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Published in:
Journal of Experimental Biology

Publication date:
1998

Citation for published version (APA):
Stamhuis, E. J., & Videler, J. J. (1998). Burrow ventilation in the tube-dwelling shrimp Callianassa subterranea (Decapoda Thalassinidea) - I. Morphology and motion of the pleopods, uropods and telson. Journal of Experimental Biology, 201(14), 2151-2158.

The Journal of Experimental Biology 201, 2151–2158 (1998)
Printed in Great Britain © The Company of Biologists Limited 1998
JEB1470

BURROW VENTILATION IN THE TUBE-DWELLING SHRIMP *CALLIANASSA SUBTERRANEA* (DECAPODA: THALASSINIDEA)

I. MORPHOLOGY AND MOTION OF THE PLEOPODS, UROPODS AND TELSON

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Accepted 5 May; published on WWW 25 June 1998

Summary

The morphology of the pleopods, uropods and telson of the tube-dwelling shrimp *Callianassa subterranea* have been studied using dissection microscopy and scanning electron microscopy. The kinematics of these appendages were examined by motion analysis of macro-video recordings of ventilating shrimps in transparent artificial burrows. The pleopods show the usual crustacean biramous anatomy, but all segments are rostro-caudally flattened. The protopodite bears a triangular medially oriented endopodite and a scoop-shaped exopodite. The contralateral endopodites are linked by the appendix interna, ensuring a perfect phase relationship between contralateral pleopods. The outer rims of the exopodites are fringed with long fern-leaf-like plumose setae bearing flattened setules. These setae have very mobile joints and can be turned caudally. The slits between contralateral endopodites have rims of leaf-like setae as well. Setae of the same leaf-like type fringe the uropods, but these are non-motile. The telson has a narrow fringe of leaf-like setae, locally interrupted by long mechanoreceptory setae.

A shrimp, wandering through the burrow or resting, holds its pleopods against the abdomen with the exopodites and their setal fringes retracted medially. The uropods are folded medially as well, probably to reduce the shrimp's drag. During ventilation, the uropods are extended against the tube wall, leaving only a small opening for flow ventral from the telson, and the pleopods beat at a frequency of approximately 1 Hz (0.9±0.2 Hz). Fourier analysis of pleopod kinematics showed that the motion pattern of the first flow-generating pleopod pair (PP1) consisted mainly of the first harmonic (75 %) and to a lesser extent of the third harmonic (20 %), resulting in almost perfect sinusoidal motion. The motion patterns of PP2 and PP3 could be modelled by assigning pure sinusoids with a 120 ° phase shift and a rostro-caudal ranking to the three pairs of pleopods.

Key words: burrow ventilation, pleopod, uropod, telson, morphology, motion analysis, tube-dwelling shrimp, *Callianassa subterranea*, ventilation posture, metachrony, kinematics.

Introduction

The abdomen of decapod crustaceans consists of six segments and the telson. The anterior five segments each bear a pair of pleopods, and the sixth segment bears one pair of uropods. The uropods and the telson form the tail-fan. Pleopod morphology is rather variable among the decapods and is related to their main function, which is commonly propulsion or reproduction (Bell, 1905). Pleopods used in propulsion usually resemble a slightly curved flat plate, a shape that is optimal for paddling (Alexander, 1968; Vogel, 1994). The pleopod area is often increased during the effective stroke by spreading the rims of the setae as well as extending the podites, and the area is decreased during the recovery stroke by folding the setae and drawing the podites together (Lochhead, 1977).

In swimming crustaceans, pleopods usually show metachronal beat patterns, which are assumed to be energetically advantageous (Lochhead, 1961; Sleigh and Barlow, 1980; Barlow and Sleigh, 1980). Metachronal wave patterns can be ad-locomotory (=antiplectic) or contra-locomotory (=symplectic), depending upon whether coordination is in the direction of swimming or in the opposite direction, respectively (Sleigh and Barlow, 1980). Depending on inter-limb distance and phase shift, single pleopods in a metachronal system may perform a complete and undisturbed beat cycle or may move together with the pleopod of an adjacent segment during part of the cycle, showing sudden advances and delays compared with an undisturbed beat cycle (Alexander, 1988; Lochhead, 1961).

