

Patterns of Heart and Scaphognathite Activity in the Crab *Cancer magister*

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ABSTRACT The respiratory system of the crab *Cancer magister* has been investigated with long-term measurements of the activity in the heart and scaphognathites of unrestrained animals settled on a natural, sandy substrate. Although crabs generally remained motionless in the experimental apparatus, except while in the dark, they initially exhibited a high degree of respiratory activity; the rates of forward pumping by the scaphognathites exceeded 90/minute, reversal incidence was less than five reversals/10 minute and heart rate was constant. Subsequently both the heart rate and the forward pumping rates of the scaphognathites declined, incidence of reversals increased and spontaneous pauses by the heart and scaphognathites began to occur. Eventually one scaphognathite ceased pumping for prolonged periods. Possible roles for reversals, pauses and unilateral pumping are discussed.

The literature on the heart and scaphognathite activities of decapod crustaceans includes descriptions of the effects of a wide variety of stimuli (tactile, chemical, thermal, hypoxic) on the rates of beating of these structures (e.g., Larimer and Tindel, '66; Uglow, '73; McMahon and Wilkens, '75). There is less information available on their natural patterns of activity; however recent studies (see DISCUSSION for references) have suggested that in the resting animal wide fluctuations in heart and scaphognathite rates may occur in addition to periods when activity may cease entirely in either one or both scaphognathites and in the heart.

In the present study the natural variability in the activity of the respiratory system of the subtidal brachyuran decapod *Cancer magister* has been investigated by long-term monitoring of unrestrained specimens settled on a natural substrate. Measurements were made by means of chronically implanted catheters (hydrostatic pressure recording) and electrodes (heart movement recording). The aim of these investigations was to construct a detailed analysis of heart and scaphognathite activity changes with time in otherwise undisturbed animals. This work provides a background for a subsequent investigation of the range of ventilatory flow and oxygen consumption in this species (McDonald, Wood and McMahon, in preparation).

MATERIALS AND METHODS

Experimental animals

Crabs used in this study were either supplied by the Vancouver Public Aquarium, collected in the waters off San Juan Island in Puget Sound, Washington or obtained from Whitney-Fidalgo Sea Foods, Inc. in Anacortes, Washington. The experiments were carried out in the marine aquarium facility at the University of Calgary and at Friday Harbor Laboratories, University of Washington. In both locations the crabs were held in large aquaria filled to a depth of 8 cm or more with fine sand and supplied with well aerated sea water at a temperature of 7-9°C. With the exception of one crab (No. 11) held for two days, the animals were held from one week to three months prior to examination and were given chopped fish twice a week. For the most part, the crabs were on an artificial 12-hour day/night cycle while in the holding facilities. They fed regularly and, in several cases, molted successfully. Only animals in intermolt stage C₄ were used for experimentation. Following experimentation recording leads and cannulae were removed and the crabs were returned to the holding facilities. These animals resumed feeding and remained in healthy condition for several months. Twelve

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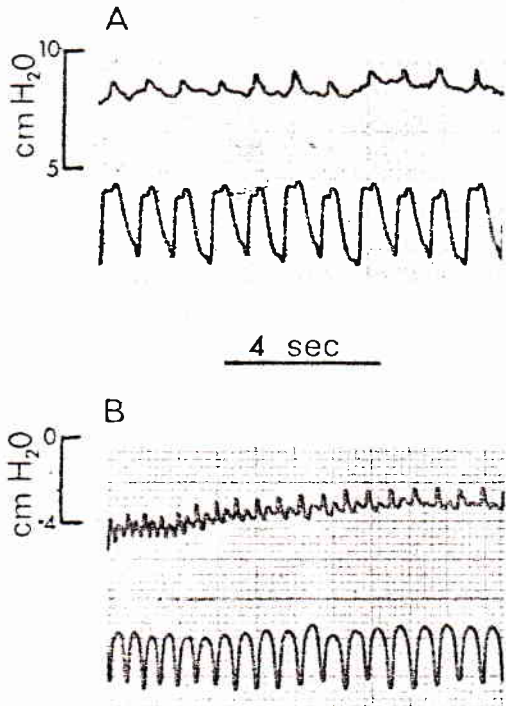


Fig. 1A Simultaneous recordings of pericardial blood pressure (top trace) and heart impedance fluctuations (bottom trace).

B Simultaneous recordings of branchial hydrostatic pressure (top trace) and scaphognathite impedance fluctuations (bottom trace).

crabs (5 females, 7 males), ranging in weight from 261 to 815 grams, were used in this study.

Recording of heart and scaphognathite (SG) activity

Heart activity was recorded by means of an impedance conversion technique. This technique has been used extensively for recording both heart and scaphognathite activity in crustaceans (see Ansell, '73, for references). Two fine wires were implanted on either side of the heart and held in place with dental dam glued to the carapace with cyanoacrylate glue. The wires were connected to an impedance converter (Biocom, Inc.) which generates a low intensity alternating current field across the implanted electrodes. Tissue movement within the field causes changes in impedance between the electrodes which are detected and transformed to a voltage output. The correspondence between the heart impedance signal and heart movement was con-

firmed with simultaneous recordings of impedance changes and blood pressure fluctuations caused by heart contraction (fig. 1A). Blood pressure in the pericardial space was monitored with a pressure transducer (Hewlett-Packard 267 BC) using a technique similar to Blatchford ('71).

