ELSEVIER

J. Exp. Mar. Biol. Ecol. 176 (1994) 167–185

JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

The effects of reduced salinity on lobster (*Homarus americanus* Milne-Edwards) metabolism: implications for estuarine populations

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(Received 3 March 1993; revision received 8 September 1993; accepted 15 October 1993)

Abstract

During periods of substantial freshwater runoff, lobsters that inhabit estuaries, such as the Great Bay Estuary in NH, are exposed for several days to weeks to seawater that is diluted as low as 10 ppt. To assess the physiological stress imposed by these conditions, we measured the oxygen consumption, heart rate, ventilation rate and hemolymph osmolarity of lobsters while sequentially exposing them, for 24-h periods, to seawater of 20, 15, and 10 ppt. Measurements of hemolymph osmolarity confirmed previous results which demonstrated that at salinties below 20 ppt lobsters are limited osmoregulators; allowing their hemolymph osmolarity to drop as the environmental salinity is reduced, but always maintaining it higher than the ambient osmolarity. All animals exposed to 10 ppt, at 15 °C, were capable of surviving for at least 72 h. There was a nearly linear increase in oxygen consumption, heart and scaphognathite rates in animals exposed to dilute seawater, with almost a twofold increase in metabolic rate when animals were moved from 20 to 15 to 10 ppt. At the lowest salinity tested (10 ppt) the average oxygen consumption was higher for females than for males. We conclude that at low salinities the energetic demands of osmoregulation are greater for females than males, and for both sexes the physiological stress imposed may determine, in part, their distribution and/or movements in estuarine habitats.

Key words: Estuary; Lobster; Metabolism; Oxygen consumption; Respirometer; Salinity

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SSDI 0022-0981(93)E0153-P

1. Introduction

American lobsters, *Homarus americanus* Milne-Edwards are considered to be poor osmoregulators (Dall, 1980). Nonetheless, their range extends into many bays and estuaries along the North Atlantic coast (Thomas & White, 1969; Briggs & Mushacke, 1979; Munro & Therriault, 1983; Reynolds & Casterlin, 1985; Estrella & McKiernan, 1989; Vetrovs, 1990; Howell & Watson, 1991; Maynard, 1991; Robichaud & Campbell, 1991; Watson & Howell, 1991). These habitats are characterized by large seasonal fluctuations in salinity due to heavy rains and runoff from melting snow, which limits occupation of these areas to species that have evolved appropriate behavioral and/or physiological adaptations (Sanders et al., 1965; Theede, 1975; Vernberg & Vernberg, 1975; Lassere, 1976).

In the upper Great Bay Estuary, N.H., the salinity drops to between 10 and 15 ppt each spring (Nelson et al., 1981, 1982; Loder et al., 1983), which is close to the lethal limit for adult lobsters (McLeese, 1956), and well below the lethal limit for molting individuals and larvae (Scarrat & Raine, 1967; Cobb, 1976; Aiken & Waddy, 1986). Although heavy benthic invertebrate mortalities, including lobsters, have been reported in several estuaries after particularly heavy spring runoffs (Thomas, 1968; Thomas & White, 1969), including in the Great Bay Estuary (Nelson, pers. comm.), it is equally important to understand the survival strategies utilized in normal years. Previous investigations indicate that lobsters may use behavioral mechanisms to avoid low salinity conditions (Munro & Therriault, 1983; Reynolds & Casterlin, 1985; Vetrovs, 1990; Howell & Watson, 1991; Maynard, 1991; Watson & Howell, 1991). In this study, we measured the hemolymph osmolarity, oxygen consumption, heart rate and ventilation rate of lobsters under conditions similar to the Great Bay Estuary during a typical spring runoff, to determine the magnitude of the physiological stress these conditions evoke, and thus the extent to which the osmoregulatory abilities of lobsters might limit their range or influence their distribution.

The lethal levels of salinity, temperature, and oxygen tension for lobsters acclimated to various combinations of these factors have been previously determined (McLeese, 1956; Charmantier et al., 1988) and imply that some intermolt adults and juveniles may be able to tolerate the range of salinities normally found within the estuary. Under "optimal" acclimation conditions in the laboratory (5 °C, 30 ppt salinity, 6.4 mg/l oxygen) the lethal salinity may be as low as 6 ppt. However, this is an unusual case and the lethal salinity is, on average, greater than 11 ppt (McLeese, 1956). McLeese also found that as the temperature increases above 20 °C, tolerance for low salinity decreases up to as high as 16.4 ppt for animals acclimated to approximately 25 °C. Therefore, it would be expected that a low salinity event that occurred in the late spring/summer, when temperatures may reach as high as 25 °C, would be more stressful than one occurring in seasons when the water is cooler.

Most studies of juvenile and adult *H. americanus* metabolism, both in terms of oxygen consumption (McLeese, 1964; McMahon & Wilkens, 1975; Penkoff & Thurberg, 1982) and heart and ventilation rates (Wilkens & McMahon, 1972; Bill & Thurberg, 1985) have been conducted under conditions of invariable, "normal" salinity (≈30–33 ppt). Their metabolic rate rises with increasing activity, feeding, and temperature (McLeese,

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1964; Leavitt, 1987) and also as molting approaches (McLeese, 1956; Penkoff & Thurberg, 1982). However, heart and ventilation rates in *H. americanus* are not affected by moderate reductions in ambient oxygen levels (McMahon & Wilkens, 1975). To our knowledge, no published data are presently available concerning the effect of low salinity on metabolic rate in *H. americanus*.

Several studies have shown that decreasing salinity effects the metabolic rate of crustaceans (Table 1). *Carcinus maenas* shows an increase in oxygen consumption as salinity is reduced (Taylor, 1977) presumably due to the increased energy necessary to actively pump ions. In the amphipod, *Onisimus glacialis*, increasing oxygen consumption was also correlated with decreasing salinity. The authors conclude that "It is questionable whether amphipods could endure such an increase in metabolic rate for long periods, and migration into seawater with higher salinity might be necessary for survival (Aarset & Aunaas, 1990)."

