AN ANALYSIS OF SCAPHOGNATHITE PUMPING PERFORMANCE IN THE CRAYFISH ORCONECTES VIRILIS: COMPENSATORY CHANGES TO ACUTE AND CHRONIC HYPOXIC EXPOSURE

WARREN W. BURGGREN AND BRIAN R. McMAHON

Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003-0027; and Department of Biology, University of Calgary, Calgary, Alberta, T2N 1N4, Canada

Ventilation volume ($\dot{V}w$), beat frequency of right scaphognathite (fR_r), total stroke volume of the scaphognathite pair (Vs_{tr}), and the amplitude of the pulse *(PP)* and mean standing pressure *(Pbr)* developed within the postbranchial chamber by scaphognathite action have been measured in the crayfish *Orconectes virilis*. Data were recorded from crayfish acclimated to normoxia ($Po_2 = 130$ mm Hg), and during acute (< 24 h) and chronic (> 4 days) exposure to hypoxia ($Po_2 = 40–60$ mm Hg). At values of fR_r below 100 beats/min $\dot{V}w$ varied as a function of both Vs_{tr} and fR_r, both in normoxic and acutely hypoxic animals. Above 100 beats/min, Vs_{tr} remained constant in both groups. In acutely hypoxic crayfish, stroke volume was elevated above normoxic values at any given fR_r. Long-term acclimation to hypoxia was accompanied by a significant decrease in $\dot{V}w$ through reduction in both fR_r and Vs_{tr}. In addition, the stroke volume at higher scaphognathite frequencies was significantly lower than in either normoxic or acutely hypoxic crayfish. Calculations of power output for scaphognathite pumping indicate that the power required to produce a given $\dot{V}w$ was unchanged by hypoxic acclimation. Scaphognathite pumping accounted for 1%, 12%, and 4% of total oxygen consumption in chronic normoxia, acute hypoxia, and chronic normoxia, respectively. The scaphognathites of the crayfish thus emerge as variable-stroke, variable-frequency ventilatory pumps. Possible active and passive mechanisms involved in modulating scaphognathite stroke volume are discussed.

INTRODUCTION

The scaphognathites of decapod Crustacea are highly modified epipodites of the second maxillae that serve as the paired respiratory pumps. As the scaphognathites oscillate in the exhalant canal and expel water anteriorly, they generate a sub-ambient pressure in the epibranchial chamber. This sucks water into the openings at the base of each thoracic limb and over the gills. Anatomical and functional details of this ventilatory system have been presented by Wilkens and McMahon (1972), Burggren, McMahon, and Costerton (1974), Wilkens and Young (1975), and Wilkens (1981).

The scaphognathite system must be able to respond to changing needs for convection of water over the gills. Scaphognathite frequency (fR) increases greatly in response to hypoxic exposure or exercise (see McMahon [1981] for review), as does gill ventilation volume ($\dot{V}w$). In fact, a nearly linear relationship between fR and $\dot{V}w$ has been assumed to occur during transient increases in fR in *Astacus fluviatilis* (Lindroth 1938), *Cancer novaezelandiae* (Pilkington and Simmers 1973), *Carcinus maenas* (Cumberlidge and Uglow 1977), *Callinectes sapidus* (Batterton and Cameron 1978), and *Cancer magister* (McDonald, Wood, and McMahon 1980). However, few detailed analyses of the dependent interactions between fR, $\dot{V}w$, scaphognathite stroke volume (Vs_{tr}) and the oscillatory pressures generated in the branchial chamber in decapods have been attempted (see Wilkens 1981), and several key questions remain unanswered. For instance, do increases in scaphognathite stroke volume occur in addition to increases in frequency? Is the ability to increase ventilatory stroke volume eventually restricted because scaphognathite excursion might be limited within the narrow exhalant canal? What proportion of the oxygen uptake by the animal is devoted to ventilatory muscle metabolism? Do any of these

ariable change during sustained high levels of scaphognathite pumping characteristic of chronic hypoxia?

The present study analyzes these aspects of scaphognathite pumping performance of the crayfish *Orconectes virilis* under both normoxic and hypoxic conditions. Investigations concerning the adaptability of scaphognathite performance under hypoxic conditions are particularly appropriate for freshwater decapods, which may often be exposed to hypoxia at both the environmental and the tissue levels (McMahon, Burggren, and Wilkens 1974; Wilkes 1980).

MATERIAL AND METHODS

Crayfish, *Orconectes virilis*, were obtained from commercial suppliers. Body mass ranged from 13 to 19 g, with a mean mass of 16.5 ± 3.0 g SD (no. = 10). The animals were held in air-equilibrated water (PO_2 130–135 mm Hg at Calgary's elevation) at 20 C under constant light conditions for a period of at least 1 mo prior to being transferred to the experimental apparatus. All experiments were performed at 18–20 C using 10 fasting crayfish that appeared to be healthy and in the intermolt condition.