Fluctuations in hydrostatic pressure in the branchial cavities caused by movement of the scaphognathites were monitored by a technique similar to that of Wilkens and McMahon ('72). Water-filled polyethylene cannulae (PE 160) connected to pressure transducers (Hewlett-Packard, 267-BC) were

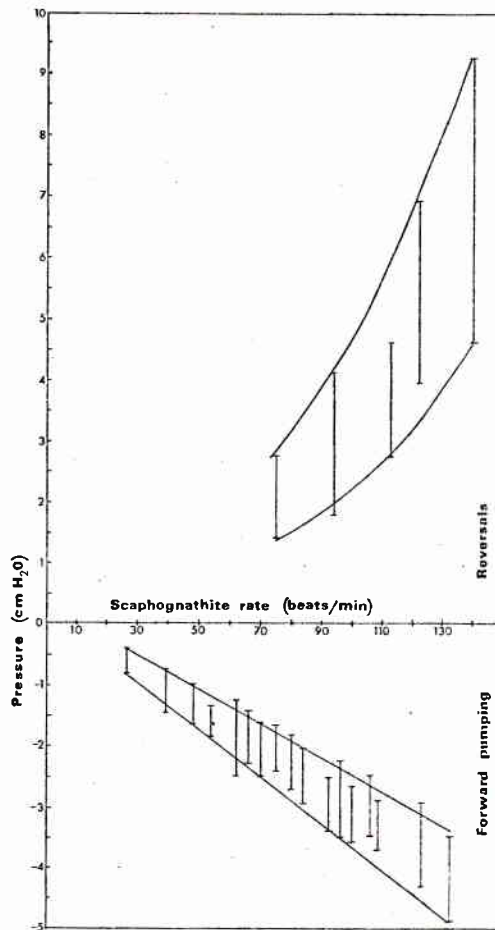


Fig. 2 Relationship between levels of hydrostatic pressure generated in the branchial cavity and the frequency of scaphognathite beating. The length of the vertical band represents the amplitude of the branchial pressure waveform. Each amplitude and rate was determined over a 30-second scaphognathite pumping period. Solid curves were fitted by inspection.

tightly fitted into both epibranchial cavities through holes drilled in the posterior margin of the carapace overlying gills 7 and 8. The observed pressure fluctuations, indicated both frequency and mode (forward or reverse) of scaphognathite (SG) beating. In three experiments, SG frequency was also monitored directly using the impedance conversion technique. Two fine wires were implanted on either side of the exhalant channels where the SG's are located and sealed in place with dental dam and cyanoacrylate glue. This method of measurement gave a clearer record of SG rate and confirmed the correlation between the branchial pressure waveform and the movement of the SG (fig. 1B) but did not indicate the mode of beating. The crabs were restrained and in air during implantation of cannulae and electrodes.

Prior to experimental recording the crabs were placed in a 100-liter aquarium filled to a depth of 8 cm or more with fine sand and supplied with well aerated sea water at the holding temperature. The sides of the aquarium were covered with opaque material to minimize visual disturbance to the animal. Recording leads and cannulae were of sufficient length to allow the crab freedom of movement within the aquarium. Output of the impedance converters and pressure transducers were displayed, after suitable amplification, on a Gilson rectilinear trace oscillograph. Recordings of heart and SG activity were made for a minimum of seven hours on each crab and for 3 of the 12 crabs examined were continued for several hours into scotophase of the 12-hour day/night cycle. For another three crabs, observations of heart and SG activity while on a sandy substrate were extended to include observations under similar conditions but with the sand removed.

Analysis of data

The total recording time for each animal was divided into 10-minute blocks starting immediately following burrowing which occurred shortly after the crabs were returned to the water (RESULTS). Within each block, five, approximately equidistant, 30-second intervals were chosen. For each interval the beat frequency of the heart and both scaphognathites was determined. All rates reported are a mean of these five measurements (\pm one standard deviation). Reversal incidence is expressed as the number of reversals occurring in ten minutes.

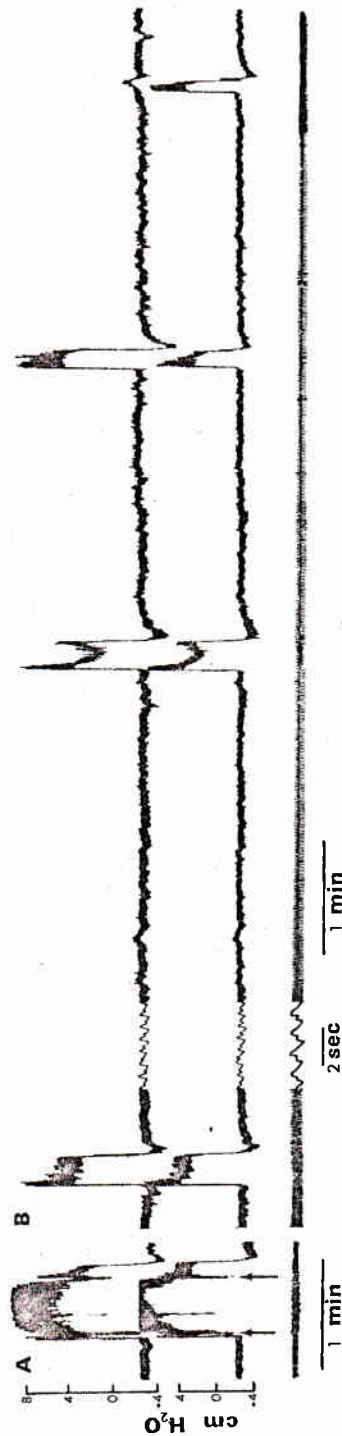


Fig. 3 Initial activities of heart and scaphognathites (crab 8). Top: right branchial pressure; middle: left branchial pressure; bottom: heart activity. Panel A: "burrowing reversal" occurring five minutes after crab returned to water; arrows indicate period over which animal burrowed. Note that pressures generated by left SG exceeded the channel width of the chart recorder. Panel B: 10-minute record of heart and SG activity (starting at +20 minutes following burrowing). The period of faster chart speed illustrates the biphasic nature of the SG pressure waveform. Note the unilateral reversal by the left SG.