The thalassinids use pleopod beating to generate a flow of water through their burrow (Dworschak, 1981). The burrow can be ventilated for filter-feeding purposes, as in most Upogebiae, or mainly for respiratory purposes, as in most Callianassidae (Atkinson and Taylor, 1988). Burrow ventilation is assumed to be energetically expensive (Atkinson and Taylor, 1988) and is always performed periodically (Farley and Case, 1968; Torres *et al.*; 1977; Felder, 1979; Dworschak, 1981; Mukai and Koike, 1984; Scott *et al.* 1988). Ventilation bouts tend to be shorter in Callianassidae than in Upogebiae (Dworschak, 1981; Mukai and Koike, 1984; Forster and Graf, 1995; Stamhuis *et al.* 1996), probably because of differences in feeding strategy. The mechanism of burrow ventilation in thalassinids has been little studied quantitatively, and very little is known about the morphology of the pleopods and their kinematics during burrow ventilation. The aim of the present study is to describe the morphology, postures and motion patterns of the pleopods, uropods and telson of the thalassinid shrimp *Callianassa subterranea* during burrow ventilation.

Materials and methods

Callianassa subterranea (Montagu) of approximately 40 mm total length were collected from box core sediment samples at the Oyster Grounds and at the Frisian Front, central North Sea, at approximately 53°45′N and 4°30′E. Sampling trips were made in October 1989 and May 1990 on the Dutch research vessel ‘*Aurelia*’. For morphological studies, approximately 20 specimens were killed on board using a 12 % solution of formaldehyde in sea water and preserved in a 4 % solution of formaldehyde in sea water. Other animals were stored separately in small containers and transported to the laboratory alive. For details of collection procedures, transport and storage conditions, see Stamhuis *et al.* (1996).

Macro- and micro-morphological studies were made of the abdominal appendages involved in burrow ventilation. A dissection microscope equipped with a *camera lucida* was used for the macro-morphological studies. Photographs of micro-structures were taken using scanning electron microscopy after preparation of the appendages involving critical-point drying and sputter coating. The abdominal appendages are classified according to Biffar (1971). For the setae, the nomenclature used by Jacques (1989) and Watling (1989) was followed.

Ventilation behaviour was studied in two experimental arrangements. Individual *C. subterranea* constructed and regularly ventilated a burrow inside narrow transparent sediment-filled cuvettes (Stamhuis *et al.* 1996). Experimental animals also showed ventilation activity inside artificial burrows made of Perspex (PMMA). The moving pleopods as well as the postures of the uropods and the telson were filmed (at 25 frames s^{-1}) from the lateral, ventral and dorsal aspects using a video camera equipped with a macro lens. The images were stored on U-matic-SP tape. Sequences of typical ventilation behaviour were digitized frame by frame. On each image from the lateral aspect, the positions of the pleopod tip and the centre of the pleopod joint were digitized manually using a cross-hair cursor, and their locations were stored. The outer rims of the exopodite’s setal fringes and the pleopod tips were located on the ventral-view frames and stored in the same way. The motion patterns of the pleopod tips were reconstructed from the time series of the stored locations. These motion patterns revealed sudden phase advances or delays in the metachronal waves due to interactions between adjacent pleopod pairs. Fourier analysis was used to study the harmonic components of the motion patterns. The resulting phase relationships and harmonic components were used to model the motion patterns of the pleopod tips. The changing postures of the uropods and telson during ventilation were drawn from the video images.

Results

Macro- and micro-morphology

The third, fourth and fifth abdominal segments each carry one pair of pleopods used to generate the ventilation current. Each pleopod consists of a rostro-caudally flattened protopodite with two rami: a scoop-shaped curved exopodite and a flat medially oriented endopodite (Fig. 1).

The left and right endopodites of each segment are interlocked at their medial rims by a short appendage called the ‘accessory ramus’ (Bell, 1905) or ‘appendix interna’ (Lemaitre and de Almeida Rodrigues, 1991) (Figs 1, 2). The exopodites are able to spread out laterally over a small angle. The lateral and ventral rims of the exopodites as well as the lateral and medial rims of the endopodites bear a row of densely implanted segmented setae (Fig. 3). The setae have infra-cuticular joints, allowing medio-lateral and dorso-ventral motions. They are of the plumose ‘leaf’ type with flattened setules. The rims of the exopodites and ventral parts of the endopodites contain a pattern of branching membranous

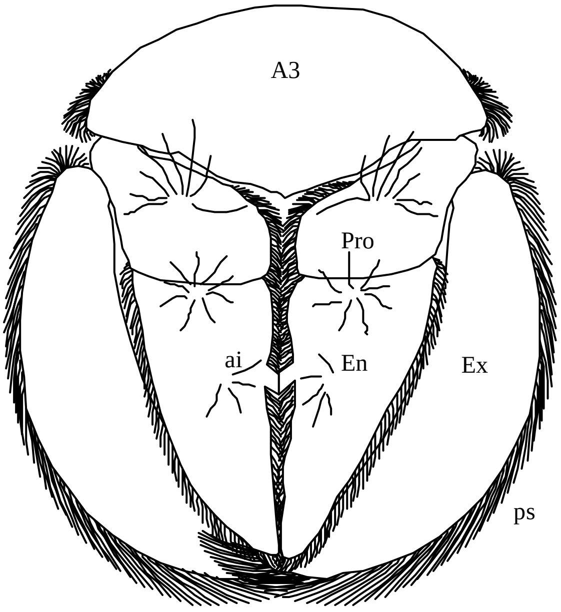

Fig. 1. Line drawing of the pleopod pair of the third abdominal segment of *Callianassa subterranea*. The pleopods of the fourth and fifth abdominal segments are similar in appearance. Viewed from the caudal aspect; A3, third abdominal segment in cross section; Pro, protopodite; En, endopodite; Ex, exopodite; ai, appendix interna; ps, plumose setae.