Respiratory variables were measured using an apparatus and techniques described in detail elsewhere (McMahon et al. 1974). Briefly, the apparatus consisted of a small Plexiglas box that was divided into a forward and a rear chamber by a thin flexible rubber membrane. A crayfish was inserted for approximately one-third of its body length through a snug hole in the membrane and was restrained by a thread tied through a small hole drilled in the rostrum. The crayfish was not held so tightly as to alter the normal contours or natural movement of the branchiostegites. The membrane formed a watertight seal around the carapace, so that only water pumped by the scaphognathites from the rear chamber and over the gills could enter the anterior chamber. This water exiting from the excurrent canal displaced an equal volume of water down a standpipe in the forward chamber that was collected periodically and recorded as the combined gill-ventilation volume from both scaphognathites ($\dot{V}w$). This factor (and others) was expressed on a mass-specific basis (μl H_2O/g body wt/min), though body mass varied only slightly in the 10 crayfish used. Standpipes in both chambers were adjusted to ensure that the apparatus induced no hydrostatic pressure gradient across the gills.

Hydrostatic pressure changes resulting from movement of the right scaphognathite were monitored via a polyethelene cannula (PE 160) inserted through the branchiostegite into the right epibranchial cavity (see McMahon et al. 1974). Pressure changes were detected by differential fluid pressure transducers (Hewlett Packard 267 BC) excited and amplified by a preamplifier (Hewlett Packard 311A). The resulting signals were displayed on an oscillographic chart recorder (Harvard Instruments).

Analysis of the characteristic branchial pressure waveforms (fig. 1) yielded the beat frequency of the right scaphognathite (fR_r), the amplitude of the pressure excursion resulting form each beat of the right scaphognathite *(PP)*, together with the mean standing pressure *(Pbr)* maintained in the right branchial cavity, both expressed in cm H_2O. The total stroke volume of the scaphognathite pair, Vs_w in μl/g, was calculated as $\dot{V}w \div fR_r$. This assumed that there was no significant difference in rate between left and right scaphognathites, i.e., $fR_r = fR_l = f\bar{R}$ (see Discussion for elaboration of this assumption).

The oxygen partial pressure of water flowing into the rear chamber (PIO_2) was manipulated by passing water through a gas-exchange column flushed with a finely controlled countercurrent stream of nitro-
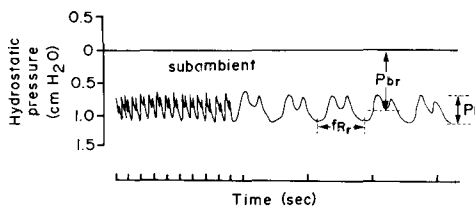

Fig. 1.—Representative pressure waveforms recorded from the left epibranchial cavity of a *O. virilis*, acclimated to normoxia. The fR_r is right scaphognathite frequency; *Pbr*, mean branchial subambient pressure; *PP*, amplitude of pressure oscillation.

gen gas or air. Water samples for P_{IO_2} analysis were drawn from just outside the Milne-Edwards openings. The P_{O_2} of these samples was measured with a Radiometer oxygen electrode (E5046) and display system (PHM 71). The electrodes were maintained at the experimental temperature and calibrated with nitrogen and air-equilibrated water.

EXPERIMENTAL PROTOCOL AND ANALYSIS OF DATA

All crayfish were allowed a 3-day normoxic period (P_{IO_2} 110–135 mm Hg, or 81%–100% air saturation at Calgary's altitude) to allow both for recovery from cannulation and for acclimation to the apparatus. A further 3–4 days of normoxia ensued, during which measurements of fR_r, Vw, P_{IO_2}, *Pbr*, and *PP* were made to establish control values. Each crayfish was monitored for 5–10 5-min periods each day without being disturbed. Details of measuring techniques are given in McMahon et al. (1974) and illustrated in figure 1. The P_{IO_2} was then reduced slowly over a 12-h period to 40–60 mm Hg. This level of hypoxia was then maintained for an additional 6–8 days. As with normoxia, 5–10 5-min monitoring periods were made daily for each crayfish.

Three categories of conditions were established. The first category (chronic normoxia) included measurements made in the post-acclimation normoxic period. The second category (acute hypoxia) included measurements taken during the 24-h period after hypoxic exposure had begun and so included measurements during both the period of P_{IO_2} reduction and during the initial 12 h at a stable level of hypoxia. The third category (chronic hypoxia) included only measurements made *after* 4 days at a stable level of hypoxia.

Data within these categories were initially analyzed as a function of P_{IO_2}, as follows. Measurements of pumping variables from an individual crayfish in a particular experimental category were placed in P_{IO_2} classes incrementing in 10-mm Hg steps. Thus data were classified into groups at a P_{IO_2} centering on 110, 120, and 130 mm Hg for chronic normoxia; 40, 50, 60, 70, 80, 90, and 100 mm Hg for acute hypoxia; and 40, 50, and 60 mm Hg for chronic hypoxia. All data collected in the same experimental category and in the same 10-mm Hg range of P_{IO_2} were pooled for each crayfish to provide a single estimator for that animal in that category and P_{IO_2} range. Mean values ± SE for the species were then calculated using the estimator for each crayfish centered on each P_{IO_2} range and category. Regression of all data points for each ventilatory parameter against all P_{IO_2}'s thus could be avoided, as such a regression masked small but significant inflections in the line describing the relationship which emerged when the mean values of a single estimator from each crayfish were plotted as a function of P_{IO_2} (or fR_r—see below).

