697–710.
- WEBB, P. W. (1979). Mechanics of escape responses in crayfish (*Orconectes virilis*). *J. exp. Biol.* **79**, 245–263.
- WEBB, P. W., KOSTECKI, P. T. & STEVENS, E. D. (1984). The effects of size and swimming speed on locomotor kinematics of rainbow trout. *J. exp. Biol.* **109**, 77–95.
- WOLVEKAMP, H. P. & WATERMAN, T. H. (1960). Respiration. In *The Physiology of the Crustacea*, vol. 1 (ed. T. H. Waterman), pp. 35–100. New York: Academic Press.

