MOVEMENTS OF TAGGED AMERICAN LOBSTER, *HOMARUS AMERICANUS*, OFF RHODE ISLAND[1]

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ABSTRACT

In 1974 and 1975 a total of 3,063 American lobster, *Homarus americanus*, were tagged and released at five sites along the Rhode Island coast and on the adjacent continental shelf. Analyses were based on 671 returns with sufficient information to assess movement patterns. Lobster movements at inshore locations were generally localized; the mean distance between release and recovery sites ranged from 5.5 to 10.4 km. Intense fishing effort in inshore areas resulted in a disproportionate number of returns within 30 days of release. Rayleigh tests demonstrated a nonuniform ($P<0.01$) distribution of return directions at each site. Mean vector angles ranged from 164.5° to 193.7° from true north at inshore locations.

Lobsters tagged and released on Cox Ledge, 35 km southeast of Narragansett Bay, migrated to the outer continental shelf in late fall and winter. The mean distance travelled was 41.6 km and the average time between release and recapture was 235.3 days. A Rayleigh test indicated that the distribution of return directions was nonuniform ($P<0.01$) and the mean vector angle was 158.8° from true north.

Analyses of the movement patterns of the American lobster, *Homarus americanus*, in coastal waters have typically revealed little evidence of extensive migrations. In a study designed to examine seasonal movements, Wilder and Murray (1958) noted a mean dispersion radius of <1.6 km for tagged lobsters released off the coast of Nova Scotia. Wilder (1963) reported movements averaging 13.5 km for tagged lobsters at large 10-12 mo off Price Edward Island. Bergeron (1967) concluded that lobsters undertake a seasonal onshore-offshore migration of about 10 km off the Magdalen Islands of Quebec. In tagging experiments conducted in the Gulf of Maine, Cooper (1970) and Krouse[5] noted generally localized movements. Dow (1974) indicated, however, that large lobsters (>127 mm carapace length, CL) may undertake migrations of over 140 km. Morrissey (1971) presented evidence for directed movements averaging 26.1 km for ovigerous and sublegal-sized lobsters in the southern Gulf of Maine. Lund et al.[6] reported that lobsters tagged in western Long Island Sound were nonmigratory while others tagged in eastern Long Island Sound undertook migrations to the edge of the continental shelf.

In contrast, Cooper and Uzmann (1971) and Uzmann et al. (1977) demonstrated an extensive inshore spring migration for lobsters tagged on the outer continental shelf. Saila and Flowers (1968) reported that ovigerous females displaced from continental shelf waters to Narragansett Bay, R.I., tended to return to the area of first capture.

The present study was designed to examine various aspects of the population dynamics of lobster off the coast of Rhode Island. In this paper we describe the movement and migratory behavior of lobster in local waters. The work was part of a coast-wide research effort sponsored by the State-Federal Lobster Management Program under the auspices of the U.S. Department of Commerce, National Marine Fisheries Service, with the objective of developing a comprehensive management strategy for lobster in the territorial waters of the United States.

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[6]Lund, W. A., L. L. Stewart, and C. J. Rathbun. 1973. Investigation on the lobster. Completion report. Commercial Fisheries Research and Development Act. Project 3-130-R, 189 p. Univ. Connecticut, Storrs, Conn.

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METHODS

In 1974 and 1975, 3,063 lobsters (55-176 mm CL) were tagged and released at five general locations off the Rhode Island coast and on the adjacent continental shelf (Figure 1).

Lobsters were tagged using the sphyrion anchor tag (Scarratt and Elson 1965). The tag consisted of an encoded yellow plastic tube (2 mm in diameter) attached to a stainless steel anchor by a monofilament thread. The anchor was inserted with a hypodermic needle into the right or left dorsal extensor muscle of the lobster through the membrane posterior to the margin of the carapace. Carapace length, sex, molt status, and physical condition were recorded for each tagged lobster. We obtained lobsters used in tagging experiments directly aboard commercial lobster vessels. Lobsters were tagged at sea and released as close to the point of capture as possible. However, on 20 December 1974, 231 lobsters captured on the mid-continental shelf (Midshelf) were released on Cox Ledge. This displacement (≈60 km) was necessary to avoid several foreign trawlers which moved into the area during tagging operations.

