



The behavior of lobsters in response to reduced salinity

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Abstract

Two experiments were conducted to measure the behavioral responses of lobsters, *Homarus americanus* (Milne-Edwards), to reductions in salinity. In the first experiment animals were placed in a 3 ft diameter tank that was divided in half by plastic mesh. Spontaneously active lobsters were able to move between the two halves of the tank by passing through either of two conduits. The conduits were equipped with optical sensors to monitor the passage of animals, and a perfusion system to control the salinity of the area in, and around, the conduit. When the salinity in the vicinity of both conduits was the same (28–32 ppt), lobsters exhibited no preference for either conduit. However, when the salinity in one of the conduits was lowered, lobsters preferred to pass through the high salinity (20–25 ppt) conduit rather than the one with low salinity (10–15 ppt). In addition, females appeared to be more selective in their preference and exhibited higher overall activity than males when exposed to reduced salinity. In the second experiment, individual lobsters were placed in a shelter at one end of a long seawater table and exposed to seawater of gradually decreasing salinity. The salinity required to cause a movement out of a shelter, i.e. an avoidance response, was recorded. On average, lobsters first ventured small distances ($< \text{one body length}$) out of their shelter when the salinity reached a level of $18.4 \text{ ppt} \pm 1.42 \text{ (SEM)}$, and definitively moved away from their shelter ($> \text{one body length}$) when levels approached $12.62 \text{ ppt} \pm 1.59$. Although it was not statistically significant, females again seemed to be either more sensitive to salinity or found it more aversive, because they tended to initiate movements at salinities greater than those required to influence males. These behavioral data indicate that: (1) adult lobsters are capable of detecting changes in salinity which are comparable to the levels found during natural fluctuations in coastal bays and estuaries; (2) when exposed to low salinity of sufficient magnitude, they attempt to avoid it, and; (3) females appear to be more sensitive to drops in salinity and/or they find it more aversive. Previous studies have demonstrated that estuarine lobster populations are dominated by males and that there are

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seasonal migrations of lobsters into, and out of, estuaries. We conclude that the behavioral responses of male and female lobsters to low salinity may determine, in part, the distribution and movements of lobsters in estuarine habitats.

Keywords: Avoidance; Crustacean; Estuary; *Homarus americanus*; Invertebrate behavior; Lobster; Salinity

1. Introduction

American lobsters, *Homarus americanus*, are traditionally considered to be stenohaline and limited to coastal and offshore habitats, where the salinity is consistently higher than 25 ppt (Dall, 1970). However, despite their limited ability to osmoregulate, recent reports suggest that lobsters commonly occupy estuarine habitats as well (Thomas & White, 1969; Reynolds & Casterlin, 1985; Vetrovs, 1990; Howell & Watson, 1991; Maynard, 1991). Furthermore, the populations that exist in estuaries have an unusually high proportion of male lobsters (Briggs & Mushacke, 1979; Munro & Therriault, 1983; Vetrovs, 1990; Robichaud & Campbell, 1991). In our studies in the Great Bay Estuary, NH, the male:female ratio is greater than 5:1 at sampling stations farthest from the coast, and it gradually decreases to 1:1 at stations on, or near, the coast. It has been suggested that these differences in sex ratio are the result of differential movements of males and females in response to salinity and/or temperature gradients (Vetrovs, 1990; Howell & Watson, 1991; Watson & Howell, 1991).

Extreme reduction in salinity is a common seasonal occurrence in the Great Bay Estuary, and estuaries in general, due to runoff from melting snow and ice, heavy rains in the spring, and occasional storms in the summer and fall (Nelson et al., 1981; Loder et al., 1983). Heavy benthic invertebrate mortalities, including lobsters, have been reported in several estuaries after extreme spring runoffs (Thomas, 1968; Thomas & White, 1969). This is not surprising given the limited osmoregulatory capabilities of lobsters. Under "optimal" experimental acclimation conditions in the laboratory (5 °C, 30 ppt salinity, 6.4 mg/l oxygen) lobsters may have a lethal salinity 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 $\approx 20^{\circ}\text{C}$, tolerance for low salinity decreases up to as high as 16.4 ppt for animals acclimated to $\approx 25^{\circ}\text{C}$. 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 was cooler. In addition, because molting individuals and larvae are even more sensitive to dilute seawater, the estuary is likely to be a lethal environment for these life history stages even during a typical year (McLeese, 1956; Scarrat & Raine, 1967; Cobb, 1976; Aiken & Waddy, 1986; Charmantier & Aiken, 1987; Charmantier, et al., 1988).

