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Lobster movements in an estuary

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Abstract The extent to which the American lobster, *Homarus americanus* (H. Milne-Edwards), utilizes estuarine habitats is poorly understood. From 1989 to 1991 we examined lobster movements in and around the Great Bay estuary, New Hampshire using tag/recapture and ultrasonic telemetry. A total of 1212 lobsters were tagged and recaptured at sites ranging from the middle of Great Bay, 23.0 km from the coast, to Isles of Shoals, 11.2 km offshore. Twenty-six lobsters equipped with ultrasonic transmitters were tracked for periods ranging from 2 weeks to > 1 year. Most lobsters moved < 5 km toward the coast, with those furthest inland moving the greatest distance. Lobsters with transmitters moved in a sporadic fashion, with residency in one area for 2 to 4 weeks alternating with rapid movement to a new location (mean velocity = 0.3 km d^{-1} , 1.8 km d^{-1} max.). Site of release influenced distance moved, but there was no significant relationship between lobster size and distance traveled, days at large, or rate of movement. Most movement into the estuary occurred in the spring, while during the remainder of the year there was a strong tendency to move downriver, toward the coast. These seasonal migrations of estuarine lobsters may enhance their growth and survival by enabling them to avoid low salinity events in the spring and fall, and to accelerate their growth in warmer estuarine waters during the summer.

Introduction

Estuarine habitats are characterized by widely fluctuating daily and seasonal changes in temperature and salinity, and some crustaceans, such as blue and Dungeness crabs, undergo seasonal migrations which may optimize their survival and growth (Diamond and Hankin 1985; Hines et al. 1987; Archambault et al. 1990; Gunderson et al. 1990; Smith and Jamieson 1991). Females move from estuaries toward the coast, or from bays to offshore areas, and release larvae; juveniles move into estuaries during the warmer months; and males and females move up into the estuary in the spring, where they molt and mate. Similar patterns have been observed in other estuarine crabs, suggesting this life history strategy is adaptive for estuarine crustaceans (*Macropipus holsatus*, Venema and Creutzberg 1973; *Scylla serrata*, Hyland et al. 1984; reviewed by Herrink 1983).

The American lobster, *Homarus americanus*, is considered to be a limited osmoregulator, and thus restricted to coastal waters (Dall 1970). Each year, in the Great Bay estuary in New Hampshire the salinity falls close to, or below, the lethal salinity for adult lobsters (McLeese 1956). Molting lobsters (Cobb 1976) and larvae (Scarrat and Raine 1967; Charmantier et al. 1987) are even more susceptible to this osmotic stress. Nevertheless, lobsters are abundant in some estuaries and, while heavy mortalities occur during years with a large spring runoff (Thomas and White 1969), it is likely that they are adapted to withstand the large fluctuations in salinity occurring during a typical year. A major goal of the present study was to determine if lobsters undertake seasonal migrations in order to avoid these intermittently deleterious estuarine conditions.

While periodic low salinity events are stressful, and occasionally lethal, elevated estuarine temperatures may be beneficial, because warmer waters enhance growth and development of eggs, larvae, juveniles, and adults (Aiken and Waddy 1986). One explanation of the

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migrations of offshore lobsters to coastal waters in the summer is that they benefit from an increased water temperature (Saila and Flowers 1968; Cooper and Uzman 1971; Pezzack and Duggan 1986; Haakonsen and Anoruo 1994). Similarly, nearshore lobsters could enhance their growth and development by moving relatively short distances into warmer estuarine waters between March and November.

While offshore American lobsters, and spiny lobsters (Herrnkind 1980), migrate considerable distances, SCUBA and tag/recapture studies of lobsters in coastal waters indicate that they seldom move long distances (reviewed by Krouse 1980; Haakonsen and Anoruo 1994; Lawton and Lavalli 1995). The general view is that coastal lobsters inhabit shelters during the day, forage at night, and then return to shelters before dawn (Cooper and Uzman 1980; Ennis 1984a). This behavior seldom results in movement of more than a few kilometers, at least during the time-frame of most investigations. In contrast, some studies indicate that coastal lobsters are capable of moderate to long-distance migrations (Fogarty et al. 1980; Ennis 1984b; Campbell and Stasko 1985; Campbell 1986; Estrella and Morrissey 1997), which are usually correlated with changing seasons and water temperature.

In the present study we examined the movements of estuarine lobsters and the relationship between these movements and changing environmental conditions. We hypothesized that lobsters use behavioral mechanisms to avoid the stressful hypoosmotic conditions common in the spring, and take advantage of the growth and reproductive benefits offered by higher temperatures in the summer. The majority of the data presented is consistent with this hypothesis.

Materials and methods

Great Bay estuarine system

The Great Bay estuarine system in the southeastern corner of New Hampshire, USA receives fresh water from seven rivers, which mixes with salt water entering from the western Gulf of Maine (Fig. 1). The salinity typically ranges from 25‰ in late summer to 15‰ in the spring, and the temperature fluctuates between 0 and 22 °C. In some years, freshwater input is more abundant, due to heavy rains and snowmelt in the spring and intermittent storms in the summer and fall (Jury et al. 1995). These low salinity events can cause salinities in the upper portions of the estuary to fall close to 0‰. The magnitude of temperature and salinity fluctuations varies as one moves from the coast into the estuary. Near the Coastal Marine Laboratory at the mouth of the Piscataqua River (Site P, Fig. 1), the salinity is relatively constant throughout the year, while 23 km up the estuary (Great Bay, Site A) the seasonal fluctuations are much greater. At each study site with UNH research traps (A, C, D, H, P, Fig. 1) temperature and salinity (YSI meter Model 33) were measured every time traps were hauled. In 1991, data were collected from surface and bottom waters. There were always < 2 °C and 2‰ differences between surface and bottom values, due to extensive vertical mixing (Loder et al. 1983). Further details about the Great Bay estuary, and its seasonal variations in temperature and salinity, can be found in Loder et al. (1983), Short (1992), or at the following Web site: http://ekman.sr.unh.edu/ids/ids_data.html.

