

## THE ROLE OF THE 'WALKING LEGS' IN AQUATIC AND TERRESTRIAL LOCOMOTION OF THE CRAYFISH *AUSTROPOTAMOBIOUS PALLIPES* (LEREBoullet)

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### SUMMARY

1. The hydrodynamic drag acting on the crayfish *Austropotamobius pallipes* is measured and it is concluded that, in the range of velocities used in walking, the drag is independent of the posture of the limbs and the direction of motion of the body. At swimming velocities the streamlining caused by promotion of the legs reduces the drag losses to half that of a crayfish moving in the forwards walking posture at the same speed.

2. The forwards walking of intact crayfish is compared with that of the same animal after amputation of one or more pairs of legs. It is concluded that the third and fourth pair of legs provide most of the propulsion under water and the second pair is not essential to locomotion under any of the conditions tried.

### INTRODUCTION

The crayfish, *Austropotamobius pallipes* spends most of its time in water, but it can live on land for several days, and when confined in a crowded tank it attempts to climb out. It walks forwards, backwards and sideways both on land and in water and is an agile climber in vegetation. It has four pairs of walking legs (pereopods) and which are anatomically distinct and are held in a characteristic posture. In *Austropotamobius* but not in the related *Homarus americanus* (Macmillan, 1974) or in *Procambarus blandingii* and *Oronectes virilis* (Parrack, 1964), the first, second and third pair of legs move more or less in phase, but the legs of the fourth pair move alternately. The horizontal angle through which the leg moves during a step is very small (Baldi, 1936) and the body is slung low between the legs. Alexander (1971) has explained the sprawling posture of the legs as an adaptation to withstand overturning in strong lateral water currents, but he did not discuss the effect of this posture on the mechanics of walking and swimming.

Much effort (see review, Lochhead, 1961; Parrack, 1964) has been devoted to describing the exact sequence of movement of ipsilateral legs of *Austropotamobius* and related species; however most of these descriptions were based on crayfish walking on land, or only partly immersed in water, and the question of whether the gait differs on land and in water was not mentioned. Baldi (1936) suggested that some of the legs of *Potambius* (*Austropotamobius*) *pallipes* served only to support the body, while others provided the propulsion, but the idea was not developed in detail and there was no experimental evidence to support it.

In this paper the effect of leg position of the mechanics of swimming is investigated, and the role of different pairs of legs in forwards walking under water is compared to their role on land.

#### MATERIALS AND METHODS

*Austropotamobius pallipes* (Lereboullet) (= *Potamobius pallipes* or *Astacus pallipes*, sometimes wrongly called *Astacus fluviatilis*) is the only indigenous species of crayfish (Crustacea, Decapoda, Astacidae) in Britain (Thomas & Ingle, 1971). Adult crayfish of both sexes were caught locally between May and September and maintained in the laboratory at room temperature. They ate raw fish, freshwater molluscs and *Elodea canadensis* and some lived as long as a year in captivity. Only those with all the walking legs intact were used, although as many as 20% of crayfish caught in the wild have damaged or amputated limbs, or limbs in the course of regeneration.

The hydrodynamic drag was measured in a tow-tank 4.5 m long and 0.6 m wide fitted with a trolley which moved above the water at various speeds. Deep frozen, dead crayfish were attached with thread to a stiff bar containing a semiconductor strain gauge and suspended from the trolley. It was essential that the corpses kept the correct orientation during movement and that they were neutrally buoyant in the water; the buoyancy and balance of the corpses were adjusted, if necessary, with air bubbles and small pieces of Plasticine inserted into the body, and the posture of the limbs, including the chelae, was manipulated by means of stiff wires inserted through the gut into the limbs. The drag on the strain gauge when the whole apparatus was moved through the water at constant velocity was measured.