TABLE 1

Activities of heart and scaphognathites over the first ten minutes following burrowing

Crab	Wt (gm)	Sex	Scaphognathite forward pumping rate [means (SD), n=5]		Reversal incidence		Heart rate [mean (SD) n=5]
			Left	Right	Left	Right	
1	261	F	106(28)	118(26)	4	4	67(0)
2	324	M	118(5)	105(3)	1	1	60(0)
3	339	F	115(3)	112(9)	2	2	58(1)
4	350	F	101(7)	88(6)	0	0	70(0)
5	367	F	90(7)	84(8)	3	4	65(1)
6	337	F	107(10)	105(17)	3	4	62(0)
7	386	M	83(12)	94(8)	0	0	65(0)
8	415	M	104(4)	104(4)	2	2	55(1)
9	417	M	87(3)	130(7)	0	0	78(1)
10	624	M	72(5)	75(7)	2	2	58(0)
11	650	M	131(11)	120(5)	3	3	78(0)
12	815	M	117(5)	133(6)	2	2	62(1)
Overall mean			103(16)	106(18)	2(1)	2(2)	65(7)

RESULTS

Behaviour

All crabs in this study were air exposed for 20 to 30 minutes while recording leads and cannulae were installed. When returned to the water, the majority of those crabs on a sandy substrate soon began to burrow into the sand in a manner similar to that described for the portunid crab *Ovalipes gadulpenis* (Caine, '74). The crabs loosened and removed sand from beneath themselves by outward extension movements of their chelipeds and walking legs. The movement of the chelipeds also served to propel the crab beneath the surface of the sand in a posterior direction. Burrowing activity could continue until only a small portion of the carapace in the region of the eyes and mouth parts was visible. This extent of burrowing was more common in the smaller crabs (200-400 grams). The larger crabs (400-900 grams) usually only burrowed until the postero-dorsal margin of the carapace was level with the surface of the sand. In the light, the crabs which had settled in the sand usually remained motionless if not unduly disturbed hence most recordings of heart and scaphognathite activity were made in the light. In the dark, crabs left the sand and became active.

Ventilatory mechanism

The action of the scaphognathites in generating ventilatory flow through the branchial cavities has been described for the crab, *Carcinus maenas* (Hughes et al., '69; Young, '75). The conclusions of these studies appear to be generally applicable to *Cancer magister*.

During forward pumping the scaphognathite (SG) produces a maintained biphasic negative pressure (e.g., fig. 3B) in the branchial cavities relative to that outside of the animal. Water is drawn into the hypobranchial cavity through openings at the base of the chelipeds and walking legs, passes through the gill sieve into the epibranchial cavity and is expelled through exhalent openings located adjacent to the mouth parts (Hughes et al., '69; Johansen et al., '70). During reversed pumping the SG produces a rhythmic maintained positive pressure and ventilatory flow occurs in the opposite direction. Both the amplitude of the pressure waveform and the pressures developed within the branchial cavity are directly related to the frequency of SG beating. This relationship is summarized for both forward and reverse SG beating in figure 2. Note that SG frequency during reverse pumping varied within smaller limits than during forward pumping. The data for this figure are derived from one crab, but are generally representative of all crabs studied. Some variability from animal to animal in branchial pressure was noted; for example at a forward SG rate of 90/minute, mean negative branchial pressures ranged from 1.5-3.5 cm H₂O. This variability was not correlated with body weight but may have been due to differences in positions of cannulae within the epibranchial cavity.

Temporal changes in scaphognathite and heart activity during bilateral pumping

Crabs burrowed for 30 to 60 seconds following their return to water and reversed pump-

