# Seasonal movement of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts

**Bruce T. Estrella**
Massachusetts Division of Marine Fisheries
50 A Portside Drive
Pocasset, Massachusetts 02559
E-mail address: Bruce.Estrella@state.ma.us

**Thomas D. Morrissey**
7 Horseshoe Circle
Sandwich, Massachusetts 02563

**Abstract.**—A total of 1,237 tagged American lobsters, *Homarus americanus*, with a carapace length (CL) range of 48 to 198 mm (mean CL of 104 mm) were liberated at three release stations off the eastern shore of Cape Cod, MA, between 1969 and 1971. By 1973, 332 (26.8%) of the tags were returned. Mean time at large was 112.5 days (range 0–897 d).

One hundred and thirty (39.2%) of the recaptured lobsters moved less than 10 km from their points of release. One hundred and fifty-one (45.5%) were recaptured within 10 to 40 km from their points of release; 51 (15.4%) at 40 km or more.

Recapture depths and distances traveled were significantly greater in colder months. The distribution of these recaptures with time, depth, and location indicates seasonal movement to and from the edge of the continental shelf between fall and spring.

The apparent reshoaling of these inshore-tagged lobsters to the eastern shore of Massachusetts in successive summers and the greater movement shown by females with ripe eggs at tagging, versus the movement of sublegal and nonovigerous female classes, suggest that the migration of this group of offshore lobsters is stimulated by seasonal changes in environmental cues in relation to hatching or reproductive needs (or both). Their relation to the Georges Bank–Southern Offshore stock unit, reproductive potential, and extensive seasonal movement into the southern and western Gulf of Maine, represent important considerations for resource managers and emphasize the need for further research on rate of stock interchange.

Manuscript accepted 11 February 1997.
Fishery Bulletin 95:466–476 (1997).

The traditional American lobster, *Homarus americanus*, fishery consists of a small-boat fleet that fishes with traps within a few miles of shore in depths up to 20 fathoms. This inshore fishery is centered in the northern Gulf of Maine and produces annually approximately 47% of the U.S. pounds landed. Massachusetts, the next largest producer, contributes about 28% of U.S. landings. Exploitation of inshore stocks is intensive. In the coastal waters of Maine, over 85% of the commercial inshore catch consists of new recruits (Krouse et al.[1]). In Massachusetts coastal waters, approximately 90% of the inshore catch falls into this category (Estrella and Armstrong[2]).

Prior to 1948, small numbers of lobsters were caught incidentally by trawls in groundfish operations. These incidental catches accounted for less than 1% of U.S. landings. About 1945, trawlers began to fish specifically for lobsters, principally in deep water in the offshore region south of the Gulf between southeast Georges Bank and Hudson Canyon. This fishery was developed moderately and by 1968 offshore lobsters accounted for 16.9% of all U.S. lobster landings (Skud and Perkins, 1969). The introduction of deep-water trap fishing in the late 1960's rapidly accelerated development of the offshore fishery. Vessels that fish with traps have largely replaced the original trawl fleet, and the number of vessels in the offshore lobster fishery have increased greatly. Substantial numbers of vessels in the 40' to 60' class, as well as larger vessels, were built or converted specifically for offshore trap fishing. Offshore landings averaged 24% of U.S. landings (3,400 metric tons [t]) between 1970 and 1974 but declined to a 1978–83 average of 17% or 2,500 t per year (NEFC, 1983). Despite short-term increases (5,000 t in 1990), offshore landings have not accounted for more than 18% of total U.S. lobster landings since the mid 1970's (NEFSC, 1994).

[1] Krouse, J. S., K. H. Kelly, G. E. Nutting, D. B. Parkhurst Jr., G. A. Robinson, and B. C. Scully. 1994. Maine Dep. Marine Resources lobster stock assessment project 3-IJ-61-2. Maine Dep. Mar. Resources, Marine Resources Laboratory, P.O. Box 8, West Boothbay Harbor, ME 04575. Annual Rep., 53 p.

[2] Estrella, B. T., and M. P. Armstrong. 1995. Massachusetts coastal commercial lobster trap sampling program, May–November, 1994. Mass. Div. Mar. Fish., 20 p.

The continued development of the offshore fishery has subjected American lobster in all remaining segments of its range to intensive exploitation. Thus, stock identification and determination of any interrelations between stocks of lobsters is of increasing importance to management of the lobster fishery (Pezzack[3]). Earlier studies indicated that lobsters were relatively nonmigratory. Numerous tagging experiments conducted primarily in more northern inshore areas showed that most lobsters usually remain within a radius of 3–5 km (Templeman, 1935, 1940; Wilder and Murray, 1958; Wilder, 1963; Cooper, 1970; Cooper et al., 1975; Krouse, 1980; Stasko, 1980; Campbell, 1982; Lawton et al., 1984). Accordingly, management practices were based largely on the concept of discrete local stocks. Findings of extensive lobster movement in tagging experiments conducted in offshore areas (Saila and Flowers, 1968; Cooper and Uzmann, 1971, 1980; Uzmann et al., 1977; Fogarty et al., 1980; Campbell et al,. 1984) and in more southern inshore areas (Morrissey, 1971; Briggs and Muschacke, 1984) show significant movement of large, sexually mature lobsters which become intermixed with the inshore resource. Thus, the concept of discrete inshore stocks, characterized by a particular size range or maturity status (Campbell and Stasko, 1986; Campbell, 1989) becomes speculative.

Intermingling of offshore lobsters with inshore stocks off southern New England is shown from recaptures of offshore-tagged lobsters in inshore areas. Cooper and Uzmann (1971, 1980) and Campbell (1986) hypothesized that seasonal depth-related movements are important to the biology of the species in providing optimal temperatures for mating, molting, egg extrusion, and egg development.