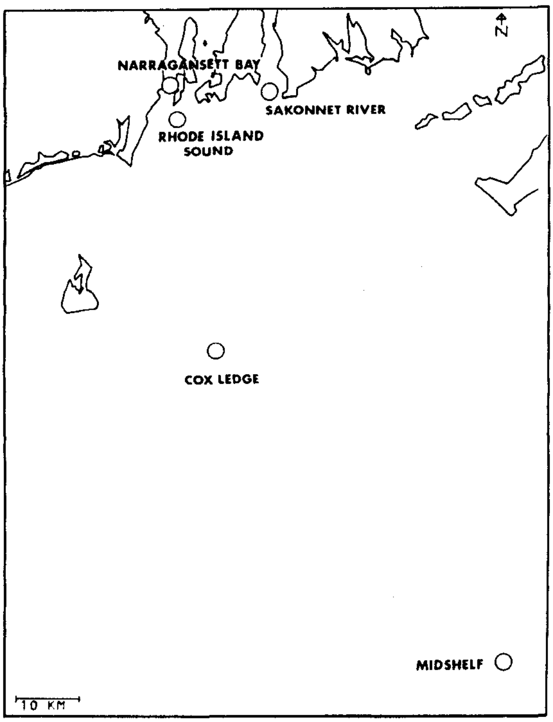


FIGURE 1.—Location of tagging sites for American lobster in the coastal waters of Rhode Island and on the adjacent continental shelf.

Rewards of $2 for the return of the tag alone and $5 for the return of the lobster and tag were paid. Information on the date and location of capture were requested for each recapture. The study was publicized through the local news media, posters describing the study distributed to shellfish dealers, and personal contact with fishermen.

For detailed evaluation of directional components of movement we followed the approach of Saila and Flowers (1968). The specific test statistics and directional components computed were

Mean vector angle $$\bar{\Theta} = \text{arc tan}\left[\frac{\sum r \sin \Theta}{\sum r \cos \Theta}\right]$$

Mean square dispersion coefficient (km²/d)

$$a^2 = \frac{1}{n}\left[\sum \frac{r^2}{t} - \frac{(\sum r \cos \Theta)^2 + (\sum r \sin \Theta)^2}{\sum t}\right]$$

North-south directional component (km/d) $$V = \frac{\sum r \cos \Theta}{\sum t}$$

East-west directional component (km/d) $$V' = \frac{\sum r \sin \Theta}{\sum t}$$

Rayleigh test statistic $$Z = R^2/n$$

where $R = [(\sum \sin \Theta)^2 + (\sum \cos \Theta)^2]^{1/2}$
n = number of individuals
Θ = direction of travel from an arbitrary reference point
t = time in days from release
r = straight line distance (km) of travel.

All angles are presented as deviations from true north (°T). The Rayleigh test is a test for uniform concentration of points around a circle of unit radius (Batschalet 1965).

The mean square dispersion coefficient is a measure of undirected or random movement based on diffusion theory (Beverton and Holt 1957; Jones 1959, 1966). The dispersion coefficient is a compound parameter dependent on both rate of travel and the mean distance travelled without directional change (Jones 1959). The quantities V and V' indicate directional or nonrandom components of movement. These parameters measure the mean rate of group movement of tagged individuals in the north-south and east-west planes.

RESULTS

Inshore Locations

To date, 450 lobsters tagged and released at coastal sites have been recovered with sufficient information to assess movement patterns (Table 1). Due to intensive fishing effort for lobster along the Rhode Island coast, a disproportionate number of tags were returned within 30 d of release (Figure 2); the mean time at large was 48.6, 34.7, and 48.6 d for lobsters released in Narragansett Bay, Rhode Island Sound, and the Sakonnet River. Most lobsters tagged at inshore locations were recaptured within 6 km of the release site (Figure 3), possibly reflecting the short time at large. The distance between release and recovery sites averaged 6.9, 10.4, and 5.5 km at the Narragansett Bay, Rhode Island Sound, and Sakonnet River locations. Distance travelled tended to increase with time up to 90 d at large at each inshore location although high variability made clear trends difficult to discern (Figure 4).

An initial examination of straight-line tracks between release and recapture sites revealed a general southerly trend in movements for lobsters released at inshore tagging sites (Figure 5). These plots also demonstrated that some inshore lobsters

TABLE 1.—Release and recapture data for American lobsters tagged in 1974 and 1975 off Rhode Island. Locales are given in Figure 1. Number recaptured refers to the number of returns with adequate information to evaluate movements. Cox Ledge-Midshelf indicates lobsters captured on the midcontinental shelf (Midshelf) and released on Cox Ledge.