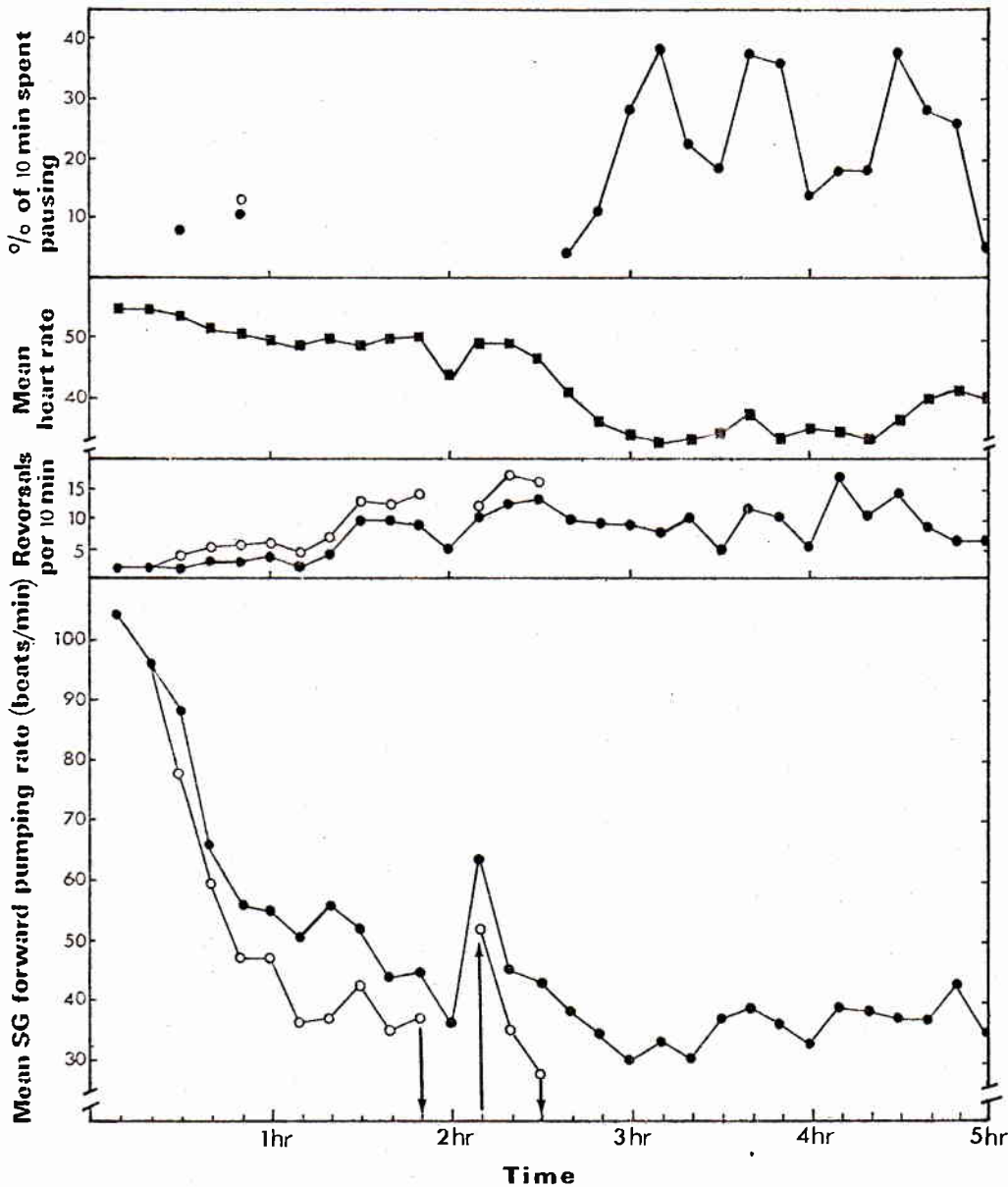


Fig. 4 Summary of heart and SG activity for crab 8 over a 5-hour period. Each rate datum is a mean of five measurements over a 10-minute period (the first datum is for the period 0 to +10 minutes, the second for +10 to +20 minutes etc.). *Open circles*: left SG; *closed circles*: right SG. The left SG ceased pumping at 1 hour 50 minutes, resumed pumping at 2 hours and ceased again at 2 hours 30 minutes (indicated by arrows). In the top panel the absence of data points for some of the 10-minute periods indicates that no pauses occurred in either the left or right SG. Once the left SG had ceased pumping, its percent time spent paused would be 100%.

ing was often initiated before and persisted after the duration of this activity (e.g., fig. 3A). The maximum positive branchial pressures exhibited during these "burrowing reversals" often exceeded 8 cm H₂O and the SG rate was as high as 150/minute. These high

pressures likely prevent sand from entering the branchial cavities.

The heart and scaphognathite activity through the first ten minutes after the crabs had settled into the sand is summarized in table 1. Initial SG mean forward pumping

rates ranged from 72 to 133 beats/minute with an overall mean of 104 beats/minute. Reversal incidence varied from 0 to 4 per ten minutes. The duration of each reversal was less than the initial "burrowing" reversal, rarely exceeding 20 seconds (e.g., fig. 3B). Heart rate ranged from 55 to 78 beats/minute but in individual crabs varied less than 2 beats/minute. No correlation was evident between body weight and either heart rate or scaphognathite rate for the animals in this study.

Over the subsequent 7 to 20 hours of recording considerable variation was observed between animals but a number of common elements were routinely observed. These elements in approximate temporal sequence were:

1. Slowing of the forward pumping frequency of both SG's accompanied by increasing incidence of periods of reversed pumping.
2. "Pausing" behavior: abrupt bilateral cessation of SG beating and a pronounced slowing of heart beating: duration variable but usually less than 30 seconds.
3. Cessation of active pumping by one SG for periods of several minutes up to several hours. Crabs occasionally returned to bilateral pumping for brief periods but once initiated unilateral pumping predominated.

The time before the onset of unilateral pumping was variable. In eight crabs unilateral pumping was observed within two hours and in three others within nine hours. However, one crab (No. 11) exhibited over 32 hours of bilateral pumping before unilateral pumping occurred. This animal was set up for recording two days after its capture in the wild. A number of factors could contribute to this variability, but the extent of prior acclimation to the holding facilities may play an important role. Animals that had been held a month or more in the holding facilities commonly exhibited unilateral pumping within two hours of being set up.

The results from one crab (crab 8: fig. 4) have been selected for detailed presentation as this animal exhibited features that were common to most of the animals in this study. Both left and right SG forward pumping rates decreased continuously over the first hour and at one hour 50 minutes the left SG ceased beating. For the first 20 minutes the rates of the two SG's were closely coupled in a manner similar to that described for the lobster *Homarus americanus* (Wilkins and Young, '75). However from 20 minutes onward the right SG consistently maintained a higher

pumping rate than the left. Such maintained differences between SG rates were observed in 9 of the 12 animals. In the remainder some degree of coupling was apparent throughout the period of bilateral pumping. Wilkins and Young ('75) described two types of relationships in bilateral coordination of SG rhythms: phase coupling or phase drifting with a tendency to couple. When coupling occurred in *Cancer magister* it more commonly took the latter form.

