VENTILATION, CIRCULATION AND THEIR INTERACTIONS IN THE LAND CRAB, *CARDISOMA GUANHUMI*

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SUMMARY

Physiological variables for ventilation (scaphognathite frequency, branchial chamber pressure and branchial air flow) and for circulation (heart rate, intracardiac and pericardial haemolymph pressure) were measured in the land crab *Cardisoma guanhumi* (Latreille). Crabs were studied both in air alone and in air with access to a shallow layer of fresh, brackish or sea water.

During complete air exposure, forward scaphognathite beating predominated and reversed scaphognathite beating was very infrequent. Periods of apnoea were rare. When crabs were able to immerse the Milne-Edwards openings to the branchial chambers in water, scaphognathite reversal occurred much more frequently, and most air flow through the branchial chambers was generated by this mode of ventilation. Changes in water salinity had no effect on respiratory patterns. The cyclic variation between forward and reversed scaphognathite beating appears to serve not only to ventilate the branchial chambers with air, but also to flush water through the branchial chambers for non-respiratory purposes such as ion, water and acid-base regulation.

Haemolymph pressures were comparatively low (14 mmHg systolic, 6 mmHg diastolic). During diastole a pressure gradient of approximately 0·6 mmHg existed between the pericardial space and the heart lumen. Pauses in heart beat were never observed. Circulatory events were closely co-ordinated with adjustments in ventilation. Reversed scaphognathite beating produced a transient increase in systolic and diastolic haemolymph pressure due to the rise in branchial air pressure acting directly upon the large, haemolymph-filled spaces lining the branchial chambers. A transient brady-cardia accompanied this brief rise in central haemolymph pressures. Possible mechanisms for the regulation of haemolymph pressure are discussed.

INTRODUCTION

The study of intertidal and terrestrial decapod Crustacea has burgeoned in recent years, partly because of the search for new insights into the evolution of air breathing,

and partly because of a specific interest in the adaptations of the land decapods *per se*. Regardless of habitat or degree of terrestrial adaptation, decapods that ventilate with air (i.e. use the paired scaphognathites to generate a flow of air through the branchial chambers) must still keep branchial respiratory structures moistened. Not only are hydrated respiratory membranes a requisite for adequate gas exchange, but in many aquatic and terrestrial decapods alike the gills are also of cardinal importance in hydromineral exchange between haemolymph and water passing through or residing within the branchial chambers (see Mantel & Farmer, 1983).

Water availability is an important limiting factor for terrestrial decapods, and numerous behavioural and morphological adaptations for water acquisition and retention are apparent. For example, many terrestrial brachyurans inhabit burrows, the lower chambers of which lie at or below the water table (Herreid & Gifford, 1963; Cameron, 1975, 1981). Thus, even though the crab may venture short distances from the burrow mouth, significant amounts of time are still spent in the presence of water at the bottom of the burrow. The ability to take a reservoir of water into an arid terrestrial environment is particularly well developed in some terrestrial hermit crabs, where a considerable volume of water may be retained in the inhabited mollusc shell (see DeWilde, 1973; McMahon & Burggren, 1979; Wheatly, Burggren & McMahon, 1984).

A number of studies have concentrated on the respiration and water relations of the land crab *Cardisoma*. Comprehensive accounts of the respiratory morphology of this genus have been provided by von Raben (1934), Gray (1957), Diaz & Rodriguez (1977), Cameron (1981) and Wood & Randall (1981). One noteworthy characteristic of *Cardisoma* is that the gills are quite small, occupying less than one-tenth of the volume of the branchial chamber. Much additional respiratory surface area is provided by extensive folding of the highly vascularized epithelial sheet lining the extensive branchial cavity.

Cardisoma is of considerable interest with respect to acquisition and retention of gill water. This genus not only makes frequent trips to burrows containing at least some water (Herreid & Gifford, 1963; Cameron, 1975, 1981), but also has been reported to retain significant quantities of water in the branchial chamber when active in air (Wood & Randall, 1981). When *Cardisoma* is completely air-exposed, it is not clear whether this branchial water reserve functions primarily as an O_2 source or a CO_2 sink (Wood & Randall, 1981), or whether its major respiratory function is to moisten the gills. Wood & Randall (1981) cut an observation port in the dorsal wall of the branchial chamber of completely air-exposed *Cardisoma carnifex* and observed that the mastigobranchs of the first, second and third maxilliped were in nearly constant motion, flicking water contained in the lower regions of the branchial chamber up over the gills. While this water was probably well aerated by this motion, forward scaphognathite beating simultaneously drew large volumes of air into the Milne-Edwards openings and expelled it out of the exhalant canals. Long periods of apnoea occurred and reversed scaphognathite beating was never observed. Similar observations of forward scaphognathite beating generating a large air flow, with very infrequent reversed beating, have also been previously reported for completely air-exposed *Cardisoma guanhumi* (Cameron, 1975; Herreid, O'Mahoney & Shah, 1979*b*; Herreid, Lee & Shah, 1979*a*).

Terrestrial migrations involving large numbers of *Cardisoma guanhumi* occur during seasonal transitions. Moreover, these crabs are frequently observed in areas with relatively dry surface soil. Thus, physiological studies of *Cardisoma* when completely air exposed, such as those mentioned above are, of course, of considerable interest and value. Unfortunately, such observations may have biased experimentation away from crabs in the natural amphibious setting. *Cardisoma guanhumi* spends considerable amounts of time in wet lowlands, and burrows excavated even in apparently dry areas often contain ground water at their deepest levels. With the progression of the dry season *Cardisoma* is rarely seen on open ground, and may even seal itself in its burrow (Herreid & Gifford, 1963). *Cardisoma* thus spends considerable time in proximity to water, but unfortunately little information exists on the respiratory or cardiovascular physiology of this genus in this normal amphibious state.

In this study on *Cardisoma guanhumi* we test the hypothesis that ventilatory patterns and performance are influenced by the available respiratory media. Additionally, we assess the extent of cardio-respiratory interactions under a variety of experimental conditions and measure basic cardiac variables to determine if the circulatory haemodynamics of land crabs differ from those of aquatic decapods.

MATERIALS AND METHODS

Experiments were performed on a total of 45 *Cardisoma guanhumi* (Latreille) (mean weight 127 ± 45 g, $\bar{x} \pm 1$ s.d.) captured on the Atlantic coast of Panama, and transported to and maintained at the Naos Marine Laboratory, Smithsonian Tropical Research Institute, on the Pacific coast of Panama. Crabs were maintained in shaded outdoor pens and experienced the normal temperature and humidity regime for the season (night temperature 25–26 °C, night humidity 75–95 %; day temperature 33–35 °C, day humidity 75–95 %). During this pre-experimental period all crabs had free access to 50 % sea water (SW) and were fed vegetable matter daily.

The experimental chamber consisted of an opaque box approximately $40 \times 20 \times 15$ cm. The chamber, which was thermostatted to 30 ± 3 °C, was covered with a translucent lid to screen movements of the investigators. In some experiments, crabs were placed unrestrained in this box. In other experiments, crabs were partially restrained by using elastic bands to secure their legs and chelae to a $15 \times 15 \times 1$ cm ceramic plate. Although restrained, such crabs could raise the carapace slightly above the plate and rotate the carapace dorso-ventrally. The restrained animal on the plate was then placed in the centre of the chamber described above. When a 2-cm water layer was placed in the chamber, voluntary rotational movements of the carapace allowed the crab either to immerse the openings to the branchial chambers at the bases of the legs, or raise these openings slightly above the water level (see below).

Ventilatory variables

Standard cannulation and measurement techniques for ventilatory pressures and impedance were employed (see Taylor, Butler & Sherlock, 1973; McDonald, McMahon & Wood, 1977). All pressure cannulae were 40-cm lengths of seawater-filled PE 160 tubing attached to Narco P–1000B pressure transducers, whose signals were displayed on a Narco MKIV rectilinear chart recorder. Each transducer was

calibrated frequently and zeroed against the level of the catheter tip. The pressure cannulae were introduced through 10-mm square pieces of rubber dam glued to the carapace over 1-mm holes drilled through the dorsal surface of each branchial chamber. Impedance electrodes (for measurement of scaphognathite frequency) were constructed from $0 \cdot 1$ mm diameter insulated copper wire. The impedance leads were introduced through 0.5-mm holes drilled in the carapace lateral to the positions of the scaphognathite and held in place by gluing a 1-cm square of rubber dam over the hole in the carapace. In some additional preparations a 5-mm diameter hole was drilled in the carapace at the top of each branchial chamber. The edges of the hole were cauterized, and a removable rubber plug was fitted into the hole. Removal of the plugs eliminated pressure fluctuations in one or both branchial chambers.