Release site	Release period	Number released	Recaptured		Carapace length (mm) at release		
			No.	%	Mean	SE	Range
Sakonnet River	15 May-31 July 1975	645	147	22.79	80.57	0.257	62.0-103.0
Rhode Island Sound	9 May-21 Aug. 1975	543	115	21.18	79.02	.286	55.0-108.0
Narragansett Bay	9 May-15 Nov. 1975	470	188	40.00	73.92	.212	58.0-102.0
Cox Ledge	11 Nov.-5 Dec. 1974	612	157	25.65	82.70	.454	62.0-134.0
Cox Ledge-Midshelf	20 Dec. 1974	231	29	12.55	96.67	1.201	64.0-167.0
Midshelf	29 Oct.-18 Nov. 1974	562	34	6.05	86.92	.637	65.0-176.0

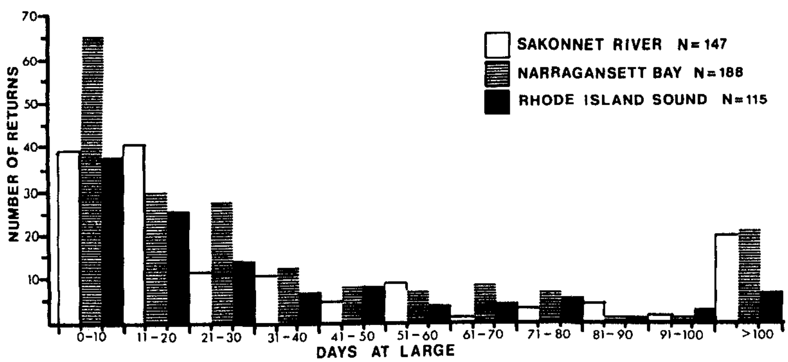


FIGURE 2.—Number of tag returns for American lobster released at inshore locations off Rhode Island as a function of time at large.

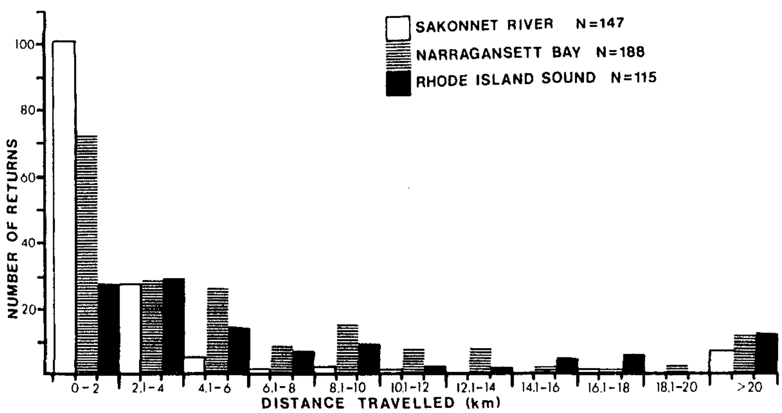
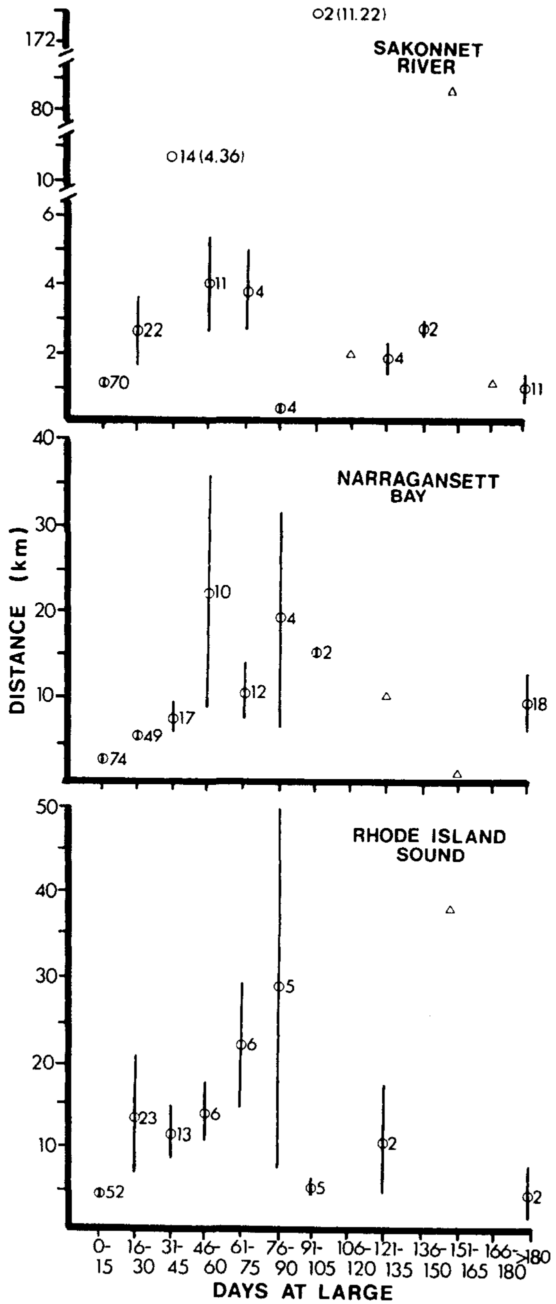


FIGURE 3.—Number of tag returns for American lobster released at inshore locations off Rhode Island as a function of distance travelled.