Lobster collection and tag/recapture data analysis

Groups of 3 to 5 wire-mesh traps were fished, from April to November, 1989 to 1995, at five study sites (A, C, D, H, P, Fig. 1). Traps were hauled two to three times each week, and all lobsters were measured, examined for sex and molt stage, marked with sphyrion lobster tags (Floy Co., Seattle, Washington), and released. Tags were inserted into the cuticle at the junction of the thorax and abdomen, so they would be retained during molting. Each tag had a number to identify the lobster and a phone number so lobstermen could call in returns. Lobstermen were also sent forms, with maps, so they could return recapture data by mail. Additional sublegal, ovigerous, and V-notch lobsters were tagged and released aboard several commercial boats, at locations throughout the estuary, along the adjacent coast, and at the Isles of Shoals (Site Q).

Results are based on recaptures from 11 143 lobsters tagged and released between 1989 and 1991 (Table 1). The number of lobsters tagged and recaptured, in 5 mm size classes based on carapace length (CL), over the course of the study are shown in Fig. 2. A total of 234 sublegal lobsters were recaptured on more than one occasion, resulting in multiple recapture/release events of these lobsters. Data from these lobsters were treated in two different ways. First, to make use of these data in the analysis of individual release/recapture events, we converted each multiple series for a given lobster into as many single release/recapture events as possible. Therefore, some analyses of movement trends are based on 1760 tag/recapture events, from 1212 different lobsters. We also used the data from multiple release/recaptures to test the seasonal movement hypothesis. If a given lobster moved in the direction predicted by the hypothesis during each sequential recapture event, then the data from that lobster were considered to support the hypothesis. If one or more of the movements were in a direction opposite to that predicted by the hypothesis, data from that lobster were considered to contradict the hypothesis.

For some analyses we used only lobsters that moved ≥ 0.5 km ("movers"). For analyses of rates of movement and seasonal movements we did not use tag/recapture events > 3 months apart, because it was difficult to determine when lobsters, which had been at large for longer periods of time, actually moved.

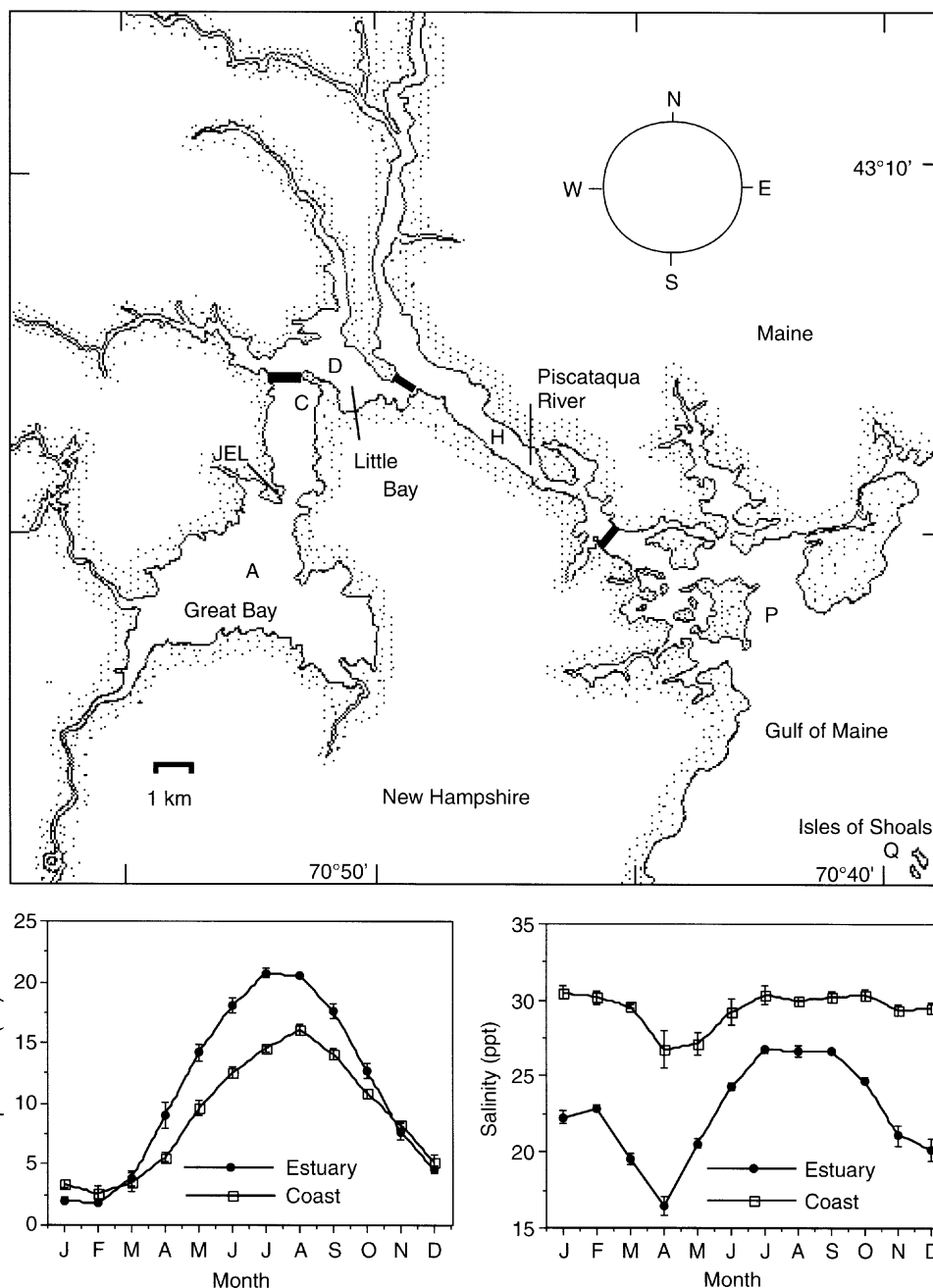
Lobsters tended to move in a linear manner, either upstream or downstream, because channels in the estuary are fairly narrow relative to their length. Therefore, the distance a lobster moved was calculated by subtracting the recapture location from the release location. The middle of Great Bay, farthest up the estuary (Site A), was assigned a value of 0 km, and all other distances were determined relative to this site.

Telemetry

From 1989 to 1991, 26 large lobsters (89.3 ± 0.2 mm CL, range 80 to 98 mm) were equipped with ultrasonic telemetry tags, which transmitted unique coded pulses with a carrier frequency of 75 kHz (Sonotronics, Tucson, Arizona). Transmitters (16 mm diam. \times 60 mm in length, weighing 8 g in water) were attached to the dorsal carapace of lobsters using a combination of duct tape, velcro, and cyanoacrylate glue. Observations of lobsters in the laboratory, and in the field using SCUBA, indicated the transmitters did not impede lobster movements or other behaviors. Individual lobsters were identified by listening for their coded pulses with a directional hydrophone and receiver (Sonotronics, Tucson, Arizona). Ultrasonic tags could be detected at a distance of approximately 0.5 km, and were capable of transmitting for approximately 12 months. Lobsters with ultrasonic tags were captured and released by commercial lobstermen on many occasions; at least four tagged lobsters were caught in traps more than 6 months after release, with their transmitters still intact.