With the varying combinations of implanted branchial impedance electrodes and pressure cannulae, ventilatory variables could be assessed for forward and reversed pumping in left and right branchial chamber. Symbols in the text representing variables measured during forward scaphognathite pumping have been assigned the superscript 'f', while the superscript 'r' has been used to designate variables measured during reversed scaphognathite beating. The variables measured, and the symbols used to represent them are given below.

F_R^f, scaphognathite frequency, forward pumping (beats min^{-1}),

P_{Br}^f, branchial pressure, forward pumping (mmHg),

P_P^f, branchial pulse pressure, forward pumping (mmHg),

F^r, frequency of reversal episodes (episodes min^{-1}),

F_R^r, scaphognathite frequency, reversed pumping (beats min^{-1}),

P_{Br}^r, branchial pressure, reversed pumping (mmHg),

P_P^r, branchial pulse pressure, reversed pumping (mmHg),

t_A, apnoea length (s).

Each of these variables could be measured independently for both left and right scaphognathite.

In five crabs ventilatory flow was measured by fitting a face mask, made from the base and neck of a rubber balloon, over the anterior portion of the carapace, as modified from McMahon & Wilkens (1977). The edges of the balloon were glued to the carapace with cyanoacrylate glue, ensuring a gas-tight seal. Inserted into the open end of the neck of the balloon was a 10-mm diameter T-connector. One open arm of the T-connector was directed ventrally to the bottom of the experimental chamber. The chamber contained a 2-cm layer of brackish water (50% sea water), so that the ventral opening of the connector always rested below the water surface. This ventral arm of the connector provided a route by which any water pumped up into the face mask during forward pumping could be drained back to the chamber. However, since its opening was below the water surface, it could not serve as a site of air entry into the face mask. The dorsally directed arm of the connector, which provided a low resistance inlet for fresh air to flow into the face mask, also contained a hot-wire anemometer (HWA 104, Thermonetics Co., San Diego), the output of which was directed to one channel of the chart recording system. A catheter inserted into the connector between the hot wire anemometer and the face mask was attached to a suction pump drawing gas at a constant rate of 45 ml min^{-1}. When the crab was in a ventilatory pause, the signal from the anemometer indicated a constant gas flow

through the mask of 45 ml min^{-1}. When the crab pumped gas forward out of the exhalant canals into the mask, the flow of fresh air past the anemometer sensor and into the face mask generated by the suction pump was reduced by the exact amount of gas added to the face mask from the branchial chambers by forward scaphognathite pumping. During reversed scaphognathite pumping, gas from the face mask was being removed to ventilate the branchial chambers, as well as being removed by the suction catheter. This combined effect resulted in an increase in flow of fresh air past the hot-wire anemometer which was exactly proportional to the ventilatory volume during reversed beating. The frequency response of this system was extremely rapid, and allowed resolution on the recorder of individual movements of the scaphognathites. After each experiment the anemometer sensor was removed from the face mask and calibrated by directing known flows of air past it.

Circulatory variables

Typically, three or four 1-mm diameter holes were drilled through the carapace in the vicinity of the heart. Copper electrodes glued into two of these holes were used for measurement of heart beat by an impedance technique. The other holes were sealed with squares of rubber dam. A 40-cm long PE 160 catheter fitted with a PE 60 tip was used for recording intracardiac haemolymph pressures. The tip of this catheter was introduced through the dam at the midline of the carapace and advanced ventrally 3 mm into the lumen of the heart. This catheter was filled with filtered sea water and attached to a P–1000B pressure transducer and the rectilinear recorder described above. The pressure signal from the transducer was also sent to a Narco Biotachometer which computed and displayed instantaneous heart rate on the recorder. A similar catheter arrangement was used for measurement of pericardial pressure immediately outside of the heart, with the catheter tip advanced ventrally 2 mm through the carapace at a position 1 cm off the crab's midline. Cardiac and pericardial cannulation caused minimal disturbance to the crab (see Results).

Experimental protocols

In some preliminary experiments, crabs fitted only with impedance electrodes were allowed overnight recovery and acclimation to the experimental chamber before measurements were begun. In the remainder of the experiments, restrained crabs were allowed at least 1 h to recover from surgery and handling during restraint before measurements were begun. Animals in the latter experiments were clearly not 'undisturbed', but had stopped struggling against restraint during this period. If released from restraint, these crabs were immediately fully active and aggressive, indicating that they were not fatigued or otherwise severely disturbed by the experimental conditions.

Instrumented crabs were examined with an experimental protocol involving several experimental conditions. Cardio-ventilatory variables were measured during a 1-h period when air was the only available respiratory medium, and for additional 1-h periods when a 2-cm aerated layer of 100 % sea water, 50 % sea water or fresh water was placed in the bottom of the chamber. Crabs were never denied access to air, since we rarely observed voluntary total submergence in water in their natural habitat on the Atlantic coast of Panama.

Statistical analyses

All data were analysed for mean values ± 1 s.e. Analysis of variance (ANOVA) was used to assess treatment effects. Where significant effects were found, Student's t-test for independent means (unless otherwise indicated) was used to determine the significance level of differences between particular means. A significance level of 0·05 was used in all statistical procedures.

RESULTS

The respiratory surfaces of *Cardisoma guanhumi* are ventilated by forward or reversed pumping by the scaphognathites located at the anterior margin of each branchial chamber. Whether water or air is the respiratory medium used by *Cardisoma* when it stands in shallow water depends largely upon the positioning of the Milne-Edwards openings and exhalant channels. During forward pumping in shallow (1–4 cm) water, an undisturbed crab adjusts its posture so that its horizontal plane is roughly parallel to the water surface. This usually places the openings of both the Milne-Edwards and exhalant channels at the air–water interface (Fig. 1A). Under these conditions much air in addition to water is drawn into the Milne-Edwards openings, and the gas exiting the exhalant canals anteriorly creates a constant stream of air bubbles at the water surface.

At the onset of a period of reversed scaphognathite beating in an undisturbed crab, a marked postural change occurs such that the plane of the carapace pivots upwards anteriorly (Fig. 1B). The crab lowers the limb bases and Milne-Edwards openings, completely submerging them in the water, and raises the openings of the exhalant channels well above the water surface. Air is drawn into the exhalant channels during reversed breathing, and a large stream of gas bubbles is forced out from the ventral region of the branchial chambers *via* the Milne-Edwards openings and rises to the water surface.

Effects of acclimation, restraint and cardiac cannulation

Since a variety of different techniques was used in this study, it was important first to define carefully the specific limitations of each technique, before discussing quantitative details of cardio-ventilatory patterns or experimental treatment effects.

Restraint

Ventilatory variables for both left and right scaphognathite as well as heart rate, all measured through impedance techniques, were measured 1–4 h after electrode attachment in both unrestrained and restrained crabs. All crabs had access either to air alone or to air and 50 % sea water as indicated above. In air alone, none of the ventilatory parameters measured for either right or left scaphognathite nor heart rate were significantly altered by restraint ($P > 0·10$).