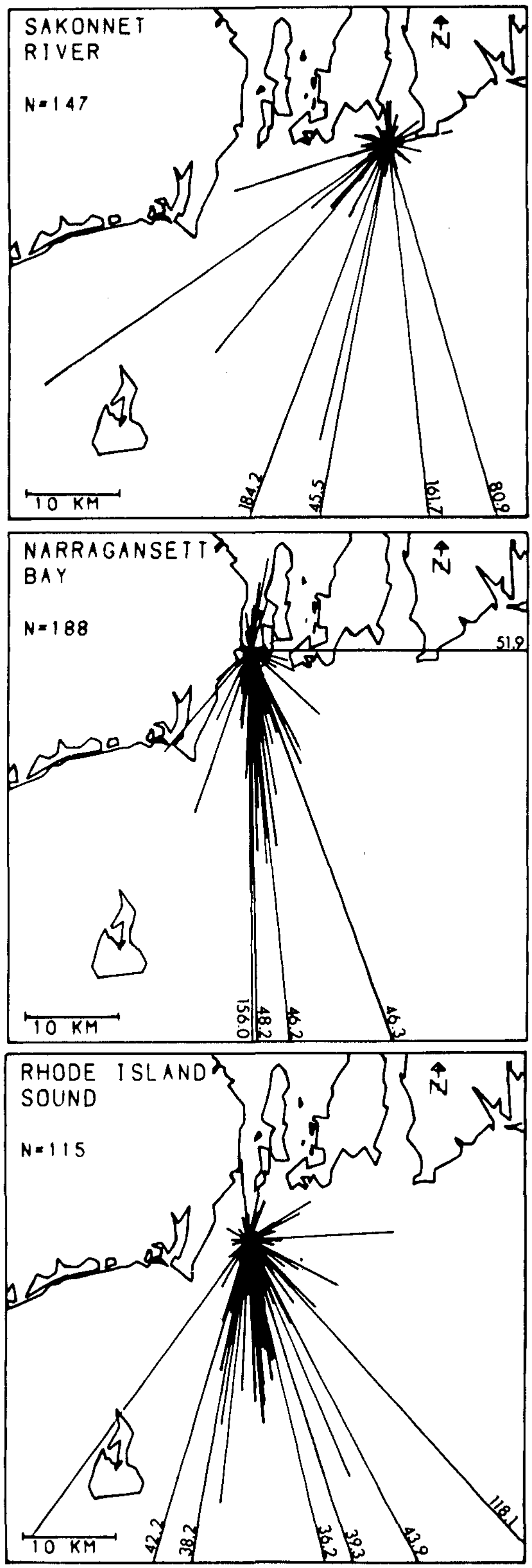


FIGURE 4.—Distance travelled ($\bar{x}\pm1$ SE) as a function of time at large for tagged American lobster released at inshore locations off Rhode Island. Open triangles denote single observations for the time period. Sample sizes are specified beside each mean with an associated standard error. Standard errors are provided in parentheses for observations falling within ranges of truncated ordinate.

FIGURE 5.—Straight line distance between release and recovery sites for American lobster at inshore locations off Rhode Island. Release locations are composites of several release sites in each area. Total distance travelled is noted for tracks which are truncated by borders.

did undertake extensive movements. Appropriate test statistics and directional components (Saila and Flowers 1968) were computed for each total data set and for data partitioned according to time at large (Table 2). Missing data for some returns prevented the use of all the recoveries for these analyses. Mean vector angles ($\bar{\Theta}$) for the three locations ranged from 164.53°(T) to 193.69°(T), and Rayleigh tests indicated a nonuniform distribution of returns at each inshore location (Table 2). In general, the north-south vector components were consistently stronger than the east-west components for each location. When partitioned by time at large, the relative magnitude of the north-south and east-west vector components were more nearly equal for the first time period (0-20 d) at the Sakonnet River site, possibly reflecting an initial random dispersal of released lobsters. The lack of a statistically significant mean vector bearing for this period (Table 2) supports this inference.