Lobsters could enhance their survival in estuarine habitats by undertaking seasonal migrations to avoid areas of the estuary with the lowest salinities during times of the year when conditions are most severe, and during life history stages when they are most intolerant. This hypothesis is supported by field studies of lobster movements in

certain Canadian estuaries (Munro & Therriault, 1983; Maynard, 1991; Robichaud & Campbell, 1991), as well as our own investigations in the Great Bay Estuary (Vetrovs, 1990; Howell & Watson, 1991; Watson & Howell, 1991). In general, lobsters move out of estuaries toward, or into, the ocean in the late summer and fall, and then into, or up, estuaries in the early summer after the spring runoff is largely completed and salinities are returning to "normal" levels.

If lobsters use such a behavioral adaptation to avoid potentially lethal salinities, it is likely that they possess the ability to sense salinity. Therefore, when subjected to a salinity gradient, a seemingly advantageous response would be to avoid potentially dangerous low salinity water and move into regions of higher or normal salinity. The goal of this study was to test this hypothesis by studying the salinity avoidance response of lobsters under controlled laboratory conditions.

We used two different behavioral assays to measure the response of lobsters to reduced salinity. In both experiments, animals avoided areas of low salinity, with females showing a greater tendency to move than males. These results support the hypothesis that lobsters are capable of sensing salinity and they may use this ability to help them move to different areas as the ambient osmolarity drops to damaging levels, or avoid low salinity regions of estuaries during certain times of the year.

2. Methods

2.1. Animals

All lobsters were caught in University of New Hampshire research traps located in the Great Bay Estuary, or in the coastal waters near the UNH Coastal Marine Laboratory, in Newcastle, NH, between March and November, 1991–1993. Animals were held in flow-through seawater tables in the Coastal Marine Laboratory, at ambient temperature (≈ 12 – 15°C) and salinity (≈ 28 – 30 ppt). Only adult (75–92 mm CL) intermolt lobsters, stages C4–D based upon shell rigidity (Aiken, 1980), were used because molting may make animals less tolerant of low salinity.

2.2. Experiments

Behavioral responses were determined by observing preference movements when exposed to high and low salinities concurrently or avoidance movements in an artificial salinity gradient. To obtain the desired salinities in all experiments fresh tap water was added to full strength sea water (28–32 ppt). All salinities were measured with a temperature-compensated refractometer.

2.3. Salinity preference

Individual lobsters were placed into a 3 ft diameter tank that was partitioned into halves by plastic mesh and then the tank was completely covered by sheets of black plastic. Two 12 inch lengths of PVC pipe served as conduits running through the mesh,

providing passageways between the two sides (Fig. 1). These “conduits” were designed as jacketed tubes with water running into the outer tube (6-inch ID) and then into the central opening (4-inch ID) via many small holes drilled in the inner tube. In the center of the conduits were paired infrared optical sensors and emitters. When the sensor detected the pulsing (1/s) infrared beam from the emitter, the circuit associated with the sensors produced a 1-V signal. However, if the beam was tripped (by a lobster passing through the conduit) then the circuit was broken and the voltage output dropped to zero. The output of this circuit was digitized, visualized and stored in computer memory using a hardware/software package called MacScope.

Animals were allowed to move freely in the tank, and they spontaneously moved through the conduits from one side to the other. All movements through the conduits were recorded for each animal throughout a 6 h run. Only animals that responded (i.e. passed through one conduit at least once during any particular trial) were used in subsequent analyses. Each conduit was continuously perfused with water at a flow rate of $\approx 4\text{--}5$ l/min. This water leached into the conduits, out into the rest of the tank, and then out through a standpipe in the center of the tank. Salinities in the “low” salinity conduit were adjusted by mixing fresh water and sea water in a Y-shaped hose connector. The conduits created a local environment of high (25–20 ppt) or low (15–10 ppt) salinity within the conduit and a small distance from either end of the tube. The rest of the tank was well mixed by vigorously bubbling the water at the center of the tank. The salinity at the bottom of the tank, between the conduits, was approximately the median of the range of salinities within the two conduits. Salinities and temperatures within the conduits were tested before and after each run by withdrawing a sample of water with a 50 ml syringe attached to tubing leading to the inside of each conduit.