In an effort to obtain information that would augment offshore tagging studies off the Massachusetts coast, we undertook a three-year tagging experiment beginning in 1969 in the inshore waters of Cape Cod where previous work (Morrissey, 1971) showed the existence of a seasonal population of large, highly mobile lobsters. Additional lobster tagging in this area in 1984–85 also confirmed highly migratory behavior.[4]

Estrella and McKiernan (1989) described the extensive size range of this segment of the lobster resource, which is only seasonally available east of Cape Cod, as characteristic of an offshore migrant group. This area exhibits the smallest percentage of sublegal-size lobsters in commercial trap catches of any other Massachusetts coastal region (10% compared with 89% in waters off Boston, MA, in 1995[5]). Catch per trap haul of sublegal-size lobster off outer Cape Cod was four to eight times lower than that for other Massachusetts coastal regions sampled in 1994 (Estrella and Armstrong[2]). Outer Cape Cod habitat is not "classic" lobster habitat conducive to supporting a resident (burrowed) resource; it is characterized by expansive sandy bottom and is dynamic owing to its exposure to strong easterly winds. Some local lobster production apparently occurs in the Nauset Marsh area of outer Cape Cod where limited numbers of early benthic-phase lobster have been found (Able et al., 1988). However, it is the larger, more common, offshore migrant lobster which supports the commercial fishermen in this area and which shapes the style of fishing deployed there. Long strings of traps are set parallel to the shoreline to intercept incoming migrations each season. In late spring, traps are initially set by day-boat lobstermen approximately thirteen miles from shore. This gear is gradually fished shoalward as migrations proceed closer to land in warmer months, until declining autumn temperatures reverse the trend.

It is informative that the intense outer Cape Cod lobster fishery has not been successful in reducing the size structure of this resource as definitively as in other inshore Massachusetts regions. A greater number of size-age groups are represented in outer Cape Cod catches. In most other inshore areas, lobsters exhibit minimal migration and are exposed to fishing pressure throughout the year. New recruits (lobsters which, upon molting, become legal size) may represent as much as 95% of the legal catch, compared with only 55% in the outer Cape Cod area. The seasonal occurrence of these offshore lobsters in the outer Cape Cod area thus limits their exposure to intense fishing pressure.

The size structure of this portion of the resource is similar to that from southern Georges Bank. Accordingly, the Sixteenth Northeast Regional Stock Assessment Workshop (16th SAW) of NMFS assigned this migratory group of lobsters to the Georges Bank-Southern Offshore stock unit (NEFSC, 1993).

Estrella and McKiernan (1989) discussed the geography as a potential factor in concentrating migrants. The outer Cape Cod area is adjacent to steeply sloping gradients which lead to a much greater depth range than that found in most other inshore regions.

[3] Pezzack, D. S. 1987. Lobster (*Homarus americanus*) stock-structure in the Gulf of Maine. Int. Counc. Explor. Sea. Shellfish Comm. Council Meeting 1987/K:17, 18 p.

[4] Estrella, B. T. 1997. American lobster tagging studies conducted in Massachusetts coastal waters. MA Div. Mar. Fish. In prep.

[5] Estrella, B. T. 1997. Massachusetts Division of Marine Fisheries, 50 A Portside Drive, Pocasset, MA 02559. Unpubl. data.

## Materials and methods

Tagged lobsters were released at three specific locations along the eastern shore of Cape Cod (Fig. 1). Lobsters used in tagging were collected in the immediate vicinity of each release station and released within a day of capture. At station 1 (Provincetown), tagged lobsters were liberated in the periods 21–25 July 1969; 6–9 July 1970; and 23–25 June 1971. Lobsters used in the tagging at station 1 were collected by SCUBA teams that attempted to capture all lobsters observed on each dive. At station 2 (Truro) and station 3 (Eastham), tagged lobsters were liberated over the period 20 July to 18 August 1970. Lobsters used at these two stations were collected in the traps of a local commercial fisherman.

Sphyrion anchor tags were used. These consisted of a coded polyvinyl-chloride-tubing pennant connected by a monofilament thread to a stainless steel anchor. The anchor was inserted in the lobsters with a hypodermic needle through the membrane connecting the carapace and first abdominal segment and implanted in dorsal extensor musculature below the carapace hypodermis as described in Cooper (1970). The implanted tag can endure successive molts.

A reward of $1 was paid for each tag, as well as the market value of each tagged lobster returned with information on the date and location of recapture. During 1971, the reward was increased to $5 for each tagged lobster submitted for examination, and the fisherman was permitted to retain possession of the lobster.

Distance traveled by recaptured lobsters was determined as the shortest distance, avoiding landmass, from point of release to point of recapture. Direction of travel was computed to the nearest 0.1 degree true north.

## Results

A total of 1,237 tagged lobsters with carapace length (CL) range of 48 to 198 mm (mean CL of 104 mm),