The consistently low estimates of V' for lobsters tagged at inshore locations were due, in part, to physiographic constraints since east-west movements were often limited by the coastline, particularly in Narragansett Bay (Figure 1). The negative north-south vector components were indicative of net southerly movement since the cosine of angles ranging from 90° to 270° would be negative. Similarly, negative values of V' imply a westerly displacement since the sine of angles from 180° to 360° would be negative.

The mean square dispersion coefficient (a^2) varied considerably by location and the time period under consideration (Table 2). The quantity a^2 measures the relative degree of undirected movement of any individual with respect to the group directional average. Some caution is necessary in interpreting these values since dispersion coefficients are likely to be overestimated when movements are nonrandom (Jones 1959).

To examine the possibility of directed seasonal movements, we pooled data from inshore release locations and regrouped them according to release period and time at large. We compared movement statistics for lobsters released prior to 1 July 1975 and recaptured prior to 1 September 1975 with those released after 1 July 1975 and recaptured prior to 1 September 1975 (Table 3). We noted a nonuniform distribution of returns at all levels of analysis (Table 3). The north-south directional components consistently dominated the east-west components for both groups. The negative V values reflect the strong southerly directionality for both groups while the east-west components (V') varied considerably when further partitioned by time at large (Table 3). For lobsters released after 1 July 1975 the north-south vector components were two to three times higher than for late spring-early summer releases, indicating a sharp in-

TABLE 2.—Mean vector angle ($\bar{\Theta}$) from true north, mean square dispersion coefficient (a^2), north-south (V) and east-west (V') directional components, Rayleigh test statistics (R and Z) and sample size (n) for lobsters released in the Sakonnet River, Narragansett Bay, Rhode Island Sound, and Cox Ledge. The mean square dispersion coefficient is a measure of random movements; V and V' indicate nonrandom components of movement. Negative values of V and V' are indicative of net southerly and westerly movements. The Rayleigh test is a test for uniform concentration of points around a circle of unit radius.

Location	Days at large	$\bar{\Theta}$ (°T)	a^2 (km²/d)	V (km/d)	V' (km/d)	R	Z	n
Sakonnet River	0-20	215.236	1.952	−0.077	−0.054	10.225	2.133	49
	21-60	211.748	4.966	− .119	− .074	11.391	4.805**	27
	>61	184.469	25.574	− .104	− .008	6.418	1.647	25
	Total	193.694	8.654	− .105	− .025	26.899	7.164**	101
Narragansett Bay	0-20	175.072	2.870	− .294	.025	34.238	13.630**	86
	21-60	178.854	11.012	− .293	.006	31.339	20.043**	49
	>61	164.301	2.471	− .054	.015	24.982	17.336**	36
	Total	173.353	5.700	− .123	.014	90.178	47.556**	171
Rhode Island Sound	0-20	167.967	8.597	− .340	.073	26.958	11.913**	61
	21-60	163.498	2.872	− .246	.073	23.207	17.951**	30
	>61	163.212	9.840	− .140	.042	12.650	7.620**	21
	Total	164.530	7.502	− .199	.055	62.241	34.589**	112
Cox Ledge	0-180	162.690	38.155	−1.244	.388	22.559	14.968**	34
	181-270	140.637	16.365	− .062	.051	8.077	1.553	42
	271-360	150.263	6.900	− .048	.027	15.856	4.261	59
	>361	150.549	14.166	− .104	.059	3.222	1.483	7
	Total	154.847	4.931	− .120	.056	37.863	10.096	142

**P<0.01.

TABLE 3.—Movement statistics for lobsters released prior to 1 July 1975 and recaptured prior to 1 September 1975 (spring-early summer) and lobsters released after 1 July 1975 and recaptured prior to 1 September 1975 (late summer). Data are pooled over release locations in Narragansett Bay, Rhode Island Sound, and the Sakonnet River. See Table 2 for explanation of symbols.

Season	Days at large	$\bar{\theta}$ (°T)	a^2 (km²/d)	V (km/d)	V' (km/d)	R	Z	n
Spring-early summer	0-15	190.657	3.038	−0.156	−0.029	22.287	5.458**	91
	16-30	165.275	1.368	− .104	.027	16.365	5.251**	51
	31-45	183.151	2.247	− .144	− .008	16.946	9.573	30
	46-60	180.343	22.126	− .249	− .001	13.945	9.260**	21
	>61	183.380	12.854	− .110	.006	22.201	14.935**	33
	Total	178.854	5.852	− .138	.003	91.056	36.687**	226
Late summer	0-15	161.321	7.121	− .473	.160	33.975	18.035**	64
	16-30	188.365	4.527	− .479	− .070	15.036	10.765**	21
	>30	202.517	8.495	− .434	− .180	4.531	4.105**	5
	Total	179.427	6.808	− .469	− .005	52.447	30.563**	90

**$P<0.01$

crease in directional movement in this period. Estimates of the mean square dispersion coefficient also increased in the late summer period, indicating a general increase in activity levels. The relative magnitude of the increase in random movement (as measured by a^2) was less striking than the increase in directed movement, however (Table 3).