When 2 cm of 50 % SW was placed in the chamber, heart rate and most parameters for forward pumping for either right or left scaphognathite were also not significantly different between restrained and unrestrained crabs. Only the length of the apnoeic
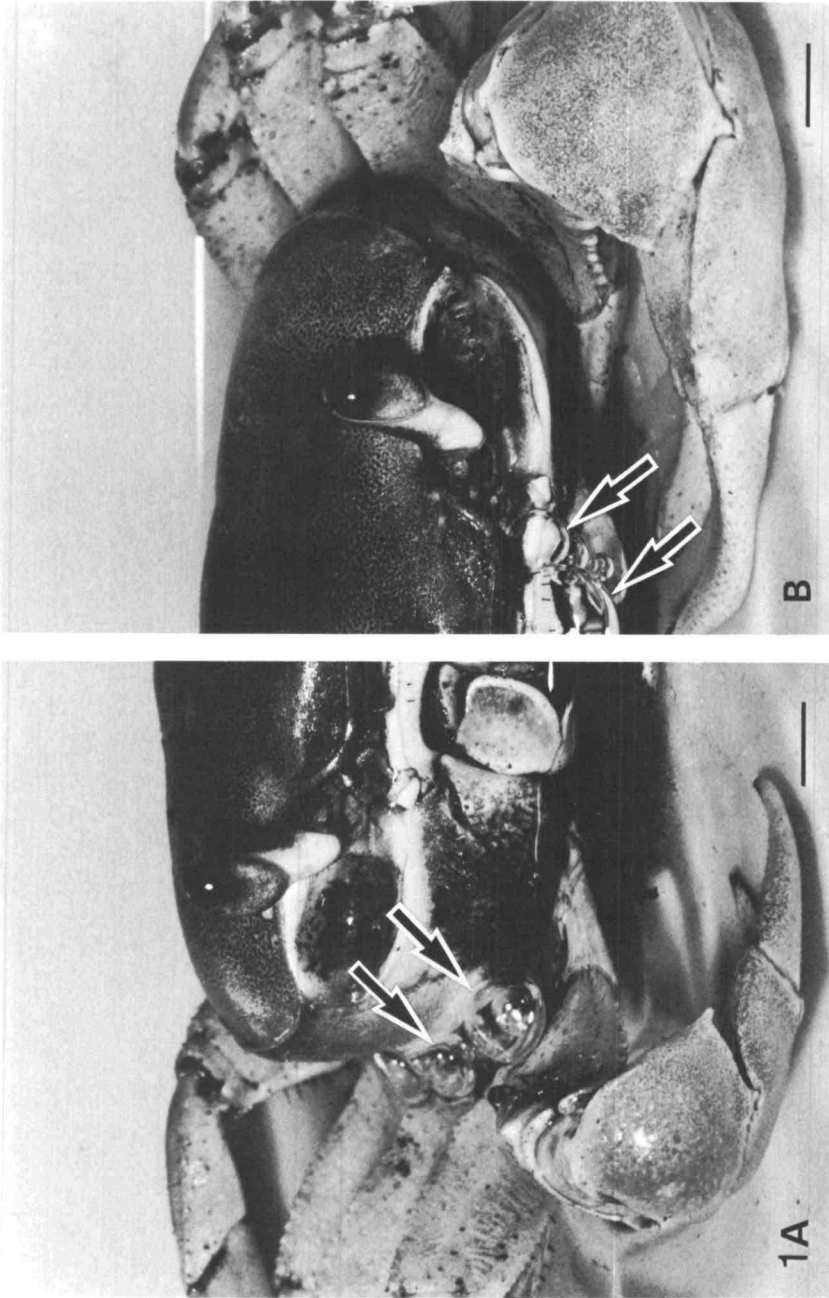
Fig. 1. Postural adjustments during branchial chamber ventilation in a land crab, *Cardisoma guanhumi*, resting in 3 cm of 50 % SW. A and B were photographed from identical camera angles. (A) The posture during forward scaphognathite beating, in which the exhalant channels are held just at or below the water level. Note the bubbles of air (arrows) gathering around the exhalant channels. (B) The posture during reversed scaphognathite beating, in which the exhalant canals are elevated well above the surface of the water to allow air entry. Note the bubbles of air gathering around the Milne-Edwards openings (arrows). Scale bars, 1 cm. See Results for further details.

period of the right scaphognathite (but not the left) was significantly affected
($P < 0.05$), decreasing from 0.5 ± 0.5 min to 0.1 ± 0.1 min, but the effect was
nonetheless not large enough to change significantly the beat frequency of the right
scaphognathite. The frequency of reversal periods by both scaphognathites ($3.3–4.9$
periods min^{-1}) was not significantly influenced by restraint in crabs in 50% SW, but
the frequency of pumping within each period of reversed beating was significantly
elevated ($P > 0.05$) in restrained crabs (23.1 beats min^{-1}) compared with
unrestrained crabs (6.8 beats min^{-1}).

Patterns in left vs right scaphognathite (i.e. 'handedness')

In some decapod Crustacea ventilatory patterns are characterized by very close
coupling of left and right scaphognathite events, while in others the scaphognathites
may drift in and out of phase, or even show unilateral pausing (Taylor, 1982;
McMahon & Wilkens, 1983). In the present experiments, if cardiac and pericardial
pressures were being measured simultaneously, the recorder channels remaining were
sufficient only to monitor ventilatory events on one side of the crab. Since it was
important to know whether the pattern of a single scaphognathite recorded under
these circumstances was representative of both scaphognathites, a series of crabs was
prepared in which both left and right scaphognathite patterns could be recorded.

Although there was very occasionally phase drifting or unilateral apnoea in *Car-
disoma*, left and right scaphognathites were usually absolutely coupled under all
experimental situations (i.e. unrestrained or restrained, in air or with access to 50%
sea water, before or after cardiac cannulation). In fact, the differences in mean values
of all ventilatory parameters for right and left scaphognathites of each crab were not
significantly different from zero ($P > 0.10$, Student's t-test for dependent means).
Thereafter patterns of scaphognathite beating recorded from one side were assumed
to be representative of both sides.

Cardiac cannulation

Ventilatory parameters and heart rate of restrained crabs with access to 50% SW
were measured immediately before and 30 min after cannulation of the heart. Cardiac
cannulation caused no significant ($P > 0.10$) change in F_R^f, P_{Br}^f, P_P^f, F^r, P_{Br}^R, P_P^R or t_A
of the right scaphognathite. Similarly, left scaphognathite pumping was not sig-
nificantly affected by cardiac cannulation, with the exception of a significant but small
decrease in F^r and rise in t_A. Importantly, heart rate was not significantly ($P > 0.10$)
altered by cardiac cannulation.

In general, then, *Cardisoma guanhumi* tolerated restraint, instrument implanta-
tion and experimental manipulation very well. Since restraint or cannulation
produced only small quantitative, rather than qualitative, changes in only a few of the
respiratory and cardiac variables (and since unrestrained *Cardisoma* showed amazing
ingenuity and dexterity in destroying implanted leads), the data which follow were
recorded solely from restrained crabs unless otherwise indicated.

Ventilatory patterns and influence of respiratory medium

When ventilating with air alone, predominantly forward directed scaphognathite
pumping generated subambient pressures in the branchial chamber. This produced

a ventilatory flow which was primarily forward through the branchial chamber and out of the exhalant canals (Fig. 2A). A quantitative analysis of ventilation (Fig. 3) reveals that scaphognathite frequencies during forward ventilation were about
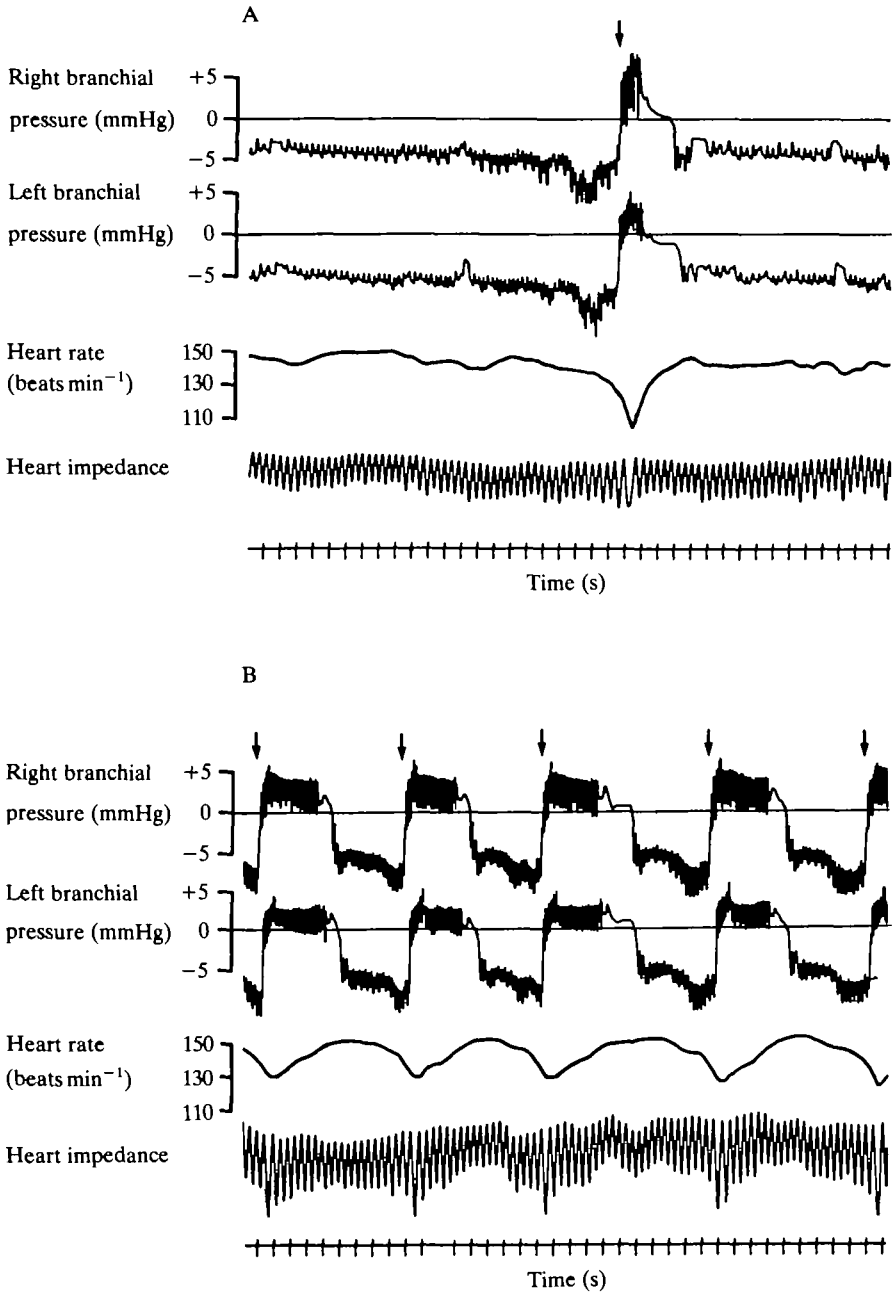