While the American lobster is a poor osmoregulator, in habitats with reduced salinity it does maintain its hemolymph osmolarity higher than the ambient environment. In this study our aim was to indirectly measure how much energy this limited osmoregulation requires, and then use this information to judge if the most energetically efficient adaptation to low salinity is increased active transport of ions or avoidance behavior. We found that lobsters consume more than twice as much oxygen at 10 ppt as compared to 20 ppt which would cause considerable stress during prolonged seasonal drops in salinity. We suggest that behavioral strategies would be more adaptive, under these circumstances, than extended periods of actively pumping ions. Furthermore, we discovered that at 10 ppt female lobsters require more energy than males to maintain the same hemolymph osmolarity. This would make the upper estuary even more stressful to females than it is to males, and may be one of the underlying causes for the observed

Table 1
Changes in metabolic rate for several decapod crustaceans exposed to low salinity

Oxygen consumption			Species	Source	Comments
Δ in ppt	Δ in ml O2/g/h	%increase/ 10 ppt			
30–5	0.0093–0.0178	36.5	*Panopeus herbstii*	Dimock & Groves, 1975	Acclimated to 30 ppt, 10 °C
30–15	0.205–0.293	28.6	*Penaeus japonicus*	Chen & Lai, 1993*	Juveniles at 15 °C
37–10	0.20–0.40	37.0	*Penaeus japonicus*	Dalla Via, 1986	Approx. values
34–12	0.030–0.052	30.3	*Carcinus maenus*	Taylor, 1977	Approx. values
30–15	0.028–0.036	19.0	*Carcinus maenus*	Taylor et al., 1977	Tested at 14 °C
26–2	0.072–0.148	44.0	*Callinectes rathbunae*	Rosas et al., 1989	
35–5	1.6–3.4	37.5	*Callinectes sapidus*	Engel & Eggert, 1974	Approx. values from excised gill
30–10	0.138–0.175	13.4	*Callinectes sapidus*	Findley et al., 1978	Approx. values acclimated to 30 ppt, 20 °C

* See for review of salinity effects on oxygen consumption rates for penaeid shrimp.

domination of the upper Great Bay estuary by male lobsters (Vetrovs, 1990; Howell & Watson, 1991).

2. Methods

2.1. Animals

Animals were collected using standard vinyl-coated wire traps in the Great Bay Estuary, between March and August of 1991 and August and September of 1992. They were held at the Jackson Estuarine Laboratory, Durham, NH, which gets its water from the Great Bay Estuary, until 2 wk before testing, when they were transferred to recirculating aquaria (15 °C, 20 ppt) at the University of New Hampshire Zoology Department. Only adult (75–92 mm CL) intermolt lobsters, stages C4-D (Aiken, 1980), were used because molting appears to increase oxygen consumption and make animals less tolerant of low salinity (Penkoff & Thurberg, 1982). In addition, lobsters were not fed for at least 48 h prior to trials, and the activity of the animals was minimized during physiological testing (McLeese, 1964; Spoek, 1974).

Twenty ppt was used as a baseline salinity level for the following reasons: (1) previous work by McLeese (1956) demonstrated that 100% of the lobsters exposed to this salinity were able to survive; (2) our preliminary experiments indicated that when animals were dropped from 30 to 20 ppt, there was relatively little change in oxygen consumption; and (3) we were attempting to mimic the type of stress they would encounter during a typical spring in the estuary, when the salinity commonly drops from $\approx$20 to 10 ppt.

2.2. Hemolymph osmolarity experiments

Animals of both sexes were housed together (six per experiment) in a recirculating, refrigerated tank maintained at 15 °C and 20 ppt. They were allowed at least 72 h to acclimate to this environment (Dall, 1970). Within this tank two smaller tanks, one at 15 ppt and one at 10 ppt, were inserted so that the temperatures in all three tanks were identical. Salinities in the tanks were checked daily using an osmometer and a temperature compensated refractometer. The experiments were designed to mimic the salinity conditions in the respirometry experiments described below, and thus provide hemolymph osmolarity data that could be compared with changes in oxygen consumption at equivalent salinity values. The protocol consisted of moving animals between tanks so that they consecutively spent 24 h at 20, 15, and 10 ppt. After 24 h in 10 ppt, three animals, chosen randomly, were placed in the 15 ppt tank for 24 h and then in the 20 ppt tank. The other three animals remained in the 10 ppt tank. Hemolymph samples were taken sequentially after 1, 3, 6, and 24 h in each successive salinity to determine how the hemolymph osmolarity changes over time. In a similar experiment on *Panopeus herbstii* it was found that repeated sampling of the same individual compared to sampling each individual only once yielded similar results (Blasco & Forward, 1988). Approximately 1 ml of hemolymph was collected from the arthroidal membranes

at the base of the walking legs using a chilled syringe. Samples were immediately placed on ice to prevent clotting. Osmolarity was measured within 20 min with a Wescor 5100C Vapor Pressure Osmometer.

2.3. Oxygen consumption experiments

The oxygen consumption of single, unrestrained lobsters was measured in a continuous flow, open respirometer (Fig. 1). Movement was kept to a minimum by using a small (3.5″ diameter) chamber, similar in size and shape to burrows found in the field (Atkinson & Taylor, 1988). The animal chamber was covered with clear, red plastic (Wald & Hubbard, 1957), and a black curtain was drawn in front of the entire apparatus to reduce visual disturbance of animals during experiments. However, the clear ends of the tube were left uncovered so that animals could be exposed to a normal photoperiod. A water jacket surrounded the 2-l animal chamber and the 100 ml oxygen electrode chambers to maintain their temperature at 15 °C. A temperature of 15 °C was chosen because it was equivalent to the average late spring temperature in the estuary (Loder et al., 1983).