A secondary data analysis was performed as described above, except that data on branchial pumping were plotted as a function of fR_r rather than P_{IO_2} (fig. 3). It should be emphasized that interactions occur between P_{IO_2} and fR_r such that at the same P_{IO_2}, fR_r varied with acclimation (fig. 2), while at the same fR_r the dependent variables vary with P_{IO_2} (i.e., acute vs. chronic hypoxia). The secondary analysis of scaphognathite pumping as a function of fR_r was not intended to identify the separate effects of scaphognathite frequency and P_{IO_2} per se but rather to indicate the integrated ventilatory response of this species to short- and long-term hypoxia.

Finally, significant differences between two means from different experimental categories at the same P_{IO_2} or fR_r were assessed with Student's two-tailed t-test, using a significance level of .05.

RESULTS

RELATIONSHIP BETWEEN SCAPHOGNATHITE
PUMPING PERFORMANCE AND INSPIRED P_{O_2}

In crayfish acclimated to a normoxic P_{O_2} range (100–135 mm Hg), both the frequency of scaphognathite pumping (fR_r) and the combined stroke volume (Vs_{tr}) of the scaphognathite pair remained relatively constant (fig. 2), with no significant differences occurring between these variables at the two P_{IO_2} extremes. Water flow over the gills (Vw). averaged about 100–200 $\mu l/g/min$. Exposure to progressive hypoxia was accompanied by a large in-

crease in branchial ventilation. Initially, 12 h of exposure at $P_{O_2} = 40$ mm Hg caused scaphognathite pumping frequency to increase threefold, but at the same time ventilation volume increased approximately eightfold (fig. 2), indicating that changes other than scaphognathite frequency are involved in the elevation of V_w. After 4 days of hypoxic exposure, gill ventilation was still significantly elevated above normoxic levels, but, at any given oxygen partial pressure, fR_r, V_w, and V_{s_w} were significantly lower than under acute hypoxia conditions. The absence of the anticipated one-to-one relationship between fR_r and V_{s_w} (see Introduction), as well as the apparent adjustments in ventilation relationships occurring during the process of hypoxic acclimation, prompted a more detailed analysis and comparison of the relationship between scaphognathite pumping variables under the three experimental conditions.

ANALYSIS OF SCAPHOGNATHITE PUMPING
PERFORMANCE

A. Normoxia and acute hypoxia.— Scaphognathite performance variables, i.e., amplitude of the pressure developed in the branchial cavity, ventilation volume, and stroke volume, were plotted against the frequency of scaphognathite pumping (fig. 3). Under normoxic conditions, fR in individual crayfish varied between 40 and 100 beats/min (the smaller range of values in fig. 2 represents *mean* values over the normoxic range of O_2 partial pressures). Mean ventilation volume measured over this range varied almost fourfold (fig. 3), indicating that the combined stroke volume of the scaphognathite pair in normoxic crayfish doubled throughout this lower range of fR_r. Examination of data for animals during the first few hours of hypoxic exposure allows extension of the relationships $\Delta V_w/\Delta fR_r$ and $\Delta V_{s_w}/\Delta fR_r$ above $fR_r = 100$
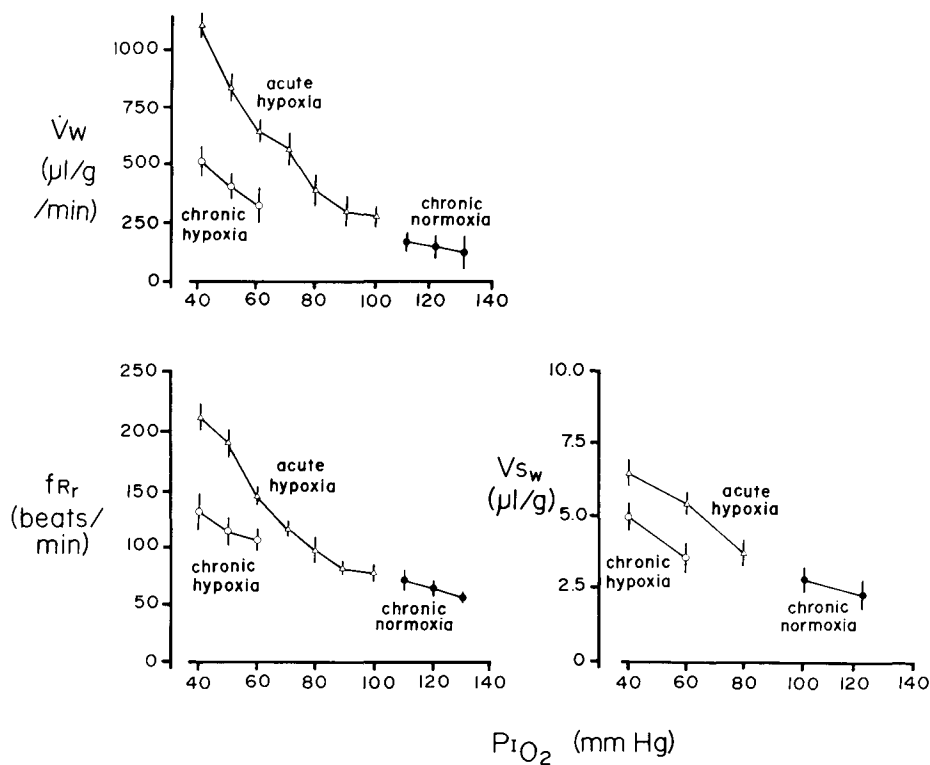