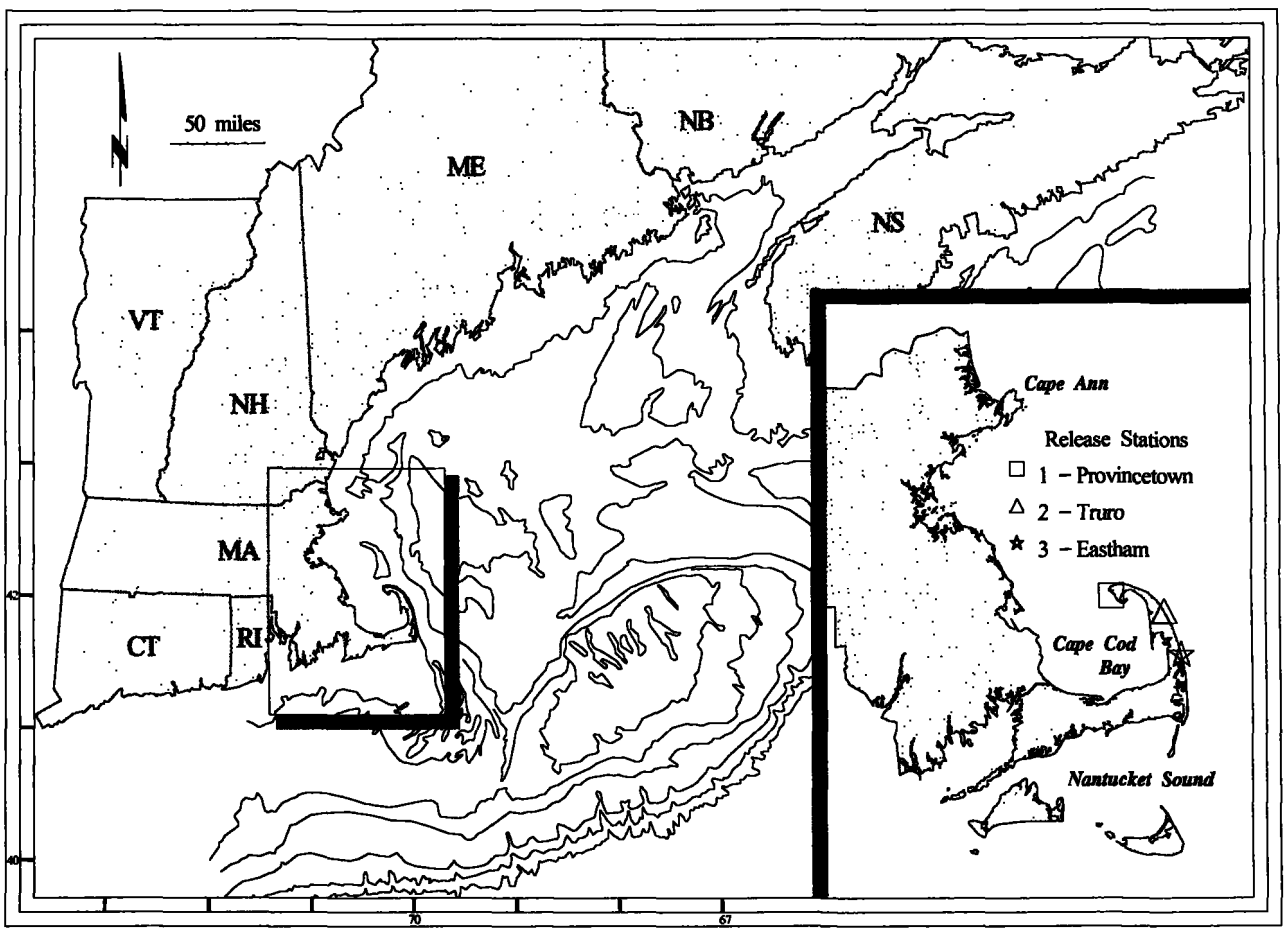


**Figure 1**

Map of northeast coast of the United States and Canada showing eastern Cape Cod, Massachusetts, release stations for tagged American lobster, *Homarus americanus*.

were liberated at three release stations (Table 1) between 21 July 1969 and 25 June 1971. By 22 December 1972, 332 or 26.8% of the tags were returned (Fig. 2). Mean distance from point of release to point of recapture was 22.6 km (median=140.4 km), mean time at large 112.5 days (median = 448.5 d).

One hundred thirty (39.2%) of the recaptured lobsters moved less than 10 km from their points of release (Table 2). One hundred fifty-one (45.5%) were recaptured within 10 to 40 km, and 51 (15.4%) were recaptured at 40 km or more from point of release. Four lobsters moved farther than 100 km, one of the four as far as 281 km.

The distances traveled by lobsters grouped in classes based on size, sex, and the presence or absence of ripe and immature external eggs at tagging are shown in Table 3A. Legal-size females without eggs moved the shortest distance of all groups. Ripe ovigerous lobster moved farthest (average 30.3 km), followed by females with immature eggs (average 23.8 km). Analysis of variance of log-transformed data indicated there were significant differences among groups ($P<0.01$). Several multiple-range test procedures, Tukey-HSD test, Student-Newman-Keuls (SNK), and Duncan, were run on log-transformed data. A common result among the tests was

**Table 1**

Tagged lobsters liberated and recaptured from three release stations at Cape Cod, Massachusetts.

| Release station | Number tagged | Carapace length (mm) | | | Tags returned | | Movement | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | Range | SD | Number | Percent recovery | Mean distance traveled (km) | Mean time at large (days) | Velocity (km/day) |
| 1 Provincetown | | | | | | | | | |
| Male | 190 | 84 | 48–198 | 25.2 | 54 | 28.4 | 22.4 | 220.4 | 0.49 |
| Female | 683 | 113 | 49–189 | 21.2 | 200 | 29.3 | 21.4 | 83.6 | 0.65 |
| 2 Truro | | | | | | | | | |
| Male | 39 | 75 | 67–80 | 3.8 | 8 | 20.5 | 25.3 | 228.9 | 0.37 |
| Female | 105 | 106 | 67–149 | 21.0 | 21 | 20.0 | 21.7 | 104.7 | 1.50 |
| 3 Eastham | | | | | | | | | |
| Male | 75 | 76 | 69–90 | 3.8 | 14 | 18.7 | 22.6 | 198.1 | 0.49 |
| Female | 145 | 96 | 66–146 | 21.6 | 35 | 24.1 | 29.6 | 55.1 | 1.18 |
| Total or weighted mean | 1237 | 102 | 48–198 | 24.9 | 332 | 26.8 | 22.6 | 112.5 | 0.72 |

**Table 2**

Distance traveled by lobsters liberated from three release stations at Cape Cod, Massachusetts.

| Distance traveled (km) | Provincetown | | Truro | | Eastham | | Total | |
|---|---|---|---|---|---|---|---|---|
| | Number of tags returned | Percent of total | Number of tags returned | Percent of total | Number of tags returned | Percent of total | Number of tags returned | Percent of total |
| Less than 10 | 100 | 39.4 | 2 | 6.9 | 28 | 57.1 | 130 | 39.2 |
| 10–19 | 49 | 19.3 | 15 | 51.7 | 1 | 2.0 | 65 | 19.6 |
| 20–29 | 26 | 10.2 | 2 | 6.9 | 2 | 4.1 | 30 | 9.0 |
| 30–39 | 46 | 18.1 | 8 | 27.7 | 2 | 4.1 | 56 | 16.9 |
| 40–49 | 20 | 7.8 | 1 | 3.4 | 5 | 10.3 | 26 | 7.8 |
| 50 or more | 13 | 5.2 | 1 | 3.4 | 11 | 22.4 | 25 | 7.5 |
| Total | 254 | 100.0 | 29 | 100.0 | 49 | 100.0 | 332 | 100.0 |

that the distance traveled by legal-size nonovigerous females was significantly shorter than that of all other groups except sublegal females.

Only fourteen of the returned lobsters molted while at large. These were distributed among most of the lobster classes. Sample size was insufficient to assess effects of molting on movement.