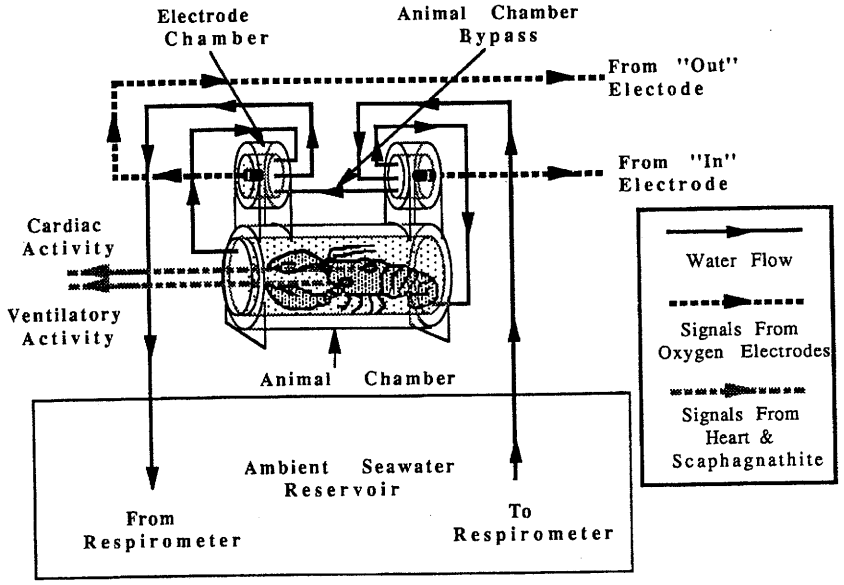

Fig. 1. Design of the flow-through respirometer. Seawater of 20, 15, or 10 ppt flowed sequentially from the ambient seawater reservoir to the "in" electrode chamber, the animal chamber, the "out" electrode chamber, and finally back to the reservoir where it was continuously aerated. All connections between the chambers were made with three-way stopcocks so that the animal chamber could be bypassed to recalibrate or zero the oxygen electrodes. The heart, scaphognathite, and common ground electrodes were run through a rubber stopper in the endcap that was sealed with two O-rings and then placed into one end of the animal chamber. Cardiac and ventilation activity were recorded on a polygraph, while the outputs of the two oxygen electrodes were digitized, stored and displayed on a computer. Note that the electrode and animal chambers were jacketed as shown, however, the plumbing for the recirculating 15 °C seawater, used to maintain these chambers at a constant temperature, is not shown for the sake of simplicity.

Seawater with a salinity of 10, 15 or 20 ppt was pumped from a 15°C holding tank to the electrode and animal chambers using a Masterflex peristaltic pump. The oxygen solubility values used for the different salinities were 20 ppt = 6.30 ml/l, 15 ppt = 6.50 ml/l, 10 ppt = 6.70 ml/l (Green & Carritt, 1967). The rate of flow varied between individuals, from ≈120–160 ml/min (7.2–9.6 l/h), depending on the oxygen demand of the animal. The flow was set in the control run, and kept constant throughout the experiment, so that the oxygen concentration of the water leaving the animal chamber was no less than half the value of the water entering the chamber (≈3 ml/l). This prevented the chamber from becoming hypoxic, which would have had additional affects on the physiology of the animal (MacMahon & Wilkens, 1975). Transitions from one salinity to the next occurred at the rate of ≈0.20 ppt/min. Salinities of the outflow were monitored intermittently using a temperature compensated refractometer or a conductivity meter.

The oxygen tension of the water entering and leaving the chambers was measured with Strathkelvein polarographic oxygen electrodes (electrode model no. 1302; meter model no. 781). The analog outputs of the oxygen meters were digitized, stored, and displayed on a computer using an 8-channel analog-digital converter and the oscilloscope simulation program MacScope. The oxygen concentration was measured initially in the "in" electrode chamber receiving completely oxygenated water. The water then ran from this chamber to the animal chamber and the oxygen concentration of the water leaving the animal chamber was measured by the "out" electrode, located in the out electrode chamber. These values could then be subtracted to determine how much oxygen the lobster extracted from the water as it passed through the animal chamber. These measurements were then converted to oxygen consumption values using the following equation:

$$\text{ml}O_2/\text{g/h} = \frac{\{[O_2^{\text{in}}(\text{ml/l}) - O_2^{\text{out}}(\text{ml/l})] \times \text{flow rate(l/h)}\}}{\text{wt of animal (g)}}$$

where O_2^{in} = oxygen tension measured at the "in" electrode, and O_2^{out} = oxygen tension recorded at the "out" electrode. Weight (wt) of animal was obtained after each trial by shaking and blotting the animal dry and then weighing it on a triple beam balance. Weight loss during a trial was assumed to be negligible. Oxygen consumption measurements were taken after 24 h at each salinity and small variations were minimized by averaging the data over at least 30 min for any one "data point" at a specific salinity for any individual (Hayes et al., 1992).

Following at least 2 wk of acclimation at 20 ppt, lobsters were placed in the animal chamber, and allowed to acclimate to the apparatus for at least another 24 h at 20 ppt and 15 °C. Sample sizes for subsequent analyses were as follows: (1) oxygen consumption of animals sequentially exposed to 20, 15, and 10 ppt ($n = 11$); (2) heart and scaphognathite rates of animals exposed to 20, 15, and 10 ppt ($n = 7$); (3) oxygen consumption, heart, and scaphognathite rates of animals spending one day at each progressive salinity from 20, to 15, to 10, back up to 15, and then returning to 20 ppt ($n = 4$). Lobsters remained in the respirometer for the entire experiment which lasted from 3–5 days. Most of the data illustrated in this paper was obtained during the final hour spent at each salinity; that is, after 24-h exposure to a given salinity.