Fig. 2.—Gill ventilation and related variables as a function of inspired P_{O_2} in *O. virilis* exposed to chronic normoxia (7–8 days), acute hypoxia (0–24 h), and chronic hypoxia (4–8 days). Mean values ± 1 SE are plotted. Number of animals for each data point in chronic normoxia, acute hypoxia, and chronic hypoxia are 10, 10, and 4, respectively. See Material and methods for experimental and analytical protocol.

beats/min. Throughout the range 100–300 beats/min, ventilation increased linearly with an increase in fR_r, but no further increase in stroke volume resulted. Thus, at the moderate scaphognathite frequencies typical of quiescent or routinely active animals, stroke volume was correlated with scaphognathite frequency, whereas throughout the range of higher fR_r typical of active, disturbed, or acutely hypoxic animals, Vs_w was constant (fig. 3). However, a further complexity is revealed by close examination of figure 3, which indicates that crayfish exposed to hypoxic conditions exhibited increased stroke volume when compared with their normoxic counterparts at the same scaphognathite frequency. This difference is apparent over the whole range of frequency overlap (60–100 beats/min) but is most pronounced between 80 and 100 beats/min, becoming significantly ($P < .05$) elevated at this highest level. Clearly, stroke volume of the scaphognathite pumps is elevated under short-term conditions of increased O_2 demand or decreased supply of oxygen, when an increase in the convective supply

of water to the gills would aid oxygen uptake.

Examination of branchial pressure waveforms and profiles recorded over a range of scaphognathite frequencies (fig. 3) in normoxic or acutely hypoxic crayfish reveals that the amplitude of the pressure pulses during individual scaphognathite cycles *(PP)* and the level of standing subambient pressure developed in the branchial cavity as a result of continual scaphognathite pumping *(Pbr)* are complexly related. At moderate frequencies (fR_r = 40–100 beats/min), little change occurred in the amplitude of PP, but the standing subambient pressure, Pbr, increased as fR_r increased (fig. 3). Above fR_r = 100 beats/min both PP and Pbr increased similarly with rising fR_r.

B. *Chronic hypoxia–effects of acclimation.*—Whereas the hypoxic-induced increases in branchial ventilation and the attendant changes in scaphognathite performance outlined above occurred within minutes of exposure to lowered O_2 partial pressure, under conditions of chronic hypoxic exposure additional large adjust-
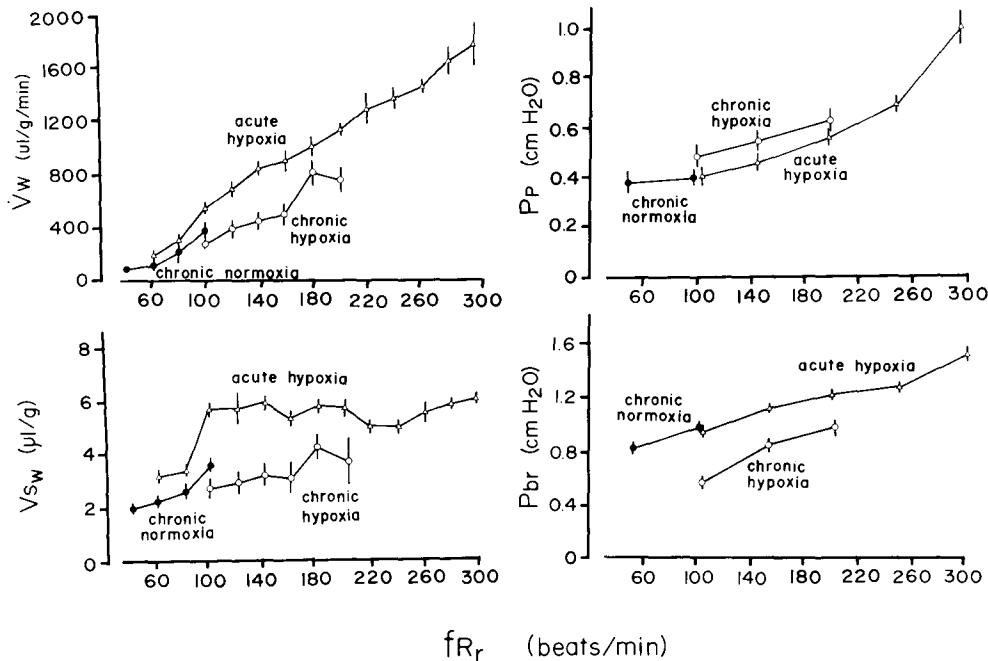

fR_r (beats/min)