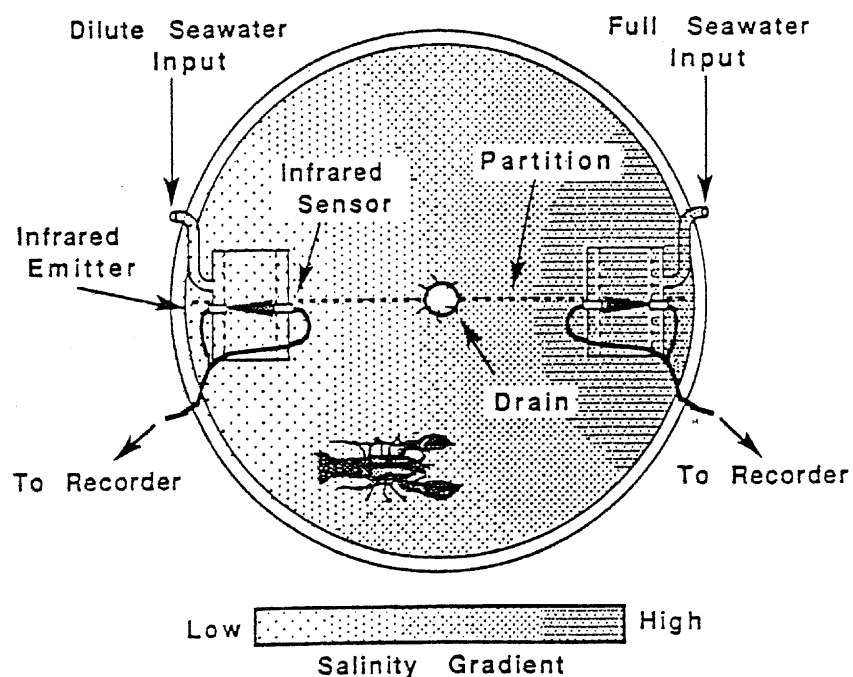


Fig. 1. Top view of the apparatus used to determine salinity preference behavior (see text for explanation).

The plumbing of each conduit was identical so that the salinity in either conduit could be adjusted to avoid a possible nonspecific preference of lobsters for one conduit or the other.

2.4. Salinity avoidance

Lobsters were placed individually within a 10 ft long, 8 inch deep, and 12 inch wide trough surrounded by a black plastic curtain, with unidirectional flow of water from an input at one end to an overflow at the other end (Fig. 2). A 1 × 1 ft board was placed over the end of the trough nearest to the input, and animals, because they were negatively phototactic (MacKenzie & Moring, 1985), would typically reside under this shelter, presumably to avoid the overhead lights.

A gradient maker, which mixed and aerated water from 50 gallon freshwater and saltwater reservoirs, created a repeatable, linear gradient of salinity from 30 to 0 ppt over ≈ 60 min (0.5 ppt/min) (Fig. 5A). This gradually diluted seawater entered at the shelter end of the trough and flowed out the other end of the trough, producing a gradient over time in the shelter, as well as a spatial horizontal gradient within the trough. This system was used in order to avoid some of the problems presented by creating a static salinity gradient (Fivizzani & Spieler, 1978; Moser & Gerry, 1989) to test the responses of benthic, mobile species. There was some minor vertical separation of water within the trough, but, by sufficiently mixing the water and using a shallow depth so that the animal was just below the surface, at least some part of the lobster came in contact with the lowest and highest salinity water in any one area of the trough. Salinities were measured via a tube that was permanently attached near the bottom of the shelter, therefore, all salinity values are conservatively high. Static horizontal gradients can be produced using a Staaland device, where the salinity gradient is also based upon density differences (Reynolds & Thomson, 1974; Fivizzani & Spieler, 1978; Reynolds & Casterlin, 1985). However, the design of the device necessitates barriers along the bottom to compartmentalize volumes of water of progressively lower salinities