A two-way fixed factor analysis of variance was used to determine the effects of size and sex on distance travelled for each inshore release location. The three inshore sites differed slightly in release periods (Table 1) and were therefore treated independently to eliminate any possible seasonal effects. Lobsters were categorized on the basis of release size (≤60, 61-70, 71-80, 81-90, >91 mm CL) and sex (male, female, ovigerous female). No significant differences ($P<0.01$) were noted by size, sex, or the size-sex interaction at any of the three release locations. The data were treated with a $\log_e(x+1)$ transform prior to analysis.

Offshore Locations

In contrast to lobsters tagged at coastal locations, those tagged and released on Cox Ledge exhibited extensive movements. The mean distance travelled was 41.6 km and the average time between release and recapture was 235.3 d. Return rates were relatively high for the first 30 d, and subsequently increased for lobsters at large over 240 d (Figure 6). Of 157 lobsters recovered with adequate information to evaluate movements, 117 (74.5%) were recaptured within 60 km of the release site (Figure 7). Examination of dispersal as a function of time at large indicated large-scale movements within 60-120 d of liberation while recoveries after 240 d were progressively closer to the release site (Figure 8). Plots of

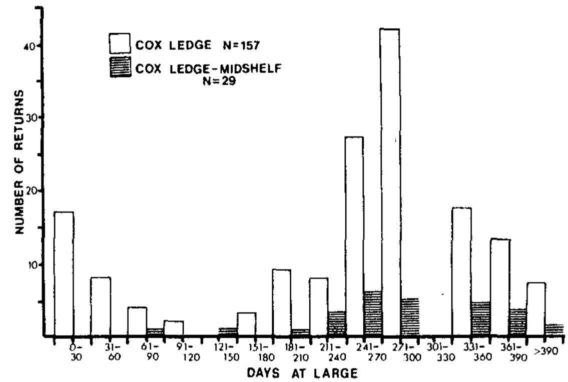


FIGURE 6.—Number of tag returns for American lobster released on Cox Ledge and lobster displaced from the Midshelf tagging site to Cox Ledge (Cox Ledge-Midshelf) as a function of time at large, Rhode Island vicinity.

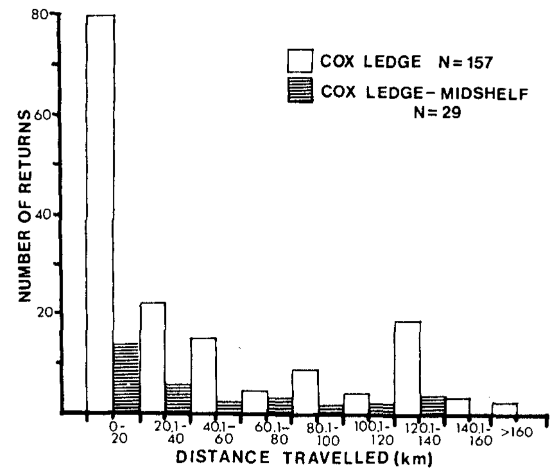


FIGURE 7.—Number of tag returns for American lobster released on Cox Ledge and lobster displaced from the Midshelf tagging site to Cox Ledge (Cox Ledge-Midshelf) as a function of distance travelled, Rhode Island vicinity.

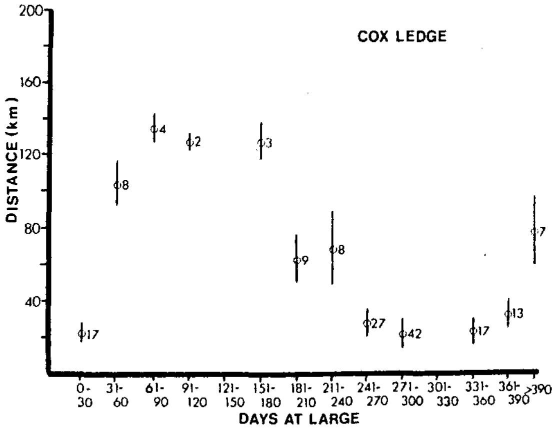


FIGURE 8.—Distance travelled ($\bar{x}\pm1$ SE) as a function of time at large for American lobster tagged and released on Cox Ledge, off Rhode Island. Sample sizes are specified beside each mean with an associated standard error.

