

W. H. Watson III · A. Vetrovs · W. H. Howell

Lobster movements in an estuary

Received: 26 January 1996 / Accepted: 22 January 1999

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 Herrinkind 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

Communicated by J. P. Grassle, New Brunswick

W.H. Watson III (✉) · A. Vetrovs¹ · W.H. Howell
Zoology Department, Center for Marine Biology,
University of New Hampshire,
Durham, New Hampshire 03824, USA

Present address:

¹Aquatic Research Instruments, P.O. Box 2214, Seattle,
Washington 98111, USA

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 Uzmann 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 Uzmann 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/idents/idents_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 sphyron 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.

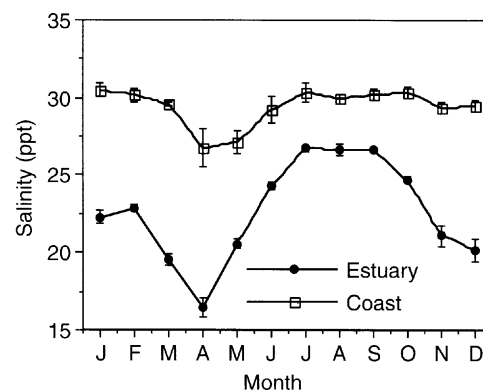
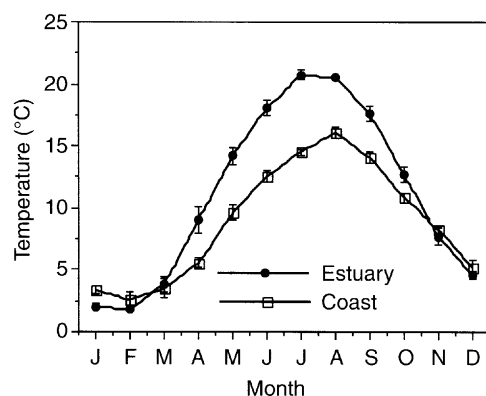
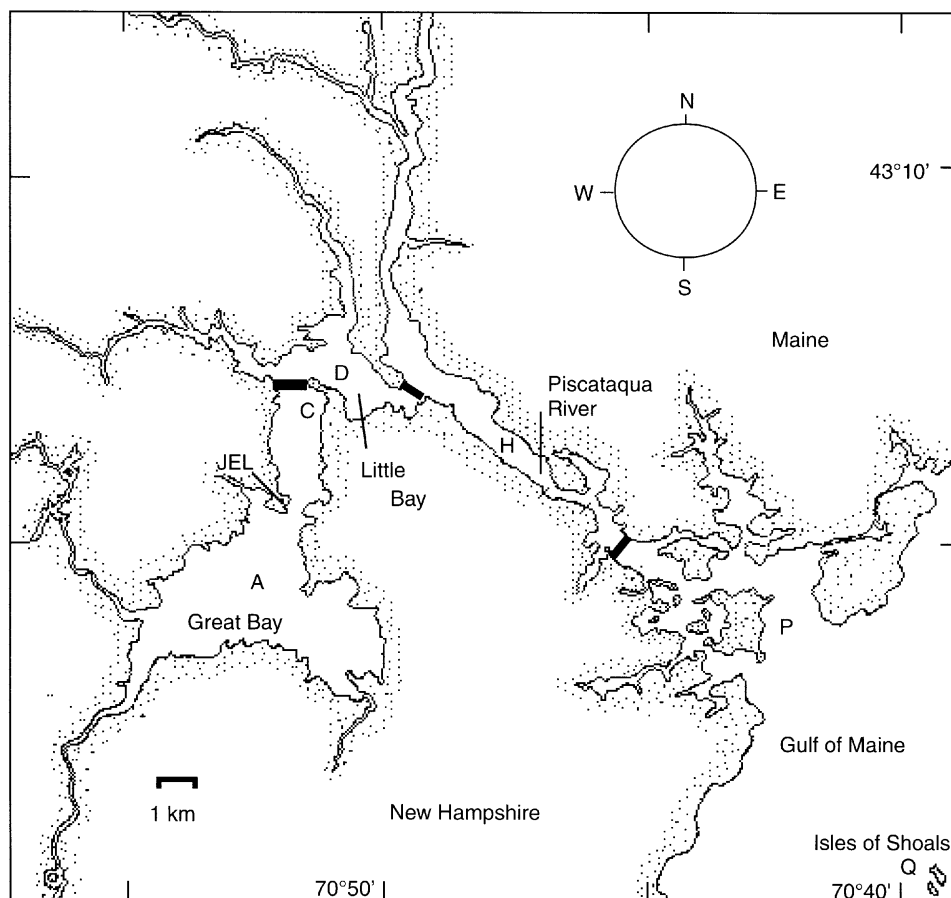
Lobsters tended to move in a linear manner, either upstream or downstream, because channels in the estuary are fairly narrow relative to their length. Therefore, the distance a lobster moved was calculated by subtracting the recapture location from the release location. The middle of Great Bay, farthest 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)