Three times each week lobsters were located, and their position was marked on a nautical chart. The distance they moved every 3 d was calculated by measuring straight-line distances on the chart. We estimate it was possible to determine changes in position > 50 m. Because this investigation focused on large-scale movements, the smallest unit of measurement used in the data analyses was 0.1 km.

Fig. 1 The Great Bay estuary. Traps were located at: Nannie Island (Site A, avg. depth 7.5 m), Fox Point (C, 13.5 m), Goat Island (D, 12 m), Simplex Wire (H, 7.5 m), and CML (P, 10.5 m). The areas described as Great Bay, Little Bay and River are divided by bold lines. Bottom panels show mean monthly salinity and temperature along the coast (data collected at the Coastal Marine Laboratory, CML, near Site P, from 1988 to 1993) and in the estuary (data collected at Jackson Estuarine Laboratory, JEL, from 1989 to 1995). Note the estuary is significantly warmer during the spring and summer, and has a lower salinity during most of the year, especially in the spring and fall



Statistical analyses

Least squares linear regression analyses were used to determine if lobster size (CL) affected days at large (DAL), distance traveled,

and rate of movement, and also to determine if distance traveled was related to DAL. Curvilinear regression analysis was used to describe the relationship between DAL and the number of recaptures. The non-parametric Kruskal-Wallis test, followed by

Table 1 *Homarus americanus*. Summary of lobsters tagged and recaptured between 1989 and 1991. Numbers in parentheses indicate the percentage of the total lobsters in a given year recaptured that number of times

Year	No. tagged	Number of lobsters recaptured:					
		1 time (%)	2 times (%)	3 times (%)	4 times (%)	5 times (%)	6 times (%)
1989	3 450	320 (9.3)	58 (1.7)	21 (0.6)	7 (0.2)	2 (.06)	0
1990	5 444	679 (12.5)	148 (2.7)	50 (0.9)	17 (0.3)	2 (.04)	1 (.02)
1991	2 249	213 (9.5)	28 (1.2)	4 (0.2)	1 (.04)	0	0
1989–1991	11 143	1 212 (10.9)	234 (2.1)	75 (0.7)	25 (0.2)	4 (.04)	1 (.01)

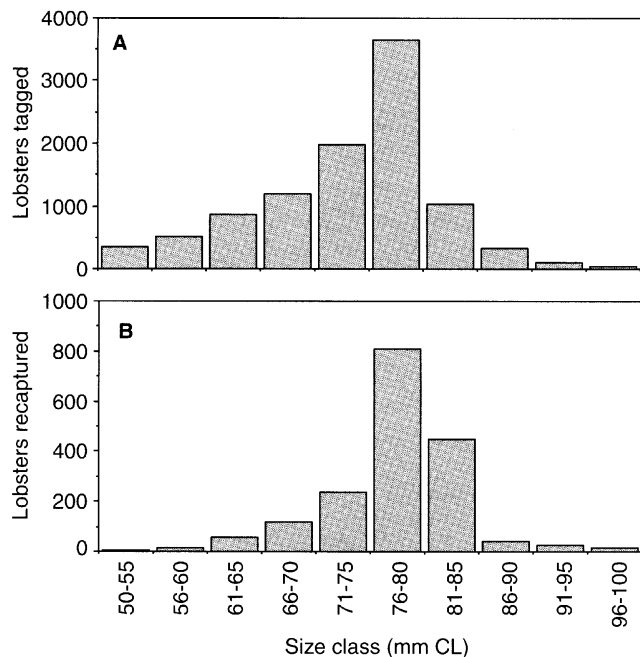


Fig. 2 *Homarus americanus*. Size distribution of lobsters **A** tagged ($n = 11\,143$) and **B** recaptured ($n = 1760$), during the study. A total of 1212 individual lobsters were recaptured, but a portion of these were recaptured and released multiple times, yielding a total of 1760 recaptures. The size distribution reflects the lobsters available and selectivity of the traps. Mean size (CL) of tagged lobsters = 76.6 ± 0.16 mm

Dunn's multiple comparison test, was used to determine if mean distances traveled and mean rates of movement differed between months and locations. This was chosen since the assumptions of analysis of variance (ANOVA) were not met. Because lobster sizes within months were normally distributed, we used ANOVA tests to determine if mean sizes differed between months. However, as lobster sizes were not normally distributed by location, we used the non-parametric test (Kruskal-Wallis) followed by Dunn's multiple comparison test to determine if mean sizes differed between locations. Rates of movement of males versus females, and ovigerous females versus non-ovigerous females were compared using t -tests.

Results

Lobsters tagged and recaptured

During the 3-year study 11 143 lobsters were tagged and released in locations, from the middle of Great Bay (Site A, Nannie Island) to the New Hampshire coastline (Site P) and out to the Isles of Shoals (Q). A total of 1212 (10.9%) lobsters were recaptured and included in the database (Table 1; Fig. 2). Most lobsters were recaptured and reported only once, despite the fact that 92% of the lobsters tagged were sublegal in size (Fig. 2A), necessitating their immediate release. A total of 234 lobsters were recaptured on more than one occasion, with one lobster experiencing six recapture/release events.

Days at large (DAL) and distance moved

Tagged lobsters remained at large for periods ranging from 1 to 863 d (mean DAL = 99.6 d). Most lobsters (73.4%) were recaptured within 100 d of being released, while 26.6% remained at large for longer periods (Fig. 3). The lobster at large the longest was a 72 mm CL male released at Site F in Little Bay in June 1989 and recaptured near the Isles of Shoals (20 km from Site F) in October 1991. The relationship between number recaptured and DAL is best described by an exponential decay curve (Fig. 3).