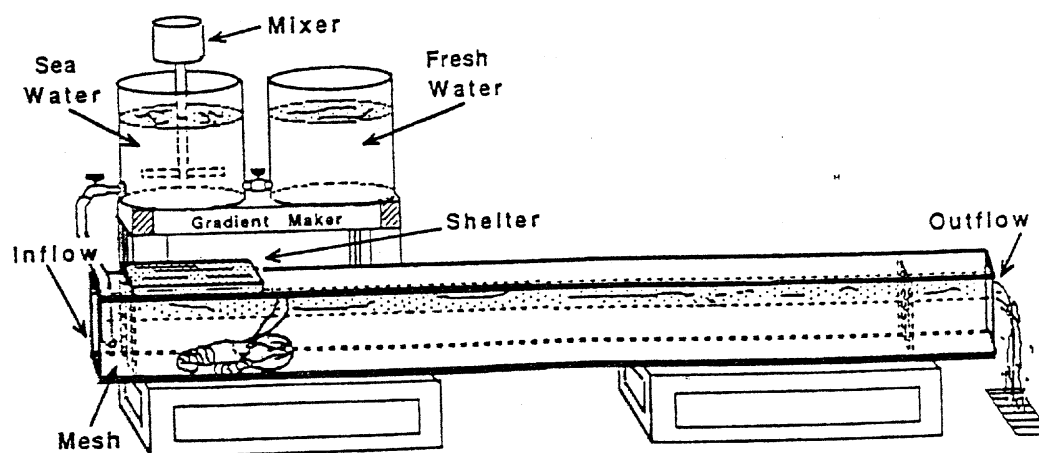


Fig. 2. Apparatus used to determine salinity avoidance behavior (see text for explanation).

and these barriers seem to impede natural movements by a benthic species moving along the bottom.

An experimental trial in the avoidance chamber consisted of > 2 h of acclimation in running sea water and then a 1-h control period during which data was collected while the animals were still exposed to 100‰ seawater. The experimental run was then conducted by exposing the animal to a salinity gradient from 30 to 0 ppt. The experimental run was terminated when the salinity reached 0 ppt, which typically required about 60 min, or when the animal moved out of the shelter, whichever occurred first. Only animals that were not spontaneously active during the last hour of the acclimation period were used for subsequent experimental runs.

During a typical experiment, an animal would remain relatively motionless within the shelter during the control run and then, as the salinity dropped below some threshold, show increased activity within the shelter. We assumed this was an indication that the animal "sensed" the reduced salinity and it usually occurred very quickly after only minor drops in salinity, i.e. 31–28 ppt. This particular experiment was not intended to test this detection threshold, however, more precise experiments are underway in our laboratory to determine these values. This experiment was designed to determine the avoidance responses by lobsters after they have sensed reductions in salinity. These responses generally consisted of an initial movement, of less than one body length, out of the shelter and usually back into the shelter. Then, as the salinity continued to drop, the animal would eventually make what we denoted as a definitive movement, of greater than one body length. This definitive movement would carry the animal out of the shelter completely and usually to the other end of the trough. Salinity values were obtained when the initial and definitive movements occurred by sampling the water within the shelter when they exhibited the aforementioned behaviors.

3. Results

3.1. Salinity preference

When given a choice between moving through high or low salinity passageways (see Fig. 1) all animals tested ($n = 41$) passed through the higher (20–25 ppt) salinity conduits more readily than the lower (10–15 ppt) salinity conduits ($p < 0.01$) (Fig. 3B); or else they did not move at all. Out of 329 passes between the two halves of the chamber by the 25 lobsters that showed some movement, only six lobsters passed through the low salinity conduit, a total of 24 times. Therefore, given 329 chances, 92.8% of the time lobsters chose the higher salinity route. In contrast, during control runs ($n = 42$), with seawater flowing through both conduits, there was no significant difference in the conduit preference of the lobsters tested ($p < 0.01$) (Fig. 3A).

Both male and female lobsters "preferred" high salinity passageways (Fig. 4). However, using the number of times animals passed through a conduit as criteria, female lobsters appeared to be much more active than males at reduced salinity. Of the animals showing some movement, males (18.4 passes/animal/trial) and females (20.7 passes/animal/trial) showed similar activity under control conditions when the average salinity in the tank was ≈ 30 ppt. However, under experimental conditions when the

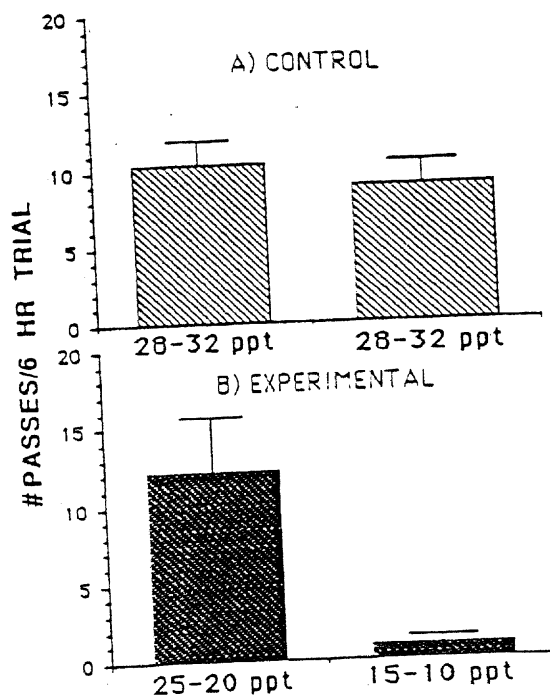


Fig. 3. Preference of lobsters for high vs. low salinity areas. When both conduits were at ≈ 30 ppt, there was no significant difference between the number of passes through one conduit or the other (A). However, there was a significant difference ($p < 0.001$) when the salinity in the vicinity of each conduit was different (25–20 ppt vs. 15–10 ppt) because animals consistently passed through the conduit with the higher salinity (B). This indicates that lobsters can detect areas of low salinity and avoid them.

