ANALYSIS OF THE SCAPHOGNATHITE VENTILATORY PUMP IN THE SHORE CRAB *CARCINUS MAENAS*

II. PUMPING EFFICIENCY AND METABOLIC COST

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**SUMMARY**

The water pumping efficiency and the metabolic costs of the scaphognathites (SC), the gill ventilating water pumps, of shore crabs have been measured. The ratio of dynamic stroke volume to static pumping chamber volume, measured over the range of ventilation frequencies (fr) of 60–300 beats min$^{-1}$, shows the water pumping efficiency to be 85%. Despite this high efficiency, the pump appears to become leaky at low fr. Reflux of water back through the pumping chamber was demonstrated by artificially increasing the pressure gradient across the SC chamber at normal fr.

The oxygen requirements of actively beating SCs, the ventilatory fraction of total metabolism, was measured by comparing oxygen consumption (MO$_2$) before and after SC ablation. The cost of ventilation for resting crabs is 30% of total MO$_2$. The oxygen requirement for a single SC beat is 0.032 µmol O$_2$ kg$^{-1}$. The high ventilatory fraction of total MO$_2$ may be one factor contributing to the low metabolic scope of most crustaceans.

**INTRODUCTION**

In brachyuran and macruran crustaceans, the scaphognathites (SC), which are at the anterior limits of the branchial chambers, pump water in either a forward or backward direction over the gills. The pumping rates closely match the behavioural state of the animal; during vigorous activity or stressful situations the rates increase, but in quiescent animals the rates are reduced and there may be intermittent pauses where either one SC pumps at a time or the animal becomes bilaterally apnoeic. These ventilatory pauses may range in duration from a few seconds to 20 min (for reviews of the variety of ventilatory patterns see McMahon, 1981; Wilkens, 1981; Taylor, 1982; McMahon & Wilkens, 1983).

The occurrence of apnoea and unilateral SC pumping in settled animals has intrigued numerous investigators. It has been suggested that these animals may not need to ventilate continuously in order to meet metabolic oxygen demands. It has
been shown that under settled conditions bilateral ventilation provides sufficient oxygen to saturate the haemocyanin and to store an additional amount of oxygen in simple physical solution in the haemolymph (*Carcinus maenas*, Taylor, 1976; *Cancer productus*, McMahon & Wilkens, 1977; *Cancer magister*, McDonald, McMahon & Wood, 1979). During apnoea, tissue oxygen demands can be initially met by utilizing the dissolved oxygen fraction, and only when haemolymph oxygen content falls below the level at which haemocyanin is saturated is ventilation again resumed (McMahon & Wilkens, 1972, 1977; Burnett & Bridges, 1981). Following a pause the SCs beat at elevated rates for a short period to repay the oxygen debt accrued during the pause.

A relatively high metabolic cost for SC beating in settled animals has been suggested as another reason for apnoea and unilateral ventilation (McDonald *et al*. 1979; Burnett & Bridges, 1981). However, until now all estimates of the SC fraction of total metabolism have been indirectly derived and the values obtained vary widely (0.02% in *Callinectes sapidus*, Batterton & Cameron, 1978; 1% in *Orconectes virilis*, Burggren & McMahon, 1983; 17-76% in *Cancer pagurus*, Burnett & Bridges, 1981 and 64% in *Cancer magister*, McDonald, Wood & McMahon, 1980). On the basis of these studies, no clear consensus regarding ventilatory metabolic cost is possible.

The purpose of the present study was directly to measure the cost of scaphognathite powered ventilation in settled shore crabs, *Carcinus maenas* (L.), in terms of oxygen consumption. Such measurements can then be used to evaluate the validity of the assumption that long duration apnoea and/or unilateral ventilation is an energy conserving strategy for settled crabs. The water pumping efficiency of the SCs was also measured. These two measurements were then used to calculate the metabolic efficiency of the scaphognathites as ventilatory machines.

**METHODS**

*Carcinus maenas* (L.) (71—133 g) were obtained from commercial suppliers on the Atlantic coast of Canada. Animals were maintained in filtered, recirculated artificial sea water for up to several weeks before use. Animals were fed twice weekly before but not during experiments. All experiments were performed in the recirculating sea water system at 12—13 °C, $P_{O_2} = 128$—129 Torr, and salinity of 32.2.