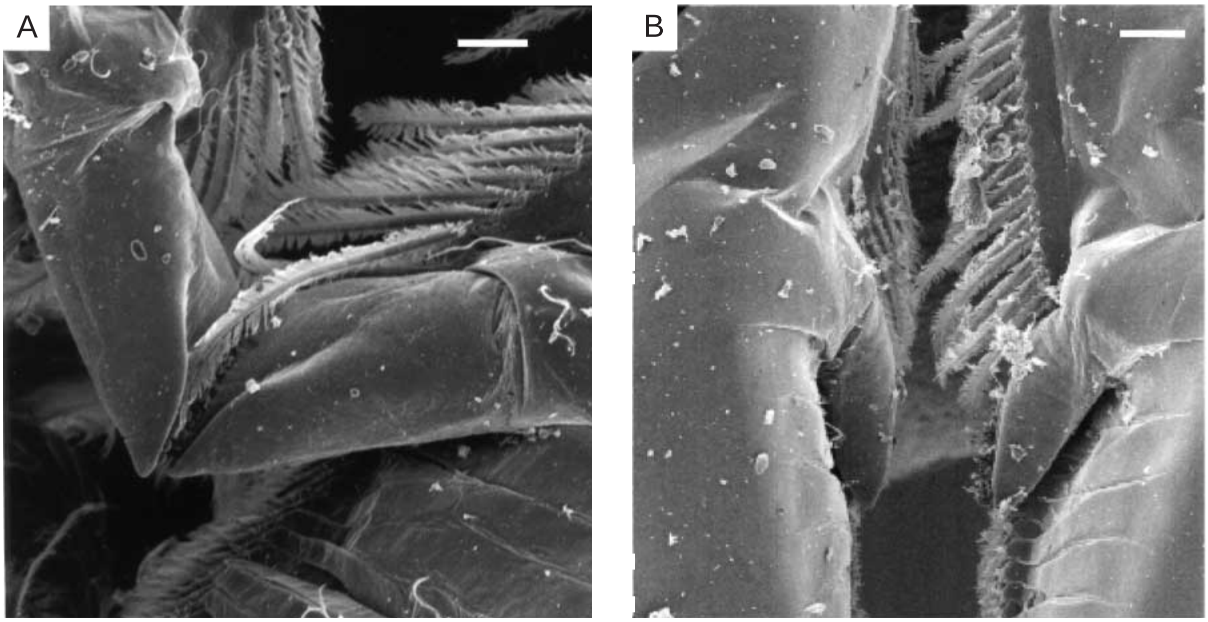

Fig. 2. Scanning electron micrographs of the appendices interna on the pleopodal endopodites of *Callianassa subterranea* that link contralateral pleopods; (A) locked, (B) unlocked. Scale bars, 0.1 mm.

cuticular folds (Fig. 4), allowing the rims to extend when the podite stretches.

The 'tail-fan' of *C. subterranea* is attached to the sixth abdominal segment and consists of a biramous uropod at each side and the telson (Fig. 5). The uropods consist of an endopodite and an exopodite. The exopodite is partly covered by a small flat basal epipodite. The fine long straight setae at the rims of the uropods are of the same plumose 'leaf' type as those of the pleopods. The setal rims on the uropodal endopodites and on the telson include a few extremely long setae. This type of seta is also found on other parts of the abdomen, e.g. on the caudal side of the telson and at the bases of the uropods (Fig. 5).

Postures of the pleopods, uropods and telson

When *C. subterranea* is not ventilating, the pleopods and the uropods are held close to the abdomen (Fig. 6A). The pleopodal exopodites and their setae, as well as the uropods, are folded medially. During ventilation, the uropods are spread until their setal fringes touch the tunnel wall. They close off the whole tunnel diameter except for the small slits between the abdomen and the uropodal exopodites, and a rectangular opening below the telson (Fig. 6B). The pleopods are spread out during the power stroke (backwards) and are folded back during the recovery stroke (forwards). During the power stroke, the exopodites are stretched and flattened, and the exopodital rims and the setae are extended, so that the setal fringe almost touches the tunnel wall.