salinity was in the range of 10 to 25 ppt, females (22.1 passes/animal/trial) were much more active than males (1.7 passes/animal/trial) (Fig. 4). In addition, 50.0% of the males were not used in subsequent analysis because they showed no passes through either conduit, whereas only 26.3% of the females did not move during the experimental trials. This contrasts with the control trials where only 15.4% of the males and 6.3% of the females showed no movement. Thus females appear to have a greater tendency to exhibit behavioral responses to changes in salinity, while males appear to be more sedentary. These data also illustrate that reductions in salinity from ≈ 30 to 20 ppt produce changes in overall activity levels with males becoming much less active and females showing reduced activity. These general changes in locomotory activity are consistent with our unpublished results from studies designed to directly measure such activity changes. Therefore, diluted seawater may produce very general changes in overall activity as well as eliciting avoidance responses.

3.2. Salinity avoidance

Some animals were remarkably hesitant to move out of their shelter despite exposure to dilute seawater. Indeed, 28% of the animals tested did not move out of their shelter even when the salinity reached 0 ppt. It is not clear why these lobsters found the stress of exposure to low salinity less aversive than leaving their shelter. When

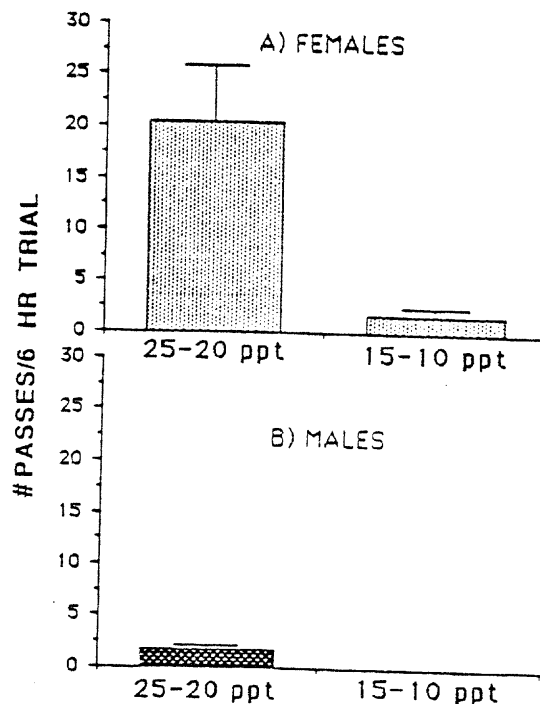


Fig. 4. Salinity preference in male and female lobsters. When exposed to high (25-20 ppt) and low (15-10 ppt) salinities concurrently, both males (B) and females (A) prefer higher salinity regions. In addition, females are comparatively more active than males at low salinities.

animals moved during the 1 hr seawater control run the trial was terminated, and these lobsters ($n = 5$) were released. Our results are based on avoidance threshold values which could only be measured when animals actually moved during the experimental runs (71% of all animals, $n = 31$).

Lobsters appeared to sense decreased salinity after only very small drops in salinity (30 to 28 ppt), as indicated by increased activity within their shelter. On average, lobsters first ventured small distances ($< \text{one body length}$) out of their shelters when the salinity reached a level of $18.4 \text{ ppt} \pm 1.42 \text{ (SEM)}$, and definitively moved away from their shelter ($> \text{one body length}$) when levels approached $12.62 \text{ ppt} \pm 1.59$. The threshold salinity that elicited the initial movement was significantly different ($p < 0.001$ independent t-test) than that required to induce the definitive movement (Fig. 5B).

The salinity avoidance response appeared to be elicited at somewhat different salinity thresholds for males ($n = 14$) and females ($n = 17$). However, these differences were not statistically significant. The initial movement by females occurred at a salinity of $19.6 \text{ ppt} \pm 1.80 \text{ (SEM)}$ which was higher than the threshold of $17.0 \text{ ppt} \pm 2.26 \text{ (SEM)}$ observed for males. The definitive movement also occurred at a higher salinity for females ($14.55 \text{ ppt} \pm 2.45$) than males ($10.5 \text{ ppt} \pm 1.86$). Thus, most of the lobsters examined, both male and female, moved to a different region of the test chamber to avoid exposure to low salinity water. These movements typically, but not always, occurred before the salinity reached a level which could cause mortality with prolonged exposure (McLeese, 1956).