During forward ventilation, water is drawn into the branchial chambers along their ventral margins and exits through anteriorly directed exhalant canals. The exhalant water was collected by covering the anterior carapace of a crab with the tight fitting neck half of a balloon (McMahon & Wilkens, 1977). The neck of the balloon was fastened to an electromagnetic flow probe (BLI 610) calibrated to read ventilation volume ($\dot{V}_w$) in units of ml min$^{-1}$. The flow probe was in turn connected to a tube which passed through the wall of the aquarium. The external end of this tube could be positioned to maintain a zero pressure head during spontaneous ventilation by controls, raised to increase the pressure gradient across the SC chamber in controls, and lowered to effect siphon ventilation in operated animals.

Heart and SC beating rates ($f_H$ and $f_R$, respectively) were measured by the impedance technique developed by Ansell (1973) and described in detail by McDonald *et al*. (1980). The change in impedance across the two electrodes caused by heart or SC activity was detected by Biocom 2991 impedance transducers.
Electromyograms (EMG) were taken from the first or second walking leg. Fine insulated copper wires (76 μm diameter) with bared tips were inserted into the depressor muscle of the coxa. The EMG signals were amplified (Grass P-15 amplifiers) and displayed along with the impedance signals on a four-channel oscillograph.

Oxygen tensions of inhalant and exhalant water and postbranchial haemolymph (P_{102}, P_{E02} and P_{ao2}, respectively) were measured with a Radiometer oxygen electrode thermostatted to the experimental temperature and displayed on a Radiometer Acid-Base Readout. From these measurements we calculated the rate of oxygen uptake (M_{o2}), the percentage oxygen extracted from the inhalant water (Ext_w), and the convection requirement for water (V_{w}/M_{o2}) using the standard equations from Dejours (1981).

Haemolymph samples used to determine postbranchial (arterial) oxygen tension (P_{ao2}) and lactate concentration were drawn from the pericardial sinus with a 1-0 ml glass syringe without disturbing the animal. Repeated sampling never removed more than 6% of the total haemolymph (haemolymph volume was taken to represent 30% of body weight, Gleeson & Zubkoff, 1977). Lactate concentrations were measured by enzymatic assay (Sigma Procedure Bulletin No. 836 UV).

After crabs had been fitted with masks and electrodes they were placed in the experimental chamber for a minimum of 16 h prior to data collection. After a number of initial measurements of M_{o2}, f_k, f_h, V_{w}, lactate and P_{ao2} had been obtained on control animals, the SCs were excised. To gain access to the SCs a piece of the branchiostegite covering each appendage was removed. Each SC was transected deeply at its base and the resulting hole was immediately stuffed with cotton to prevent blood loss. The cotton was fixed in place by a surface application of a drop of cyanoacrylate cement. The exhalant channels were not obstructed by the cotton. The previously removed branchiostegite pieces were cemented back into their original positions and the replacement of the balloon accurately restored the shape of the exhalant aperture. In addition, a small hole (approx. 5 mm^2) was made in the posterior portion of the branchiostegites in order to ensure correct irrigation flow patterns over the gills (see below). The entire procedure required less than 10 min. After surgery the crab was returned to the experimental chamber and artificially ventilated at 3–4 times the control value for V_{w} for 24 h to allow recovery. Subsequent measurements of M_{o2}, P_{ao2}, lactate and EMG recordings were made at ventilation volumes which were very similar to the control values for each individual animal. While the surgery is undoubtedly traumatic, the heart rate, EMG activity and haemolymph lactate and oxygen levels all indicate that the animals were in a stable condition.

An important requirement in evaluating oxygen consumption after SC ablation is to ascertain that siphon ventilation is an effective way to irrigate the gills. P_{ao2} and lactate levels were used as indices of haemolymph oxygenation and delivery, respectively. Preliminary studies demonstrated that operated animals often had low P_{ao2} and/or elevated lactate concentrations which could not be corrected by increasing the rate of artificial ventilation to between three and four times the control value of V_{w}. This implied that there might be differences in water flow patterns over the gills under the two conditions.