The longer lobsters were at large, the farther they moved. A least squares linear regression of kilometers traveled versus DAL, using all recaptures, showed a significant ($P < 0.001$) positive relationship ($\text{km} = 2.039 + 0.008 \text{ DAL}$). Because many tagged lobsters did not move at all, there was a great deal of scatter in the data, so only about 5% of the variation in distance moved was explained by DAL ($R^2 = 0.05$). When the relationship between distance traveled and DAL was examined using only lobsters that moved ≥ 0.5 km, there was a similar, significant ($P < 0.001$) positive relationship ($\text{km} = 3.260 + 0.008 \text{ DAL}$), but again, DAL explained only about 5% of the variation in distance moved ($R^2 = 0.05$).

Effects of lobster size

Linear regression analyses were used to determine if lobster size (CL) influenced distance traveled, DAL, or rate of movement (Fig. 4). Lobster size explained only 1% of the variation in distance traveled (Fig. 4A), but the slope of the least squares linear relationship (-0.05) was significantly different than zero ($P < 0.001$), indicating that distance traveled decreased with lobster size. A significant ($P < 0.001$) inverse relationship was also found between DAL and lobster size (Fig. 4B). Smaller lobsters remained at large for longer periods than larger ones, but CL

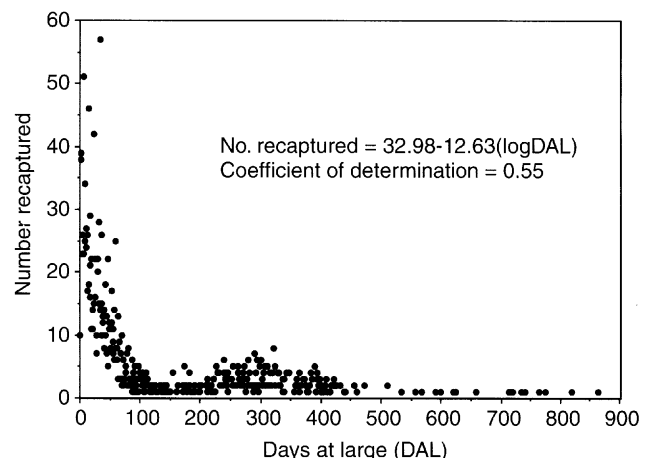


Fig. 3 *Homarus americanus*. Number of recaptures versus DAL. The equation relating these two variables is based on 1760 recaptures

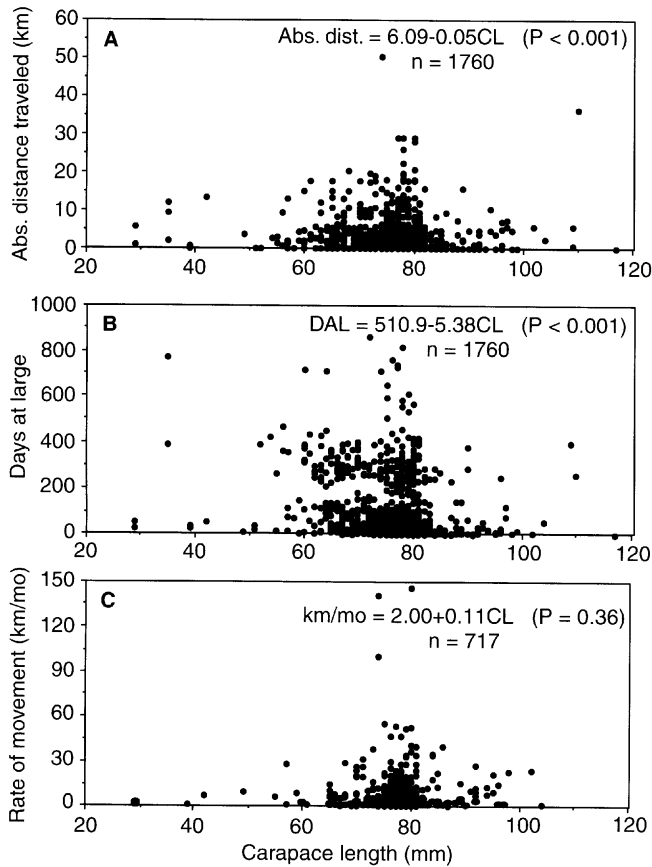


Fig. 4 *Homarus americanus*. Relationships between lobster size and **A** absolute distance traveled, **B** DAL, and **C** rate of movement. Data in **C** are from 717 lobsters recaptured ≥ 0.5 km from their point of release, which were at large ≤ 90 d. *P*-values given in each panel resulted from testing the null hypothesis that the slope of the relationship was zero

explained only 8% of the variation in DAL. This is probably due to trap selectivity. Because smaller lobsters remained at large for longer periods (Fig. 4B), and because this could, in turn, affect distance traveled (Fig. 4A), the relationship between lobster size and mobility was expressed as rate of movement. Using all recaptures ($n = 1760$), regardless of distance moved or DAL, the slope of the linear relationship was positive (0.09), but not significantly different than zero ($P > 0.05$), indicating that lobster size does not affect rate of movement. The relationship between lobster size and rate of movement using only lobsters moving > 0.5 km, and at large for ≤ 90 d ($n = 717$) (Fig. 4C) again showed that there was no significant relationship between lobster size and rate of movement ($P > 0.05$). We conclude that lobster size has a very slight influence on the distance lobsters move and DAL, but not on rate of movement.

Movement by location

Some lobsters were recaptured at the same location ("non-movers"), some were recaptured further up, and some were recaptured further down the estuary toward

the coast. At the uppermost estuarine location all recaptures occurred at the point of release, or further down the estuary (Fig. 5A). Overall, there was a clear tendency for estuarine lobsters to move downriver toward the coast. There were significant differences (Kruskal-Wallis statistic, $P < 0.05$) between the mean distances traveled by lobsters released in different regions of the study area, with the exception of the river and coastal locations (Table 2; Fig. 5B). In four of the five locations the mean distance traveled by "movers" (those that moved > 0.5 km) was toward the coast. Lobsters that moved the furthest downriver were captured and released in Great Bay.