Thirty crayfish were used for the walking experiments, including 14 males (mean live weight in air 30.7 g, S.D. 6.0) and 16 females (mean live weight in air 23.6 g, S.D. 5.2). They walked either on a smooth sheet of plate glass, or on a rough substrate consisting of three layers of cloth firmly bound to a sheet of glass. These substrates were placed either in a large tank containing aerated water at least 10 cm deep, or on a level surface in air. Most crayfish walked straight across these substrates as soon as they were put down on them. A few, especially males, persistently adopted the threat posture and walked backwards or in circles. Usually this behaviour disappeared after a few minutes of handling, but if it did not, that crayfish was abandoned. The crayfish were never removed from the water for more than five consecutive minutes so the limb tips in contact with the substrate were always wet. Ten bouts of straight, forwards walking under each of the four conditions were recorded on videotape and the stepping frequency and average distance moved per step were measured using the slow motion facility. The walking of the intact animal was compared to that of the same animal after one or more pairs of legs had been amputated, either by inducing autospasy, or by cutting the limb in the normal breakage plane. The crayfish was allowed to recover overnight after each operation; about 25% of them died within the first three hours of the operation, but the remainder survived for at least three days after the experiment, and many underwent another moult.

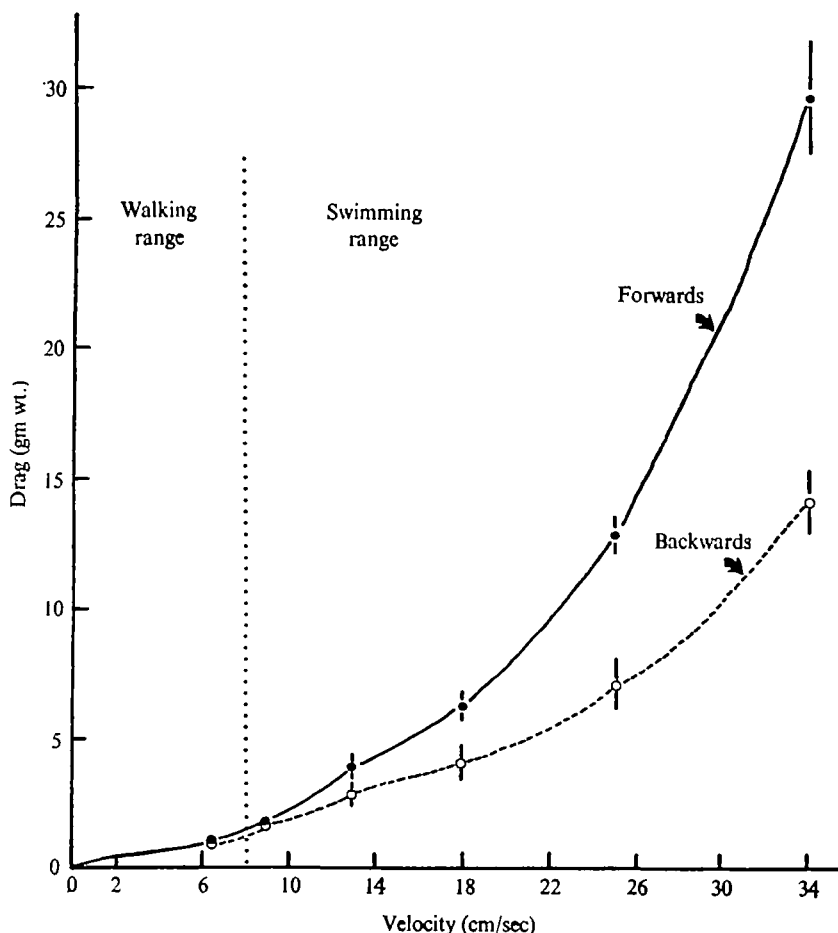


Fig. 1. The hydrodynamic drag of a crayfish corpse (fully extended length 15.1 cm) against velocity of movement through water. Each point is the mean of ten measurements and the standard deviation is shown.