To observe branchial water flow, large portions of the branchiostegites which cover the gills were replaced with moulded celluloid windows (Hughes, Knights & Scammell,
Small streams of milk used as a dye were added by cannulae to inhalant water. The flow patterns for intact crabs agreed with those observed by Hughes et al. (1969). The largest portion of water entered through the Milne-Edwards openings above the chelae and this stream divided along the hypobranchial space to perfuse gills 1 to 8. Lesser amounts of water entered the much more restricted openings above the pereiopods to ventilate the posterior gills. In marked contrast, during siphon ventilation this water column did not become divided and virtually all water entering via the Milne-Edwards openings immediately went out of the exhalant openings. Consequently, only the podobranch gills 1 and 2, which arise from the epipodites of the 2nd and 3rd maxillipeds, were perfused. Complete branchial irrigation could be re-established by removing a 5 mm² piece of the ventral branchiostegite posterior to the hindmost gill located above the 3rd and 4th pereiopods. Dye streams indicated that approximately 50% of the ventilation water now entered from the rear and perfused the entire gill network, the remaining 50% still entered through the Milne-Edwards openings. This manipulation allowed sufficient irrigation of the gills to maintain arterial oxygen tensions and lactate concentrations at control levels at values of \( V_w \) equal to those generated by SC pumping. Data from an operated animal were only accepted if haemolymph \( P_{\text{O}_2} \) was >70 Torr and lactate concentrations were <1.19 mmol l⁻¹. Scaphognathite ablation was performed on nine crabs and five met the criteria for acceptance.

Autopsies performed at the termination of experiments showed that no more than 8–10% of the SC musculature remained after ablation. The proximal bits of muscles were severed from their insertions and it is unlikely that they received innervation since motor neurones invade these muscles in the mid-regions before branching (A. J. Mercier, unpublished observations).

Calculations of the water pumping efficiency (%) of the SCs were derived from the relationship:

\[
\text{Physical pump efficiency (\%)} = \frac{V_s}{V_{\text{static}}} \times 100, \tag{1}
\]

where \( V_s \) (ml kg⁻¹ beat⁻¹) is the dynamic stroke volume derived from the ratio \( \dot{V}_w/\dot{F}_R \) and normalized for animal weight. After the dynamic stroke volume had been measured, the pumping chamber with SC intact was filled with molten dental impression wax. The wax cast was dissected out and weighed. By dividing this weight by a density conversion factor for the wax and normalizing for animal weight the static volume \( V_{\text{static}} \) was obtained.

Statistical analyses were performed using the Student’s \( t \)-test for unpaired data. Statistical differences refer to the 0.05 level of significance or greater for a two-tailed test. All values are presented as the mean ± one standard error of the mean (\( X \pm 1 \text{ S.E.M.} \)).

RESULTS

The ventilatory costs to be measured are those resulting from SC muscular contractions; however, the common denominator in control and operated animals was ventilation volume rather than ventilation frequency. It is therefore necessary to relat
Cost of ventilation in a crab

Fig. 1. Ventilation volume ($\dot{V}_w$) as a function of total scaphognathite rate (right plus left). The SCs fail to generate a net flow at about 40 beats min$^{-1}$. This $f_R$ is also the lowest rate at which the SCs normally beat. Regression line: $y = 3.9x - 443, r = 0.79$.

$\dot{V}_w$ to $f_R$. Fig. 1 indicates that $\dot{V}_w$ varies linearly with $f_R$, even though the scatter of points shows that stroke volume is variable. It is noteworthy that control crabs never ventilated the gills at individual SC rates of less than 40 beats min$^{-1}$ and that $\dot{V}_w$ becomes zero at about this $f_R$.