The relatively long mean distances traveled by sublegal male and female lobster groups (22.5 km and 17.0 km, respectively) were likely due to their number of days at large being, on average, considerably greater than the number of days at large for other lobster groups (Table 3A). The mean time at large was less for legal-size females with and without external eggs than for legal-size males and sublegal males and females.

Lobster "velocities" greater than 3 km/day were not exhibited by individual sublegal males or sublegal females. However, these rates were calculated for the larger lobsters, including 6.6% of legal-size males, 1.1% of legal-size nonovigerous females, 7.6% of females with immature eggs, and 4.2% of females with ripe eggs. Females with immature and ripe eggs exhibited greatest mean velocities (1.55 and 0.95 km/day, respectively, Table 3A).

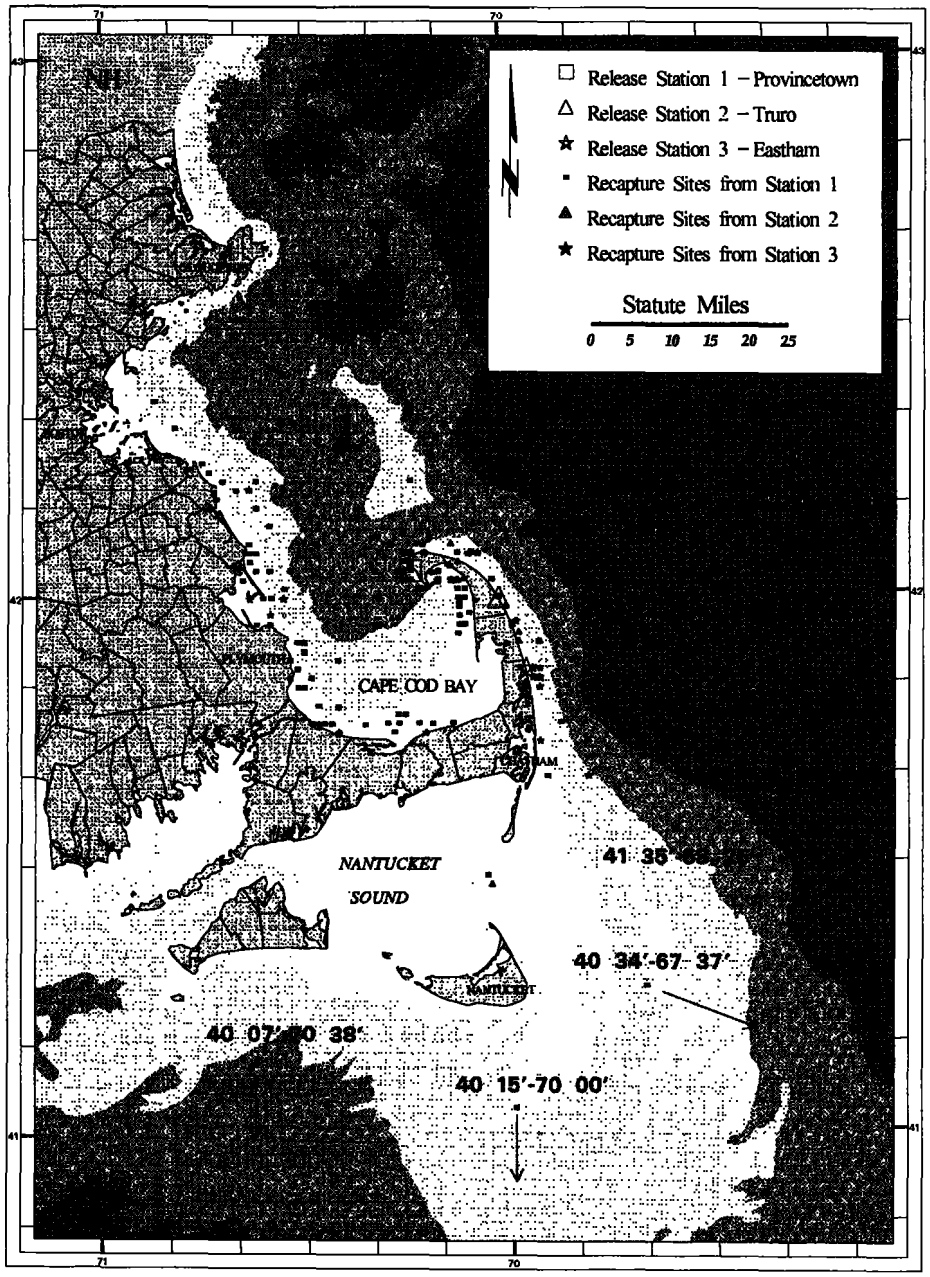


**Figure 2**

Tagged American lobster, *Homarus americanus*, release stations and return locations off the coast of Massachusetts. Some inshore recapture sites represent multiple recaptures.

Because variability in days at large among classes of lobster could affect comparisons of distance traveled, standardization was warranted. An additional data analysis was conducted which was limited to lobsters at large < 200 days (Table 3B). This eliminated potential misleading recapture locations that could occur after circuitous (homing) movement patterns, i.e. those from lobsters which, after tagging, may move offshore and return inshore in the following year, and subsequent years. Because lobsters were tagged and released in the months of June through August, a 200-day limit was considered reasonable to avoid spring recaptures in our data treatments.