Fig. 3.—Gill ventilation and related variables as a function of scaphognathite frequency in *O. virilis* exposed to chronic normoxia (7–8 days), acute hypoxia (0–24 h), and chronic hypoxia (4–8 days). Mean values ± SE are plotted. Number of animals for each data point in chronic normoxia, acute hypoxia, and chronic hypoxia are 10, 10, and four, respectively. See Material and methods for experimental and analytical protocol.

ments in scaphognathite pumping performance developed over the course of 1–3 days and were essentially complete within 4 days of the start of hypoxic exposure (figs. 2, 3). At most scaphognathite frequencies, stroke volume was reduced significantly by 30%–50% compared with crayfish in normoxic or acute hypoxia. As with the first two experimental conditions, however, Vs_{tr} was largely independent of fR_r over the entire observed range of 100–200 beats/min. The $\dot{V}w$ in these hypoxic-acclimated crayfish paralleled that of acutely exposed animals but, as a consequence of the large decrease in stroke volume, was lower at any given fR_r.

The changes in branchial pressures were less clear, with the *Pbr* lowered but *PP* not significantly changed at any fR_r.

DISCUSSION

Large increases in scaphognathite frequency resulting from hypoxic exposure have been commonly reported in decapod crustaceans (Amberson, Mayerson, and Scott 1924; Fox and Johnson 1934; Thomas 1954; Larimer and Gold 1961; Winget 1969; McMahon et al. 1974; Taylor, Butler, and Al-Wassia 1977; Wilkes and McMahon 1982). The increased frequency generally results in enhanced branchial water flow and, at least in resting undisturbed animals, in maintained or even elevated oxygen uptake—despite the reduction in ambient oxygen levels (Taylor et al. 1977; Wilkes and McMahon 1982).

The scaphognathite system of decapods has been generally described as a constant-stroke volume pump (Larimer 1961; Pilkington and Simmers 1973; Cumberlidge and Uglow 1977; McDonald 1977; Batterton and Cameron 1978; McMahon and Wilkens 1975; McDonald et al. 1980), with adjustments in $\dot{V}w$ thus affected solely by changes in scaphognathite frequency. However, in *Orconectes virilis,* this is the case only at higher levels of scaphognathite pumping typical of active, disturbed, or acutely hypoxic animals. At more moderate rates, stroke volume is adjustable and so could play a major role in the regulation of ventilation volume under less extreme conditions. Wilkens (1981) suggests that Vs_{tr}

may also vary independently of fR_r in both *Carcinus maenas* and *Homarus americanus,* while our reexamination of the published data on two species for which constancy of stroke volume is claimed, i.e., *Cancer magister* (McDonald 1977), and *Carcinus maenas* (Cumberlidge and Uglow 1977), indicates that a progressive increase in stroke volume of the scaphognathite pump may occur between an fR_r of 60 and 100 beats/min.

One potentially complicating factor in the analysis of stroke volume is the possible lack of beat-to-beat coupling between left and right scaphognathites. A higher frequency in either the right or the left scaphognathite is apparent in quiescent *O. rusticus* (Wilkes and McMahon 1982), but they rapidly begin to beat in unison as fR rises with activity or hypoxia. If this lack of coupling occurred in *O. virilis,* then a disproportionate increase in $\dot{V}w$ (in relation to scaphognathite frequency) could result if the trailing scaphognathite accelerated to match its partner as fR increased. This could be misinterpreted as an increase in Vs_{tr} of a scaphognathite pair assumed to be acting totally in unison, at a common frequency. The present study measured only right scaphognathite performance, but there is essentially no scaphognathite dominance (i.e., $fR_r = fR_l$) in *O. virilis* under the stated experimental conditions (Algarin, unpublished). The fourfold rise in combined stroke volume between 60 and 100 beats/min must therefore be largely produced by changes in the stroke volume of each scaphognathite, which we consider to be acting essentially in unison.