Motion analysis of ventilation viewed ventrally showed that the pleopods are spread actively in the rostral-most position before starting the power stroke and retracted actively in the caudal-most position at the start of the recovery stroke (Fig. 7).

The small slits between the exopodites and the endopodites, and the slit between the left and right endopodite, are closed off during the power stroke by the endopodital setal fringes (Fig. 6). The projected area of the pleopods including the setal fringes is 1.7–2.0 times as large during the power stroke as during the recovery stroke.

Stroke pattern of the pleopods

During ventilation, the pleopods perform a rhythmic

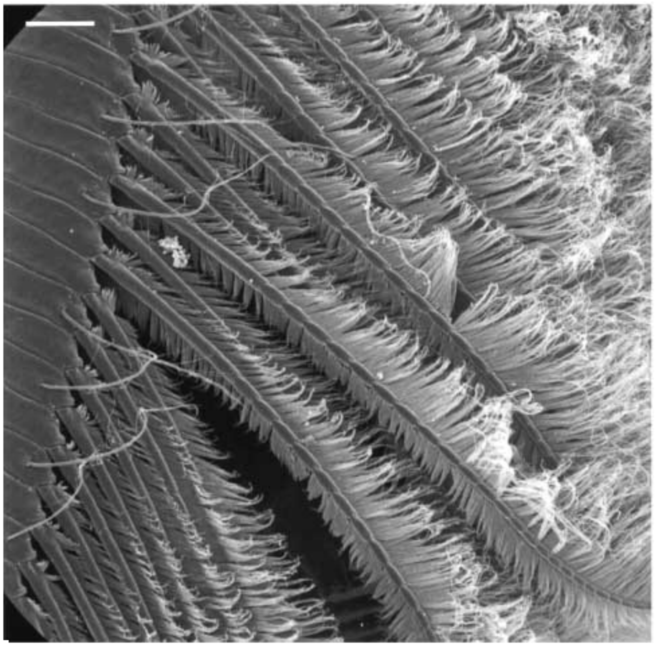

Fig. 3. Scanning electron micrograph of the lateral rim of the pleopodal exopoditeite of *Callianassa subterranea* showing a row of segmented plumose setae with flattened setules implanted obliquely with respect to the rim. Scale bar, 0.1 mm.

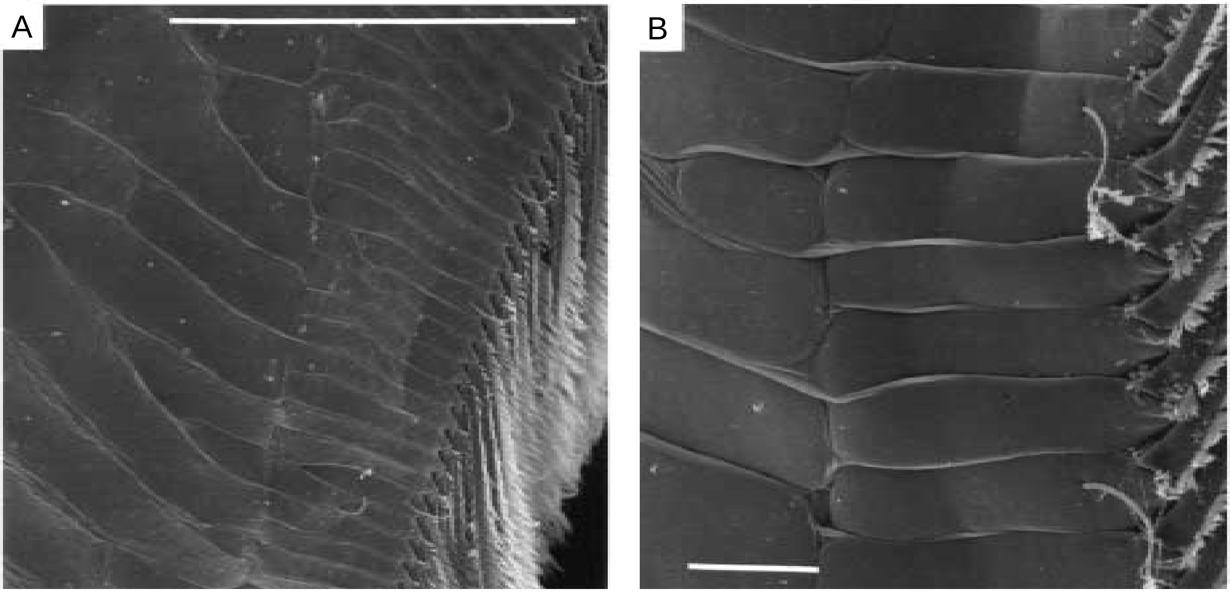

Fig. 4. Scanning electron micrographs of the branching cuticular folds in the rim of the pleopodal exopoditeite of *Callianassa subterranea*. (A) Overview showing the branching pattern of the cuticular folds. Scale bar, 1 mm. (B) Detail showing the membranous folds. Scale bars, 0.1 mm.