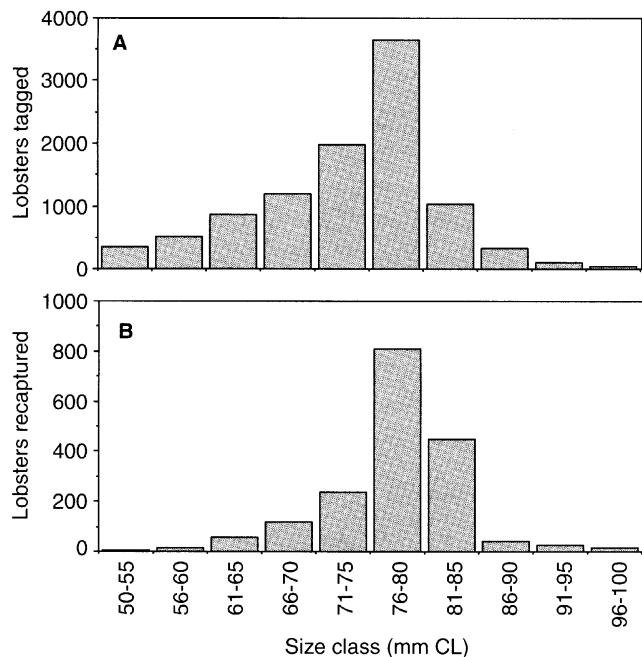


Fig. 2 *Homarus americanus*. Size distribution of lobsters **A** tagged ($n = 11\,143$) and **B** recaptured ($n = 1760$), during the study. A total of 1212 individual lobsters were recaptured, but a portion of these were recaptured and released multiple times, yielding a total of 1760 recaptures. The 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

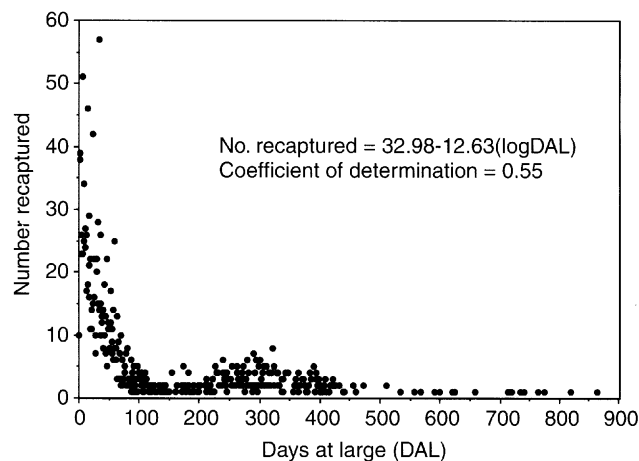


Fig. 3 *Homarus americanus*. Number of recaptures versus DAL. The equation relating these two variables is based on 1760 recaptures