Analysis of these "standardized" data reaffirmed that legal-size females with ripe external eggs exhibited the greatest mean distance traveled, 25.6 km, followed by females with immature external eggs, 24.2 km. Legal-size males ranked third, with a mean of 16 km; nonovigerous females and sublegal females and males averaged 12.2 km, 13.1 km, and 14.2 km, respectively. Analysis of variance of log-transformed distance data indicated that there were signifi-

**Table 3A**

Tag returns from various classes of lobsters liberated at Cape Cod, Massachusetts, for all days at large.

| Lobster class | Number liberated | Number recovered | Percent tag recovery | Mean carapace length (mm) | Mean distance traveled (km) | Mean time at large (days) | Velocity (km/day) |
|---|---|---|---|---|---|---|---|
| Male sublegal-size[1] | 213 | 46 | 21.6 | 72 | 22.5 | 308.0 | 0.31 |
| Female sublegal-size without external eggs | 128 | 20 | 15.6 | 75 | 17.0 | 153.0 | 0.37 |
| Male legal-size | 91 | 30 | 33.0 | 106 | 23.1 | 79.0 | 0.74 |
| Female legal-size without external eggs | 295 | 91 | 30.8 | 106 | 13.4 | 77.0 | 0.46 |
| Female with immature external eggs | 130 | 26 | 20.0 | 112 | 23.8 | 34.2 | 1.55 |
| Female with ripe external eggs | 380 | 119 | 31.3 | 118 | 30.3 | 83.0 | 0.95 |
| Total or weighted mean | 1,237 | 332 | 26.8 | 104 | 22.6 | 112.5 | 0.72 |

[1] Lobsters less than 81 mm carapace length. During this study, the minimum legal carapace length in Massachusetts was 3 and 3/16 inches (80.96 mm).

**Table 3B**

Tag returns from various classes of lobsters liberated at Cape Cod, Massachusetts, which were at large <200 days.

| Lobster class | Number liberated | Number recovered | Percent tag recovery | Mean carapace length (mm) | Mean distance traveled (km) | Mean time at large (days) | Velocity (km/day) |
|---|---|---|---|---|---|---|---|
| Male sublegal-size[1] | 213 | 21 | 9.9 | 75 | 14.2 | 34.1 | 0.59 |
| Female sublegal-size without external eggs | 128 | 14 | 10.9 | 75 | 13.1 | 47.2 | 0.51 |
| Male legal-size | 91 | 26 | 28.6 | 104 | 16.0 | 38.1 | 0.82 |
| Female legal-size without external eggs | 295 | 81 | 27.5 | 106 | 12.2 | 35.0 | 0.51 |
| Female with immature external eggs | 130 | 25 | 19.2 | 112 | 24.2 | 22.8 | 1.61 |
| Female with ripe external eggs | 380 | 107 | 28.2 | 117 | 25.6 | 36.1 | 1.04 |
| Total or weighted mean | 1,237 | 274 | 22.2 | 107 | 19.1 | 35.2 | 0.85 |

[1] Lobsters less than 81 mm carapace length. During this study the minimum legal carapace length in Massachusetts was 3 and 3/16 inches (80.96 mm).

cant differences among groups ($P<0.01$). Tukey-HSD, SNK, and Duncan test results were similar to results from tests on all data. They indicated that distances traveled by sublegal and legal nonovigerous lobster groups were significantly less than those of egg-bearing female groups ($P=0.05$). The trend in mean velocity and proportion of lobsters traveling greater than 3 km/day was similar to that calculated for each lobster class from all data. Maximum velocities, calculated by lobster class, were 2.98 km/day for a 79-mm-CL sublegal male, 2.36 km/day for sublegal females (80 mm CL), 5.19 km/day for legal size males (106 mm CL), 4.15 km/day for legal-size nonovigerous females (101 mm CL), 7 km/day for le-

gal-size females with immature eggs (103 mm CL), and 5.8 km/day for females with mature eggs (118 mm CL).

Time at large for recaptured lobsters ranged from 0 to 897 days (Table 4). Approximately 78% of recaptured lobsters were at large less than 60 days. The number of tags returned and the percentage recovery of tagged lobsters at large decreased sharply in the fourth month after release (October) coincident with the start of the fall season. Only three tags were returned from lobsters recaptured in the colder months from December through April (all years combined). All three tagged lobsters were recovered in deep water. Two were recaptured on 7 and 22 March 1972, at depths of 54 m and 59 m, respectively, off Provincetown, MA, and the third was recaptured offshore on 22 December 1972, at a depth of 95 m, NE of Veatch Canyon.

Depth of recapture data were log-transformed and analyzed with equality of means test and found to be related to season (Welch: $F$=4.41, $P$=0.0411; Brown-Forsythe: $F$=4.41, $P$=0.0411). Depth of recapture for the combined months of June through September (63 m) was significantly different from October through May (93 m).

Distance traveled was also significantly different by season ($t$=–3.50, $P$=0.001). Distance from release site was greatest during the October–May period of recapture (41.3 km), in comparison with June–September period of recapture (22.5 km).

Distance of travel northeastward of the Cape Cod landmass was apparently limited compared with distance of travel in other directions; recapture points tend to be distributed in a northwest-southeast plane (Fig. 2).

To test inshore versus offshore migrational tendencies, tag-return locations were grouped with consideration for the curvature of the "arm" of the Cape. Exclusive of lobster recaptured within Cape Cod Bay, recapture points east to south of all landmass between 90° and 225° true north (for lobsters liberated at stations 2 and 3), and 1° and 225° (for lobsters

**Table 4**

Tags returned by month of recapture and days at large for tagged lobsters liberated at Cape Cod, Massachusetts (recapture years combined).

| Recapture month | Mean days at large | Number of returns | Tags returned | | Mean distance (km) | Mean depth (meters) |
|---|---|---|---|---|---|---|
| | | | Percent of total | Cumulative percent | | |
| **1st season** | | | | | | |
| June | 4.0 | 2 | 0.6 | | 3.2 | 70.0 |
| July | 10.1 | 70 | 21.1 | 21.7 | 10.1 | 62.5 |
| August | 33.2 | 112 | 33.7 | 55.4 | 20.0 | 53.0 |
| September | 50.6 | 76 | 22.9 | 78.3 | 26.2 | 78.5 |
| October | 89.9 | 9 | 2.7 | 81.0 | 21.1 | 81.2 |
| November | 111.0 | 5 | 1.5 | 82.5 | 19.5 | 128.2 |
| **2nd season** | | | | | | |
| March | 258.0 | 1 | 0.3 | 82.8 | 4.6 | 176.0 |
| May | 302.1 | 10 | 3.0 | 85.8 | 69.7 | 91.3 |
| June | 338.8 | 9 | 2.7 | 88.5 | 22.5 | 54.3 |
| July | 359.8 | 5 | 1.5 | 90.0 | 37.0 | 33.8 |
| August | 381.6 | 8 | 2.4 | 92.4 | 33.1 | 51.9 |
| September | 434.5 | 2 | 0.6 | 93.0 | 7.6 | 92.5 |
| October | 449.8 | 4 | 1.2 | 94.2 | 39.8 | 48.3 |
| November | 486.0 | 1 | 0.3 | 94.5 | 33.8 | 50.0 |
| **3rd season** | | | | | | |
| March | 582.0 | 1 | 0.3 | 94.8 | 38.5 | 192.0 |
| May | 670.0 | 2 | 0.6 | 95.4 | 19.9 | 30.5 |
| June | 703.5 | 2 | 0.6 | 96.0 | 35.7 | 60.5 |
| July | 726.3 | 6 | 1.8 | 97.8 | 23.2 | 81.5 |
| August | 742.5 | 2 | 0.6 | 98.4 | 33.9 | 93.0 |
| October | 807.5 | 2 | 0.6 | 99.0 | 30.2 | 70.0 |
| November | 843.5 | 2 | 0.6 | 99.6 | 11.5 | 61.0 |
| December | 897.0 | 1 | 0.3 | 99.9 | 223.5 | 312.0 |