metachronous stroke pattern with a mean frequency of approximately 1 Hz (0.9±0.2 Hz, mean ± S.D., N=20). The pleopod pairs have a mean phase shift of 0.31±0.02 (N=20) cycle from caudal to rostral segments, resulting in an ad-locomotory metachronal wave (Fig. 8). The pleopod pair of the third abdominal segment (PP1) performs a simple harmonic motion. The pleopod pair of the fourth abdominal segment (PP2) describes its own characteristic harmonic curve, until it touches PP1. Then, it moves together with PP1 until their paths no longer coincide. The same applies to the pleopod pair of the fifth abdominal segment (PP3), which moves together with PP2 as well as PP1 during parts of the cycle. Fourier analysis of the pleopod motion patterns yields valid results only for the first pair of pleopods. The first- and the third-order harmonics are the most important components, explaining 75 % and an additional 20 % of the motion pattern, respectively, resulting in a nearly perfect sinusoidal motion pattern.

The motion patterns recorded for PP2 and PP3 are reconstructed in a simple model by assigning first-order harmonic functions to all three pairs of pleopods, setting a phase shift between, and an order on, the subsequent pleopod pairs. The pleopods have a phase shift of one-third of the cycle, from caudal to rostral (ad-locomotory): PP3 runs 120 ° ahead of PP2; PP2 runs 120 ° ahead of PP1. The order is imposed on the pleopod pairs from rostral to caudal: PP1 performs an undisturbed complete cycle; PP2 follows PP1 during interactions; PP3 follows PP2 during interactions. The patterns for pleopod tip position *versus* time and pleopod angle *versus* time resulting from the model reconstruction (Fig. 9A,B) closely resemble the observed patterns (Fig. 8).

Discussion

The morphologies of the uropods and telson of the Callianassidae and other thalassinids are well described in the literature because they were used as taxonomic characters (e.g. Stevens, 1928; Biffar, 1971; Williams, 1986). This is not the case for the flow-generating pleopods. Kinematic data on the movements of these abdominal appendages are not available for thalassinids.

When comparing the morphology of the uropods and telson of *Callianassa subterranea* with that of other Callianassidae (Stevens, 1928; Biffar, 1971) and with that of the Upogebiae (Williams, 1986), some similarities as well as some differences can be found. Callianassidae have relatively large uropods with fringes of long setae, and a small telson with a fringe of short

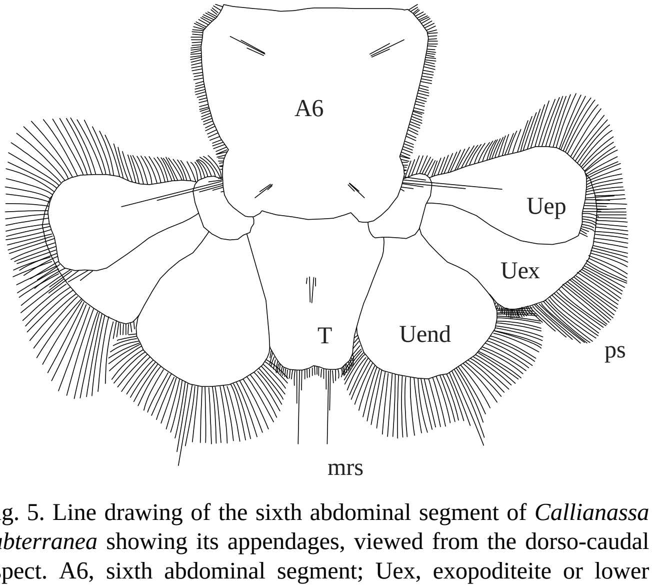

Fig. 5. Line drawing of the sixth abdominal segment of *Callianassa subterranea* showing its appendages, viewed from the dorso-caudal aspect. A6, sixth abdominal segment; Uex, exopoditeite or lower exopodital plate; Uep, epipodite or upper exopodital plate; Uend, endopoditeite; T, telson; ps, plumose setae; mrs, mechanoreceptory setae.