The mechanisms used in this increase of stroke volume could be either "active" or "passive" in nature. In decapods, each scaphognathite is a flexible blade (the exopodite of the second maxilliped) which oscillates within a narrow channel. There are two propulsion strokes per beat cycle in which the posterior and anterior tips of the scaphognathite blades alternately and sequentially elevate and depress, each trapping a volume of water and expelling it forward through the excurrent canal (Paterson 1968; Wilkens and McMahon 1972; Young 1975). Each power stroke generates subambient pressure in the

branchial cavity (fig. 1), but following each propulsion stroke the scaphognathite is fully apposed to the channel wall, leaving the scaphognathite channel open. Under these interbeat conditions, branchial pressure rises toward ambient as water enters the branchial cavity (Wilkens and McMahon 1972). The presence of this "open" interbeat phase in the cycle could allow the following, passive mechanism of varying stroke volume with increasing fR. During these interbeat intervals reflux of water could occur back through the open scaphognathite channel, simply following water pressure gradients. As fR falls, the interbeat interval increases, and reflux could become progressively more significant, effectively reducing stroke volume. Below a certain critical beat frequency, which in $O.$ $virilis$ may be 40 beats/min, reflux could reach levels which render the pump ineffective. This may explain why these lower frequencies rarely occur in decapods (McDonald et al. 1980; McMahon and Wilkens 1975; Wilkens 1981).

These contentions are supported by examination of branchial pressure waveforms and profiles recorded over a range of scaphognathite frequencies (fig. 3). At moderate frequencies ($fR_r = 40\text{--}100$), little change occurred in PP, but the subambient standing pressure (Pbr) increased markedly as fR_r increased (fig. 3), perhaps reflecting reduction in water reflux past the scaphognathite blades and thus a progressive increase in stroke volume. Above $fR = 100$, both PP and Pbr increased similarly with increase in fR_r. This probably involves the greater power required to promote increased ventilatory flow at high frequencies and perhaps changes in output resistance, though this remains to be tested.

The present study also provides evidence for active control of scaphognathite stroke volume, since acute exposure to hypoxia resulted in increased stroke volume compared with that at the same frequency during normoxia. Under conditions of chronic hypoxia exposure, these elevated stroke volumes were not maintained but fell to levels well below those measured during acute exposure. These data clearly show that $O.$ $virilis$ has the ability to actively raise or to lower not only

frequency but also stroke volume of the scaphognathite pump. Such integrated responses are clearly advantageous as the water convection requirement rises steeply during acute hypoxic exposure and then decreases as hypoxic acclimation develops (McMahon and Wilkens 1982; Wilkens and McMahon 1982). No unequivocal evidence as to the active mechanism(s) involved can be advanced at this time. However, in the acute stage of hypoxic exposure, stroke volume increased about twofold over that of normoxic animals at comparable fR_r (fig. 3) with no change in either the amplitude of the scaphognathite waveform or in the standing subambient branchial pressure. This necessarily involves a decrease in the resistance of the water pathway through the branchial system. Changes in branchial input resistance may occur relatively easily either at the branchial inhalant openings, which are influenced by positional movements of the limb bases, or possibly at the level of the gills by variation of the internal dimensions of the branchial cavity. In addition, variations in output resistance may result from movements of the maxillary appendage overlying the excurrent channel.

Variation in the effectiveness of the scaphognathite pump might also result from active changes in the position or tension (flexibility) of the scaphognathites or from changes in the geometry of the scaphognathite channel itself. For example, the floor of this channel is composed of the epipodites of the first maxillipeds, which can be actively raised or depressed (Wilkens 1981). While the scaphognathite blade appears sufficiently flexible to maintain functional integrity within an enlarged channel (Young 1975), changes in diameter need not be large since the volume pumped will vary with the fourth power of the radius for the same hydrostatic pressure gradient (assuming the channel to be cyclindrical). Muscle-mediated adjustments either to scaphognathite shape or to exhalant channel geometry could improve pumping performance by increasing the "sealing" between scaphognathite blade and the channel walls.

Whatever combination of factors results in changes in scaphognathite perfor-

...ance, acclimation to chronic hypoxia is not immediate. As long as 3–4 days are required for stroke volume to decrease from the high levels measured during initial exposure to low O_2 partial pressure. Whether the acclimation rate of scaphognathite performance is fixed or may vary with degree of hypoxia or other factors is unknown.

Finally, a new approach to the study of the capabilities of the scaphognathite pump was attempted by estimation of the power developed during scaphognathite pumping and the O_2 cost of changes in ventilatory work under various acclimation conditions. Given the mean pressure gradient across the gills (Pbr) and the mean ventilation volume (Vw), then the external power generated can be approximated using the mathematical expression $Pbr \times Vw$ (see Alexander 1967; Batterton and Cameron 1978). Assuming 20% efficiency of the scaphognathite muscles (Bartholomew 1977) and an oxygen consumption of 50 μl O_2/J expended (see Dejours 1981), then the O_2 cost of a change to a different level of scaphognathite performance can be estimated.

The power developed during ventilation, reflecting the O_2 cost, increased exponentially with increasing fR_r for all three experimental situations (fig. 4). It is important, however, that the power developed at any given fR_r and the ventilation volume achieved for any given power development during scaphognathite pumping were similar before and after acclimation to hypoxia (fig. 4), even though stroke volumes were considerably different (fig. 3). These data indicate that the reduction of Vs_{tr} during chronic hypoxic exposure is not associated with a marked decrease in power output or fall in the O_2 cost of ventilation.