### RESULTS

On Fig. 1 the drag on crayfish moving backwards and forwards at various speeds is compared. The corpses were mounted so that they were in the normal backwards swimming position (see Wine & Krasne, 1972, their Fig. 5) when moving backwards; the legs were splayed out in the walking posture when moving forwards. Each point is the mean of fifty observations, ten from each of five crayfish 12.5–16 cm from tip of outstretched chelae to tip of telson. The results for forward movement fit the equation:

$$\text{Drag} \propto \text{velocity}^{2.05} \quad (1)$$

and for backwards movement:

$$\text{Drag} \propto \text{velocity}^{1.6} \quad (2)$$

Equation (1) is very close to the results which would be expected for the drag on a cylindrical body moving slowly enough to maintain laminar flow around it (Alexander, 1968). In walking the legs project at least 2.5 cm from the body surface. The Reynolds number in walking is approximately  $3 \times 10^3$  so such projections would be expected to

Table 1. *Average walking performance of twenty-nine intact crayfish*

Substrate	Mean distance (cm) moved per step	S.D.	Mean stepping frequency Hz	S.D.	Mean velocity (cm/sec)
Air/smooth	2.2	0.30	0.7	0.19	1.5
Water/smooth	2.6	0.32	1.2	0.26	3.1
Air/rough	2.5	0.29	0.6	0.17	1.5
Water/rough	3.0	0.32	1.1	0.21	3.3

make a considerable difference to the drag. When moving backwards in the swimming posture the legs project only 0.5–1 cm from the body so the body is partly streamlined. The reduction in drag is only significant above 13 cm/sec.

On Table 1 the average distance moved per step\*, stepping frequency and velocity are shown for 29 intact crayfish. There was no correlation between the weight of the crayfish and its walking velocity under any conditions, and no evidence to support Baldi's (1936) suggestion that smaller crayfish walk better in water and large ones on land. Burrows & Hoyle (1973) also found little correlation between the size of *Ocypode* crabs and their average running speed. There was no correlation between the walking velocity of a crayfish on the same substrate on land and in water, although there was a significant ( $p < 0.05$ ) correlation between the walking velocity on different substrates in the same medium. Crayfish step significantly faster in water than in air ( $p \leq 0.001$ ) and in both media the distance moved per step is significantly greater ( $p < 0.001$ ) on the rough than on the smooth substrate. On land they also take more steps per second on a smooth than on a rough substrate ( $p < 0.02$ ) so the average velocity is the same in both cases.

Table 2 shows the effect of amputation of pairs of walking legs on the performance of thirty crayfish. In each experiment the average of ten bouts of walking under the control and experimental conditions were taken as significantly different at  $p < 0.05$ . Ten crayfish were used for each of groups A, B and C; group D contains the results from six experiments from crayfish which were also used for group B or C. In group A there is no change in distance moved per step or in stepping frequency in the majority (60%) of the experiments, and in the remainder the change in distance moved per step is equally divided between increases and decreases. The same results are obtained when the second pair of legs is amputated from a crayfish which has already lost one other pair (group D) except that there are no experiments in which amputation causes a greater distance to be covered per step. Taking groups A and D together, half of all the cases in which amputation of the second pair of legs caused a decrease in the distance moved per step were recorded when the crayfish was walking on a smooth substrate on land.

Amputation of the third and fourth pair of legs causes a decrease in the distance moved per step in water but not in air ( $p < 0.001$ ). In all four groups the stepping frequency was constant in at least half of the experiments; all nine cases in which amputation caused a significant increase in stepping frequency were recorded when the crayfish was walking in water.

\* In this paper the term 'step' means the complete cycle of movement of a leg.

Table 2. *The effect of amputation of pairs of legs upon walking. In each experiment the average of ten bouts of walking of the intact crayfish is compared with ten bouts of walking after amputation of one or more pairs of legs. The differences are significant at  $P < 0.05$ .*