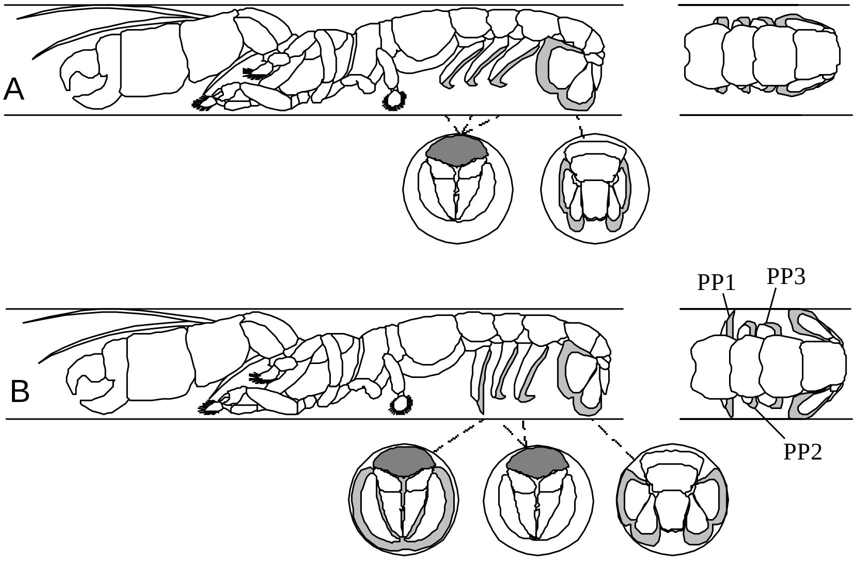

Fig. 6. Typical postures of *Callianassa subterranea* in a tube during walking through the burrow (A) and during ventilation (B), viewed from the lateral and dorsal aspects and in cross-sectional views from the caudal aspect. Note that the pleopods and uropods are retracted during walking (A). In B, the pleopod pair of the third abdominal segment (PP1) is drawn during its power stroke with spread podites and setal rims (shaded), and the pleopod pairs of the fourth (PP2) and and fifth (PP3) abdominal segments are drawn during their recovery stroke with retracted podites and setae. The uropods are extended to the tube wall.

setae. The uropods and the telson of Upogebiae are of rather uniform size and shape, and their setae are of similar length. According to Scott *et al.* (1988), filter-feeding Upogebiae lift their uropods and telson when generating a water current through the burrow for feeding purposes. The flow, passing the animal on the ventral side, may be regulated by adjusting the posture of the tail-fan (Scott *et al.* 1988). We found that *C. subterranea* behaved differently during ventilation, closing the tube with the uropods and leaving only a small opening below the telson for the water to pass through. Ventilation in *C. japonica* results in a flow rate of 0.6–5.5 ml min^{-1} (Mukai and Koike, 1984), and in adult *C. subterranea* of average to large size (approximately 40 mm) the flow rate ranges from 2.7 to 9.5 ml min^{-1} (Forster and Graf, 1995; Stamhuis and Videler, 1997), whereas a filter-feeding *Upogebia pusilla* of the same size produces a flow of approximately 20 ml min^{-1} through its burrow (Dworschak, 1981). Differences in the posture of the tail-fan might therefore be associated with differences in ventilation mechanism in relation to flow rate (Stamhuis and Videler, 1997).

In *C. subterranea*, the relatively large area of the pleopods during the power stroke is achieved by active extension of the exopodites and spreading of the wide fringes of plumose setae on these exopodites. Additionally, the area of the exopodites themselves (and to a smaller extent the endopodites as well) is enlarged by flattening and stretching them. This is achieved by spreading the membranous folds in the lateral and ventral rims, a feature that, to our knowledge, has not been described before for pleopods. The slits between the podites of each pleopod pair are closed off by rims of plumose setae, preventing leakage of water.

Metachrony in swimming legs is often displayed with phase shifts equal to one cycle divided by the number of appendages involved (Barlow and Sleigh, 1980). The phase shift may be actively influenced by an animal. An increase in beat frequency, for example, most commonly results in a decrease in phase shift (Sleigh and Barlow, 1980). The phase shift between the pleopod pairs of *C. subterranea* was found to be approximately one-third of a cycle. There are indications (based on observations of individuals trying to swim out of a cuvette with a pleopod beat frequency of approximately 2.5 Hz) that *C. subterranea* applies a smaller phase shift at higher beat frequencies.