2.4. Ventilation and heart rates

Oxygen consumption was used to indirectly measure relative changes in metabolic rate and throughout this manuscript we use the terms interchangeably. However, the two terms are not identical and it is certainly possible that there were times when our oxygen consumption measurements did not fully reflect 100% of the ongoing metabolic activity. Heart and ventilation rate are also sensitive measures of metabolic rate in crustaceans (Wilkens & MacMahon, 1972; MacMahon & Wilkens, 1975; Hume & Berlind, 1976; Cumberlidge & Uglow, 1977; Dyer & Uglow, 1977; Mercaldo-Allen & Thurberg, 1987; Hamilton & Houlihan, 1992). To confirm that changes in oxygen consumption were related to variations in oxygen uptake and circulation, we also monitored the heart and ventilation rates of several animals while they were in the respiration chambers. A pair of copper wire electrodes was implanted dorsal to the cervical groove to record heart activity and another pair was placed laterally above one of the branchial chambers to monitor scaphognathite movements. Signals were amplified and displayed on a Grass Model 7D Polygraph, and simultaneously transformed into instantaneous rate by a tachograph. The output of the tachograph was displayed on the polygraph along with the original heart and scaphognathite signals, and also digitized and stored along with the oxygen consumption data.

To confirm that the signal recorded from the lateral electrodes was an accurate indicator of gill bailer activity, simultaneous recordings were obtained with the Grass Polygraph and a UFI model 2991 impedance transducer (Dyer & Uglow, 1977; Bill & Thurberg, 1985) using electrodes implanted at the same location in the carapace. This technique verified that the signal was representative of water flow through the branchial chamber and thus a valid indicator of ventilation.

Heart and scaphognathite activity, as well as oxygen consumption, were measured after 24 h at each successive salinity. Measurements were also taken for 1 h prior to, and 2 h after, the transition to the next salinity. To assess any short term effects of salinity change during the transition period, short samples of heart and scaphognathite rate were taken throughout each trial.

3. Results

In both male and female lobsters, decreases in hemolymph osmolarity paralleled reductions in ambient osmolarity (Fig. 2). There were no significant differences between the sexes in their ability to maintain their hemolymph slightly hyperosmotic to the surrounding seawater ($p > 0.70$, independent t-tests). However, the lobsters always regulated their internal osmolarity at a level that was 50–100 mOsm higher than ambient levels ($p < 0.05$ for both sexes at all salinities tested, except for females at 20 ppt, where $p = 0.075$, independent t-tests). Thus, as shown by Dall (1970), lobsters are limited osmoregulators at salinities below 20 ppt.

The degree to which lobsters osmoregulate seems to be related to the amount of osmotic stress they encounter. At salinities of 20–30 ppt there is comparatively little difference between their internal osmolarity and the osmolarity of the surrounding

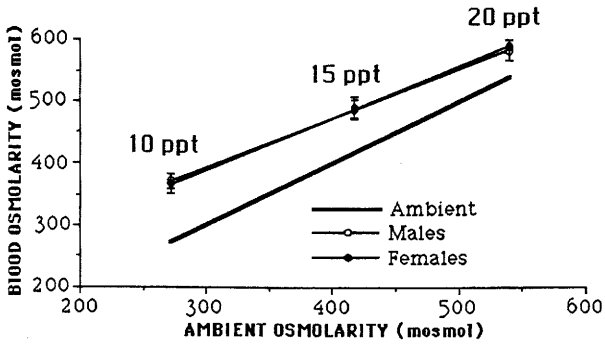

Fig. 2. Hemolymph osmolarity as a function of ambient osmolarity. Samples were obtained after 24- exposure to each osmolarity in succession, from 20 to 15 to 10 ppt. Below 20 ppt, lobsters maintain the internal osmolarity at levels above ambient salinity ($p < 0.05$ for all animals except females at 20 ppt whe $p = 0.075$, independent t-tests), but the hemolymph concentration continues to decrease as the salinity drop Thus, they are considered limited osmoregulators. Each point represents the mean of either 12 males 16 females ± SEM.

seawater (Dall, 1970). However, as the salinity is reduced toward 10 ppt, the differenc between the ambient and hemolymph osmolarities increases. As the salinity drops, mos of the concurrent drop in hemolymph osmolarity occurs within the first hour and the stabilizes at a lower, albeit hyperosmotic, level after ≈6 h (Fig. 3), which is similar t the value of 4 h found for *P. herbstii* exposed to an 8 ppt drop in ambient salinity (Blasc & Forward, 1988). Lobsters are able to maintain this osmolarity set point for severa days, but as shown below, this requires a considerable expenditure of energy at lowe salinities.

There was a close relationship between oxygen consumption, scaphognathite beat and heart rate (Fig. 4). This has also been demonstrated in a number of other marin

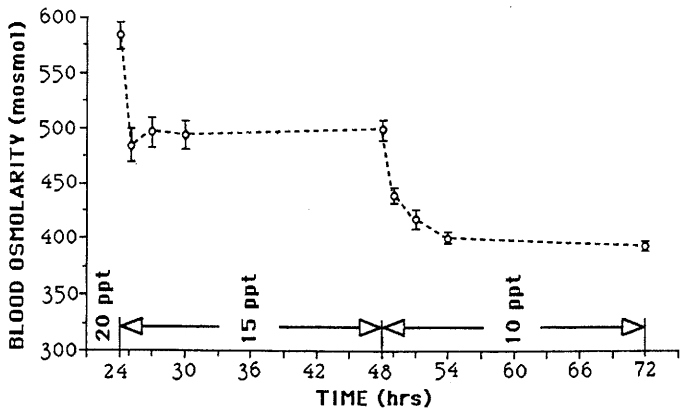

Fig. 3. Changes in hemolymph osmolarity over time. Hemolymph samples were taken after 1, 3, 6 an 24 h at each successive salinity, from 20 to 10 ppt. The most significant drop occurs within the first hou of exposure to the next lower salinity, and there is little change between 6- and 24-h exposure. Each poin represents the mean ± SEM ($n = 23$); except at 25 h ($n = 6$) and 54 h ($n = 12$).