liberated at station 1) were grouped as southeast (offshore) in direction. All other recapture points, including those within Cape Cod Bay, were grouped as northwest (inshore) in direction. Inshore versus offshore travel was tested with chi-square by month of recapture for lobsters at large up to one year and which traveled more than 3.7 km. Direction of travel was biased significantly toward inshore during warmer months (Table 5).

## Discussion

Our findings of greater directed movement toward the north and west during summer months is in agreement with the summer movement along the eastern shore of Cape Cod and into Cape Cod Bay as reported by Morrissey (1971). The Cape Cod landmass is interjacent to inshore grounds to the north and west and offshore grounds along the edge of the continental shelf to the south and east. The overall northwest-southeast distribution of recapture points suggests an interchange of inshore and offshore stocks in the Cape Cod area. Cooper and Uzmann (1971) and Uzmann et al. (1977) found that lobsters tagged in offshore canyon areas moved into shoal water in late spring and early summer, returning to deep water in late fall and early winter. Lobsters migrating from that offshore area to the inshore area of eastern Massachusetts would pass along the eastern shore of Cape Cod. The northwest-southeast pattern of recapture locations is consistent with movement to and from the Georges Bank and southern offshore canyon area which exhibits a similar population structure to the lobster group which is only seasonally available east of Cape Cod.

**Table 5**

Seasonal distribution of recapture points of lobsters at large up to one year and that had traveled more than 3.7 km.

| | Direction of travel | | | |
|---|---|---|---|---|
| Recapture period | Number inshore | Number offshore | Total | $\chi^2$ |
| 1st season of release | | | | |
| July–August | 106 | 43 | 149 | $P<0.0001$ |
| September–October | 59 | 15 | 74 | $P<0.0001$ |
| 1st winter of release | | | | |
| November–May | 11 | 5 | 16 | $P=0.134$ |
| 2nd season of release | | | | |
| June–August | 8 | 4 | 12 | $P=0.248$ |
| Total | 184 | 67 | 251 | |

Lawton et al. (1984) found minimal movement in an inshore tagging study of 4,761 sublegal lobster at nearby Rocky Point, Plymouth, Massachusetts during 1970–75. Only 19 lobsters (<1% of returns) were retrieved 16 or more km from their release points and all 19 were within state territorial waters. A study by Fair[6] on legal-size lobster in the same area several years later yielded similar results. Additional studies affirmed the nonmigratory nature of inshore lobsters (Templeman, 1935; Wilder, 1963; Cooper et al., 1975; Krouse, 1980; Stasko, 1980; Campbell, 1982). Ennis (1984) noted small-scale seasonal depth movements in relation to temperature with lobsters moving to shallow water in warmer months and deeper water in colder months. More extensive seasonal migrations were demonstrated by Campbell (1986) and Pezzack and Duggan (1986).

We conclude that lobsters tagged in the present experiment are onshore migrants from an offshore stock that seasonably becomes "superimposed" on the endemic inshore stock. Recapture depths were significantly greater in colder months than during summer. The movement of lobsters off southeastern Massachusetts is cyclical, with lobsters moving to deep water in late fall. Uzmann et al. (1977) found that lobsters returned to the continental shelf margin and slope in fall and winter. In our study only three lobsters were recaptured during December through April, consequently, we did not clearly establish if lobsters winter specifically on the edge of the shelf or in deep-water areas in general. However, four of our lobsters were recaptured in clearly offshore areas: at 40°07', 70° 38', 119 m depth, on 26 September 1970; at 40°34', 67°37', 110 m depth, on 9 May 1970; at 41°35', 68°25', 55 m depth, on 23 May 1971; and at 40°15', 70°00', 95 m depth, on 22 December 1972. The occurrences of these recaptures in time, depth, and location suggest seasonal movement to and from the edge of the continental shelf between fall and spring. With an average recovery rate of only 7.0% of lobsters tagged offshore by Cooper and Uzmann (1971), it is probable that substantial numbers of our inshore tagged lobsters wintered on the edge of the continental shelf.

Cooper and Uzmann (1971) concluded that offshore lobsters actively orient to optimum temperature according to season. Uzmann et al. (1977) provided further sup-

[6] Fair, J. J., Jr. 1977. Lobster investigations in management area 1: southern Gulf of Maine. NOAA, NMFS State-Federal Relationships Div., Mass. Lobster Rep. No. 8, 21 April 1975–20 Apr. 1977, 8 p. Appendix, 5 p.

port with their finding that through random or directed movements (or both), the offshore lobster population maintains itself within temperatures of 8°–14°C. Cooper and Uzmann (1971) hypothesized that seasonal shoalward migration to warmer water compensates for a lack of sufficiently high temperature during summer in the continental slope habitat to permit extrusion and hatching of eggs and subsequent molting and mating. They found that offshore lobsters that demonstrated the most extensive onshore migrations were predominately females and that the migration of offshore lobsters to inshore grounds is generally confined to areas south and west of Cape Cod (no recoveries were made north of Cape Cod in the Gulf of Maine proper).