Fig. 2 Representative records of branchial pressures and heart impedance and rate in a restrained, 151 g *Cardisoma guanhumi*. (A) Patterns measured during total air exposure, which resulted in primarily forward scaphognathite beating. (B) Ventilatory patterns with frequent periods of reversals (arrows) stimulated by placement of the crab in 2 cm of 50 % SW.
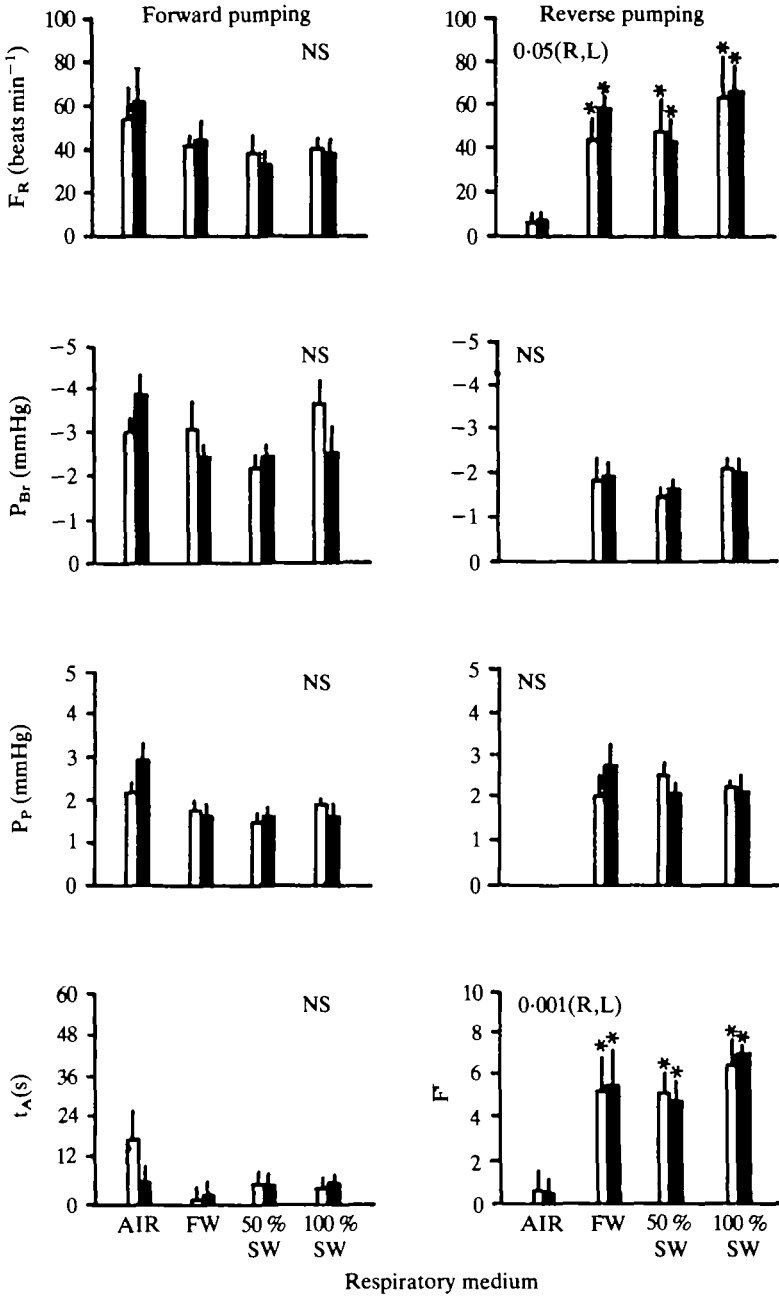
Fig. 3. Effect of ventilatory medium on scaphognathite frequency (F_R), branchial (P_{Br}) and branchial pulse (P_P) pressures, length of apnoea (t_A) and frequency of reversal episodes (F^r) during forward and reversed beating in *Cardisoma guanhumi*. Mean values ± 1 S.E. are presented for both left (L, white bars) and right (R, black bars) scaphognathites. Number of crabs analysed for each ventilatory medium are AIR = 8, FW (fresh water) = 7, 50 % SW = 8, and 100 % SW = 8. Results of analysis of variance for effect of ventilatory medium are shown in the upper region of each panel. Where significant treatment effects were indicated, *t*-tests were performed to reveal significant differences between ventilatory media. Thus, asterisks indicate significant differences from values measured with air as the ventilatory medium. *, $P<0.05$; **, $P<0.01$. See text for additional details. NS, not significant.

50–60 beats min^{-1}. Apnoeic episodes were infrequent and irregular (1 episode every 3–5 min) and lasted only 5–20 s. Intrabranchial pressures during forward beating were 3–4 mmHg subambient, with a pulse pressure of 2–3 mmHg. When ventilating with air, less than one reversal episode occurred per minute.

When *Cardisoma* was provided access to water and could thus partially submerge one or both of the Milne-Edwards openings, several important aspects of the ventilatory patterns were affected. Whereas F_R^F, P_{Br}^f, P_P^F and t_A remained unchanged, the frequency with which reversals occurred increased 10–15 times (Fig. 3). Not only did reversals occur more often, but the frequency of scaphognathite beating during these reversals was elevated several times compared with strictly aerial ventilation. Apnoeic episodes of significant length still occurred quite infrequently and irregularly when access to water was provided, although in some crabs a ventilatory pause of a few seconds occasionally followed a period of reversed scaphognathite beating.

Values for each ventilatory parameter measured when the crab had access to fresh water, 50 % sea water or 100 % sea water were statistically identical. Therefore, these changes in respiratory pattern were apparently related to use of water *versus* air as a respiratory medium, rather than to water quality *per se*.