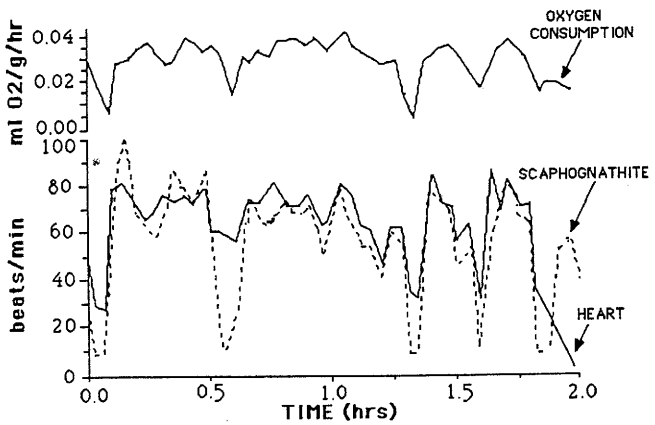

Fig. 4. A continuous 2-h record of oxygen consumption, heart rate, and ventilation rate, recorded from an adult lobster, at 20 ppt and 15 °C. There is a close relationship between oxygen consumption, heart and scpahognathite rates. Heart and scaphognathite activity, along with pO2 values from the respirometer, were obtained as described in the Methods section. In order to induce large fluctuations in respiration and circulation the outside of the respirometer was intermittently tapped. Note that there is a slight delay between changes in ventilation and heart rates and changes in oxygen consumption. This is due to the delay inherent in the flow-through respirometer.

crustaceans (*Cancer pagurus*: Ansell, 1973; *H. gammarus*: Spoek, 1974; *C. maenus*: Cumberlidge & Uglow, 1977; Taylor, 1977; Hamilton & Houlihan, 1992). Covariation of cardiac and ventilatory rhythms in *H. americanus* has been reported previously (MacMahon & Wilkens, 1975; Mercaldo-Allen & Thurberg, 1987) and was observed in these experiments as well (Fig. 4). For example, during periods of little or no scaphognathite activity and associated bradycardia, there were clear drops in oxygen consumption, whereas oxygen consumption increased when heart and ventilation rates were elevated. In *C. maenus* there is a closer correlation between oxygen consumption and ventilation than oxygen consumption and heart rate (Cumberlidge & Uglow, 1977; Taylor, 1977; Hamilton & Houlihan, 1992) and this appears to be true for *H. americanus* as well (Fig. 5). Thus, for certain types of studies, once the precise relationship has been established, heart or ventilation rates could be used to indirectly monitor oxygen consumption.

Exposure of lobsters to low salinities, representative of those found in the estuary, caused an increase in their oxygen consumption, heart, and scaphognathite rates. As the ambient salinity was reduced from 20 to 15 to 10 ppt there was a nearly linear increase in oxygen consumption (Fig. 6), with significant differences between the metabolic rates at each salinity ($n = 11$) ($p < 0.001$, repeated measures ANOVA; Scheffe's F-test). There were also significant differences in heart and scaphognathite rates between 20 and 10 ppt ($n = 7$) ($p < 0.01$, repeated measures ANOVA; Scheffe's F-test) but these differences were not significant between 20 and 15, or 15 and 10 ppt. As the salinity was gradually restored to 20 ppt, oxygen consumption, heart and scaphognathite rates approached the levels found prior to the "low salinity event" (Fig. 7 A,B).

Although male and female lobsters showed a similar ability to maintain their

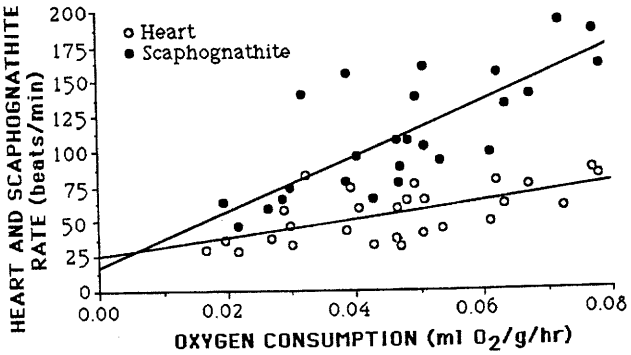

Fig. 5. Correlation of lobster oxygen consumption, heart and scaphognathite rates. Both heart ($Y = 24.04 + 658.24X$, $R^2 = 0.37$) and ventilation ($Y = 17.21 + 1969.20X$, $R^2 = 0.60$) rates were associated with changes in oxygen consumption. All values were taken from lobsters which had been at a particular salinity (20, 15, or 10 ppt), for 24 h. Data points represent values which were averaged over ≈30-min intervals. Data from seven different lobsters were used for this plot to provide a wide range of values.

hemolymph slightly hyperosmotic to the surrounding seawater (Fig. 2), at low salinities there exists an apparent sex related difference in the amount of energy required for this osmoregulatory activity (Fig. 8). There is no significant difference between male ($n = 6$) and female ($n = 5$) percent increase in oxygen consumption at 15 ppt, but at 10 ppt there is a strong trend for the proportional increase in metabolic rate of females to be greater than that observed for males (presumably due to differential osmoregulatory abilities) ($p = 0.08$, independent t-test on log-transformed data). The slopes of the regression lines for the percent increase in metabolic rate at 15 and 10 ppt, from 20 ppt were also significantly different between males and females (ANCOVA, $p < 0.01$). Upon recovery, males ($n = 2$) consumed 0.039 ± 0.0118 ml O2/g/h at 15 ppt and 0.026 ± 0.0041 ml O2/g/h at 20 ppt, whereas females ($n = 2$) consumed 0.057 ± 0.003