While diving to collect lobsters for tagging at station 1, we observed lobsters always to be concentrated in a narrow stratum where a thermocline intercepted the steeply sloping surfaces of a sandy escarpment paralleling the beach in that area, about 1.8 km from shore. Morrissey[7] conducted semiweekly SCUBA surveys throughout the summer of 1966 at Provincetown, where station 1 is located, and found lobsters only in close proximity to the thermocline-sediment interface, which occurred at 24 m in late May and ranged between 9 and 19 m during June, July, and August. During a vertical transect along the bottom from the shoreline to a depth of 22 m, 14 July 1966, 15 of 16 lobsters observed were within a stratum (11 to 14 m) in which a bathythermograph cast showed a change of 12.8°C in water temperature. On the basis of observed activity of individual lobsters, he concluded that the lobsters were not concentrated by a thermal block but rather were attracted to the warmer epilimnion layer and used the reduced light intensity associated with the thermocline as cover. These observations support the conclusion of Cooper and Uzmann (1971) and Uzmann et al. (1977) that offshore lobsters orient to optimum temperature.

Our test results indicated that sublegal and legal-size females with no eggs moved significantly less than egg-bearing female groups. An explanation for why legal-size females without eggs move less than those with eggs may be that they tend to congregate in the warmer shoal water where egg extrusion occurs. During this study, three tagged females, which extruded eggs after tagging, moved only an average distance of 4.2 km before recovery. Although this sample size is small, the inference from it is supported by fishing activity in this area. Fishermen report concentrations of females with immature eggs in the shoals east of Cape Cod during August and September.

The fact that tagged inshore female lobsters with ripe external eggs moved greater distances than other classes of tagged lobsters may be a verification of the findings of Cooper and Uzmann (1971), that offshore lobsters demonstrating the most extensive inshore migrations are predominantly female. However, unlike Cooper and Uzmann (1971), our recoveries indicate that lobster migration occurs north of Cape Cod into at least the southwestern portion of the Gulf of Maine with one recovery made as far north as latitude 42°39'. Our subsequent tagging work in this study area (1984–85) yielded the return of a female after 362 days at large from even farther north, 43°33' (off Cape Elizabeth, Maine).[4]

None of our lobsters were recovered in the inshore grounds south and southwest of Cape Cod where most of the inshore recoveries were made by Cooper and Uzmann. The distribution of recapture points of the 58 lobsters recovered after their first season of release (Table 4) suggests that our inshore tagged lobsters returned to the shoal waters along eastern Massachusetts in successive summers.

The movement described by the findings of Cooper and Uzmann (1971) suggests that offshore lobsters migrate to secure more suitable hydrographic conditions. The areas involved, i.e. the edge of the continental shelf and shoaler waters extending into inshore grounds south and west of Cape Cod, are quite generalized. The apparent return of our inshore tagged lobsters to the eastern shore of Massachusetts in successive summers, and the greater movement shown by females with ripe eggs at tagging, suggest that the migration of offshore lobsters may be anastrophic or gametic (Heape, 1931; Wilkinson, 1952) in character, i.e. nonrandom, stimulated by metabolic needs or reproductive cues. Campbell (1986) provided calculations that suggest ovigerous lobster need to make seasonal deep-shallow water migrations to obtain sufficient heat units for egg development within any 9–12 month period. Using a threshold temperature of 3.4°C, he determined that shallow water had more degree days than deeper water in summer months and that the reverse was true in winter months.

Although significant American lobster migrations have been reported, Saila and Flowers (1968) provided the first reference in the literature to long-distance homing by this species. They found a pronounced directional tendency toward the original area of capture in the movements of berried female lobsters transplanted from Veatch Canyon on the edge of the continental shelf to Narragansestt Bay,

[7] Morrissey, T. D. 1970. Observations on behavior of the American lobster, *Homarus americanus*, at Provincetown, Massachusetts during the summer of 1966. MA Div. Mar. Fish., 50 A Portside Drive, Pocasset, MA 02559.

Rhode Island. They concluded that the lobsters tended to remain in shoal waters in suitable spawning habitat until they had shed their eggs or had molted, or both. Cooper and Uzmann (1971) referred to seasonal movement to and from generalized areas: the edge of the continental shelf and the shoaler waters of southern New England. Campbell (1986) and Pezzack and Duggan (1986), however, provided evidence from Canadian waters that lobsters undertake regular migrations between widely spaced and well-defined areas.

In contrast, the European lobster, *Homarus gammarus*, although biologically similar to *H. americanus*, displays minimal migratory behavior (Bannister and Addison, 1995). Tagging studies have shown that both juveniles and adults exhibit "strong site loyalty." The distribution of the *H. gammarus* resource and fishery is primarily coastal; "offshore" distribution occurs only 20 km from shore. The lack of substantial long-distance movement may be due to the more moderate water temperature off the British Isles (compared with the NW Atlantic) caused by proximity to the Gulf Stream. This may mitigate the biological "need" for extensive seasonal inshore-offshore movement by *H. gammarus*.[8]

There is an apparent affinity between the migratory group of lobsters east of Cape Cod, which are examined in this study, and those from Georges Bank and southern offshore canyons. Our evidence for movement of these lobsters north of Cape Cod into the Gulf of Maine seasonally, implies that genetic interchange between stock units continues, despite high exploitation rates. In light of this, management of fishing mortality rates on the offshore resource becomes an issue of increasing importance.

There is also increasing information on movements of lobster larvae, the distribution and behavior of newly settled and juvenile lobsters, concentrations of egg-bearing females, and the occurrence of long-distance homing behavior in American lobster both in the northern Gulf of Maine and southern New England waters. Some progress has been made in roughly delineating stock structure with the help of larval dispersion, hydrodynamic, and migration studies (NEFSC, 1993). Interpretation of these data, however, is tentative because migratory habits of larger lobsters appear extensive and may transcend the boundaries that some researchers attempt to draw solely on the basis of larval distribution. Despite many years of larval and postlarval lobster monitoring, a definitive stock-recruitment relation has yet to be determined, although ecological knowledge has been enhanced. The relative importance of the offshore lobster resource to recruitment in shoaler waters of the Gulf of Maine or other areas must be assessed. We need to know the degree of interchange between the two lobster groups in order to refine stock assessments.

[8] Bannister, R. C. 1997. The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, England NR33 0HT. Personal commun.