The x-intercept of the frequency-flow relationship suggests that inherent leakiness of the physical SC pump may become significant at low pumping rates. Table 1 shows that the efficiency of the pump expressed as the ratio of the dynamic stroke volume ($V_d$) to the static chamber volume ($V_{static}$) is on average 85%, implying that the pump has a dead space or leakiness of up to 15%. This ratio holds over the range of $f_R$ of 40–300 beats min$^{-1}$ (the range at which $V_d$ remains fairly constant). Since C. maenas does not beat the SCs at individual rates of less than 40 beats min$^{-1}$, but rather alternates between apnoea and this low rate, it is not possible to evaluate pump efficiency at lower frequencies. However, reflux of water back through the SC chamber can be shown by gradually increasing the height of the exhalant water

Table 1. Efficiency of the scaphognathite-driven ventilatory pump

<table>
<thead>
<tr>
<th>Animal</th>
<th>$f_R$ (beats min$^{-1}$)</th>
<th>$\dot{V}_w$ (ml min$^{-1}$)</th>
<th>$V_d$ (ml kg$^{-1}$ beat$^{-1}$)</th>
<th>$V_{static}$ (ml kg$^{-1}$)</th>
<th>Efficiency</th>
<th>$\frac{V_d}{V_{static}}$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>144.8 ± 15.1</td>
<td>278.5 ± 28.3</td>
<td>2.0 ± 0.2</td>
<td>3.35</td>
<td>59.7</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>232.7 ± 16.3</td>
<td>669.8 ± 47.3</td>
<td>2.9 ± 0.1</td>
<td>3.25</td>
<td>89.2</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>140.4 ± 14.0</td>
<td>360.0 ± 40.1</td>
<td>2.6 ± 0.1</td>
<td>2.76</td>
<td>93.0</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>173.1 ± 22.1</td>
<td>479.2 ± 59.3</td>
<td>2.8 ± 0.1</td>
<td>3.03</td>
<td>92.3</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>171.4 ± 16.4</td>
<td>446.5 ± 39.1</td>
<td>2.7 ± 0.1</td>
<td>2.81</td>
<td>89.4</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>172.5</td>
<td>446.8</td>
<td>2.6</td>
<td>3.04</td>
<td>84.7</td>
<td></td>
</tr>
</tbody>
</table>
The rate of oxygen uptake ($\dot{M}_{O_2}$) for control (O) and operated (X) animals as a function of ventilation volume ($\dot{V}_w$). For controls $y = 0.033x + 6.97$, $r = 0.84$; for operated animals $y = 0.009x + 11.65$, $r = 0.50$.

Collecting tube. $\dot{V}_w$ falls to zero when the overflow tube has been raised by a distance equal to the branchial pressure head (2 cm when branchial pressure is $-2 \text{ cmH}_2\text{O}$). At this point reflux must equal efflux.

The relationship between $\dot{M}_{O_2}$ and $\dot{V}_w$ for control and operated crabs is presented in Fig. 2 and Table 2. All values reported represent animals in which haemolymph $\text{PaO}_2$ and lactate concentrations met the criteria for adequate branchial oxygen exchange. The $\dot{M}_{O_2}$ of operated animals was, taken as a group, 7.4 $\mu$mol O$_2$ kg$^{-1}$ below that of controls (Table 2) and is taken to represent the ventilatory fraction of total $\dot{M}_{O_2}$. Even though there is some overlap of data points between these two groups as displayed in Fig. 2, for each crab taken alone the $\dot{M}_{O_2}$ after SC ablation was significantly lower than before.

Operated animals exhibited a significant decrease in the percentage oxygen extracted ($\text{Ext}_w$) from the inhalant water at matched ventilation volumes (Table 2, Fig. 3A). This indicates that the rate of oxygen uptake is lower in the experimental than in control conditions. Since ventilation volumes are comparable, the convection requirement ($\dot{V}_w/\dot{M}_{O_2}$) for water increased (Table 2, Fig. 3B), although there is considerable overlap of points for $\text{Ext}_w$ and $\dot{V}_w/\dot{M}_{O_2}$ between the two conditions. However, differences become more pronounced at higher values of $\dot{V}_w$.