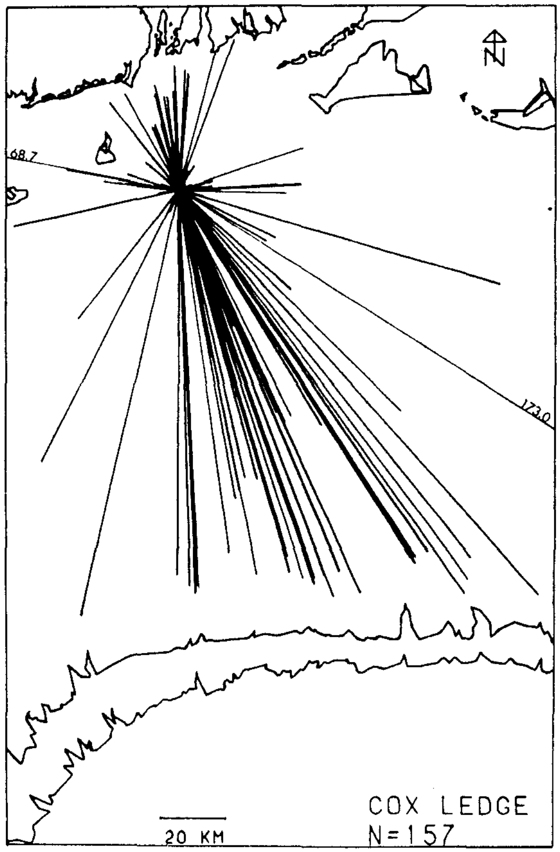


FIGURE 9.—Straight line distance between release and recapture sites for American lobster tagged and released on Cox Ledge, off Rhode Island. Release location is a composite of four release sites on Cox Ledge. Total distance travelled is noted for tracks which are truncated by borders.

straight-line distance between release and recovery sites indicated that these long distance migrants travelled to the outer continental shelf (Figure 9).

Tagging experiments conducted on the outer continental shelf revealed a shoalward migration in late spring and summer (Cooper and Uzmann 1971; Uzmann et al. 1977). The offshore migration in late fall and winter observed in the present study complements these findings and indicates a seasonal interchange between areas.

The mean vector angle for recovered tagged lobsters was 154.8°(T) at the Cox Ledge site and Rayleigh tests indicated a nonuniform distribution of returns (Table 2). The north-south vector component was substantially higher than the east-west component for the first 180 d at large, reflecting the strongly directed offshore movement. The relative magnitude of the north-south and east-west vector components were more nearly equal for lobsters at large over 180 d, indicating little directed movement. This is reflected in the nonsignificant mean vector bearing for lobsters at large between 181 and 270 d (Table 2).

A two-way fixed factor analysis of variance was used to examine the effects of size and sex on distance travelled for lobsters tagged and released on Cox Ledge. Lobsters were grouped by release size (≤90, 91-100, 101-110, 111-120, 121-130, ≥131 mm CL) and sex (male, female, ovigerous female) and the data were transformed ($\log_e x+1$) prior to analysis. No significant differences ($P<0.01$) were noted by size, sex, or the size-sex interaction.

Low return rates ($n=29$) for lobsters displaced from the Midshelf site to Cox Ledge prevented detailed analysis of movement patterns. The displaced lobsters were treated independently of the lobsters tagged and released on Cox Ledge at all levels of analysis. The mean distance travelled for lobsters transplanted from the Midshelf site to Cox Ledge was 41.6 km with an average of 274.7 d between release and recapture. The mean vector bearing for Cox Ledge-Midshelf lobsters was 170.5°(T); however, the hypothesis of a uniform distribution of return directions was not rejected ($P<0.01$) when the data were subjected to a Rayleigh test.

Return rates for lobsters tagged and released on the Midshelf fishing grounds were also low, preventing detailed analysis. The mean distance travelled for 34 recovered lobsters was 18.2 km and the mean time at large was 26.9 d. The mean vector angle for Midshelf lobsters was 167.1°(T) and the distribution of return directions was nonuniform (Rayleigh test; $P<0.01$).

DISCUSSION

Tagging experiments conducted in the coastal waters of the western North Atlantic have demonstrated generally localized lobster movements. Recent in situ observations in restricted regions of the Gulf of Maine (Cooper et al. 1975) and in Long Island Sound (Stewart 1972) have supported these results using seasonal underwater census techniques. Morrissey (1971) and Dow (1975) demonstrated, however, that lobsters tagged at inshore locations were capable of undertaking large-scale movements. Lund et al. (footnote 6) reported that some lobsters tagged in eastern Long Island Sound migrated to the outer continental shelf. Direct comparisons among these inshore studies are often not possible due to differences in tagging methodology, seasonal deployment of tags, and size range of lobsters tagged.