The progressive decrease in forward pumping rate that was observed in all animals was accompanied by an increase in the incidence of reversals. The extent of the increase was, however, variable ranging from 3 to 4/10 minute in crab 11 to 4 to 19/10 minute in crab 6 (tables 1 and 2). In general reversals occurred about equally in both SG's throughout the period prior to the onset of unilateral pumping. However, over the 10 to 20 minutes preceding unilateral pumping the reversal incidence in the SG that eventually ceased pumping often, though not always, rose above the other (table 2). Crab 8 (fig. 4) was unusual in this respect in that the reversal incidence in the SG that ceased pumping was higher throughout.

About 10 to 20 minutes after returning the crab to the water pauses of up to 1-minute duration could be induced by mechanical disturbances such as tapping the carapace. Crabs rapidly become refractory to such disturbance. The beginning of pausing was marked by the abrupt and simultaneous cessation of pumping by both SG's and by the heart. Within 10 to 20 seconds of the beginning of a pause the heart may resume pumping at a slow and erratic rate. Pausing of apparently spontaneous origin was initially uncommon; crab 8 (fig. 4) for example, exhibited only two pauses over the period prior to the first onset of unilateral SG pumping. Spontaneous pauses were usually short, rarely exceeding 30 seconds duration.

The minute to minute variation in heart rate during forward bilateral SG pumping was very small and rarely exceeded 1 to 2 beats/minute. However, over the period from the return to the water to the onset of unilateral pumping, the heart rate decreased slightly (mean = 10%, tables 1, 2) in a majority of animals. Initially reversals had little or no effect on heart rate (e.g., fig. 3B) but after 20 to 30 minutes a slowing of heart rate concomitant with reversals was observed in some ani-

TABLE 2

Activities of heart and scaphognathites over ten minutes prior to the initial onset of unilateral pumping. SG that ceases pumping is underlined

Crab	Scaphognathite forward pumping rate (mean (SD), n=5)		Reversal incidence		Heart rate (mean (SD), n=5)
	Left	Right	Left	Right	
1	<u>60(6)</u>	67(10)	<u>9</u>	7	70(0)
2	72(5)	<u>56(8)</u>	4	<u>4</u>	46(5)
3	<u>39(12)</u>	46(13)	<u>10</u>	11	49(1)
4	40(6)	<u>50(4)</u>	8	<u>9</u>	59(4)
5	84(9)	<u>80(7)</u>	9	<u>13</u>	64(1)
6	76(7)	<u>1</u>	5	<u>19</u>	55(1)
7	<u>46(11)</u>	44(7)	<u>2</u>	5	58(1)
8	<u>37(2)</u>	45(4)	<u>14</u>	8	50(0)
9	43(10)	<u>43(5)</u>	7	<u>8</u>	78(1)
10	<u>27(3)</u>	34(3)	<u>8</u>	8	53(1)
11	<u>47(9)</u>	38(10)	<u>4</u>	4	70(1)
12	41(7)	<u>39(9)</u>	3	<u>3</u>	53(2)
Overall mean	51(18)	49(14)	7(3)	8(4)	59(10)

¹ Reversal incidence too high to allow measurement of forward pumping rate.

mals (not illustrated). The extent of this slowing ranged from a lengthening of the inter-beat interval for one to three heart beats at the beginning of a reversal (6 animals) to complete cessation of heart beating for almost the duration of the reversal period (3 animals). Changes in heart rate were more common when reversals occurred simultaneously on both sides. In three of the six animals that exhibited only slight changes in heart rate, these changes were commonly associated with a short pause immediately preceding the reversal.

Activities of scaphognathites and heart during unilateral pumping

At the onset of unilateral pumping there was no change in the rate of the SG that continued pumping (e.g. figs. 4, 5A). Although the pumping rate of the active SG subsequently varied about this initial level, rates of less than 30/minute were rarely observed. Brief periods (10-20 minutes) of bilateral pumping occasionally reoccurred in the apparent absence of any disturbance (fig. 4). Strong stimuli such as lifting the crab out of the sand, were required to induce a prolonged return to bilateral pumping; smaller disturbances such as tapping the carapace usually produced pausing behaviors.

A feature of unilateral pumping was the appearance in most crabs of slow erratic fluctuations in pressure within the branchial cavity of the non-beating SG (figs. 5A,B). These slow pressure fluctuations usually varied about the zero reference pressure. In a few cases pressure fluctuations on the paused side obviously reflected pressure changes on the actively ventilated side particularly during reversed pumping (e.g., fig. 5A). However in the majority of cases, these anomalous fluctuations could not be correlated with events on the active side. Impedance records showed that no SG movements were occurring during this time. Measurements of branchial oxygen tension (samples with drawn via the pressure cannulae) revealed very low pO_2 's (10-20 mm Hg), suggesting that no active ventilation results from these pressure fluctuations. Indeed, standing negative or positive pressures sometimes developed in the non-ventilated side suggesting that the cavity may be actively sealed off from the external environment. It is possible that movements of the epidermal retractor muscles (which insert on the roof of the branchial membrane; Pearson, '08) and/or the flabellae (gill cleaning appendages) are involved in these phenomena.