The differences in the rate of oxygen uptake between the two conditions constitutes the ventilatory or SC fraction of the total $\dot{M}_{O_2}$ and can be used to estimate the single beat metabolic equivalent (SBME) where

$$\text{SBME} (\mu\text{mol O}_2 \text{ kg}^{-1} \text{ beat}^{-1}) = \frac{\text{Ventilation fraction of total } \dot{M}_{O_2}}{f_R}$$  (2)
Table 2. *Respiratory performance of control and operated* Carcinus maenas

<table>
<thead>
<tr>
<th>No. animals</th>
<th>Wt. (g)</th>
<th>fr (beats min⁻¹)</th>
<th>V̇e (ml min⁻¹)</th>
<th>fH (beats min⁻¹)</th>
<th>ṀO₂ (μmol kg⁻¹ min⁻¹)</th>
<th>V̇e/ṀO₂</th>
<th>Extro (°)</th>
<th>Pao₂ (Torr)</th>
<th>Lactate (mmol l⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control 5</td>
<td>108 ± 7</td>
<td>231 ± 10</td>
<td>551 ± 36</td>
<td>81·8 ± 2·0</td>
<td>25·0 ± 1·4</td>
<td>22·1 ± 0·8</td>
<td>22·8 ± 1·2</td>
<td>75 ± 8</td>
<td>0·28 ± 0·07</td>
</tr>
<tr>
<td>Operated</td>
<td>653 ± 36</td>
<td>92·2 ± 2·3</td>
<td>17·6 ± 0·7</td>
<td>37·6 ± 2·4</td>
<td>15·0 ± 1·4</td>
<td>15 (35)</td>
<td>79 ± 3</td>
<td>0·54 ± 0·20</td>
<td>5 (35)</td>
</tr>
<tr>
<td>t values</td>
<td>NS</td>
<td>0·01</td>
<td>0·001</td>
<td>0·001</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>

The branchial flow patterns of operated crabs were modified so that all of the gills were ventilated.
Data expressed as mean ± s.e.m., no. of observations in parenthesis. NS, not significant.
and is calculated to be $0.032 \mu\text{mol O}_2 \text{kg}^{-1} \text{beat}^{-1}$. This estimate is derived from settled crabs and may not hold for active animals where it is known that the work and power requirements increase exponentially with $f_R$ (Mercier & Wilkens, 1984).

Although animals were allowed 16–24 h recovery after manipulation they were restrained throughout the experiments. It was thus important to have some evaluation of the level of activity in the crabs other than visual observations alone. Electromyograms were recorded from coxal depressor muscles in the 1st or 2nd
Table 3. Bursts of potentials (EMG) in the coxal depressor muscles of the first or second walking leg of control and operated crabs

<table>
<thead>
<tr>
<th>Condition</th>
<th>Total determinations</th>
<th>Mean ± S.E.M.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intact (N = 8 animals)</td>
<td>70</td>
<td>6.25 ± 1.07</td>
</tr>
<tr>
<td>Without scaphognathites</td>
<td>39</td>
<td>3.45 ± 0.60</td>
</tr>
<tr>
<td>(N = 3 animals of above 8)</td>
<td></td>
<td>(0-11)</td>
</tr>
</tbody>
</table>

Range in parenthesis.

walking legs. As these are postural muscles, the EMG record allowed evaluation of both bursts of activity, which are associated with leg movements, and tonic activity, which would reflect the heightened tonus of a non-resting state. As indicated in Table 3, the average number of EMG bursts was less than 6.25 h⁻¹ with only occasional short periods of higher frequency, the latter usually associated with visible leg movements. There was very little tonic activity recorded from these muscles during the long interburst intervals. After surgery, the mean EMG rate was further depressed from that of controls. However, operated crabs were still responsive to tactile stimuli, responding by movements of the legs and general struggling.

From the data presented here and in the companion paper (Fig. 4 of Mercier & Wilkens, 1984) it is possible to calculate the work efficiency of the SC pump where

\[
\text{SC work efficiency (\%)} = \frac{\text{hydrodynamic power output}}{\text{metabolic energy input}} \times 100. \tag{3}
\]

The hydrodynamic power output (branchial pressure × \(\dot{V}_w\)) can be expressed in terms of oxygen consumption (1 W = 0.133 mmol O₂ kg⁻¹ min⁻¹, Dejours, 1981), which, at \(\dot{V}_w = 600\) ml kg⁻¹ min⁻¹ is equivalent to 0.24 μmol O₂ kg⁻¹ min⁻¹. The SC-specific \(\dot{M}_O_2\) at this \(\dot{V}_w\) is 7.4 μmol O₂ kg⁻¹ min⁻¹ (Table 2). The work efficiency of the SC pump at this flow rate is 3.15 %.