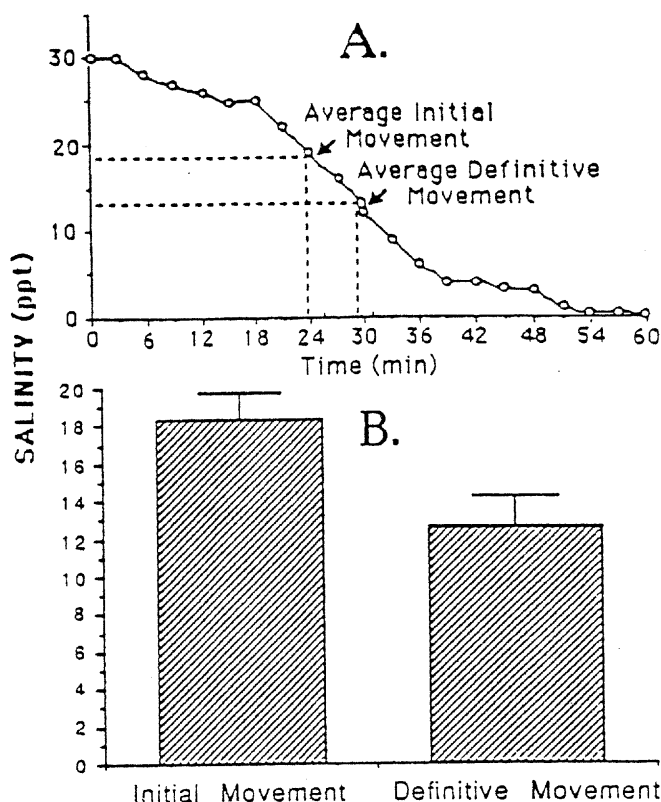


Fig. 5. Avoidance responses of lobsters exposed to a declining salinity gradient. All animals ($n = 43$) were subjected to a salinity gradient from 30 to 0 ppt in a flow-through trough, over ≈ 60 min (A). As the salinity was reduced, lobsters showed two types of responses. Their initial movement was defined as any movement out of the shelter which was < 1 body length and their definitive movement was any movement > 1 body length. The salinity of the water at the location of the lobster was recorded at the time of occurrence of each of these movements (B). Of the animals that showed some response ($n = 31$), avoidance behaviors resulted from salinities which were, on average, above their lethal limits (as determined in separate laboratory studies by McLeese, 1956).

4. Discussion

This study demonstrates that adult American lobsters, *H. americanus* (Milne-Edwards), are capable of sensing and avoiding areas of reduced salinity. If the salinity was lowered in the vicinity of their shelters, most lobsters observed moved to avoid harsh conditions before the osmotic stress reached potentially lethal levels. When lobsters were free to move through areas of high vs. low salinity, they usually selected routes that avoided dilute seawater. In addition, the consistent behavioral differences observed between male and female lobsters suggest that they either perceive low salinity differently or have evolved different strategies to adapt to low salinity conditions.

The sensory mechanisms used by lobsters to detect changes in salinity have received little attention in the past, probably because it has been generally considered that "...both homarid and palinurid lobsters occupy stable, fully marine habitats, are stenohaline, do not normally enter low salinity estuaries, and consequently hold little interest for the student of osmoregulation" (Dall, 1980). Nevertheless, decapods living within

an estuarine environment, characterized by large salinity fluctuations, are likely to have some sensory mechanism to detect salinity, either directly or indirectly (McLeese, 1970; Tazaki & Tanino, 1973; Atema, 1985). Behavioral studies on Dungeness crabs, *Cancer magister*, have demonstrated that they can sense very small (31–29.9 ppt) changes in salinity (Sugarman et al., 1983). The only evidence that receptors for salinity or osmolarity exist in lobsters comes from a study by Tazaki (1975), in which he showed that *Panulirus japonicus* have modified mechanoreceptors on the base of the antennae that may also act as osmoreceptors. Preliminary studies in our laboratory indicate that *H. americanus* is likely to have receptors sensitive to changes in salinity both on the antennules and in the branchial chamber (Jury et al., unpubl. data).