Lobsters in different locations did not have the same tendency to move (Table 2). At three of the five locations $> 50\%$ of the lobsters moved ≥ 0.5 km before they

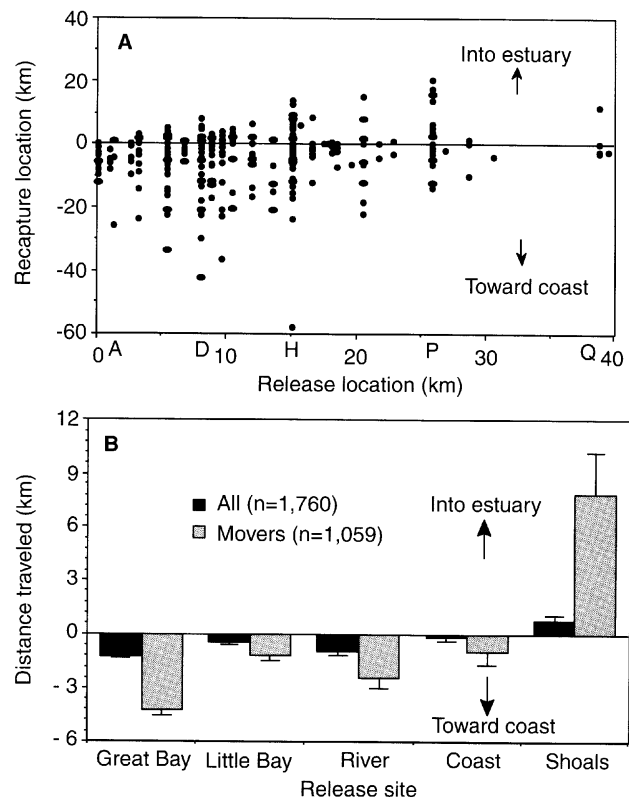


Fig. 5 *Homarus americanus*. **A** Scatter plot of release and recapture locations ($n = 1760$). Release locations range from 0 to 40 km, corresponding to linear distances from the upper estuarine site (Site A, 0 km), to the Isles of Shoals (Site Q) approximately 39 km away. Recapture locations are similarly depicted. Locations of Sites A, D, H, P, and Q shown on the x-axis. Horizontal line at 0 km represents no detectable movement. Negative values indicate lobsters recaptured further toward the coast, or further offshore, than their release location (traveled "downstream"); positive values represent lobsters recaptured further up the estuary than their release location (traveled "upstream"), or toward the coast if they were released offshore. **B** Mean (\pm SEM) distance traveled by lobsters released at different locations, from the upper estuary (Great Bay) to the Isle of Shoals (Site Q). Areas Great Bay, Little Bay, River, and Coast delimited by dark lines in Fig. 1. Positive values, movement into the estuary and negative values, movement toward the coast. Data provided for "movers" (traveled ≥ 0.5 km), and all lobsters

Table 2 *Homarus americanus*. Summary of recapture information based on release location. Numbers in parentheses are one standard deviation. For mean distance traveled (km), negative mean numbers represent movement toward the coast. Movers are defined

as lobsters that moved ≥ 0.5 km from their release location. All locations except Shoals represent more than one site, and these regions of the estuary are delimited by dark lines on the map in Fig. 1 (DAL days at large)

	Great Bay	Little Bay	River	Coast	Shoals
Number recaptured	670	483	275	263	69
Number of movers	378	357	198	113	13
Percent of movers	56.1	73.9	72.0	43.0	18.8
Mean km traveled (movers)	-4.25 (4.77)	-1.21 (5.20)	-2.40 (8.89)	-0.96 (7.70)	7.89 (8.32)
Mean DAL (all)	81.3 (104.0)	84.5 (111.0)	173.6 (166.7)	70.5 (106.7)	93.2 (129.3)
Mean DAL (movers)	89.0 (113.3)	88.9 (108.5)	200.5 (174.9)	101.7 (122.1)	131.7 (129.4)
Mean km d ⁻¹ (movers)	0.21 (0.77)	0.10 (0.19)	0.16 (0.55)	0.21 (0.37)	0.14 (0.02)
Mean CL (mm) (all)	77.5 (0.2)	76.7 (0.3)	71.2 (0.5)	78.1 (0.3)	80.9 (1.0)
Mean CL (mm) (movers)	77.5 (5.9)	76.6 (6.1)	71.0 (9.0)	77.4 (5.2)	85.0 (11.0)

were recaptured, with nearly 75% moving at two of these locations (Little Bay, River). At the Isles of Shoals only 18.8% of the lobsters moved between release and recapture, and many of these were recaptured >1 year after release. In fact, the mean DAL (Table 2) for all Shoals lobsters (93.2 d) was greater than all but one of the other locations (River, 173.6 d). These data suggest that lobster movements are influenced by habitat characteristics.

The mean rate of lobster movement (km d⁻¹) varied significantly between locations (Kruskal-Wallis statistic ($P < 0.001$), ranging from 0.1 to 0.21 km d⁻¹ (Table 2). Dunn's multiple comparison test indicated that Great Bay lobsters moved significantly faster than those in Little Bay and the River ($P < 0.001$), and that Coast lobsters moved significantly faster than those in Little Bay ($P < 0.001$). Isles of Shoals lobsters moved at an intermediate rate, not significantly different than the rate of movement of lobsters in any other location ($P > 0.05$). Although mean lobster size differed significantly (Kruskal-Wallis statistic, $P < 0.001$) between all locations (Table 2), it is unlikely that differences in mean rates of travel were due to differences in lobster size. Lobsters were largest at the Isle of Shoals, and smallest in the River area, yet they traveled intermediate distances relative to lobsters in the other areas. Moreover, large lobsters did not move significantly faster than small lobsters, within the size range examined (Fig. 4C).

Seasonal movements

We had insufficient data in the winter to draw reliable conclusions about movement at this time. The few lobsters tagged in the late fall, and recaptured in the early spring, moved very little, if at all. During the rest of the year (May to November), there was considerable variability in the magnitude and direction of movement in different months (Table 3; Fig. 6). In the early spring (May), the mean direction of movement was positive (up estuary). There was relatively little net movement in June, and from July through October there was a tendency for lobsters to move downriver toward the coast. Statistical differences in the distance traveled by "mov-

ers" each month (Kruskal-Wallis, Dunn's multiple comparison test, $P < 0.05$) were found between: (1) lobsters recaptured in May and those recaptured in July, August, and September; (2) lobsters recaptured in June and those recaptured in July, August, and September; (3) lobsters recaptured in July and August; and (4) lobsters recaptured in August and October. These data suggest a net movement of lobsters downriver toward the coast during most months of the year, except during the spring when there is a tendency to move up into the estuary.