Fig. 4 shows a representative recording of branchial pressures and gas flow at the exhalant canals during forward and reversed beating in a *Cardisoma* with access to both air and 50 % sea water. Mean values ($N = 5$ crabs) of right scaphognathite
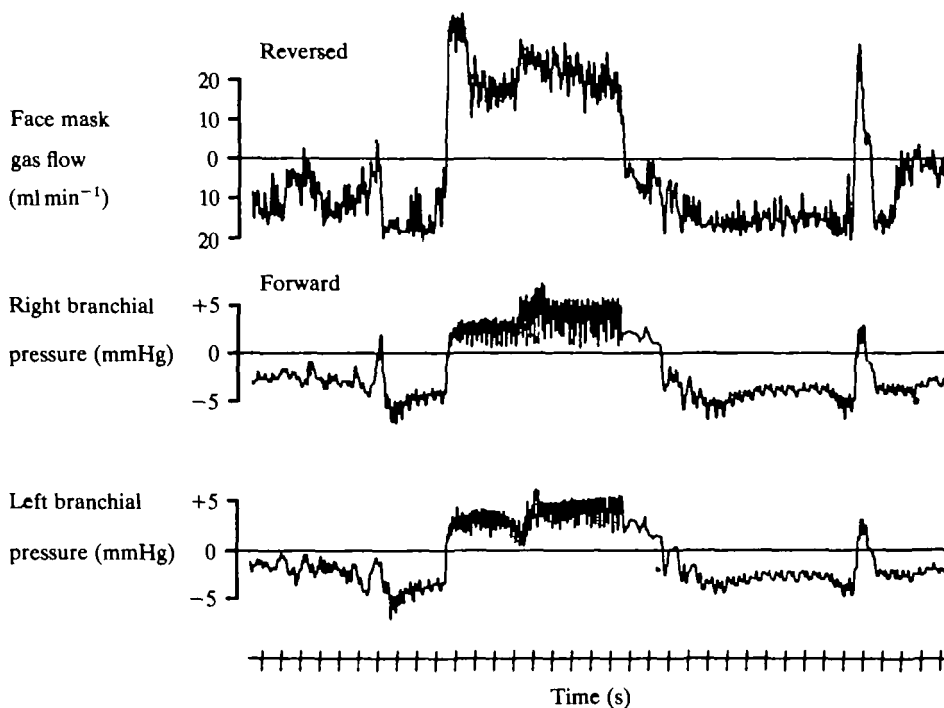

Fig. 4. Representative records of branchial pressures and of gas flow through the face mask of an 80 g *Cardisoma guanhumi* resting in approximately 2 cm of 50 % SW. Periods of reversed scaphognathite beating are characterized by positive branchial pressures and reversed gas flow through the face mask.

frequency, total gas flow into and out of the face mask during forward and reverse flow, respectively, and stroke volume of the scaphognathite pair (assuming equal frequency of left and right scaphognathites, see above) are presented in Fig. 5. Both stroke volume and gas flow were significantly greater during reversed beating than forward beating. From mean values for restrained crabs without face masks (Fig. 3),
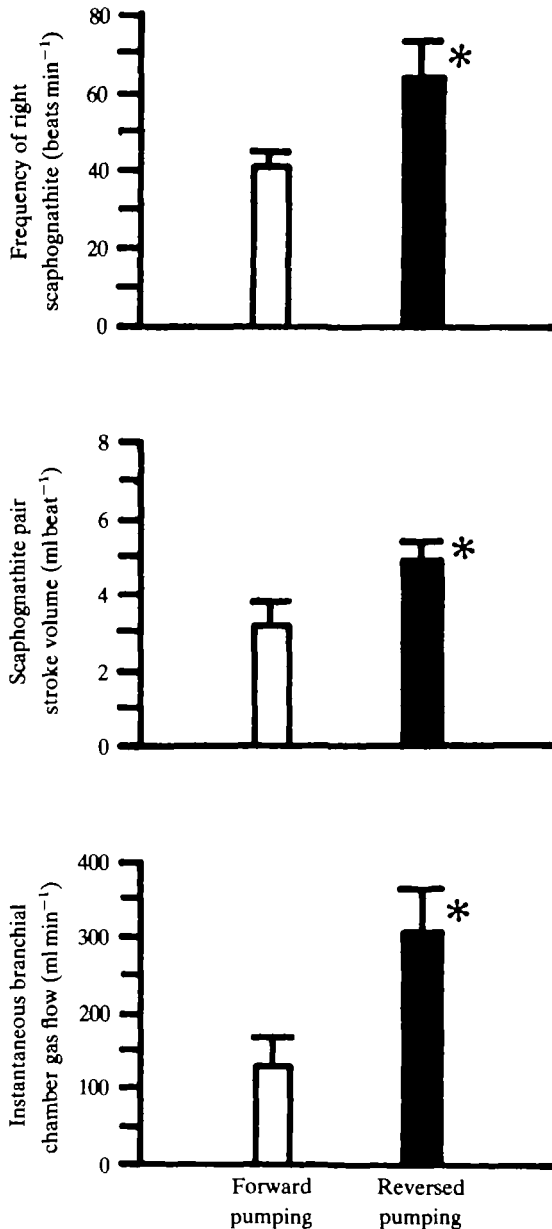

Fig. 5. Scaphognathite frequencies, stroke volumes and gas flows measured during forward and reversed pumping in five *Cardisoma guanhumi*. Mean values ± s.e. are given. Asterisks next to data for reversed pumping indicate significant difference ($P<0.05$) from forward pumping.

it can be calculated that, during constant ventilation in *Cardisoma* with access to both 50 % SW and air, forward ventilation occupies 36 s of every minute compared with 24 s for reversed ventilation. Given the differences in flow rates for the two directions of pumping (Fig. 5), this indicates that for every minute of scaphognathite ventilation approximately 125 ml kg^{-1} of gas are pumped out posteriorly from the Milne Edwards openings and 70 ml kg^{-1} of gas are pumped out anteriorly through the exhalant channels. This corresponds to 34 % of total gas flow being generated by forward pumping compared with 66 % by reversed pumping.

Measurements of forward and reversed gas flow were not made in crabs with access to air only, and we do not know if scaphognathite stroke volume changes under this condition. However, assuming an identical stroke flow to that measured when access to 50 % SW was provided, and using the mean ventilatory rates and ratios of totally air-exposed crabs provided in Fig. 3, then estimated forward and reverse gas flow changed dramatically to approximately 98 % and 2 % of total flow, respectively.

Circulatory patterns and cardio-respiratory interaction

Circulatory variables, including haemolymph pressure, were measured in a total of 24 *Cardisoma guanhumi* exposed to air but with access to 50 % SW. Mean values are

Table 1. *Circulatory variables measured in the land crab* Cardisoma guanhumi

	Mean ± 1 s.e.	Number of crabs measured
Heart rate (beats min^{-1})	134 ± 7	18
Intracardiac systolic pressure (mmHg)	14·1 ± 0·7	24
Intracardiac diastolic pressure (mmHg)	5·5 ± 0·7	24
Pericardial systolic pressure (mmHg)	8·4 ± 2·9	5
Pericardial diastolic pressure (mmHg)	6·1 ± 2·5	5

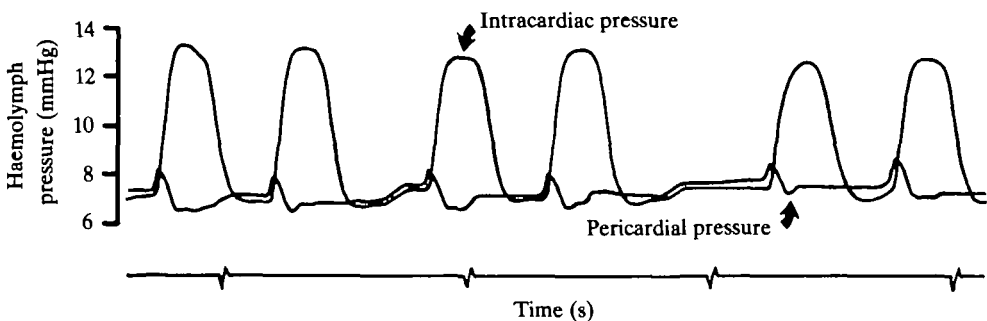Crabs were restrained and had access to a 2-cm layer of 50 % SW.

Fig. 6. Haemolymph pressure measured in the pericardial space and in the heart of a 159 g *Cardisoma guanhumi*.

given in Table 1, while Fig. 6 shows representative simultaneous recordings of intracardiac and pericardial pressures.

As is typical for the few decapod circulations investigated to date, intracardiac systolic pressure was generally below 20 mmHg and diastolic pressure several mmHg above ambient pressure. A pressure gradient from pericardial space to heart lumen of about 0·4–1·0 mmHg existed throughout diastole, and provided the driving pressure for cardiac filling. At the onset of systole, haemolymph pressure in the pericardium began to rise concomitantly with intracardiac pressure, suggesting open communication of the pericardium with the interior of the heart. After increasing by 1–3 mmHg, pericardial pressures fell back to diastolic levels while intracardiac pressures continued to rise, indicating effective closure of the ostial valves at this time.