In this study we were simply using movement out of a shelter, or through a conduit, as an assay to determine if lobsters would avoid areas of low salinity. A secondary goal was to measure the approximate magnitude of salinity drop necessary to elicit this behavior. In the salinity avoidance experiment it is likely that because we were attempting to drive lobsters away from something for which they had such a strong attachment, their shelter (Cobb & Phillips, 1980), the values we obtained for our avoidance thresholds were skewed toward the low end of the salinity range. The strong affinity of lobsters for their shelters is illustrated by the fact that a number of lobsters (28%) in the trough experiments did not respond, even when the salinity was lowered to 0 ppt. In addition, there was a considerable amount of variability in the avoidance thresholds of those animals that did respond (e.g. the salinity eliciting a definitive movement varied from 4 to 27 ppt depending upon the individual tested). If we assume that the ability to sense changes in salinity or osmolarity is roughly similar in all adult lobsters then it is likely that at least some of the variability in responsiveness is due to the relative affinity of individual lobsters for their shelters. If one could devise a more sensitive assay, lobsters would probably avoid salinity levels that were much higher than those obtained in this study. On the other hand, if one assumes that most lobsters in the field are in close association with shelters (Cobb & Phillips, 1980), then our average values are probably good indicators of how drops in salinity might affect the overall movements and distribution of this species in an estuary. The data from both experiments indicate that lobsters detect and respond to dilute seawater at levels that are higher than their lethal limits. These data greatly expand upon the observations, made using a modified Staaland device, that *H. americanus* avoid salinities lower than 20 ppt (Reynolds & Casterlin, 1985). Lobster larvae actively avoid salinities below 21.4 ppt which is well above their lower lethal limit of ≈ 13.6 ppt (Scarratt & Raine, 1967). In the adult lobsters used in our experiments, the salinity avoidance response was first observed at 18.42 ppt. Preliminary laboratory studies indicating that *H. americanus* exhibits a bradycardia response to salinity drops from 30–25 ppt (Jury et al., unpubl. data) and our observations in the avoidance experiments of increased activity within the shelter at salinities of > 28 ppt suggest that lobsters can detect very small reductions in salinity. This degree of sensitivity approaches that observed by Sugarman et al. (1983) in *Cancer magister*. Nevertheless, despite sensing that the salinity was dropping, definitive avoidance movements did not occur in lobsters until ≈ 12.6 ppt which appears to be just above their lethal limit. The lower lethal limit of adult lobsters exposed to various dilutions of seawater is generally between 8 and 14 ppt, depending upon temperature,

oxygen and acclimation conditions (McLeese, 1956). Salinities of 10 ppt or lower yield particularly robust physiological changes and are extremely "stressful" even if animals manage to survive during short-term exposure (McLeese, 1956; Jury et al., 1992). Thus, it is adaptive for lobsters to be able to detect and respond to drops in salinity before they reach levels that are potentially lethal, as occurs during a typical spring in the Great Bay Estuary.

Estuarine lobster populations undergo seasonal changes in abundance which are correlated with fluctuations in temperature and salinity (Vetrovs, 1990; Howell & Watson, 1991; Watson & Howell, 1991). Furthermore, several groups have documented differences in the composition of lobster populations within estuaries, such as the large number of males as compared to females (Briggs & Mushacke, 1979; Munro & Therriault, 1983; Vetrovs, 1990; Howell & Watson, 1991; Robichaud & Campbell, 1991). It is our contention that these differences can be partially explained in terms of behavioral responses of lobsters to reductions in salinity. Salinity, or salinity-temperature interactions, have been implicated in the movements and distribution patterns of many species residing in estuaries (Hettler, 1976; Reynolds & Casterlin, 1985; Moser & Gerry, 1989; Moser & Hettler, 1989; Gutermuth & Armstrong, 1989; Rosas et al., 1989; Pihl et al., 1991). These studies have demonstrated a relationship between environmental influences and intraspecific, or interspecific, distributional differences. For example, larvae appear to 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). Using the onset of swimming activity in progressively decreasing salinity as an assay of avoidance, Venema & Creutzberg (1973) showed that *Macropipus holsatus* have a reliable mechanism to avoid adverse salinities by rising from the bottom during ebb tides and being carried in the "correct" current direction to higher salinity waters. It has been suggested that the distribution of several species of mobile estuarine macrofauna is, in part, determined by their behavioral responses to natural physiochemical gradients (Reynolds & Casterlin, 1985). It is likely that the seasonal changes in lobster abundance in estuaries, and the predominance of male lobsters, is also due, in part, to seasonal migrations (Campbell, 1986; Vetrovs, 1990; Howell & Watson, 1991; Maynard, 1991; Robichaud & Campbell, 1991; Watson & Howell, 1991). These movements may be controlled and regulated by their ability to detect changes in salinity and avoid stressful and possibly lethal osmotic conditions.