When all recaptures were considered, the rate of movement (km d⁻¹) was significantly different between all months (Kruskal-Wallis, Dunn's multiple comparison test, $P < 0.001$) (Table 3). In May, lobsters moved an average of 0.14 km d⁻¹. This rate decreased in June, rose slightly in July, and peaked in August (0.27 km d⁻¹), when temperature and salinity were the highest (Fig. 1). Rate of movement slowed in the fall to levels comparable to those in the spring and early summer. For lobsters moving >0.5 km, rate of travel (km d⁻¹) was significantly slower ($P < 0.05$) in June than in any other month except November, and slower in July (0.23 km d⁻¹) than in August (0.43 km d⁻¹) ($P < 0.05$) (Dunn's multiple comparison test). Because there was no significant difference (ANOVA, $P > 0.05$) in the mean CL of lobsters recaptured in different months (Table 3), it is extremely unlikely that lobster size affected these seasonal patterns.

Lobsters tagged and recaptured several times

Many sublegal lobsters were captured and released several times. A total of 234 lobsters were recaptured twice, 75 three times, 25 four times, 4 five times and 1 six times. Thus, in 339 instances lobsters were released and recaptured more than once (Table 1). These lobsters provided a limited opportunity to "track" the movement of a specific lobster and to "test" the seasonal movement hypothesis previously described. In 30 (9%) cases lobsters were recaptured at very long or very short intervals, which precluded drawing any conclusions about seasonal trends. In 40% of the remaining 309 recapture

Table 3 *Homarus americanus*. Summary of recapture information based on recapture month. Numbers in parentheses are one standard deviation. For mean distance traveled (km), negative numbers

represent movement toward the coast. Movers are defined as lobsters that moved ≥ 0.5 km from their release location. Only movers at large for ≤ 90 d are reported in this table

	May	Jun	Jul	Aug	Sep	Oct	Nov
Number recaptured	32	279	297	307	216	128	37
Number of movers	17	186	168	193	88	51	14
Percent of movers	53.1	66.7	56.5	62.9	40.7	39.8	37.8
Mean CL of movers	77.6 (2.3)	77.6 (3.1)	77.7 (6.6)	77.6 (4.7)	76.4 (10.3)	77.7 (5.9)	79.4 (7.9)
Mean km traveled (all)	0.78 (1.82)	-0.13 (2.19)	-1.10 (2.98)	-2.27 (6.09)	-0.94 (4.19)	-0.80 (4.71)	0.18 (4.31)
Mean km traveled (movers)	1.43 (2.28)	-0.19 (2.69)	-1.96 (3.77)	-3.60 (7.35)	-2.30 (6.34)	-1.69 (6.78)	0.49 (7.16)
Mean km d ⁻¹ (all)	0.14 (0.23)	0.08 (0.15)	0.13 (0.27)	0.27 (1.06)	0.12 (0.44)	0.09 (0.18)	0.12 (0.34)
Mean km d ⁻¹ (movers)	0.25 (0.26)	0.12 (0.17)	0.23 (0.32)	0.43 (1.31)	0.30 (0.65)	0.22 (0.24)	0.31 (0.49)

events lobsters did not move at all, consistent with data already presented. Fourteen percent moved in a manner that could not be assigned a trend. Of the remaining 142 release/recapture events, 87% (123) demonstrated movement consistent with the hypothesis of an up-estuary migration in the spring followed by down-estuary movement in the summer and fall. In only 6% (19) of the cases lobsters moved in directions different from those predicted by the hypothesis.

Telemetry

A total of 26 lobsters were tracked for an average of 242.7 ± 6.1 d (range = 13 to 489, seven lobsters >1 year). Eighteen were males, because few large females reside in the upper estuary. Of the eight females, four were ovigerous.

Movement consisted of intermittent locomotion punctuated by long periods with little apparent movement (Fig. 7). Lobsters often remained in the same area for several weeks to months, and then moved about 1 km to a new location. On average lobsters stayed in one area for 163.6 ± 4.8 d (range 0 to 475), or 67% of the time they were tracked. This pattern differed between

summer and winter, supporting the contention that lobsters are less active in winter. During the summer, lobsters stayed in one area for 29.3 ± 1.3 d, while in the winter periods of decreased mobility they remained 193 ± 3.9 d.

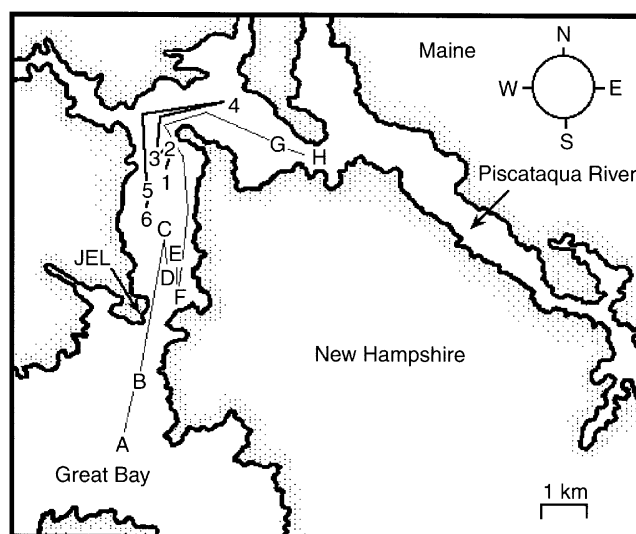


Fig. 7 *Homarus americanus*. Movements of two lobsters tracked in Great Bay estuary with ultrasonic telemetry. One 90 mm CL male lobster was released 16 August 1990 in the middle of Great Bay. Subsequent movements indicated by interconnected letters (A–H). Shortly after release it moved several kilometers downriver to B, where it remained from 17 to 24 August. It was then localized in the following areas on dates indicated: C (28–30 Aug), D (4 Sep–17 Oct), E (21–28 Oct), and F (2 Nov). Between 2 and 9 November it moved rapidly downriver to Little Bay (G), where it apparently spent the winter. Early the following spring (Apr) it was captured in approximately the same area (H). During the 258 d at large it moved 10.5 km, with most movement occurring during a small portion of that time. The track of the other lobster (98 mm CL male, track indicated by 1–6) illustrates movement downriver in the fall and upriver in the spring. It was released in the fall (16 Sep 1989) and after remaining in approximately the same location for 1 month (Location 2, 12 Sep), it was trapped and released again at Location 3 on 6 October. It subsequently moved downriver in late October early November (Location 4, 11 Nov). The following spring it moved up into the estuary (Location 5, 12 May 1990; Location 6, 25 May to 1 Jun). The distance traveled was >4.5 km in 268 d. It may have moved further, but it was not possible to track from November to March due to ice and weather restrictions