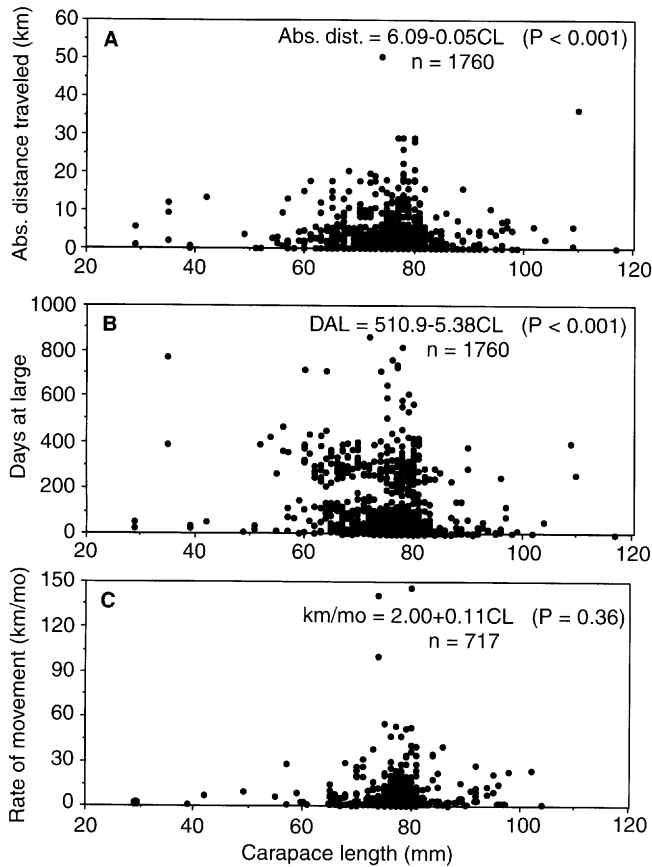


Fig. 4 *Homarus americanus*. Relationships between lobster size and **A** absolute distance traveled, **B** DAL, and **C** rate of movement. Data in **C** are from 717 lobsters recaptured ≥ 0.5 km from their point of release, which were at large ≤ 90 d. *P*-values given in each panel resulted from testing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

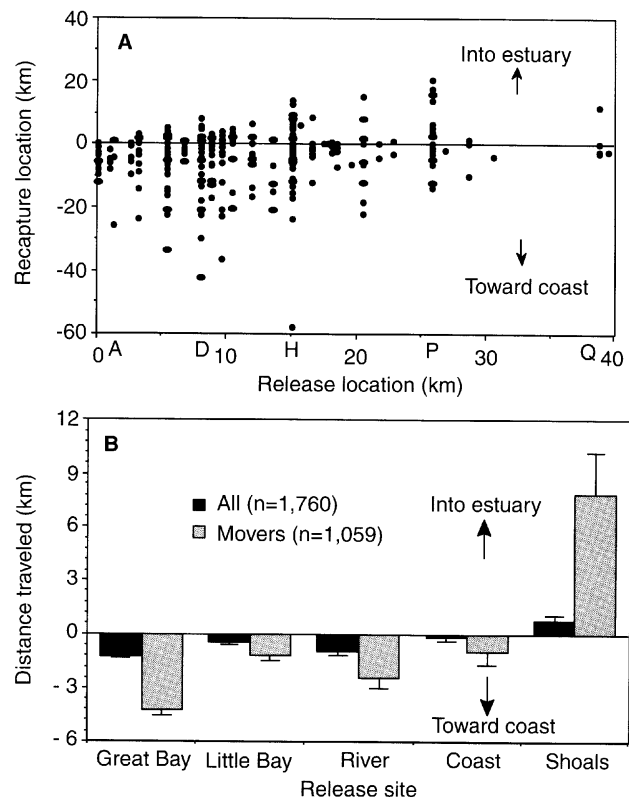


Fig. 5 *Homarus americanus*. **A** Scatter plot of release and recapture locations ($n = 1760$). Release locations range from 0 to 40 km, corresponding to linear distances from the upper estuarine site (Site A, 0 km), to the Isles of Shoals (Site Q) approximately 39 km away. Recapture locations are similarly 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

	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)

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)

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