Although mean circulatory variables were quite constant in individual crabs over an extended time period, both locomotor activity and changes in ventilatory patterns induced transient changes. The most consistent changes in circulatory parameters accompanied the transient changes from forward to reversed beating (Figs 7,8). Both systolic and diastolic intracardiac pressure began to increase within 0·5–2 s of the onset of a reversal, with both values having risen significantly (ANOVA, $P < 0.001$) by approximately 2–3 mmHg by the end of the reversal period. A significant decrease in heart rate of about 10 beats min^{-1} occurred concomitantly with reversal of scaphognathite beat and rise in intracardiac haemolymph pressure. Immediately after the end of the reversal episode, both heart rate and intracardiac haemolymph pressure returned
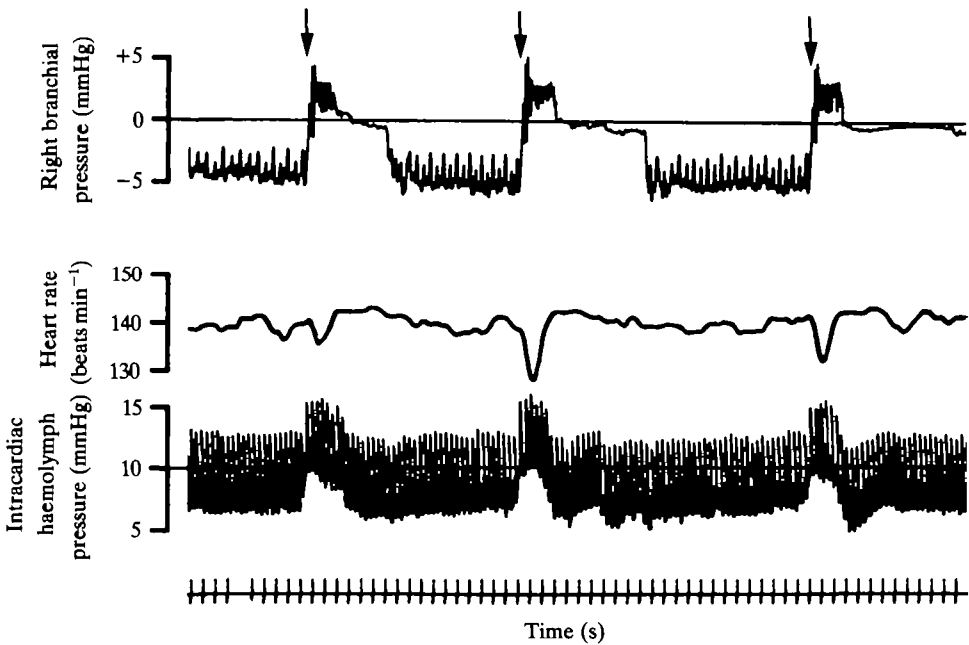

Fig. 7. Representative records of branchial gas pressure, intracardiac haemolymph pressure and heart rate during periods of both forward and reversed scaphognathite beat in a 142 g *Cardisoma guanhumi* with access to 50 % SW. Periods of reversed scaphognathite beating occur when branchial pressure swings to positive values (arrows).
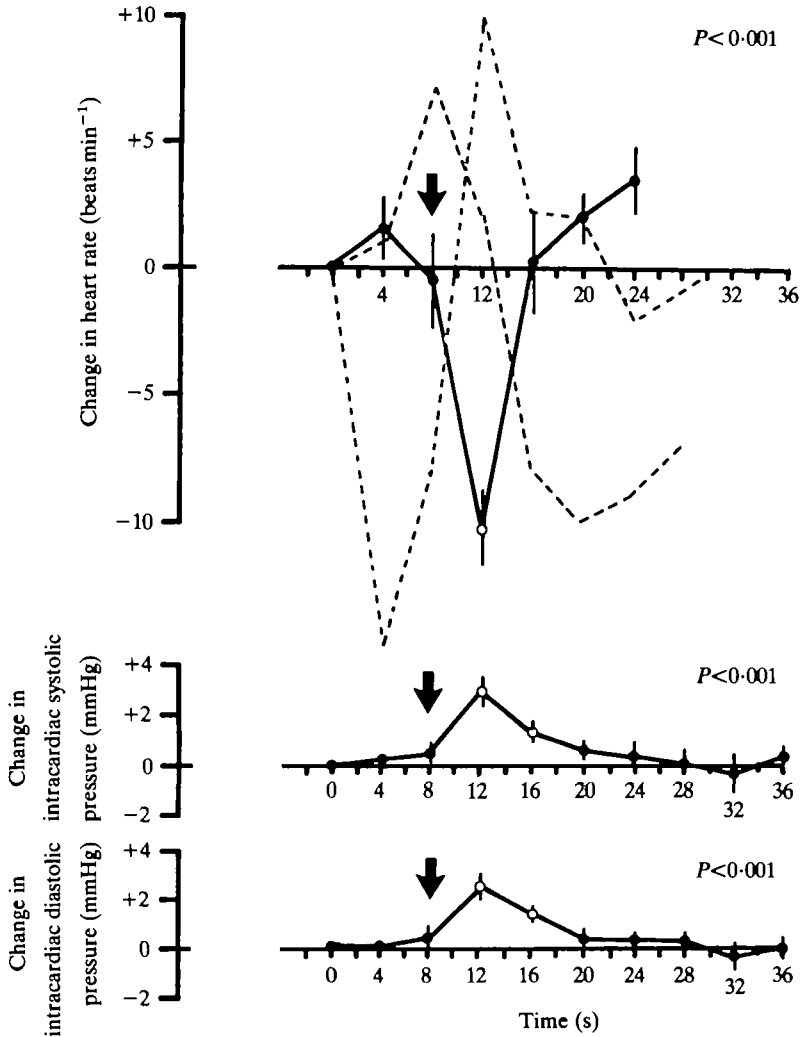
Fig. 8. Changes in heart rate and in intracardiac systolic and diastolic pressure before, during and after reversed scaphognathite beating in *Cardisoma guanhumi*. All crabs had access to 50% SW. Mean values ± 1 s.e. for five crabs are presented. Arrows indicate the onset of reversed beating, which lasted 4–10 s. Results of analysis of variance of means of each time class are shown in the upper right of each panel. Open circles represent means significantly different from values at time zero. The dashed lines indicate heart rate for two additional crabs showing atypical time courses associated with the onset of reversed scaphognathite beating.

to levels not significantly different ($P > 0.10$) from before the onset of the reversal.

Interestingly, in two otherwise apparently normal crabs, quite different heart rate patterns were associated with spontaneous scaphognathite reversals (dashed lines, Fig. 8). In both these individuals, heart rate began to change 3–6 s before the onset of reversal, and in one crab the bradycardia was greatest about 10 s after the end of the reversal episode.

Additional experiments were performed on those *Cardisoma guanhumi* fitted with rubber plugs in the carapace. When the branchial plugs were in place, normal

pressures above and below ambient accompanied reversed and forward beating, respectively, and a transient bradycardia occurred during episodes of reversed beating. Removal of the rubber plugs inserted into the 5-mm diameter hole in the top of each branchial chamber, which opened the system to the atmosphere, eliminated
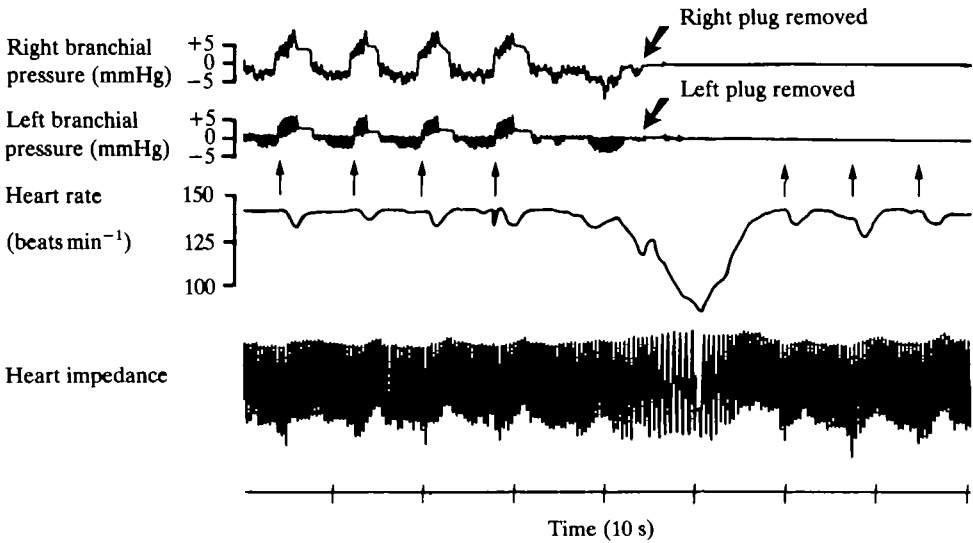