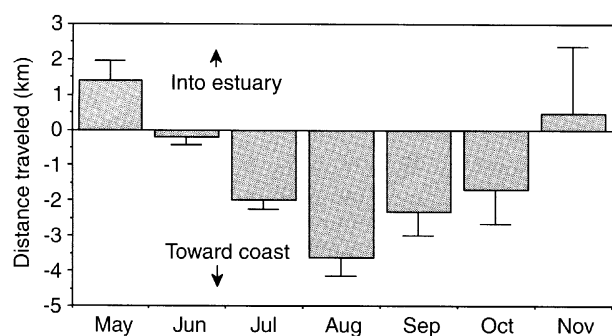


Fig. 6 *Homarus americanus*. Seasonal movements of lobsters that moved ≥ 0.5 km, and were at large for ≤ 90 d ($n = 717$). A plot (not shown) using all lobsters was very similar, but values were reduced due to the large number of lobsters that moved little between tagging and recapture. Positive mean distances represent movement into the estuary relative to release location, while negative distances represent movement toward the coast. Error bars = standard errors

On average, lobsters with ultrasonic transmitters moved 4.68 ± 0.13 km, with several moving >9 km, and some moving very little. As observed during the tag/recapture studies, most lobsters (24 of 26, 92%) moved downriver, 4.13 ± 0.15 km. Many of these were tagged in the middle of the summer (to avoid losing the tags due to molting), in the upper regions of the estuary. In contrast, the few lobsters tracked during the spring moved slightly upriver.

The average rate of travel for all lobsters tracked was 0.13 km d^{-1} . This calculation includes all days when lobsters remained in one area. To calculate their velocity during actual locomotion, while moving from one area to another, periods of apparent inactivity were excluded from the analysis. The average corrected rate of travel for all 26 lobsters was $0.29 \pm 0.02 \text{ km d}^{-1}$. The maximum rate observed was 1.82 km d^{-1} by a large male, which moved 9.1 km downriver in 5 d. Males ($n = 18$) and females ($n = 8$) moved at about the same rate ($0.33 \pm 0.09 \text{ km d}^{-1}$ males, $0.18 \pm 0.04 \text{ km d}^{-1}$ females, *t*-test, $P = 0.36$). Similarly, there was little difference in the rate of travel of ovigerous ($n = 4$) and non-ovigerous ($n = 4$) mature females ($0.16 \pm 0.04 \text{ km d}^{-1}$ ovigerous females, $0.22 \pm 0.05 \text{ km d}^{-1}$ non-ovigerous mature females, *t*-test, $P = 0.35$).

There was a general tendency for lobsters to move up into the estuary in the spring and early summer, and downriver, toward the coast, during the summer and fall (Fig. 7). Lobsters tagged in the summer and fall remained in the general vicinity of their release site during the summer and moved downriver in the fall. Lobsters tagged in the spring often moved upriver. Of most interest were the lobsters tracked during the spring and fall, when they changed their direction of migration. Five lobsters moved downriver in the fall, overwintered within the estuary, and then moved back up into the estuary the following spring (one example shown in Fig. 7). Two lobsters moved upstream in the spring, and back downriver in the summer. The overall trend was a net movement downriver, which was most intense during the late summer and fall, and a shorter upward excursion in the spring. Thus, the results from tracking individual lobsters using ultrasonic telemetry confirmed the tag/recapture data obtained from a greater number of lobsters of a much broader size range.

Discussion

Three types of lobster movements were evident in this study: local meandering or foraging in one area, medium distance (0.3 to 1.0 km), rapid excursions to a new location, and longer migrations. Previous studies have also shown that most coastal lobsters are recaptured <5 km from their site of release after carrying out localized movements of $<0.3 \text{ km d}^{-1}$ (reviewed by Krouse 1980; Stasko 1980; Haakonsen and Anoruo 1994; Lawton and Lavalli 1995). However, 2% of the lobsters tagged in this study moved longer distances. For example, one lobster

traveled 49.6 km in 15 d (3.3 km d^{-1}), 30 traveled >16 km, and 40 moved $>0.8 \text{ km d}^{-1}$. This range of movements is not uncommon. Dow (1974) reported that 6% of the large lobsters tagged in Penobscot Bay traveled >100 km; Campbell and Stasko (1985) found that 19.7% of the mature lobsters released along the coast of Nova Scotia moved >90 km; approximately 10% of the lobsters Fogarty et al. (1980) released along the coast of Rhode Island traveled >35 km; and Krouse (1981) reported that 1% of the lobsters tagged at various locations along the coast of Maine traveled >18 km. It is unclear why some lobsters travel long distances and others very little, and why in some areas a high percentage of lobsters move a great deal while in other regions extensive migration is rare. Estrella and Morrissey (1997) reported a similar, but more extreme, range of distances traveled in their study of lobster movements near Cape Cod, Massachusetts, and they concluded that the population of lobsters they studied included both offshore and nearshore lobsters; with the offshore lobsters moving the greatest distances. It is unlikely that many of the lobsters we tracked originated in offshore waters. A more likely possibility is that lobsters move more often, and for longer distances, in areas with suboptimal shelters, food, temperature, or salinity. In our study lobsters tended to move less in some locations, such as the Isles of Shoals ($>80\%$ did not move between tagging and recapture), than in others, such as Little Bay and the River (26 to 28% did not move). In addition, the lobsters that moved the furthest in the estuary were the ones released in Great Bay, which were exposed to the most extreme fluctuations in temperature and salinity.

The advantage of telemetry is that it reveals daily changes in activity, not just the overall distance moved. The method revealed that the lobsters in our study traveled in spurts, remaining in one location for about 30 d, and then rapidly moving to another area at 0.26 km d^{-1} . This same pattern (meandering at 0.24 km d^{-1} alternating with rapid excursions at 1.2 km d^{-1}) has also been observed while tracking estuarine blue crabs (Hines et al. 1995). The fastest speed we observed using telemetry was 1.6 km d^{-1} , while one tagged lobster apparently moved 3.4 km d^{-1} . This is similar to the migratory speeds of large female lobsters in the Bay of Fundy (2.5 km d^{-1} , Campbell and Stasko 1986), but slower than offshore lobsters which move as fast as 4.2 km d^{-1} (Uzmann et al. 1977). Thus, lobsters are clearly capable of traveling at rates of 1 to 4 km d^{-1} over considerable distances, although slower, local movements are more typical.

