RESPIRATORY FUNCTION DURING EXERCISE IN THE AMERICAN LOBSTER, HOMARUS AMERICANUS

Darwin Jorgensen[1,2], and Todd Millbrandt[1]
[1]Biology Department, University of Puget Sound, Tacoma, WA 98416
[2] present address: Biology Department, Roanoke College, Salem, VA 24153

Lobsters move about by two means: swimming through the water column and walking along the substrate. For lobsters, swimming consists of short duration (a few to several seconds) backward movements with the animal being propelled by rapid flexures of the tail (the so-called tail-flip or escape response). To move any considerable distance (beyond a few meters), lobsters will walk along the substrate in the forward direction with the chelipeds raised off the substrate. We are interested in how the cardiovascular and respiratory systems function to support locomotion in these commercially important crustaceans. The purpose of the present study was to characterize some aspects of the respiratory function response to steady state pedal locomotion in the American lobster, Homarus americanus.

Lobsters have two gill sets, each set residing in a separate branchial chamber. The branchial chambers are located mid-laterally on either side (and along the entire length) of the cephalothorax. Each branchial chamber is equipped with a muscularly-driven pump, the scaphognathite (scaph), which rocks back and forth cyclically, creating a slight negative pressure in the branchial chamber and pulling water past the gills unidirectionally. Exhalant water exits the branchial chambers at their anterior margins, lateral to the mouth. To collect exhalant water, we placed a flexible mask fashioned from clear acrylic over the anterior end of the animal. The mask enclosed all of the mouthparts excluding the 3rd maxillipeds and was attached to the animal with strips of thin latex rubber and cyanoacrylate glue. An opening at the tip of the mask accepted an 8 mm diameter cannulating-type electromagnetic flow probe (connected to a Zepeda Instruments flowmeter) so that total ventilation rate (right + left branchial chambers) could be monitored continuously. The tip of a length of small diameter (ID=1.3mm,OD=2.3mm) microbore Tygon tubing was positioned in the center of the mask outflow channel so that mixed exhalant water could be sampled repeatedly.

The status of the scaphs was monitored by measuring the hydrostatic pressure in each branchial chamber with seawater-filled catheters (ID=1.3mm,OD=2.3mm) connected to strain gage pressure transducers (Gould P23X). Catheter tips were inserted through 2.5 mm diameter holes drilled through the carapace over the middle of the branchial chamber. Branchial chamber pressure is pulsatile and the pressure waveform reflects scaph movement so that the number of scaph movement cycles per unit time (scaph beat rate) could be determined from the pressure record. The volume of ventilatory water pumped per complete scaph movement cycle or scaph beat (scaph stroke volume) was calculated as:

$$SV_{SC} = \dot{V}_W \,.\, \dot{SR}^{-1} \qquad (1)$$

where, SV_{SC} = scaph stroke volume (ml), $\dot{V}_W$ = ventilation rate ($ml \cdot kg^{-1} \cdot min^{-1}$), and $\dot{SR}$ = scaph beat rate ($beats \cdot min^{-1}$). Oxygen uptake was calculated as:

$$\dot{M}_{O_2} = \dot{V}_W \cdot \beta \cdot [(Pi_{O_2} - Pe_{O_2}) \cdot (Pi_{O_2})^{-1}] \qquad (2)$$

where, $\dot{M}_{O_2}$ = oxygen uptake ($\mu mole \cdot kg^{-1} \cdot min^{-1}$), Pi_{O_2} and Pe_{O_2} = inhalant and exhalant water pO_2 (torr), $\dot{V}_W$ = ventilation rate ($ml \cdot kg^{-1} \cdot min^{-1}$), and β = ventilatory water O_2 capacitance ($\mu mole \cdot liter^{-1} \cdot torr^{-1}$).

The animals walked on a submerged treadmill at a rate of 0.2-0.9 $km \cdot h^{-1}$ for 0.5-1 h depending upon the animal. An animal was free to move on the treadmill and was restrained only by Plexiglas strips positioned at the sides and ends of the treadmill (so the animal would remain on the treadmill). The animals walked in still water. Masks were placed on an animal at least 48 hr before an experiment was commenced to give the animal time to become accustomed to it. Branchial chamber pressure catheters and the flow probe were positioned the day of the experiment. The animal was allowed to rest on the treadmill after instrumentation until it was quiescent as evidenced by periods of unilateral ventilation (ventilatory pumping on one side only) or bilateral pausing (complete cessation of ventilation). This time period varied from about 2-5 hr depending upon the animal.

Figs. 1 and 2 show results for a single treadmill experiment. In Fig. 1, ventilation rate and scaph beat frequency (right + left side) are shown for an animal (body mass = 0.697 kg) before during and after a 40 min walk at 0.4 $km \cdot hr^{-1}$. In this experiment, ventilation rate increased about 7X during the exercise period (as compared to rest) while scaph beat frequency increased 5-6X. Scaph stroke volume increased by about 50%. In this same experiment, oxygen uptake increased by about 5.5X (Fig. 2) while the % oxygen extracted from the ventilatory water by the gills decreased by 40% as might be expected considering the extensive increase in ventilation rate. The efficiency of the gas exchange apparatus will depend also, of course, upon what is happening on the hemolymph side of the gill epithelium (i.e. gill perfusion) and this aspect of respiratory function must be considered if a complete picture of the gas exchange process (as it relates to the support of the exercising lobster) is to be developed.