More consistent long-range movement patterns have been noted for lobsters tagged and released on the outer continental shelf (Cooper and Uzmann 1971; Uzmann et al. 1977). Saila and Flowers (1968) had earlier demonstrated that ovigerous female lobsters were capable of extensive movements when displaced from offshore sites to Narragansett Bay.

In the present study, the movements of lobsters tagged and released at inshore locations were typically localized. We attributed the small dispersion radius, in part, to high exploitation rates which resulted in rapid recovery of released lobsters. Examination of recapture records indicated that some inshore lobsters at large for over 180 d exhibited little movement. Unfortunately, it is impossible to determine the actual trajectories of recovered lobsters and the true extent of movements between release and recovery is unknown. Employing an ultrasonic tag, Lund et al. (footnote 6) tracked individual lobster movements and concluded that most lobsters undertake only minor (<30 m) daily movements in eastern Long Island Sound.

We consistently noted southerly movements for recaptured lobsters released at inshore locations. Constraints on east-west and northerly movements imposed by geographical features of the area undoubtedly contributed to this result although movement was not totally precluded in these directions (Figure 1). The Rayleigh test gives equal weight to each return direction and therefore any detectable movement in any direction would be represented in the analysis.

Nonuniform distribution of fishing effort further complicates the interpretation of these results and the potential bias introduced by this factor cannot be ignored. Nonhomogeneous sampling effort can result in an apparent directional tendency when superimposed on random movements. In the lobster fishery, effort is concentrated primarily in areas with available shelter where lobster density is highest. Lund et al. (footnote 6) reported that lobster movements at inshore locations were often transitions between areas of suitable habitat. Dispersal of this type is therefore likely to be detected through returns from the commercial fishery. Due to high demand for lobster, the coverage exerted by the fishery is extensive and it has expanded to areas which were formerly considered marginal in terms of catch per unit effort or where operational costs were prohibitive (as on the outer continental shelf). The distribution of effort therefore generally approximates the distribution of lobster.

Comparisons between lobsters released at inshore locations in spring and early summer with those released in late summer indicated a sharp increase in directed movements in the latter period. A concommitant increase in the mean square dispersion coefficient indicated that random movements also increased, possibly as a result of increased activity and catchability. The timing of release differed slightly at each of the inshore locations; of the 147 lobsters recovered from the Sakonnet River tagging, 119 (80.9%) had been released prior to 1 July while 123 (65.4%) and 59 (51.3%) of the Narragansett Bay and Rhode Island Sound lobsters were released prior to 1 July. Since the three inshore release sites were located in close proximity and were similar habitat types, we attributed the differences in movements between locations to the timing of release. Stewart (1972) noted increased activity and movements in summer for lobsters tagged in Long Island Sound.

In constrast to the limited movements noted at inshore release locations, lobsters tagged on Cox Ledge migrated to the outer continental shelf in late fall and winter. Little evidence of lateral movement was noted despite an active fishery to both the east and west of Cox Ledge. Coupled with observations of an inshore spring migration from the outer continental shelf (Cooper and Uzmann 1971; Uzmann et al. 1977), these data indicate an intermixing between offshore and inshore lobster populations. Independent confirmation of seasonal inshore-offshore movements has been obtained using a stratified random trawl survey conducted in spring and fall by the National Marine Fisheries Service (Burns et al.[7]).

Lobster stock identification studies based on electrophoretic techniques (Tracey et al. 1975) and linear discriminant analysis of morphometric data (Saila and Flowers 1969) indicated that inshore and offshore groups are discrete. Tracey et al. (1975) noted generally low levels of genetic variability, but inshore and offshore lobsters were differentiable at one locus of the 44 examined. Saila and Flowers (1969) reported significant profile differences between inshore and offshore lobsters. These studies would indicate that inshore and offshore groups retain their genetic identity despite seasonal intermixing. Migrational studies do indicate the possibility of genetic exchange between areas, perhaps explaining the low levels of genetic variability (Tracey et al. 1975) and some of the inconsistencies noted by Saila and Flowers (1969). The period of intermixing does correspond to periods of molting and mating activity. Further research on inshore-offshore stock interactions is clearly needed to resolve these questions. This factor assumes particular importance since it is possible that coastal sites are dependent on recruitment from offshore areas to sustain inshore populations that are subjected to extremely high levels of fishing mortality.

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