For lobsters, the major disadvantages of residency in an estuary are the metabolic demands imposed by periodic drops in salinity, and high temperatures ($>20^\circ\text{C}$). The primary advantage is likely to be enhanced growth and development in warmer estuarine waters (Aiken and Waddy 1986) from March through November. While food, shelter, and other factors are likely to influence the movements of estuarine lobsters,

temperature and salinity probably have the greatest impact (Haakonsen and Anoruo 1994). Our working hypothesis is that seasonal shifts in lobster populations result from the influences of temperature and salinity on the behavior of individual lobsters, causing them to avoid dangerously low salinity in the spring and during storm events (Jury et al. 1994b, 1995), and to seek areas as close as possible to their preferred temperature of 16.5 °C (Crossin et al. 1998) throughout the year, in order to enhance growth and reproduction.

The summer downriver movement of estuarine lobsters is most likely a response to high summer temperatures, and not declines in salinity. American lobsters prefer water between 12 and 18 °C, and avoid water > 20 °C (Reynolds and Casterlin 1979; Crossin et al. 1998). If lobsters move in order to occupy their preferred thermal niche, the expected pattern would be: movement up into warming estuarine water in the spring, movement downriver from the upper estuary when it exceeds 20 °C during the summer, and then further movement downriver in the fall, as the estuary becomes cooler than the coastal waters. This is exactly the pattern emerging from our field studies. Lobsters outside of estuaries also appear to carry out seasonal migrations (Ennis 1984b), and changing water temperatures, or seasonal variations in turbulence, are thought to be the driving force (Pezack and Duggan 1986; Haakonsen and Anoruo 1994).

The upper regions of the Great Bay estuary are approximately 5 to 10 °C warmer than coastal waters in the summer, which has the potential to significantly enhance growth and development. Our preliminary molt frequency and size at maturity data support this hypothesis. Warmer water temperatures increased the molt frequency of the lagoon lobsters investigated by Munro and Therriault (1983), and Dungeness crabs in warm bays grow significantly faster than cohorts in coastal waters (Gunderson et al. 1990). Thus, the thermal preference of lobsters may have evolved, in part, to drive them towards warmer water to enhance growth.

The tendency of female lobsters to seek optimal conditions for incubation and release of larvae may also explain certain movements and patterns of distribution. One of the most striking differences between estuarine and coastal lobster populations is that there are proportionately more males than females in the estuary; with the greatest deviation from a 1:1 ratio in areas furthest from the coast (Vetrovs 1990; Howell et al. in preparation). A similar skewed sex ratio has been reported for lobsters in other estuaries and embayments (Munro and Therriault 1983; Robichaud and Campbell 1991) and for blue crabs in Chesapeake Bay (Hines et al. 1987). One explanation of why males outnumber females in estuaries is differential migration of sexually mature male and female lobsters, with females migrating toward, and remaining at, the coast, where they can release larvae in a more favorable habitat. Studies of the behavior, physiology, and distribution of estuarine lobsters (Munro and Therriault 1983; Wahle 1993; Jury et al. 1994a, b; Houchens 1996; Crossin et al. 1998; Howell

et al. in preparation) have provided considerable data supporting this hypothesis. However, at the present time our movement data are equivocal. Lobsters of both sexes moved comparable distances, at comparable rates, and their direction of movement (up or down the estuary) was similar. We propose that the behavioral mechanisms giving rise to the skewed sex ratio in the Great Bay estuary result from the same type of differential migrations documented for lobsters in the Îles de la Madeleine in Canada (Munro and Therriault 1983). Lobsters of both sexes move out of the estuary in the fall, and a higher proportion of males return the following spring.

The four ovigerous females we tracked moved short distances, comparable to the movements of mature females without eggs (0.16 vs 0.22 km d⁻¹, respectively). A more extensive telemetry study of ovigerous females in Jeddore Harbour and Clam Bay, Nova Scotia indicated that they also move very short distances (< 1.2 km), especially in suitable lobster habitat (Jarvis 1989). Two of the females we tracked increased their activity shortly after releasing their larvae. One traveled very little for several months, then suddenly moved downriver, and when it was captured most of the eggs had hatched. Another female exhibited increased mobility just after the predicted time of hatching, based on staging of eggs when the transmitter was attached. A similar correlation between locomotion and hatching has been reported for offshore lobsters (Saila and Flowers 1968). However, these data contrast with studies showing that some ovigerous lobsters are very active. In coastal Canadian waters, ovigerous females carried out relatively short, seasonal, inshore-offshore migrations, in an apparent effort to maximize egg development through exposure to higher temperatures (Campbell 1986), and along the coast of Cape Cod, ovigerous females moved the farthest of all groups studied (30.3 km, 0.95 km d⁻¹, Estralla and Morrissey 1997).

Although earlier studies (McLeese and Wilder 1958; Reynolds and Casterlin 1979) suggest that lobster locomotion increases at higher temperatures, our data are somewhat ambiguous on this issue. Despite the wide range of temperatures experienced by the lobsters in this study, the average distance traveled in different months was fairly constant, and the relationship between temperature and locomotion was not strong. For example, between May and July the average temperature increased from 12 to 22 °C (Fig. 1), yet there was no significant increase in rate of locomotion (Table 3). The only clear increase occurred in August, typically the warmest month. It is not clear whether increased mobility in August is due to the direct influence of temperature on metabolism, behaviors associated with molting, or avoidance of water warmer than 20 °C (Crossin et al. 1998).

The behavioral responses of lobsters to salinity may also have an impact on their distribution and abundance. Lobsters exhibit aversive movements in response to experimental reductions in salinity, moving out of

their shelters when salinity in the shelter is $<12\text{‰}$ (Jury et al. 1994b). This suggests that in the field lobsters will move downriver when runoff reduces the salinity below 12‰ . In fact, when Hurricane Bob caused a significant drop in salinity in the estuary, lobsters moved toward the coast into deeper, higher salinity water (Jury et al. 1995). We have also found that while lobsters moved upriver in the spring, they typically did not appear in Great Bay until after the salinity became $>15\text{‰}$ in June (unpublished catch data), suggesting that while warmer water drives them upriver, low salinities in the spring slow their progress. Similar complex interactions probably take place in the fall as well. In order to reach a more complete understanding of lobster movements in estuaries it is important to determine how lobsters respond to seasonally relevant, simultaneous changes in temperature and salinity.

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