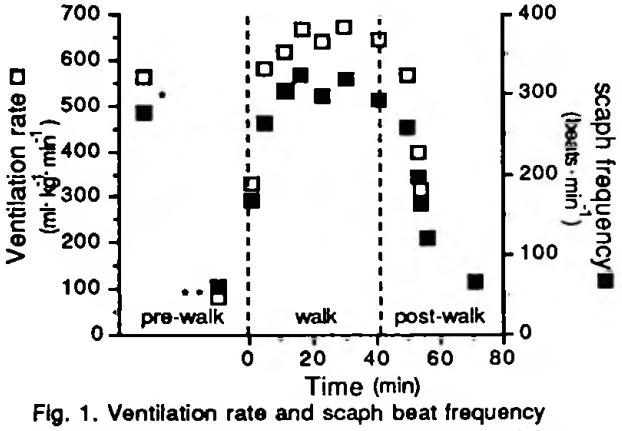

Fig. 1. Ventilation rate and scaph beat frequency before, during, and after a 40 min walk for a lobster. • = immediately after instrumentation, •• = just prior to walk. Symbols on the dashed line at time 0 represent data for the time (1-2 min) after the treadmill had been started but before the animal was walking steadily.

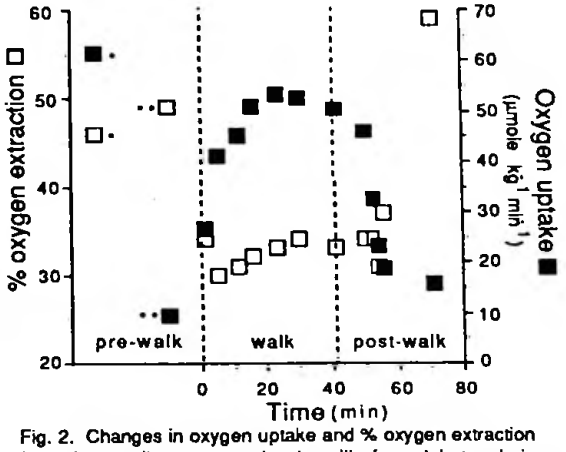

Fig. 2. Changes in oxygen uptake and % oxygen extraction from the ventilatory water by the gills for a lobster during a 40 min walk. • = immediately after instrumentation, •• = just prior to walk. Symbols on the dashed line at time 0 represent data for the time (1-2 min) after the treadmill was started but before the animal was walking steadily.

Table 1 summarizes respiratory function changes associated with an exercise bout for 6 lobsters. All changes, of course, are compared to resting values. Lobsters are extremely sensitive to disturbance and it is critical to allow the animal enough time to settle down after it has been handled during the instrumentation and experimental set-up procedure. In our experiments, there

was a 7.5X increase in oxygen uptake during exercise. Interestingly, this is similar to the 8-fold increase in oxygen uptake reported for a fast-swimming trout of about the same body mass (Kiceniuk, J. and D.Jones. J. Exp. Biol. 69:247-260, 1977). The ventilatory apparatus responds rapidly and substantially to the exercise situation. In our experiments, roughly 5X more water was pumped per unit time through the gill chambers during a typical exercise bout and a small, although not insubstantial, proportion of this increase was mediated by an increase in the volume of water pumped per scaph beat.

	pre-walk	walk	increase with exercise
ventilation rate ($ml \cdot kg^{-1} \cdot min^{-1}$)	106.9 (32.6)	501.1 (61)	4.7X
scaph frequency ($beats \cdot min^{-1}$)	89.5 (16.8)	318.8 (8.9)	3.6X
scaph stroke volume ($ml \cdot kg^{-1}$)	1.16 (0.3)	1.56 (0.2)	1.3X
oxygen uptake ($\mu mole \cdot kg^{-1} \cdot min^{-1}$)	5.7 (1.3)	43.0 (4.0)	7.5X

Table 1. Summary of changes in respiratory variables accompanying steady state treadmill exercise in Homarus americanus. Pre-walk and walk values are $\bar{X}$ (SE) for 6 animals. Treadmill speed ranged from 0.2 to 0.7 $km \cdot h^{-1}$ depending upon the animal.

Respiratory function data for organisms that move about underwater by walking are few and it is interesting to compare the metabolic cost of this type of locomotion with the cost incurred by other organisms that move about by different means. Such a comparison has been made (Schmidt-Nielsen, K. Science 177:222-228, 1972) for animals that use a variety of locomotion methods (e.g. flying, running and swimming). One can calculate the metabolic cost independent of speed of movement by dividing mass specific oxygen uptake (converted to $cal \cdot g^{-1} \cdot hr^{-1}$) by speed of movement ($km \cdot hr^{-1}$). For a lobster, the cost is about 0.5 $cal \cdot g^{-1} \cdot km^{-1}$. This value falls near those for swimming fish and about an order of magnitude lower than those for similar-sized terrestrial animals that walk or run. These data indicate that walking is a relatively efficient way for a lobster to move about underwater.

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