Substrate	Distance moved per step			Stepping frequency		
	Increase	Decrease	No change	Increase	Decrease	No change
A. Amputation of second pair of legs alone						
Air/smooth	0	3	7	0	3	7
Water/smooth	2	3	5	3	3	4
Air/rough	1	2	7	0	5	5
Water/rough	4	1	5	0	1	9
Total	7	9	24	3	12	15
B. Amputation of third pair of walking legs						
Air/smooth	0	0	10	0	4	6
Water/smooth	0	8	2	2	0	8
Air/rough	0	2	8	0	1	9
Water/rough	0	6	4	1	3	6
Total	0	16	24	3	8	29
C. Amputation of the fourth pair of walking legs						
Air/smooth	0	0	10	0	2	8
Water/smooth	1	6	3	1	3	6
Air/rough	0	1	9	0	3	7
Water/rough	0	7	3	1	5	4
Total	1	14	25	2	13	25
D. Amputation of the second pair of walking legs and one other pair						
Air/smooth	0	4	2	0	2	4
Water/smooth	0	0	6	0	3	3
Air/rough	0	1	5	0	3	3
Water/rough	0	0	6	1	2	3
Total	0	5	19	1	10	13

The chelae are normally held clear of the substrate when the crayfish is walking fast in water, and only touch the ground and perform step-like movements when four or more of the legs are amputated. The chelae perform significantly more ( $p \ll 0.001$ ) 'steps' on land than in water but on a flat surface there is no detectable difference between the velocity of walking of the same crayfish whether the chelae are held clear of the ground or performing 'steps'. All three experiments in which the first pair of legs or the chelae were removed resulted in no change in the walking.

#### DISCUSSION

The maximum walking velocity ever recorded was 7 cm/sec (on the smooth substrate in water); it can be calculated from Wine & Krasne's data (op. cit. their Fig. 5) that *Procambarus* of similar size to the *Austropotamobius* used in these experiments reached a velocity of at least 40 cm/sec during swimming. The hydrodynamic drag at walking speeds is independent of the body posture and its direction of motion and hence is probably not a factor determining the form of the leg movements of walking in slow moving water. Crayfish often live in fast flowing streams, but they walk only on the mud or stones on the bottom, where the water velocity is much reduced. One advantage of the sprawling posture of the limbs, is that progression is possible

(although not very fast) with the ventral surface of the thorax raised only a few millimetres from the substrate, and even in fast walking the body is raised only about a centimetre. Thus the posture serves to keep the body in the boundary layer, away from the adverse effects of fast flowing water. The ability to promote the legs during backwards swimming is an important adaptation to increase the distance travelled for the same thrust by reducing the kinetic energy lost as drag. The need to promote the limbs may account for the wide excursion angle of all the legs including the fourth pair whose full range of movement is not used during walking.

Crayfish walk nearly twice as fast under water as on land (see Table 1), the difference being mainly due to the much higher stepping frequency under water. The opposite result would be expected if drag from the water were preventing rapid movement of the limbs. Both in water and in air the distance moved per step is significantly reduced on a slippery substrate. On land the apparent weight of the body is 400–600% greater than in water and each step lasts much longer, probably because crustacean muscles take a long time to reach maximum tetanus (Burrows & Hoyle, 1973). The greater coefficient of friction between the limb tips and the substrate might be expected to produce a greater thrust per step on land, but this effect seems to be outweighed by the limitation of supporting a much greater weight in air. It is interesting that crayfish walk as fast on a slippery substrate as on a rough one owing to the increase in stepping frequency on a smooth substrate which compensates for the reduction in distance moved per step. Wille (1920) found that adult male cockroaches ran on dry plate glass at only 39% of their average speed on sandpaper; the first instar juveniles which have suckered tarsi ran on glass at 150% of their velocity on paper.

The results on Table 2 suggest that the second pair of legs are always redundant for normal forwards walking and the third and fourth pairs are not essential to walking on land. There are several previous observations which are consistent with this suggestion. Wood & Wood (1932) investigated the occurrence of autotomy and autospasy in various species of Decapod Crustacea and reported that nearly all species could be induced to shed damaged or restrained limbs, and many species autotomized limbs in response to non-localized stimuli such as an electric shock. After the loss of one limb, a greater stimulus is required to make the crab *Hemigrapsus oregoniensis* autotomize another leg, and some legs are more readily autotomized than others (Easton, 1972). Clearly the loss of one leg does not greatly impair the fitness of the crab, but the stimulus to autotomy must be greater before it will shed two limbs. In crayfish and lobsters, the chelae are the most expendable limbs, but there are no data on the relative ease of shedding of the walking legs, as there are for crabs (Easton, 1972). The autotomized limbs soon regenerate (Bliss, 1960) and even undersized, partially regenerated walking legs are moved in a stepping sequence in locomotion (personal observation). Burrows & Hoyle (1973) found that at moderate speeds of sideways running the crab, *Ocypode ceratophthalma* used only three of a possible eight legs for propulsion at any one time, and at high speeds it only used two legs, the remainder being held off the ground or used as skid planes. These data, and those presented here, are consistent with the suggestion that not all the legs of crustaceans are essential to all forms of walking and that some legs can act vicariously for the missing ones and hence allow for autotomy without impairing the walking performance. Unfortunately, neither Hughes & Mill (1974) nor Delcomyn (1971) nor Graham