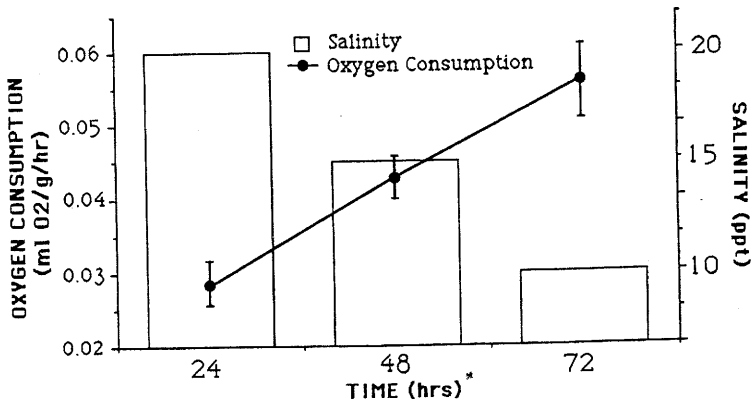

Fig. 6. The relationship between oxygen consumption and ambient salinity. Salinity was gradually dropped in 5 ppt increments each day, from 20 to 15 to 10 ppt. Test animals ($n = 11$) had significantly greater oxygen consumption at each decreasing salinity ($p < 0.001$, repeated measures ANOVA; Scheffe's F-test).

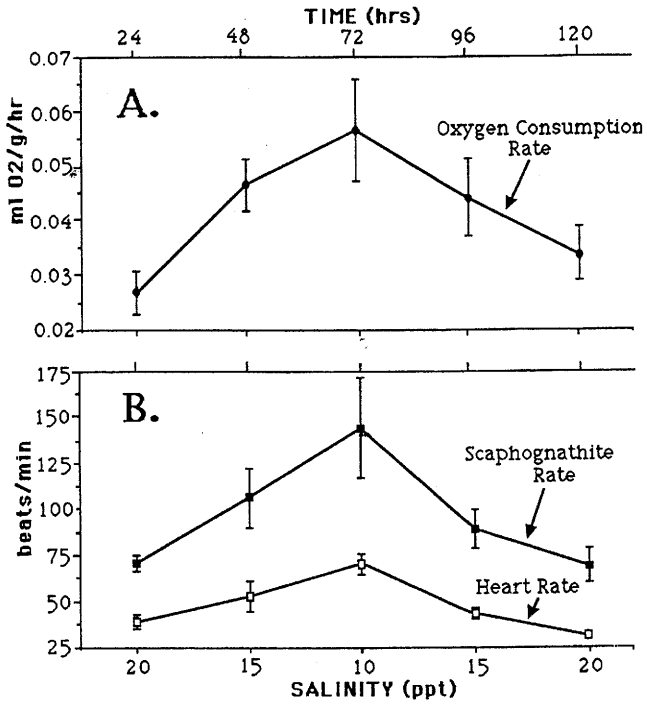

Fig. 7. Oxygen consumption (A), as well as heart and ventilatory (B), responses during decreases, and subsequent increases, in ambient salinity levels. The oxygen consumption, heart rate and scaphognathite rates ($\pm$ SEM) of mature lobsters ($n = 4$) were measured after 24 h of continuous exposure to the following sequence of salinities: 20, 15, 10, 15, and 20 ppt. It is likely that the changes in oxygen consumption, heart rate, and ventilation rate recorded from these otherwise quiescent lobsters are a manifestation of changing osmoregulatory demands.

and 0.045 ± 0.0022 at the same salinities. Because of small sample sizes the significance of this data is unclear, but it seems to indicate that females recovered more slowly than the males as the salinity was subsequently increased. Thus, at salinities below 15 ppt it appears as though male lobsters are more efficient osmoregulators than female lobsters.

4. Discussion

Lobsters and other estuarine invertebrates encounter large seasonal drops in salinity that may last from several days to weeks. Previous studies (Dall, 1970), and those reported here, indicate that lobsters are only limited osmoregulators, allowing their hemolymph osmolarity to drop, but always maintaining it 50–100 mOsm higher than their ambient environment. Osmoregulation in lobsters appears to require a significant amount of energy, especially at the low salinities characteristic of estuarine habitats in a typical spring. In our experiments, at 20 ppt, lobsters consumed 0.029 ± 0.003 ml of oxygen/g/h, which is very similar to the values reported in the literature at compa-

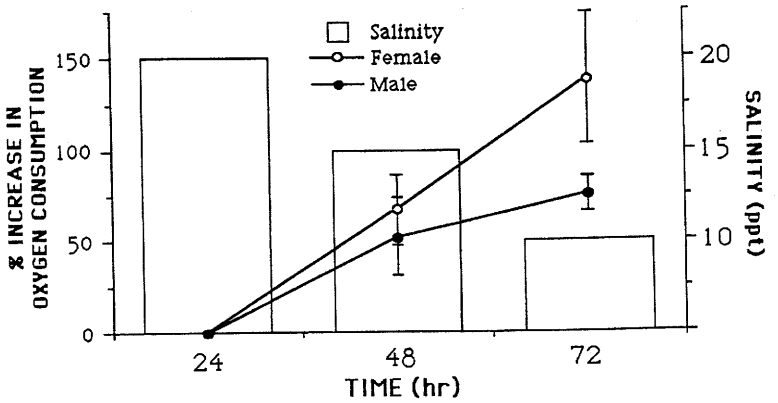

Fig. 8. Oxygen consumption at different salinities for male ($n = 6$) vs. female ($n = 5$) lobsters. Lobsters were continuously exposed to a sequence of salinities from 20, 15, to 10 ppt for 24 h each. The percent increase in oxygen consumption at 15 and 10 ppt from the basal rate at 20 ppt were averaged and plotted for each sex ($\pm$ SEM). Although initially males and females show equivalent responses to reductions of salinity from 20 to 15 ppt, at 10 ppt females show a higher percent increase in oxygen consumption ($p = 0.08$, independent t-test). In addition, females show a significantly greater percent increase in oxygen consumption from 15 to 10 ppt than do males ($p < 0.01$, ANCOVA). These data suggest that males may be more efficient osmoregulators and therefore better adapted to exposure to low salinity environments.