The motion patterns of the pleopods of *C. subterranea* (e.g. Fig. 8) suggest that each pleopod has its own internal oscillator generating a motor output pattern driving the pleopod (Sleigh and Barlow, 1980). Feedback mechanisms overrule the motion pattern as adjacent pleopods touch one another, with a preset hierarchy from rostral to caudal. When two pleopod pairs touch, the caudal-most pair is forced to move with the rostral-

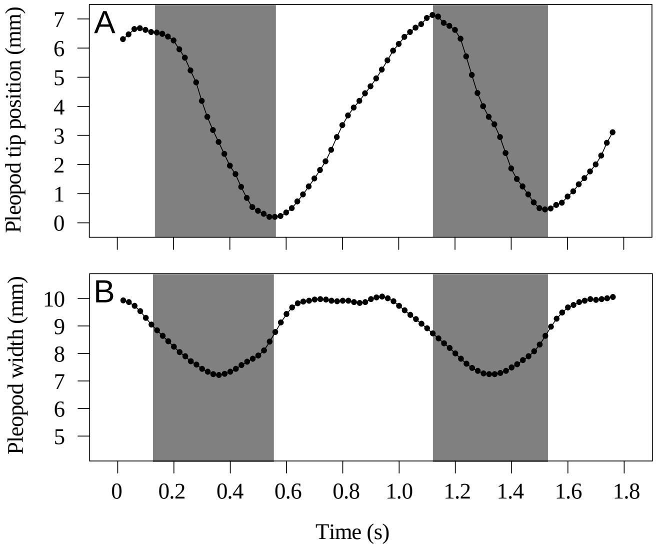

Fig. 7. Pleopod width as a function of stroke type during ventilation in *Callianassa subterranea*. (A) Position of the pleopod tip with respect to its most rostral position. (B) Total width of the pleopod, including the setal rims. Unshaded area, power stroke; shaded area, recovery stroke.

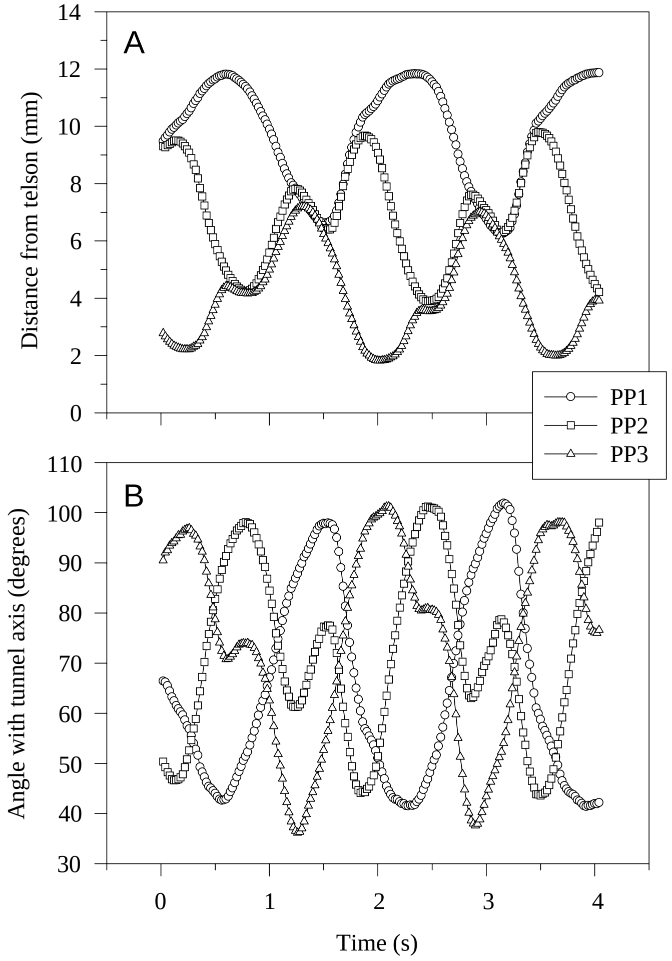

Fig. 8. Pleopod kinematics of *Callianassa subterranea* during ventilation. (A) Pleopod (PP1–PP3; see Fig. 6) tip position with respect to the telson as a function of time (distance decreases during the backward power stroke). (B) Angle between the pleopod and the tunnel axis as a function of time (0 °, pleopod pointing in the rostral direction).