Fig. 9. Effects on branchial pressure and heart rate of *Cardisoma guanhumi* produced by removal of 'branchial plugs' from the carapace (large arrows). Small, upward pointing arrows indicate brief periods of reversed scaphognathite beating. Note that branchial gas pressure fluctuations disappear after the plugs are removed, but that the transient bradycardia associated with reversed scaphognathite beating persists. See text for details.
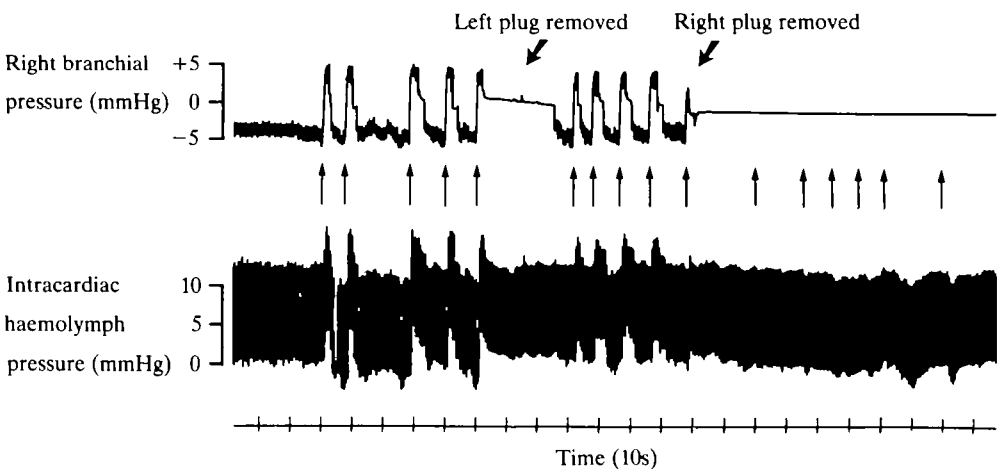

Fig. 10. Effects of sequential removal of left and right 'branchial plugs' on intracardiac haemolymph pressure in a 198 g *Cardisoma guanhumi* with access to 50 % SW. Upward arrows indicate brief periods of reversed scaphognathite beat.

all transient changes in air pressure within the branchial chambers. When both plugs were removed simultaneously, the transient changes in intracardiac haemolymph pressure that accompanied reversals were also eliminated (Fig. 9). Removal of only the left plug, which eliminated branchial pressure fluctuations in the left branchial chamber only, reduced by approximately one-half the size of the transient change in intracardiac haemolymph pressure that had previously occurred during reversals (Fig. 10). Subsequent removal of the right plug essentially eliminated all fluctuations in haemolymph pressure normally associated with reversals. Although bilateral removal of plugs eliminated branchial and intracardiac pressure transients, a brief bradycardia accompanying reversed scaphognathite beating usually persisted.

DISCUSSION

Ventilation patterns

Qualitatively, the basic ventilatory patterns and mechanisms in *Cardisoma guanhumi* are similar to those found in other brachyuran crabs, both marine and semi- or fully terrestrial (see reviews by McMahon, 1981; Taylor, 1982; McMahon & Wilkens, 1983). However, the present study reveals many quantitative differences in ventilation in *Cardisoma guanhumi* which set this species apart from other brachyurans.

Unilateral beating of one scaphognathite, a common feature of branchial ventilation in brachyuran crabs (E.W. Taylor *et al*. 1973; McDonald *et al*. 1977; Butler, E.W. Taylor & McMahon, 1978; A.C. Taylor & Davies, 1982; McMahon & Wilkens, 1983), was observed only rarely in *Cardisoma guanhumi*, where coordinated bilateral ventilation definitely prevailed under all experimental conditions. Interestingly, Wood & Randall (1981) reported that unilateral scaphognathite beat was the normal mode of ventilation in air-exposed *Cardisoma carnifex* at 25 °C, with coordinated bilateral ventilation only occurring during exercise. It has been suggested that experimental disturbance or handling results in constant, bilateral ventilation in decapod crustaceans (see McDonald *et al*. 1977; Taylor, 1982; McMahon & Wilkens, 1983). However, disturbance does not appear to account for this pattern in *Cardisoma guanhumi* in the present study, since unrestrained, air-exposed crabs allowed overnight acclimation to experimental conditions in the present study still exhibited very close coordination of left and right scaphognathite beating. Interestingly, increased bilateral pumping was observed upon aerial exposure in the intertidal crab *Cancer productus* (DeFur & McMahon, 1984).

Another feature of branchial ventilation tending to set *Cardisoma guanhumi* apart from other brachyuran crabs and even from *Cardisoma carnifex* (Wood & Randall, 1981) is the infrequent occurrence and relatively brief duration of apnoeic periods. Even after overnight acclimation, undisturbed and unrestrained *Cardisoma guanhumi* ventilating with air but with access to 50% sea water rarely stopped scaphognathite beating for more than 1 min. Given the high oxygen capacitance of air and the fact that at least in *Cardisoma carnifex* branchial chamber P_{O_2} rarely falls below 130 mmHg, even during periods of apnoea of several minutes (Wood & Randall, 1981), it is unlikely that continuous branchial ventilation in *Cardisoma guanhumi* is related to requirements for branchial O_2 uptake. Constant ventilation may instead

relate to non-respiratory processes that require water movement within the branchial chamber. Certainly, the complex ventilatory patterns seen when small amounts of water are available undoubtedly not only maintain gas flow through the upper regions of the branchial chamber, but also provide water irrigation of the gills in the lower regions of the branchial chambers. The gills and perhaps other structures in the branchial chamber of brachyurans are involved in water and ion regulation and acid-base balance (see Mantel & Farmer, 1983), and these functions would be facilitated by, if not totally dependent upon, turnover and agitation of water in the lower regions of the branchial chamber. Constant scaphognathite motion required primarily for non-respiratory, iono-regulatory functions may generate gas flow through the upper regions of the branchial chamber whether required for gas exchange at that time or not.

Interestingly, the ionic composition of the water available to *Cardisoma* had no significant influence on ventilatory patterns, at least during the relatively brief period of water exposure. Rather, the presence or absence of water *per se* was the important feature. This is quite unlike the effect of brief salinity stress in some euryhaline decapods (Taylor, Butler & Al-Wassia, 1977; Wheatly & McMahon, 1982). *Cardisoma guanhumi* is adept at regulating blood ion concentrations with water sources of varying salinities (Herreid & Gifford, 1963; M. Wheatly, unpublished) and apparently can achieve this without adjusting branchial ventilation pattern to water salinity.

Perhaps the most distinctive feature of branchial ventilation in *Cardisoma guanhumi* is the prominence of reversed scaphognathite beating. Most aquatic, intertidal or terrestrial brachyuran crabs maintained in normoxic, normocapnic environments may show a reversed beat or small group of reversed beats (see McMahon & Wilkens, 1983; E.W. Taylor, 1982; A.C. Taylor & Davies, 1982; DeFur & McMahon, 1984), but they are normally infrequent and in some species are apparently absent altogether (e.g. *Cardisoma carnifex*, Wood & Randall, 1981). However, scaphognathite reversal occurs frequently in *Cardisoma guanhumi* in air with access to water and, we believe, makes a major contribution not only to the turnover of gas but also of water within the branchial chambers. This may be important, not only for hydration of the respiratory membranes, but also for ion, water and acid-base regulation by the gills.