**DISCUSSION**

The difference between the oxygen uptake before and after removing the scaphognathites from a crab should reflect the amount of oxygen required by those appendages to pump water over the gills. This assumes that the methods used, i.e. restraining, masking and SC ablation, did not impose a lasting stress on the animals and that our measurements reflect resting metabolism. There are a number of observations which support this contention.

Both pausing and unilateral pumping behaviour were observed within 16 h of placing control crabs in the experimental apparatus. As mentioned in the Introduction, these ventilatory patterns are characteristic of crabs in a resting state (McDonald, McMahon & Wood, 1977).

The rates of oxygen uptake measured for operated and control crabs are comparable to resting values reported for other species of crustaceans (McMahon & Wilkens,
and for *C. maenas* specifically (Taylor, Butler & Sherlock, 1973; Taylor, Butler & Al-Wassia, 1977; Taylor & Butler, 1978). Although it is not certain that the siphon-generated gill perfusion pathways were counter-current to haemolymph flow, observations through branchiostegite windows confirmed that all of the gills were perfused and that the arterial oxygen tension was maintained in operating crabs.

The EMG recordings showed a very low level of tonic activity in the postural muscles of the legs and also a low frequency of leg movements.

Crabs appeared not to be damaged by SC ablation, as judged by \( \text{MO}_2 \), \( \text{fH} \) and overall responsiveness, for at least 5 days following surgery.

On the basis of the above points it is assumed that the comparison of \( \text{MO}_2 \) in the two conditions as a measure of the costs of ventilation is valid.

The cost of ventilation in settled *C. maenas* in this study was approximately 7.4 \( \mu \text{mol} \text{O}_2 \text{kg}^{-1} \text{min}^{-1} \) or 30% of total \( \text{MO}_2 \). In both control and operated crabs, the oxygen tensions in all samples of arterial haemolymph were high enough to exceed the point at which haemocyanin would be fully saturated (Truchot, 1971; Taylor *et al.* 1973; Taylor, 1976). Since oxygenation of arterial haemolymph was unchanged in the operated condition, it is reasoned that the reduced \( \text{MO}_2 \) and \( \text{Ext}_w \) was the result of an increase in the venous oxygen reserve. Without SC musculature activity less oxygen is removed from the post-branchial haemolymph, the arterial-venous oxygen tension differential is reduced, and the oxygen pressure gradient across the gill epithelium is reduced.

Oxygen consumption can be described by the following relationship (Dejours, 1981)

\[
\text{MO}_2 = V_b (P_{ao2} - P_{vo2}) (\alpha_{O2}),
\]

where \( V_b \) is cardiac output, \( P_{vo2} \) is venous oxygen tension and \( \alpha_{O2} \) is the solubility coefficient for oxygen. In the present experiments \( \text{MO}_2 \) was reduced in operated crabs while \( P_{ao2} \) was maintained. Thus, there must have been an increase in the venous reserve and/or a decrease in cardiac output. Since \( fH \) remained stable the present data are interpreted as resulting from an increase in \( P_{vo2} \).

The cost of ventilation increases linearly with increasing \( \text{fR} \) (Fig. 2 where \( \text{fR} \) is proportional to \( V_w \)) over the limited range shown by settled animals. It would be expected that this cost would increase exponentially at the increased frequencies shown by active animals (see Mercier & Wilkens, 1984, for power-\( \text{fR} \) relationships); however, it is not possible to measure the ventilatory costs in active or stressed crabs since under these conditions the locomotor muscles and other tissue metabolic rates would also be elevated above resting by unquantifiable amounts.