Using values for the rate of O_2 uptake in O. virilis maintained under identical conditions (McMahon et al. 1974), and estimates of the oxygen consumption ascribed to specific levels of ventilation as derived from figure 4, the oxygen cost of ventilation as a proportion of total $\dot{V}O_2$ can be calculated for varying experimental conditions (table 1). This admitted approximation of mean conditions ignores O_2 consumption resulting from processes re-

lated to water pumping, such as maintenance of respiratory elements of the nervous system, etc. For quiescent, normoxic O. virilis, the oxygen cost of scaphognathite pumping is approximately 1% of the total oxygen uptake of the crayfish. Unfortunately, few data on oxygen cost of ventilation exist for Crustacea. The present estimate is much higher than that of only 0.02% of total $\dot{V}O_2$ given for Callinectes sapidus by Batterton and Cameron (1978) (who assumed a 10% muscle efficiency), and considerably less than the estimate of 17%–34% calculated for Cancer pagurus (Burnett and Bridges 1981). During acute hypoxic exposure in the crayfish, the oxygen cost of the increased ventilation is proportionately 12 times greater, while whole animal oxygen uptake only rises 1.7 times, so the scaphognathites must progressively usurp the aerobic demands of other tissues.
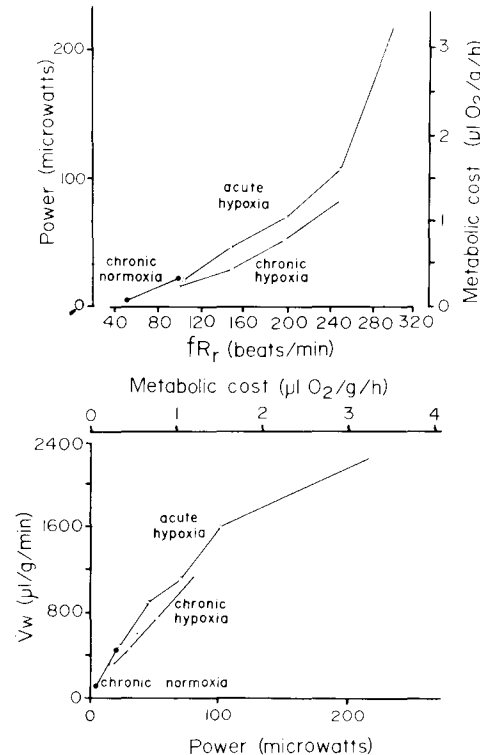

Fig. 4.—Relationships between gill-ventilation, power-generated, and metabolic cost in the crayfish O. virilis exposed to chronic normoxia (7–8 days), acute hypoxia (0–24 h), and chronic hypoxia (4–8 days). Data for O. virilis from McMahon et al. (1974) as well as present study are included. See Discussion for assumptions and calculations.

TABLE 1

GILL VENTILATION, OXYGEN UPTAKE, AND THE AEROBIC COST OF SCAPHOGNATHITE VENTILATION
IN *Orconectes virilis* AT 18–20 C

	fR, (beats/min)	Vw ($\mu l/g/min$)	Vs_n ($\mu l/g$)	Vo_2 (total) ($\mu l\ O_2/g/h$)	Vo_2 (scaph.) ($\mu l\ O_2/g/h$)	$\dfrac{Vo_2\ (scaph.)}{Vo_2\ (total)} \times 100$
Chronic normoxia	67	130	1.9	10	.10	1%
Acute hypoxia	170	830	4.9	17	.70	12
Chronic hypoxia	100	280	2.8	14	.3	4

NOTE. Data means for *O. virilis* from McMahon et al. (1974) as well as the present study are included. See Discussion for assumption and calculations.

Following acclimation to hypoxia, a two-thirds reduction in the oxygen cost of scaphognathite pumping occurred (table 1), emphasizing the importance of the changes in scaphognathite performance, the decrease in ventilation, and the underlying increases in efficiency of oxygen uptake (Wilkes and McMahon 1982) which occur at this time.

In summary, analyses of changes in scaphognathite performance in crayfish under normoxic conditions and during acute and chronic exposure to hypoxic conditions reveal that, while the scaphognathite pump may operate at fixed stroke volume above certain frequencies and under various specific conditions, the pump does exhibit variable stroke volume under conditions commonly encountered in the natural environment. Under normoxic conditions, effective stroke volume varies, with frequency progressively amplifying the incremental change in Vw as frequency rises within the range normally shown by quiescent normoxic animals. Under hypoxic conditions, the scaphognathite pump rapidly reaches frequencies at which the pump itself operates at fixed volume but stroke volume is nonetheless variable, perhaps activated by movements of the floor of the scaphognathite channel and/or by changes in conformation or force of the scaphognathite beat.

LITERATURE CITED

ALEXANDER, R. S. 1967. Functional design in fishes. Hutchinson, London. 160 pp.