(1972) give any data on the effect of amputation of insect legs upon their stepping frequency or the distance travelled per step.

It is difficult to determine the centre of gravity of a crayfish precisely because the weight of the movable appendages such as the chelae is large compared to the weight of the rest of the body; I found it to be above and slightly anterior to the point of insertion of the third pair of legs. I could not confirm Baldi's suggestion (op. cit. his Fig. 5) that the centre of gravity is located at the point of intersection of the lines of thrust of the four pairs of legs.

The crayfish body is slung low between recurved legs (Manton, 1952) when it is at rest or moving slowly, and is raised further from the substrate during rapid locomotion. The first and second pairs of legs normally rest with the dactylopodites (the most distal digit) placed in front of the plane of the insertion of the coxa onto the carapace. During the powerstroke the legs are flexed at the meropodite-carpopodite joint and swung outwards at the coxa. The fourth pair of legs is normally bent backwards and its powerstroke consists of a pushing movement caused by extension of the M-C joint from the rest position. The third pair of legs normally rests with the dactylopodite just in front of the plane of the coxa but its powerstroke ends with the dactylopodite pointing backwards. The powerstroke of the third pair of legs consists of an initial phase of pulling followed by a pushing movement.

When walking under water the crayfish moves forward smoothly, while on land its movement is lurching. Non-jerky movement is achieved by most or all the legs supplying a small thrust by turns, while lurching motion is observed when most of the propulsion is due to only one pair of legs. The weight of the crayfish in air is 400–600% greater than the weight in water; the load will increase the friction between the dactylopodite and the substrate so that even limbs which do not carry as high proportion of the load can obtain a firm grip for an effective powerstroke. The results suggest that under water both the third and fourth pairs of legs are contributing to propulsion, but on land any pair of legs which has obtained a grip provides the thrust. The remaining legs make a negligible contribution, but the legs can substitute for each other when one or more pairs is missing. Under 'slippery' conditions, such as under water or on a smooth substrate in air the contribution of the second pair of legs becomes important and half of all observations (taking groups A and D together) show a reduction in the distance moved per step following amputation of the second pair of legs. The results also suggest that the pushing movement of the third and fourth pairs of legs is more important under water than on land, but it is not clear why this is so.

In the gaits most frequently observed by Parrack (op. cit. his Table 2) the legs were moved in the order: 1–4–2–3 (50% of all observations) or 1–3–2–4 (25% of observations). In both these gaits (and only in these gaits) the second leg is moved between the movement of the two principal pushing legs (the third and fourth), as would be expected if the second pair of legs (and to some extent the third, moved just after the second in the commonest gait) is supporting the body while the third and fourth pairs of legs propel it forwards.

From the diagrams supplied by Voelkel (1922) and Baldi (op. cit. his Fig. 22) it can be calculated that at least three and often four of the legs of a walking crayfish are always stationery on the ground, thus enabling the animal to anchor itself firmly to

the substrate between strides, which may be an important adaptation to walking in swiftly flowing water.

The effects of leg amputation on walking behaviour on land and under water indicate that the mechanics of walking are very different in the two situations, and hence one must be cautious about extrapolating from stepping patterns observed in crayfish walking under different conditions. It is important to establish that the action of a particular limb is functionally relevant to the locomotion under investigation before attaching too much importance to the details of the form and timing of its movements.

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