The relatively high metabolic costs of crab ventilation led us to calculate the efficiency with which the scaphognathites perform work. By converting hydraulic power output of the pump (Mercier & Wilkens, 1984) into oxygen equivalents (Dejours, 1981), i.e. the theoretical amount of oxygen consumption required to move a given amount of water, and dividing this by the power input or SC-specific oxygen consumption we obtained an overall system efficiency of 3.15% (equation 3). While this value is almost an order of magnitude lower than the 20% muscular efficiency of a man riding a bicycle ergonometer (Hill, 1939; Gaesser & Brooks, 1975; Tucker, 1975; Goldspink, 1977), we believe it may reflect factors not present during the
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human determinations, namely the combined effects of the turbulent water flow through the pumping chamber (Mercier & Wilkens, 1984), the inherent leakiness of the pumping chamber, the reflux of water through the pump especially at low beat frequencies, and the hydraulic drag against the SC blade (Alexander, 1968).

The scaphognathites operating over the normal range of frequencies (fr = 40–300) achieve pumping efficiencies (85 %) as great as good turbine pumps (Perry & Chilton, 1973) and the 15 % leakiness is fairly constant at these frequencies. However, the x-intercept of Fig. 1 indicates that leakiness or the reflux of water back through the pumping chamber must increase rapidly below some critical fr. The present study of a crab and that of Burggren & McMahon (1983) of a crayfish show that the SCs cease to pump water effectively at about fr = 40. That reflux back past the SC is possible was demonstrated in the crab by artificially increasing the pressure gradient across the SC. At twice the normal branchial pressure net Vw was reduced to zero even though fr was unchanged at about 150 beats min⁻¹.

At least four other attempts have been made to evaluate the cost of ventilation in crustaceans. Very low values were obtained by Batterton & Cameron (1978) who calculated that 0.02 % of total M02 is required for power ventilation in C. sapidus at rest and Burggren & McMahon (1983) who estimated the aerobic cost of ventilation in Orconectes virilis to be 1 % of the total M02.

McDonald et al. (1980) observed that M02 of resting C. magister decreased by 32 % when the crab switched from bilateral to unilateral ventilation. This value must overestimate the metabolic cost of bilateral ventilation (64 % of total) since in their study (i) there was a concomitant 14 % decrease in heart rate and decreased oxygen requirement at the onset of unilateral ventilation and (ii) the increased oxygen extraction efficiency measured during unilateral pumping may have arisen from a steeper diffusion gradient into the haemolymph when only one gill chamber was ventilated.

Burnett & Bridges (1981) used two methods to calculate the cost of ventilation in C. pagurus: (i) comparison of the rates of oxygen uptake before and after ventilatory pauses and (ii) measurements of the depletion of haemolymph oxygen content during pausing. The ventilatory fraction obtained from these two methods was 17 % and 76 %, respectively. From the first method it was assumed that the incremental increase in M02 after a pause represented payment of an oxygen debt incurred during the pause. However, this postpause deficit includes three variables: the oxygen consumed to replenish haemolymph oxygen stores, to oxidize accumulated anaerobic end products produced during the pause, and to power the scaphognathites. The actual ventilatory fraction is difficult to estimate from measurements of ΔM02. The second method must represent an overestimation since their records (Fig. 1), as well as several other studies (McMahon & Wilkens, 1972, 1977; Cumberlidge & Uglow, 1977; McDonald et al. 1977), show that spontaneous ventilatory pauses are accompanied by bradycardia or cardiac arrest. Thus the 76 % reduction in pausing M02 must represent savings from both the SCs and the heart.

If the cardiac metabolic fraction were subtracted from the estimates of McDonald et al. (1980) and Burnett & Bridges (1981) there might be close agreement that the ventilatory fraction of total metabolism in resting crabs is approximately 30 %. This high cost of ventilation has an important consequence with regard to the metabolic scope of crustaceans. Although there are a few exceptions in the literature (Belman
& Childress, 1976; Rutledge, 1981) the maximum increase in oxygen uptake during exercise is reported to be only 4–6 times the resting level (McMahon et al. 1978; Booth, McMahon & Pinder, 1982). The low metabolic efficiency of the scaphognathites as pumps and the O₂ consumed by the SC muscles contracting at high frequency during exercise may both limit the residual oxygen available for the locomotory muscles.

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