Increased reversed beating in other decapods has been observed with increased environmental temperature (Taylor & Butler, 1973), decreased environmental oxygen (Herreid *et al.* 1979*a,b*) and during burrowing activity (McDonald *et al.* 1977). The function of reversed scaphognathite beating in decapods has variously been attributed to cleaning of the branchial chamber, flushing poorly ventilated regions of the branchial chamber, and sampling water anterior to the animal (Hughes, Knights & Scammel, 1969; Johansen, Lenfant & Mecklenburg, 1970; Berlind, 1976; McDonald *et al.* 1977). In addition to the 'flushing' function for reversals which we propose for *Cardisoma guanhumi*, reversed scaphognathite beating and the positive branchial pressures it produces also may act to 'wring out' stagnant pools of haemolymph in poorly perfused regions of the gills and vascular bed lining the branchial chamber.

The large increase in net retrograde flow of gas through the branchial chamber when water becomes available occurs not only by increases in the number of reversal episodes in any given time period (Figs 2, 3), but also by increases in both frequency

and stroke volume of scaphognathite beat during reversal periods (Fig. 5). Increased scaphognathite frequency during reversed beating has also been reported for the marine crab, *Cancer magister* (McDonald *et al.* 1977), but in this crab scaphognathite stroke volume decreases rather than increases and so total ventilatory flow is reduced. Both acute and chronic adjustments in these aspects of scaphognathite performance have been reported for decapods (Burggren & McMahon, 1983; J.A. Mercier & J.L. Wilkens, unpublished), and adjustments in scaphognathite stroke volume or frequency reflect a particular set of physiological or environmental conditions rather than a species-specific characteristic.

Cardiovascular patterns

Heart rate in *Cardisoma guanhumi*, approximately 100–150 beats min^{-1} even in undisturbed, unrestrained crabs, was quite high compared with values which have been reported for other decapod Crustacea. However, most previous measurements on temperate marine or freshwater species or on tropical land crabs have been made at body temperatures of only 8–25 °C. Assuming a Q_{10} value for heart rate of approximately 2, *Cardisoma* would have a heart rate of 75–100 beats min^{-1} at 25 °C, which is comparable with heart rates for *Cardisoma carnifex* and *Cardisoma guanhumi* measured at that temperature (Herreid *et al.* 1979a,b; Wood & Randall, 1981). The high heart rates typical of *Cardisoma* at normal environmental temperatures indicate that filling of the heart with venous blood *via* the cardiac ostia must be a relatively rapid process, since the length of diastole (and thus the length of the time available for cardiac filling) will be correspondingly brief.

These experiments present the first measurements of haemolymph systolic pressures in a terrestrial decapod, and at 15–25 mmHg are comparable with systolic arterial pressures recorded for marine crabs (see Belman, 1976; McMahon & Wilkens, 1983). The relatively high diastolic intracardiac pressures in *Cardisoma*, usually several mmHg above ambient pressure (Fig. 6), indicate that post-branchial venous and pericardial pressures are similarly elevated above ambient. Simultaneous measurement of pericardial and intracardiac haemolymph pressures confirm this, and reveal that a gradient for haemolymph flow from the pericardium into the heart prevails for the entire diastolic period, or approximately half of the cardiac cycle. Since heart rates are high and diastolic periods consequently short (see above), a sustained pericardium-to-heart pressure gradient probably adds significantly to the effectiveness of cardiac filling in *Cardisoma* and may contribute to the high cardiac outputs calculated for this genus (C.M. Wood, R.G. Boutilier & D.J. Randall, unpublished data).

Pressure events in the pericardial space and heart during the earliest phases of systole – i.e. the near simultaneous rise in both compartments followed by a fall in pressure on the venous side as systole continues – resemble central cardiovascular events during similar cardiac phases in the vertebrate circulation. The ostial valves may well be closed by brief retrograde haemolymph flow from the heart just as the atrio-ventricular valves are closed in the vertebrate heart. Moreover, the valves remain closed against moderately high pressures, since no intracardiac pressure event is transmitted back to the pericardial space during systole.

Finally, although terrestrial and aquatic brachyurans have fundamentally the same

cardiovascular and respiratory arrangement, the effects of gravity imposed on terrestrial forms may introduce circulatory complexities to tissue perfusion. For example, branchial resistances may be higher in terrestrial forms, where there is no buoying effect of water to prevent partial collapse of the gill filaments. The gills of terrestrial crabs are structurally modified to help prevent collapse in air (see von Raben, 1934; Gray, 1957; Diaz & Rodriguez, 1977) and the net circulatory effects of these modifications to branchial blood flow are currently unknown. Gravity acting on terrestrial crabs may also interfere with circulatory function by causing venous haemolymph to pool in tissue sinuses, analogous to that occurring in man during prolonged standing without movement. Additionally, the typical threat posture of *Cardisoma guanhumi*, involving elevation of the large, heavy chelae high over the carapace, may introduce several haemodynamic adjustments (e.g. increased venous return, increased arterial impedance) that would not occur in a crab making similar postural adjustments under water.

Ventilatory-circulatory interactions

Correlation of ventilatory and cardiovascular performance is a general feature of gas transport physiology in crustaceans (Taylor, 1982; McMahon & Wilkens, 1983), but the extent and constancy of interaction of these physiological processes in *Cardisoma guanhumi* is remarkable. The most striking correlation is between heart rate and direction of scaphognathite beating. Most crabs that were examined showed a consistent and marked bradycardia concomitant with the onset of reversed beating (Figs 6, 7, 8). A bradycardia during reversed beating has also been described for the marine crab *Cancer magister* in normoxic conditions (McDonald *et al.* 1977), though a tachycardia accompanies reversed beating stimulated by hypoxia in the shore crab *Carcinus maenas* (Taylor *et al.* 1973).

Measurements of intracardiac pressure in *Cardisoma guanhumi* revealed that scaphognathite reversal also caused transient increases in haemolymph pressure. Perturbations in heart rate and haemolymph pressure coincident with scaphognathite reversal could be accounted for by at least three mechanisms: (1) direct mechanical effects on the haemolymph spaces by the elevated epibranchial pressures generated during reversed beating; (2) reflex interactions involving circulatory baroreceptors; and/or (3) direct interactions between respiratory and cardiac elements of the central nervous system. Experiments in which the branchial pressure transients produced by reversed scaphognathite beating were experimentally reduced or eliminated (Figs 9, 10) strongly indicate that the elevated branchial pressure resulting from reversals is directly transmitted through the thin branchial vascular wall into the haemolymph spaces. This phenomenon has been considered, though not demonstrated, to be a factor in ventilatory-circulatory interactions in other crustaceans (Blatchford, 1971; Taylor, 1982; McMahon & Wilkens, 1983). The elevation of central haemolymph pressure by scaphognathite reversal appears to be a mechanical event.

Why then does a bradycardia occur during these transient changes in haemolymph pressure induced by scaphognathite reversal? Preliminary (unpublished) evidence suggests that there is a baroreceptor reflex in *Cardisoma guanhumi*. Given a constant peripheral resistance, a decline in cardiac output due to a decline in heart rate — reflexly mediated or otherwise — might minimize any factors tending to increase

haemolymph pressure. Regulation of blood pressure in *Cardisoma guanhumi* may be vital in maintaining cardiac output, since a small pressure perturbation represents a proportionately much larger pressure adjustment in an animal with a comparatively low mean blood pressure.

Heart rate adjustments at the same time as scaphognathite reversal may also reflect some direct interaction of central neural elements controlling ventilation and circulation (Wilkens, Wilkens & McMahon, 1974; Taylor *et al.* 1973; Young, 1978; Young & Coyer, 1979; Pasztor & Bush, 1983*a,b*; Bush & Pasztor, 1983). Transient bradycardia associated with scaphognathite reversal persisted in some (but not all) crabs in the present experiments when the branchial chambers were opened to ambient pressure, eliminating all transient changes in haemolymph pressure (Figs 9,10). Thus, haemolymph pressure changes are not an absolute requisite for the bradycardia response. The time courses of the onset of reversals and bradycardia are also in support of some degree of central neural interaction of ventilatory and circulatory elements. Whereas changes in heart rate and haemolymph pressure were usually very closely linked in time, in a few crabs (dashed lines, Fig. 8), heart rate adjustments either began several seconds before reversed scaphognathite beating began, or persisted for several seconds after forward beating resumed. These atypical ventilatory-circulatory interactions nonetheless suggest that not all such phenomena are mediated by tightly linked 'cause-and-effect' events involving peripheral reflexes.

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