rable oxygen tension, salinity, and temperature levels. Examples of these values include: 0.02–0.36 ml oxygen/g/h (Penkoff & Thurberg, 1982); an average of 0.0395 ml oxygen/g/h at 15 °C (McLeese, 1964); 0.021–0.037 ml oxygen/g/h in *H. vulgaris* (Thomas, 1954); and 0.015–0.035 ml oxygen/g/h in *H. gammarus* (Spoek, 1974) (for a chronological review of *Homarus* spp. oxygen consumption data see Leavitt (1987)). However, in our experiments, when the ambient salinity was lowered to 10 ppt, lobsters consumed 0.056 ± 0.005 ml of oxygen/g/h, almost a twofold increase. These are the only data available on the energetic demands of osmoregulation in *H. americanus*, but data from several other decapod crustaceans indicate that every 10 ppt drop in salinity results in increases in oxygen consumption of between 13 and 100%, depending on the species (Table 1). This range of values could be a reflection of the methods used or the relative ability of each species to osmoregulate. Thus, in lobsters, and perhaps a number of other marine decapods, even though they might be capable of withstanding brief exposure to low salinity conditions, the energetic demands of osmoregulation could limit their ability to occupy certain habitats for prolonged periods of time.

Crustaceans utilize a number of different mechanisms to control the osmolarity of their body fluids, perhaps the most important, and energetically costly way, is the active pumping of ions via Na,K-ATPase and other enzymes across the gills (Dall, 1970; Magnum & Towle, 1977; Neufeld et al., 1980; Lucu, 1990). Passive mechanisms, such as decreased cuticle permeability (Cantelmo, 1977; Lucu, 1990) or the cellular release of organic osmolytes (i.e. amino acids) into the blood (Pierce, 1982; Gilles & Pequeux, 1983), may be equally important in maintaining internal osmolarity and they may also require less energy. Increased urine production alleviates some of the problems of volume regulation at low salinities, but this mechanism will not reclaim lost ions (Dall,

1980; Gilles & Pequex, 1983). Salts that are lost by diffusion must be reclaimed by active transport. However, the actual energetic requirements of this transport is a matter of some debate (Lange et al., 1972; Taylor, 1977). Our data show that osmoregulation in *H. americanus* exposed to low salinities requires a significant increase in oxygen consumption, and, therefore, the evolution of physiological and/or behavioral mechanisms to help reduce this demand would be adaptive for lobsters inhabiting estuaries.

Behavioral osmotic control appears to be utilized by several euryhaline, mobile decapods (Davenport, 1985), to limit their exposure to potentially stressful conditions (*C. magister*, Sugarman et al., 1983; *C. maenus*, McGaw & Naylor, 1992a,b). Active avoidance of low salinity areas implies that animals have the ability to sense changes in osmolarity or the concentration of certain ions; however, little is known about how *H. americanus* senses changes in salinity. Mechanoreceptors, that may also serve as osmoreceptors, appear to be located on lobster antennules (*Panulirus japonicus*; Tazaki & Tanino, 1973) as well as in their branchial chambers (*H. americanus;* Kinnison et al., unpubl.). Presumably they use these receptors to aid in the selection of high salinities over low ones in preference and avoidance experiments.

The seasonal movements of lobsters into the Great Bay Estuary in the late spring/early summer as salinities and temperatures are increasing; their subsequent departure in the summer and fall; and the apparent absence of lobsters in the upper part of the estuary in the spring of each year (Vetrovs, 1990; Watson & Howell, 1991) also support the hypothesis that lobsters use behavioral as well as physiological adaptations for living in estuarine habitats. Tracking lobsters with sonar transmitters and a more detailed analysis of tag/recapture data, immediately before and after major storm events, reveal that lobsters travel short distances down the estuary into deeper water in response to comparatively brief, but unseasonal, drops in salinity. Studies on the costs of locomotion in *H. americanus* have indicated that after 40 min of walking on a submerged treadmill at 0.2–0.9 km/h oxygen uptake was 5.5 times greater than resting values (Jorgensen & Millbrandt, 1993). Similar studies with *C. maenas* (Hamilton & Houlihan, 1992) have demonstrated that moderate locomotor activity results in a 3–5-fold increase in oxygen consumption. Thus, the cost of locomotion is approximately twice the increase observed in our oxygen consumption experiments during a drop from 20 to 10 ppt. Given this difference in energy requirements, the most efficient response to a brief low salinity event is probably to move short distances to deeper water, burrow, and use available energy reserves for osmoregulation. However, during long duration declines in salinity it is probably more adaptive to invest energy in migration to higher salinity areas, rather than remain in low salinity areas and osmoregulate for extended periods. This is not necessarily a "decision" a lobster can make in response to the large, long-duration drops in salinity that commonly take place each spring, because the combined stress of locomotion and constant exposure to water of 10 ppt would probably be lethal. Rather, we suggest they have evolved a life history strategy that involves seasonal migrations; moving down river in the fall, remaining there until after the seasonal spring runoff, and then returning to the upper estuary in the summer. This behavioral adaptation would decrease their chances of being in the upper estuary during times of the year when salinity drops are most drastic and long-lasting.