Periods of unilateral pumping were not usually equally distributed between the two

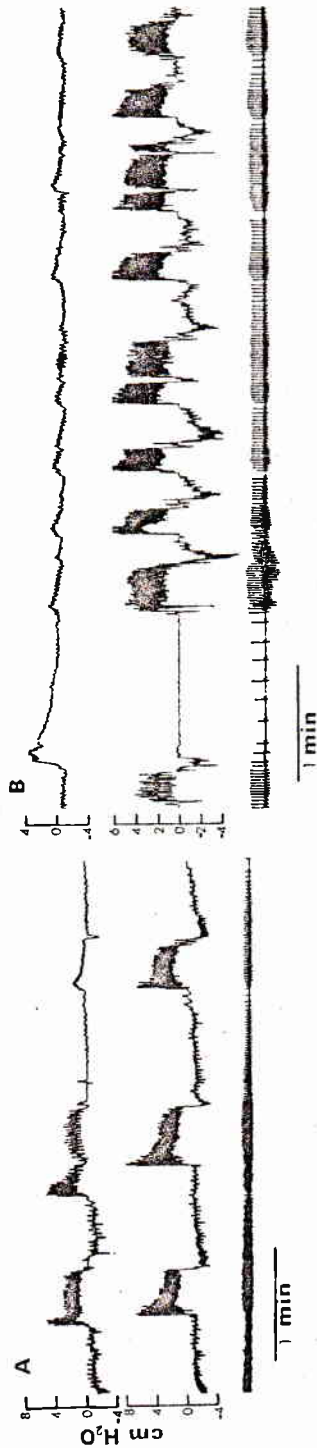


Fig. 5 Activities of heart and SG during unilateral pumping. *Panel A* Record showing onset of unilateral pumping in crab 10 at + 65 minutes. *Panel B* Typical record of unilateral pumping showing high reversal incidence, from crab 4 at + 9 hours. In both A and B; *top trace*: right branchial pressure; *middle*: left branchial pressure; *bottom*: heart.

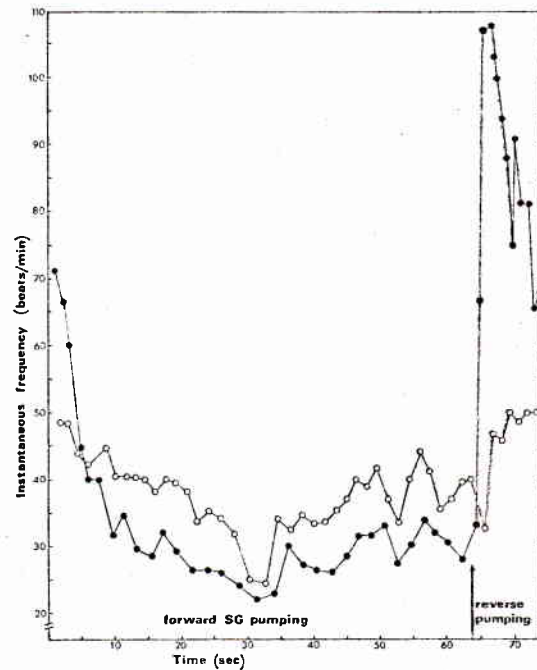


Fig. 6 Beat to beat analysis of heart and SG activity during unilateral pumping (crab 10). Instantaneous frequency (1/interbeat interval) is plotted against accumulated period length. Open circles: heart rate; closed circles: SG rate. Time 0: forward pumping immediately following a reversal.

SG's. As mentioned above, maintained differences in SG rate during bilateral pumping were observed in nine crabs. For seven of these crabs the lower rate SG ceased pumping initially and the major portion of unilateral pumping (94-100%) was performed by the faster SG. For the other two crabs the situation was reversed. In the remaining three crabs where the SG rates tended to couple, the subsequent incidence of unilateral pumping was approximately equal between both sides.

During unilateral pumping, the reversal incidence was more variable than during bilateral pumping partly due to the rise in the incidence of pausing as discussed below. In general, however, reversal incidence dropped initially at the onset of unilateral pumping (e.g., fig. 4 at 2 hours) and then subsequently rose to at least the maximum levels observed during bilateral pumping. The duration of reversal pumping periods also tended to increase during unilateral pumping. For example in crab 8 the reversal duration during bilateral pumping ranged from 4 to 16 seconds, mean 10 seconds; during unilateral

pumping the duration of reversals ranged from 4 to 48 seconds, mean 16 seconds. In some animals continuous reversal periods of up to five minutes in length were occasionally observed. In consequence reversed pumping tended to become the predominant mode of SG pumping in the latter portions of extended unilateral pumping periods (e.g., fig. 5B).

Spontaneous pauses became more common during unilateral pumping. Pauses varied considerably but rarely exceeded three minutes duration. The mean duration varied from 10 seconds (range 4-17, crab 5) to 84 seconds (range 24-295, crab 3). Crab 7 exhibited a marked departure from the norm; pauses exceeding 19 minutes were routinely observed in this animal. The incidence of spontaneous pauses also showed considerable variability ranging from three 10 to 20-second pauses over a 4-hour period (crab 10) to 110 pauses of 4 to 120-second duration over a 3.5-hour period (crab 8).

At the onset of unilateral pumping the heart rate in a majority of animals began to vary in concert with the SG rate. A typical example of this coordination of heart and SG rhythms is illustrated in figure 6. In general, increases in SG rate either during forward or reverse pumping led to increases in heart rate but only to the maximum levels that occurred during bilateral pumping. As in bilateral pumping, the transition from forward to reverse beating was usually marked by a brief slowing of the heart rate. Eight of the 12 crabs examined exhibited a coupled heart rate, in the remainder there was no appreciable change in the heart rate with the onset of unilateral pumping.