## Acknowledgments

We greatly appreciate the help of M. P. Armstrong and S. X. Cadrin with initial data collation, and the data mapping assistance received from T. B. Hoopes in cooperation with MassGIS. R. A. Cooper assisted with 1969–71 field activities, including lobster tagging. Tagging assistance during 1984–85 was provided by M. Borgatti, D. McKiernan, M. Syslo, and J. O'Gorman.

## Literature cited

**Able, K. W., K. L. Heck Jr., M. P. Fahay, and C. T. Roman.**
**1988.** Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. Estuaries 11:83–86.

**Bannister, R. C. A., and J. T. Addison.**
**1995.** Investigating space and time variation in catches of lobster (*Homarus gammarus* (L.)) in a local fishery on the east coast of England. ICES Mar. Sci. Symp. 199:334–348.

**Briggs, P. T., and F. M. Mushacke.**
**1984.** The American lobster in western Long Island Sound: movement, growth and mortality. N.Y. Fish Game J. 31(1):21–37.

**Campbell, A.**
**1982.** Movements of tagged lobsters released off Port Maitland, Nova Scotia, 1944–80. Can. Tech. Rep. Fish. Aquat. Sci. 1136, 41 p.
**1986.** Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 43:2197–2205.
**1989.** Dispersal of American lobsters, *Homarus americanus*, tagged off southern Nova Scotia. Can. J. Fish. Aquat. Sci., 46:1842–1844.

**Campbell, A., D. E. Graham, H. I. MacNichol, and A. M. Williamson.**
**1984.** Movements of tagged lobsters released on the continental shelf from Georges Bank to Baccaro Bank, 1971–73. Can. Tech. Rep. Fish. Aquat. Sci. 1288, 16 p.

**Campbell, A., and A. B. Stasko.**
**1986.** Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy. Mar. Biol. (Berl.) 92:393–404.

**Cooper, R. A.**
**1970.** Retention of marks and their effects on growth, behavior, and migrations of the American lobster, *Homarus americanus*. Trans. Am. Fish. Soc. 99:409–417.

**Cooper, R. A., R. A. Clifford, and C. D. Newell.**
**1975.** Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. Trans. Am. Fish. Soc. 104(4):669–674.

**Cooper, R. A., and J. R. Uzmann.**
**1971.** Migration and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash. D.C.) 171:288–290.
**1980.** Ecology of juvenile and adult Homarus. *In* Vol. 11: J. S. Cobb and B. F. Phillips (eds.), The biology and management of lobsters, p. 97–142. Acad. Press, N.Y.

**Ennis, G. P.**
**1984.** Small-scale seasonal movements of the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 113:336–338.

**Estrella, B. T., and D. J. McKiernan.**
**1989.** Catch-per-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: description and trends. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 81, 21 p.

**Fogarty, M. J., D. V. D. Borden, and H. J. Russell.**
**1980.** Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. Fish. Bull. 78:771–780.

**Heape, W.**
**1931.** Emigration, migration, and nomadism. W. Heffer and Sons, Ltd., Cambridge, England, 369 p.

**Krouse, J. S.**
**1980.** Summary of lobster, *Homarus americanus*, tagging studies in American waters (1898–1978). *In* Proceedings of the Canada-U.S. workshop on the status of assessment science for NW Atlantic lobster (*Homarus americanus*) stocks, St. Andrews, NB, Oct. 24–26, 1978, p. 135–140. Can. Tech. Rep. Fish. Aquat. Sci. 932.

**Lawton, R. P., G. Luders, M. Kaplan, P. Brady, C. Sheehan, W. Sides, E. Kouloheras, M. Borgatti, and V. Malkoski.**
**1984.** The commercial lobster pot-catch fishery in the Plymouth vicinity, western Cape Cod Bay. *In* Vol. 11: Lecture notes on coastal and estuarine studies: observations on the ecology and biology of western Cape Cod Bay, Massachusetts, p. 131–150. Springer-Verlag, New York, N.Y.

**Morrissey, T. D.**
**1971.** Movements of tagged American lobster, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100(1):117–120.

**Northeast Fisheries Center.**
**1983.** American Lobster. *In* Status of the fishery resources off the northeastern U.S. for 1983, NOAA Tech. Memorandum NMFS-F/NEC-29, 132 p.

**Northeast Fisheries Science Center.**
**1993.** Report of the sixteenth northeast regional stock assessment workshop (16th SAW), Stock Assessment Review Committee (SARC), consensus summary of assessments. Woods Hole, MA, NOAA/NMFS/NEFSC. NEFSC Ref. Doc. 93-18.
**1994.** American Lobster. *In* Status of the fishery resources off the northeastern U.S. for 1994, NOAA Tech. Memorandum NMFS-F/NEC-108, 140 p.

**Pezzack, D. S., and D. R. Duggan.**
**1986.** Migration and homing tendencies of offshore lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43:2206–2211.

**Saila, S. B., and J. M. Flowers.**
**1968.** Movements and behavior of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. Perm. Int. Explor. Mer 31(3):342-351.

**Skud, B. E., and H. C. Perkins.**
**1969.** Size composition, sex ratio, and size at maturity of offshore northern lobsters. U.S. D.I. Bur. Comm. Fish. Spec. Sci. Rep.—Fisheries 598, 10 p.

**Stasko, A. B.**
**1980.** Tagging and lobster movements in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932:141–150.

**Templeman, W.**
**1935.** Lobster tagging in the Gulf of St. Lawrence. J. Biol. Board Can. 1(4):269–278.

**Templeman, W.**
**1940.** Lobster tagging on the west coast of Newfoundland, 1938. Dep. Nat. Res. Fish. Bull. No. 8, 16 p.

**Uzmann, J. R., R. A. Cooper, and K. J. Pecci.**
**1977.** Migration and dispersion of tagged lobsters, *Homarus americanus*, on the southern New England continental shelf. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-705, 92 p.

**Wilder, D. G.**
**1963.** Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20(2):305–318.

**Wilder, D. G., and R. C. Murray.**
**1958.** Do lobsters move offshore and onshore in the fall and spring? Fish. Res. Board Can. Prog. Rep. Atl. Coast 69: 12–15.

**Wilkinson, D. H.**
**1952.** The random element in bird navigation. J. Exp. Biol. 29:532–560.