AMBERSON, W. R., H. S. MAYERSON, and W. J. SCOTT. 1924. The influence of oxygen tension upon metabolic rate in invertebrates. J. Gen. Physiol. 7:171–176.

BARTHOLOMEW, G. A. 1977. Energy metabolism. *In* Animal physiology: principles and adaptations. Macmillan, New York.

BATTERTON, C. V., and J. N. CAMERON. 1978. Characteristics of resting ventilation and response to hypoxia, hypercapnia and emersion in the blue crab *Callinectes sapidus*. J. Exp. Zool. 203(3):403–418.

BURGGREN, W. W., B. R. MCMAHON, and J. W. COSTERTON. 1974. Branchial water- and blood-flow patterns and the structure of the gill of the crayfish *Procambarus clarkii*. Can. J. Zool. 52(12):1511–1518.

BURNETT, L. E., and C. R. BRIDGES. 1981. The physiological properties and functions of ventilatory pauses in the crab *C. pagurus*. J. Comp. Physiol. 45:81–88.

CUMBERLIDGE, N., and R. F. UGLOW. 1977. Size, temperature, and scaphognathite frequency-dependent variations of ventilation volumes in

Carcinus maenas (L.). J. Exp. Marine Ecol. 30:85–93.

DEJOURS, P. 1981. Principles of comparative respiratory physiology. 2d ed. North-Holland, Amsterdam. 253 pp.

FOX, H. M., and M. L. JOHNSON. 1934. The control of respiratory movements in Crustacea by oxygen and carbon dioxide. J. Exp. Biol. 11:1–10.

LARIMER, J. L. 1961. Measurement of ventilation volume in decapod Crustacea. Physiol. Zool. 34:158–166.

LARIMER, J. L., and A. H. GOLD. 1961. Responses of the crayfish, *Procambarus simulans* to respiratory stress. Physiol. Zool. 34:167–176.

LINDROTH, A. 1938. Atmungsregulation bei *Astacus fluviatilis*. Ark. Zool. 30:1–7.

MCDONALD, D. G. 1977. Respiratory physiology of the crab *Cancer magister*. Ph.D. thesis. University of Calgary.

MCDONALD, D. G., C. M. WOOD, and B. R. MCMAHON. 1980. Ventilation and oxygen consumption in the Dungeness crab, *Cancer magister*. J. Exp. Zool. 213:123–136.

MCMAHON, B. R. 1981. Oxygen uptake and acid-base balance during activity in decapod crustaceans. Pages 299–335 *in* C. F. HERREID II and

R. FOURTNEIR, eds. Locomotion and energetics in arthropods. Plenum, New York.

MCMAHON, B. R., W. W. BURGGREN, and J. L. WILKENS. 1974. Respiratory responses to long term hypoxia stress in the crayfish *Orconectes virilis*. J. Exp. Biol. **60**:195–206.

MCMAHON, B. R., and J. L. WILKENS. 1975. Respiratory and circulatory response to hypoxia in the lobster *Homarus americanus*. J. Exp. Biol. **62**:637–655.

MCMAHON, B. R., and WILKENS, J. L. 1982. Ventilation, perfusion and oxygen uptake. Pages 289–371 *in* D. BLISS and L. H. MANTEL, eds., Physiology of the Crustacea. Academic Press, New York.

PATERSON, M. S. 1968. The anatomy of the cape rock lobster *Jasus lalndi*. Ann. South Afr. Mus. **1**:1–232.

PILKINGTON, J. B., and A. J. SIMMERS. 1973. An analysis of bailer movements responsible for gill ventilation in the crab, *Cancer novae-zelandiae*. Marine Behav. Physiol. **2**:73–95.

TAYLOR, E. W., P. J. BUTLER, and A. AL-WASSIA. 1977. Some responses of the shore crab, *Carcinus maenas* (L.), to progressive hypoxia at different acclimation temperatures and salinities. J. Comp. Physiol. **122**:391–402.

THOMAS, H. J. 1954. The oxygen uptake of the lobster *Homarus vulgaris*. J. Exp. Biol. **31**:228–251.

WILKENS, J. L. 1981. Respiratory and circulatory coordination in decapod crustaceans. Pages 277–299 *in* C. F. HERREID II and C. R. FOURTNEIR, eds. Locomotion and energetics in arthropods. Plenum, New York.

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.

WILKES, P. 1980. Compensation to hypoxia in the crayfish *Orconectes rusticus*. M.Sc. thesis. University of Calgary.

WILKES, P., and B. R. MCMAHON. 1982. Effect of maintained hypoxic exposure on the crayfish *Orconectes rusticus*. I. Ventilatory, acid-base and cardiovascular adjustments. J. Exp. Biol. **98**:119–138.

WINGET, R. R. 1969. Oxygen consumption and respiratory energetics in the spiny lobster, *Panulirus interruptus*. Biol. Bull. **136**:301–312.

YOUNG, R. E. 1975. Neuromuscular control of ventilation in the crab *Carcinus maenas*. J. Comp. Physiol. **101**:1–37.