Respiratory behavior during spontaneous activity

Spontaneous locomotor activity was observed in three crabs (1, 2 and 8) for which recording periods were extended into the dark. The patterns of respiratory behavior during spontaneous activity were very different from the "active" patterns observed when the animals were initially returned to the water after air exposure. Reversal incidence was usually much higher and spontaneous pauses were common. A typical example of activity is illustrated in figure 7 (crab 1). This animal became active at A and was almost continuously active until C. Normally a return to bilateral pumping followed soon after the onset of locomotor activity (B: fig. 7) and

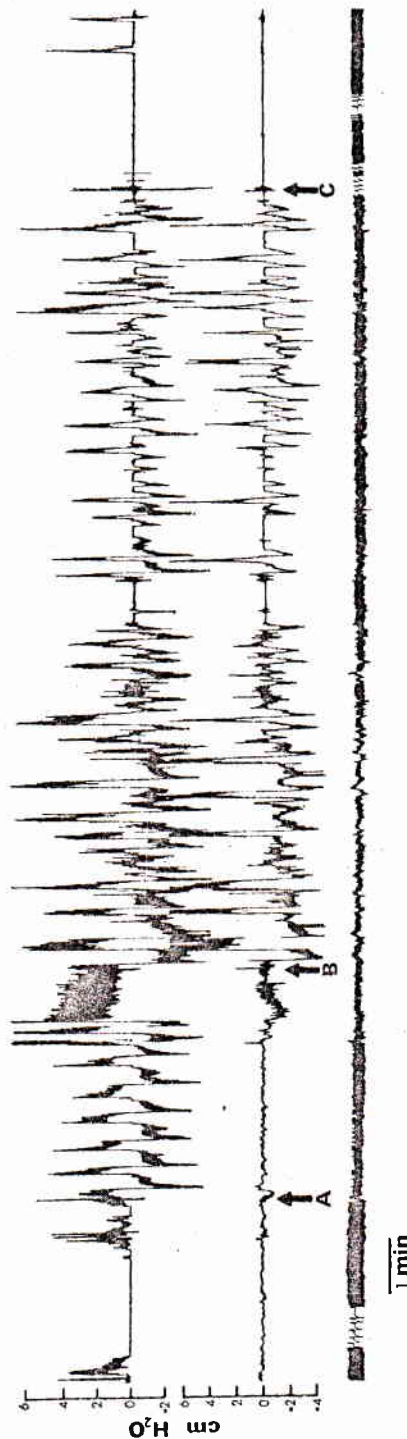


Fig. 7 Activities of heart and SG during locomotor activity (crab 1). 25-minute record, six hours after animal returned to water, 40 minutes after overhead lights turned out leaving animal in dim light. Animal almost continually active between A and C. At B bilateral pumping resumes. The large pressure fluctuations at A and C were caused by movement of the pressure cannulae by the animal. Note that movements can occur during pauses.

was the predominant respiratory pattern while the animal was active.

Comparisons between crabs on hard and sandy substrates

The overall patterns of heart and SG activity from three crabs (1, 5 and 10) recorded while the animals were on a hard, smooth substrate were compared to records obtained for the same animals on a sandy substrate. There were no obvious or consistent differences in respiratory behaviors on the two substrates. These observations tend to rule out the possibility that exposure to a natural sandy environment *per se* plays an important role in determining heart and SG activity.

DISCUSSION

The respiratory behavior of *Cancer magister* is complex and highly variable. Although there have been few long-term studies on unrestrained animals there is a growing body of evidence that suggests the respiratory patterns of other decapod species might be similarly complex. Pausing behavior now appears to be a common phenomenon at least among decapod crustaceans and has been described for the macrurans *Homarus americanus* (McMahon and Wilkens, '72), *H. gammarus* (McMahon, unpublished) and *Nephrops norvegicus* (Ansell, '73), for the branchyurans *Cancer pagurus*, *Macropipus puber* (Ansell, '73) and *Carcinus maenas* (Hughes et al., '69; Taylor et al., '73), for the terrestrial brachyurans *Gecarcinus lateralis* and *Cardisoma guanhumi* (Cameron, '75) and for the terrestrial anomuran *Birgus latro* (Cameron and Mecklenberg, '73). Unilateral pumping has also been observed in these terrestrial species (Cameron, '75), in *Carcinus maenas* (Taylor et al., '73) and in the lobster *Homarus gammarus* (McMahon, unpublished). The present study is the first demonstration of the predominance of this behavior in the resting crab.

The frequent occurrence of pauses during unilateral pumping suggests, at least in *C. magister*, that resting oxygen demands can be more than adequately met by low level ventilation of a single branchial cavity. Unilateral ventilation is apparently preferred over a system whereby the same total flow would be generated by both SG's pumping at an even lower rate. The reasons for this are unclear but there may be a minimum rate below which the scaphognathite can no longer effectively pump water. SG rates below 30/

minute were rarely observed in the present study; similar findings have been reported for the lobster *Homarus americanus* (McMahon and Wilkens, '75). Also unilateral pumping may be a mechanism to reduce the metabolic cost of ventilation. No information on the cost of ventilation has been published for any crustacean species, but estimates on the rainbow trout *Salmo gairdneri* (Jones and Schwarzfeld, '74) indicate that at a ventilatory flow of 250 ml/kg/min and an oxygen consumption of 0.8 ml/kg/min approximately 10% of the oxygen uptake is used to power the breathing muscles. The data of Johansen et al. ('70) on *C. magister* indicate that for a somewhat lower oxygen consumption (0.5 ml/kg/min) a bilateral ventilatory flow of 650 mls/kg/min is required and thus the metabolic cost of ventilation could be substantially higher. A transition to unilateral pumping accompanied by a decreased ventilatory flow and increased oxygen extraction from the water (McDonald, Wood and McMahon, in preparation) would clearly reduce this cost.