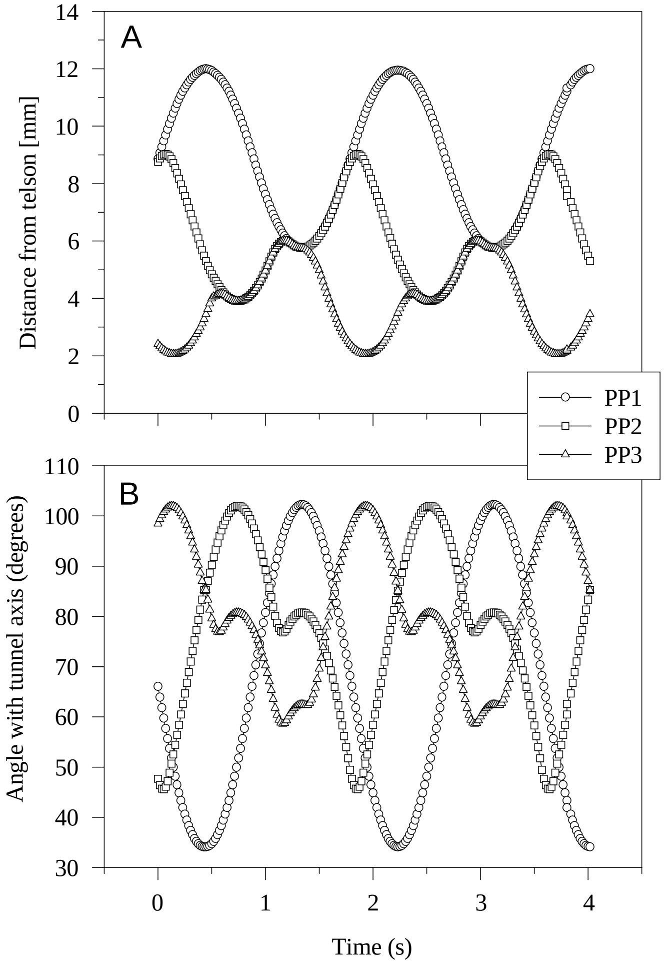

Fig. 9. Pleopod kinematics for *Callianassa subterranea* ventilation modelled from pure sinusoidal movements and phase shifts. (A) Pleopod (PP1–PP3; see Fig. 6) tip position *versus* time with respect to the telson. (B) Angle between the pleopod and the tunnel axis *versus* time (0 °, pleopod pointing in the rostral direction).

most one, resulting in a motion pattern similar to its own, but shifted in phase. As soon as the pleopod pair is able to catch up with its own motion pattern, it follows its own internal oscillator again. The second and third pleopod pairs of *C. subterranea* therefore show a motion pattern consisting of two or three principal harmonics, relatively shifted in phase. Fourier analysis of such a pattern does not provide meaningful results because it divides a periodic signal into harmonics of different order and is unable to distinguish among two or three harmonics of the same order in one signal. Analysis of the motion pattern of the first pleopod pair showed that the first harmonic component was the most important, but the third harmonic also contributed significantly to the pleopod motion pattern. Direct interactions between the pleopod pairs and pressure effects probably induce a secondary motion with a frequency of three times the principal frequency.

Similar pleopod beat patterns to those in *C. subterranea* have been found in some swimming decapods, e.g. the crayfish *Procambarus* (Stein, 1974) and the lobster *Homarus americanus* (Davis, 1968). Steady swimming speeds are observed in the adult stages of the branchiopod *Artemia* (Barlow and Sleigh, 1980; Williams, 1994), and in the mysid *Praunus flexuosus* (Laverack *et al.* 1977). The swimming legs of both these species beat with an ad-locomotory metachronal wave with a phase shift equal to or larger than the cycle divided by the number of swimming legs.

Idotean isopods (Alexander, 1988), as well as some copepod species, e.g. *Cyclops* sp. (Strickler, 1975), *Pleuromamma xiphias* (Morris *et al.* 1985) and *Acanthocyclops robustus* (Morris *et al.* 1990), display a different swimming leg (‘pleopod’) beat pattern in which the pairs of legs demonstrate a phase shift during the power stroke only, taking less than half of the total cycle time. In these small crustaceans, the swimming legs start their power stroke in an ad-locomotory metachronal pattern. After completion of the power stroke, the legs stay in their caudal-most position until all the pairs have completed their power stroke. The recovery stroke is performed by all legs simultaneously. The advantage of this motion pattern might be that maximum thrust is produced because all four pairs of swimming legs are able to perform a complete power stroke. The drag of the swimming legs experienced during the recovery stroke is approximately equal to the drag of only one pair of legs, because all pairs act as one during the recovery stroke. A disadvantage of this motion pattern might be that the thrust generated by the animal will not be evenly distributed over the beat cycle, and the animal can be expected to display a staccato velocity pattern. Intermittent velocity patterns are indeed observed in 'pleopod'-swimming copepods (Strickler, 1975; Morris *et al.* 1985, 1990).

Forster and Graf (1995) report on a pulsating ventilation flow in *C. subterranea*. This is contrary to expectations based on pleopod kinematics when assuming the same relationships between beat pattern and smoothness of flow, as in swimming crustaceans. A quantitative study of the ventilation flow of *C. subterranea* indeed shows a non-pulsatile flow (Stamhuis and Videler, 1997).

We thank the crews of the Dutch research vessel '*Aurelia*' for their assistance during the sampling trips. Jan Zagers (Department of Electron Microscopy, University of Groningen) and Birgit Dauwe are acknowledged for their assistance with scanning electron microscopy. Yvonne van Etten kindly surveyed the literature.

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