One of the most striking features of lobster populations in some bays and estuaries is the abundance of males in comparison to females (Briggs & Mushacke, 1979; Munro & Therrialt, 1983; Karnofsky et al., 1989; Vetrovs, 1990; Howell & Watson, 1991). At the New Hampshire coast, the sex ratio is ≈1:1, but the further one samples up into the estuary, the greater the male:female sex ratio, until it reaches ≈4:1 in upper Great Bay (Vetrovs, 1990; Howell & Watson, 1991). One explanation for this skewed sex ratio is that females are not able to osmoregulate as effectively as males, and this limits their survival or restricts their ability to inhabit these areas. It is known that the basal metabolic rate of male and female *H. vulgaris* is the same in full strength seawater (Thomas, 1954) and the oxygen consumption data presented in this paper indicate that male and female *H. americanus* have equivalent increases in metabolic rate when the salinity was dropped from 20 to 15 ppt. However, at lower levels (10 ppt) females appear to use more energy than males to maintain the same osmotic balance (Fig. 8). It has already been demonstrated that lobster eggs and larvae are much less tolerant of reduced salinity than adult lobsters (Scarrat & Raine, 1967; Charmantier et al., 1988; Forward, 1989; Anger, 1991). If, in addition, females are less efficient osmoregulators, then the areas of the estuary with the lowest salinities would certainly be less favorable habitats for females, and this might lead to differences in sex ratios due to reduced survival of females or their avoidance of the upper estuary.

The euryhaline blue crab, *Callinectes sapidus* shows seasonal patterns of abundance and distribution within estuaries that are similar to those of the lobsters of the Great Bay estuary (Hines et al., 1987), and may be the result of the same underlying mechanisms. The sex ratio is skewed toward males in the upper estuary and especially in low salinity tidal creeks (Hines et al., 1987; Hill et al., 1989; Shirley et al., 1990). Tan & Van Engel (1966) have suggested that this distribution is due, in part, to differences in the osmoregulatory abilities of male and female blue crabs. They found that when crabs were exposed to low salinity conditions females were unable to maintain their average hemolymph osmolarity as high as males. It has also been reported that excised gills from male and female blue crabs consume different amounts of oxygen when exposed to very low salinities (Engel & Eggert, 1974). Therefore, as we have suggested for *H. americanus*, it is likely that female blue crabs move toward higher salinity waters in order to protect themselves, their developing eggs and/or released larvae, from osmotic stress (Magnum & Towle, 1977; Hill et al., 1989) and this migratory behavior gives rise to skewed sex ratios in estuarine habitats.

Male and female blue crabs may vary in their ability to osmoregulate because of underlying differences in the ion pumps located on their posterior gills. Neufeld et al. (1980) found that when blue crabs were exposed to low salinity conditions there was a significant increase in gill Na,K-ATPase activity. At the lowest salinity tested the increase was greater in males than in females. This change in Na,K ATPase requires 1–2 wk to be completed and thus it would be a long-term response to chronic low salinity. It remains to be definitively determined if the differential distribution of male and female blue crabs is caused by their differing abilities to osmoregulate. However, sex should undoubtedly be considered as a variable in future studies of osmoregulation and the metabolism of estuarine and marine decapods.

In our experiments we found that male and female lobsters maintained the same

internal osmolarity at all salinities tested, but male lobsters required less energy to accomplish this task at 10 ppt. The synthesis of additional Na/K pumps, or the modulation of existing enzymes would presumably allow males to tolerate lower salinities than females, but it would not necessarily make them more efficient osmoregulators, because of the additional energy required to pump more ions. The hypothesis we favor is that males more effectively utilize various passive mechanisms to help them osmoregulate at low salinities, and this enables them to maintain a given internal osmolarity with less energy expenditure than females. Differences between the sexes may exist in the utilization of various passive mechanisms such as tissue permeability changes (Cantelmo, 1977; Lucu, 1990); cellular release of organic osmolytes (Pierce, 1982; Gilles & Pequeux, 1983); and/or behavioral mechanisms such as "pulsing" (Sugarman et al., 1983) and closure (Cawthorne, 1979; Davenport, 1985). We have observed several events that appear to be similar to pulsing in lobsters exposed to low salinities and further studies are presently underway to determine if this behavior or one of the aforementioned passive mechanisms might account for the differences we observed in male and female oxygen consumption upon exposure to low salinity.

Salinity, or salinity-temperature interactions, have been implicated in the movements and distribution patterns of many estuarine species including several teleosts (Hettler, 1976; Moser & Gerry, 1989; Moser & Hettler, 1989) and decapods (Gutermuth & Armstrong, 1989; Rosas et al., 1989; Pihl et al., 1991). These studies relate environmental influences to intraspecific and interspecific distributional differences. For example, larvae may utilize vertical salinity gradients to orient themselves in the proper currents for mobilization into, or out of, the estuary for settlement in the proper habitat (Forward, 1989; Gunderson et al., 1990; Anger, 1991). Adults and juveniles may also use salinity to trigger migration or movements in a horizontal salinity gradient depending on the time of the year, life history stage (Gunderson et al., 1990), or other covariables such as temperature and oxygen (Venema & Creutzberg, 1973; Vetrovs, 1990). Thus, salinity, temperature, and/or oxygen concentration seems to be at least partially responsible for habitat partitioning within species, as well as between species (Moser & Gerry, 1989; Pihl et al., 1991). In the case of *H. americanus*, we believe that salinity may have a profound effect on the distribution of male and female lobsters in estuarine habitats, and give rise to lobster populations which are strikingly different from those typically found, and extensively studied, in coastal waters.

5. Acknowledgements

This paper is funded in part by a grant from the National Oceanic and Atmospheric Administration (SJ). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. This work was also funded in part by the University of New Hampshire/UMaine Sea Grant Program (WW & WH), and the USDA (Hatch Program) (WW & WH). We thank Drs. J. Boreman, J. Sasner, C. Walker, D.C. Edwards, B. Nutting, and J. Roberts for comments on all aspects of this work. The faculty and staff of the Zoology Departments of the Universities of Massachusetts and New Hampshire, the UMASS/NOAA CMER Program, Environmental Institute, UNH Coastal Marine Laboratory, and the Jackson Estuarine

Laboratory were extremely helpful in providing space and assistance. Comments by two anonymous reviewers also improved the final version of this paper. Special thanks go to C. Becker, D. Lilly, E. Heaphy, J. Delaney, and the NH Lobstermen Association for assistance in collecting and maintaining lobsters. This is contribution number 290; of the Center for Marine Biology/Jackson Estuarine Laboratory series.

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