In the present study, ventilation levels similar to those reported by Johansen et al. ('70) were seen only after air exposure or other disturbance. Under these circumstances increased oxygen demand is met by increased SG frequency and correspondingly increased ventilatory flow. Pausing is initially absent and the incidence of reversed pumping is low. Reversals may lower the effectiveness of gas exchange by disrupting counter current water flow across the gills (Hughes et al., '69; Johansen et al., '70). As the animal acclimates, oxygen demand falls and patterns of heart and scaphognathite activity which may have little or no respiratory function begin to appear.

Non-respiratory roles have been proposed for both reversed pumping and pausing behavior. Addition of charcoal particles to the ambient water increased the incidence of reversals in *Carcinus maenas* (Berlind, '76) and the present study suggests that reversals serve to prevent sand from entering the branchial cavities during burrowing. Pausing may play a defensive role (McMahon and Wilkens, '72) by suppressing electrical or hydrodynamic activity that might alert a predator. It is evident however, that much of the reversal and pausing behaviors observed may be occurring in the apparent absence of extrinsic stimuli. It is thus possible that both pauses and reversals occur intrinsically as a

result of pre-programmed motor output from the CNS (as suggested by McMahon and Wilkens, '77). The actual incidence of reversed pumping and pausing at any one moment may then be the result of modulation of this program by oxygen demand, circulating hormonal levels and/or external stimulation.

The nervous control of respiratory activity in decapod crustaceans (reviewed by Wilkens, '76) includes elements which modulate heart rate in association with changes in the scaphognathite rate. The present study provides further evidence for this coordination of heart and scaphognathite activity in that a close coupling of their frequencies is often apparent during unilateral pumping (fig. 6).

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LITERATURE CITED

- Ansell, A. D. 1973 Changes in oxygen consumption, heart rate and ventilation accompanying starvation in the decapod crustacean *Cancer pagurus*. *Neth. Jour. Sea. Res.*, 7: 455-475.
- Berlind, A. 1976 Neurohumoral and reflex control of scaphognathite beating in the crab *Carcinus maenas*. In press.
- Blatchford, J. G. 1971 Haemodynamics of *Carcinus maenas*. *Comp. Biochem. Physiol.*, 39A: 193-202.
- Caine, E. A. 1974 Feeding of *Ovalipes gadulpensis* (Saussure) (Decapoda Brachyura; Portunidae) and morphological adaptations to a burrowing existence. *Biol. Bull.*, 147: 550-559.
- Cameron, J. N. 1975 Aerial gas exchange in the terrestrial brachyura *Gecarcinus lateralis* and *Cardisoma guanhumi*. *Comp. Biochem. Physiol.*, 52A: 129-134.
- Cameron, J. N., and T. A. Mecklenberg 1973 Aerial gas exchange in the coconut crab *Birgus latro* with some notes on *Gecarcoidea lalandii*. *Resp. Physiol.*, 19: 245-261.
- Hughes, G. M., B. Knights and C. A. Scammel 1969 The distribution of pO₂ and hydrostatic pressure changes within the branchial chambers in relation to gill ventilation of the shore crab *Carcinus maenas* L. *J. exp. Biol.*, 51: 203-220.
- Johansen, K., C. Lenfant and T. A. Mecklenberg 1970 Respiration in the crab *Cancer magister*. *Z. vergl. Physiol.*, 70: 1-19.
- Jones, D. R., and T. Schwarzfeld 1974 The oxygen cost to the metabolism and efficiency of breathing in trout *Salmo gairdneri*. *Resp. Physiol.*, 21: 241-254.
- Larimer, J. L., and J. R. Tindel 1966 Sensory modifications of heart rate in crayfish. *Anim. Behav.*, 14: 239-245.
- McMahon, B. R., and J. L. Wilkens 1972 Simultaneous apnoea and bradycardia in the lobster *Homarus americanus*. *Can. J. Zool.*, 50: 165-170.
- 1975 Respiratory and circulatory responses to hypoxia in the lobster *Homarus americanus*. *J. exp. Biol.*, 62: 637-655.
- 1977 Integrates respiratory and circulatory responses in the red rock crab *Cancer productus*. *J. Exp. Zool.*
- Pearson, J. 1908 *Cancer*. L.M.B.C. Mem. typ. Br. mar. Pl. Anim. XVI.
- Taylor, E. W., P. J. Butler and P. J. Sherlock 1973 The respiratory and cardiovascular changes associated with the emersion response of *Carcinus maenas* (L.) during environmental hypoxia at three different temperatures. *J. comp. Physiol.*, 86: 95-115.
- Uglow, R. F. 1973 Some effects of acute oxygen changes on heart and scaphognathite activity in some portunid crabs. *Neth. Jour. Sea. Res.*, 7: 447-454.
- Wilkens, J. L. 1976 Neuronal control of respiration in decapod crustacea. *Fed. Proc.*, 35(9): 2000-2006.
- Wilkens, J. L., and B. R. McMahon 1972 Aspects of branchial irrigation in the lobster *Homarus americanus* I. Functional analysis of scaphognathite beat, water pressures and currents. *J. exp. Biol.*, 56: 469-479.
- Wilkens, J. L., and R. E. Young 1975 Patterns and bilateral coordination of scaphognathite rhythms in the lobster *Homarus americanus*. *J. exp. Biol.*, 63: 219-235.
- Young, R. E. 1975 Neuromuscular control of ventilation in the crab *Carcinus maenas*. *J. comp. Physiol.*, 101: 1-37.