Possibly the most relevant example illustrating how an estuarine habitat can influence the demographics of a crustacean population comes from studies of the euryhaline blue crab, *Callinectes sapidus*. This crab has seasonal patterns of abundance and distribution within estuaries that are similar to the patterns observed in the Great Bay Estuary for lobsters (Hines et al., 1987; Shirley et al., 1990). This appears to be the result of differential migration of females, but not males, to the mouth of the estuary to release their larvae. Lobster larvae are much more susceptible to damage by dilute seawater than adult lobsters (Scarratt & Raine, 1967; Charmantier & Aiken, 1987;

Anger, 1991), and thus it may be adaptive for reproductive females to remain near the mouth of the estuary where conditions are more stable. It is unclear why "nonreproductive" females do not remain in the upper estuary or return there to gain the same estuarine benefits of increased temperatures, food, shelter, etc. (see below), as males. Perhaps, the net "gains" are not as high for females as they are for males because the reproductive and energetic "costs" of low salinity are proportionally greater for females (Jury et al., 1992). We found that females are more active at low salinities than males, and have a greater tendency to avoid areas of reduced salinity. Therefore, in a salinity gradient, such as the one that naturally exists in most estuaries, it is probable that females would tend to be distributed toward the ocean while males could remain in the upper reaches of the estuary, at least during some seasons.

Despite the fact that estuaries are often stressful (Jury et al., 1992) due to seasonal drops in salinity, some lobsters live there throughout the year, and many migrate up into estuaries in the late spring and early summer (Munro & Therriault, 1983; Vetrovs, 1990; Howell & Watson, 1991; Maynard, 1991; Robichaud & Campbell, 1991; Watson & Howell, 1991). They may be utilizing the increased temperatures in the estuary to accelerate molting and growth (Aiken & Waddy, 1986; Hines et al., 1987; Gunderson et al., 1990), which is an explanation often put forth to explain the summer inshore migration of offshore lobsters (Saila & Flowers, 1968; Cooper & Uzman, 1971). Alternatively there may be more food and shelter (Shirley et al., 1990), or reduced competition (Gunderson et al., 1990; Whale & Steneck, 1991) in estuaries. Another speculative theory is that lobsters in the upper estuary may consist of "surplus", subdominant individuals using the estuary as an underexploited, although suboptimal, habitat. A species of echinoderm, *Asterias rubens*, survives both in the North Sea (salinity = 31 ppt) and in the Baltic Sea (salinity = 15 ppt). However, these invertebrates can only reproduce in the higher salinities of the North Sea. Therefore, the movement to the Baltic Sea is assumed to be a density dependent response of "excess" animals from the North Sea population utilizing a suboptimal habitat over a highly competitive habitat with a better physio-chemical environment (Kirschner, 1991). It is possible that "excess" male lobsters, and females to a lesser degree, that are low on the dominance hierarchy move into the estuarine habitat temporarily until they are large enough to be reproductively successful in a more densely populated environment.

Whatever the impetus, the pattern of seasonal migration into, and out of, the estuary is likely to be driven by a combination of temperature and salinity effects. It is possible that the behavioral response of lobsters to salinity may vary with temperature, as demonstrated by Taylor et al. (1977) for the shore crab, *Carcinus maenas*. This crustacean osmoregulates more effectively at 10 °C, representative of winter temperatures, than at 18 °C, representative of summer temperatures. However, crabs acclimated to 10 °C are more active in response to rapid decreases in salinity than those acclimated at 18 °C. This suggests that these crabs exhibit different avoidance responses depending upon the season, and it is certainly an issue that should be addressed with *Homarus* as well. This may explain why animals move into a salinity gradient in the late spring/early summer, and down a salinity gradient toward the ocean in the fall.

In conclusion, salinity appears to be one of the most important factors dictating the abundance and distribution of *H. americanus* in estuaries. The salinity avoidance

responses exhibited by all lobsters examined may strongly influence the seasonal movements of lobsters in the salinity gradients characteristic of estuaries. While this behavior may not explain the migration of animals to deeper water in the summer and fall, it could account for their avoidance of the upper estuary in the spring. The more robust salinity avoidance behavior of females relative to males may also account for the paucity of large reproductive female lobsters in the upper estuary. Therefore, the previously undocumented ability of adult lobsters to discriminate between water of different salinities, and avoid potentially lethal conditions, may allow them to take advantage of a habitat that has been considered to be far too stressful for this somewhat "stenohaline" animal.

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