NOAA Technical Report NMFS SSRF-747

Movement, Growth, and Mortality of American Lobsters, *Homarus americanus*, Tagged Along the Coast of Maine

Jay S. Krouse

September 1981

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Malcolm Baldrige, Secretary
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CONTENTS

Figures

Tables

Movement, Growth, and Mortality of American Lobsters, *Homarus americanus*, Tagged Along the Coast of Maine[1]

JAY S. KROUSE[2]

ABSTRACT

During the spring of 1975, 2,882 American lobsters, *Homarus americanus*, were tagged at three locations off Maine. Four months after release 65% of the lobsters had been returned and by the completion of the study in September 1977, 2,188 (75.9%) lobsters had been recaptured. Most returns (88%) occurred within a 5 n.mi. (9.3 km) radius of the release site and only about 1% of the recaptured lobsters had moved more than 10 n.mi. (18.5 km). Movement and catchability did not vary significantly by sex nor size. The majority of lobsters traveled shoreward or along the coast on a west to southwesterly course with minimal easterly movement. All long distance migrants (>20 n.mi. or 37.0 km) followed a south to southwesterly course. Extremely high annual instantaneous fishing mortality rates (4.0-7.3) estimated for each release area confirm the overexploitation of the Maine inshore lobster fishery.

INTRODUCTION

During the past decade concern for the future well-being of the Maine American lobster fishery has intensified as levels of fishing effort have increased and catches have generally declined. In response to this interest in Maine's most valuable commercial fishery, the Lobster Research Project of the Maine Department of Marine Resources (DMR), initiated in 1966 extensive studies of various facets of the fishery (Thomas 1973; Krouse and Thomas 1975; Krouse 1978) and biology of the lobster (Krouse 1973). Even though information from these studies has provided some basis for scientific management of the lobster fishery, additional research is required in many areas. One important area with a paucity of information is that of lobster movement along the Maine coast. To date there have been three tagging studies with Maine lobsters. Harriman[3] and Cooper (1970) tagged lobsters at Monhegan Island [about 10 n.mi. (nautical miles), 18.5 km offshore] and determined that those lobsters were nonmigratory since most recaptures were recovered within a 2 n.mi. (3.7 km) radius of the island. In contrast, Dow (1974) reported that 5 of 162 lobsters (23 returns in all) tagged by commercial fishermen off the Maine coast traveled 75-138 n.mi. (138.9-255.6 km) toward Cape Cod. Four of these migrant lobsters were larger than the Maine maximum legal size of 127 mm CL (carapace length) when tagged, indicating a positive relationship between a lobster's size and movement.

In view of the limited size and scope of these lobster tagging studies conducted previously in Maine waters, we decided to undertake a coastwise tagging project. Objectives of this present study were to provide new information on growth, mortality, and movement or migration patterns of legal-sized lobsters (81-127 mm CL).

METHODS

Tagging Areas

Three tagging sites, Kennebunkport, Boothbay Harbor, and Jonesport, representing the western, central, and eastern sections of the Maine coast (Fig. 1), were selected on the basis of geographical location and local availability of lobsters.

Well in advance of the scheduled dates for tagging, certain lobster dealers were contacted at each tagging area, and arrangements were made to purchase about 1,000 lobsters from each area. It was specified that these lobsters be locally caught and not sorted by size. These requirements would ensure that the tagged lobsters were characteristic of the area studied in terms of size, movement, and catchability.

To determine whether the tagged lobsters were representative in size of those lobsters caught commercially, length-frequencies were plotted by 1 mm increments for lobsters tagged at each tagging site (Fig. 2). Because of the likeness between size composition data of this present study and data obtained from Maine's Commercial Sampling Program (Thomas 1973), we are confident that the lobsters tagged were typical of the legal size range of lobsters along the Maine coast.

Tagging

The sphyrion tag developed by Scarratt and Elson (1965) and later modified by Cooper (1970) was selected as the primary mark as it can be retained through a molt. The model we used in this study consisted of a supple yellow PVC (polyvinylchloride) tube (2 mm diameter × 55 mm long) attached by a thin polyethylene thread to a 7 mm long stainless steel anchor. Tags were attached according to the technique described by Cooper (1970).

In order that the magnitude of tag loss could be evaluated a secondary tag was used. The tag selected was the Floy cinch-up which was secured to the pincer claw by either fastening it around the proximal end of the propodus or around the carpus of lobsters >100 mm CL. Although this tag would be lost after ecdysis, we anticipated that a sufficient number of lobsters would be recaptured prior to molting, to enable estimation of

[1]This study was conducted in cooperation with the Department of Commerce, National Marine Fisheries Service, under Public Law 88-309 as amended, Commercial Fisheries Research and Development Act, Project 3-228-R.

[2]Marine Resources Laboratory, Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[3]Harriman, D. M. 1952. Progress report on Monhegan tagging 1951-52. Unpubl. manuscr., 8 p. Maine Dep. Mar. Resour., W. Boothbay Harbor, ME 04575.

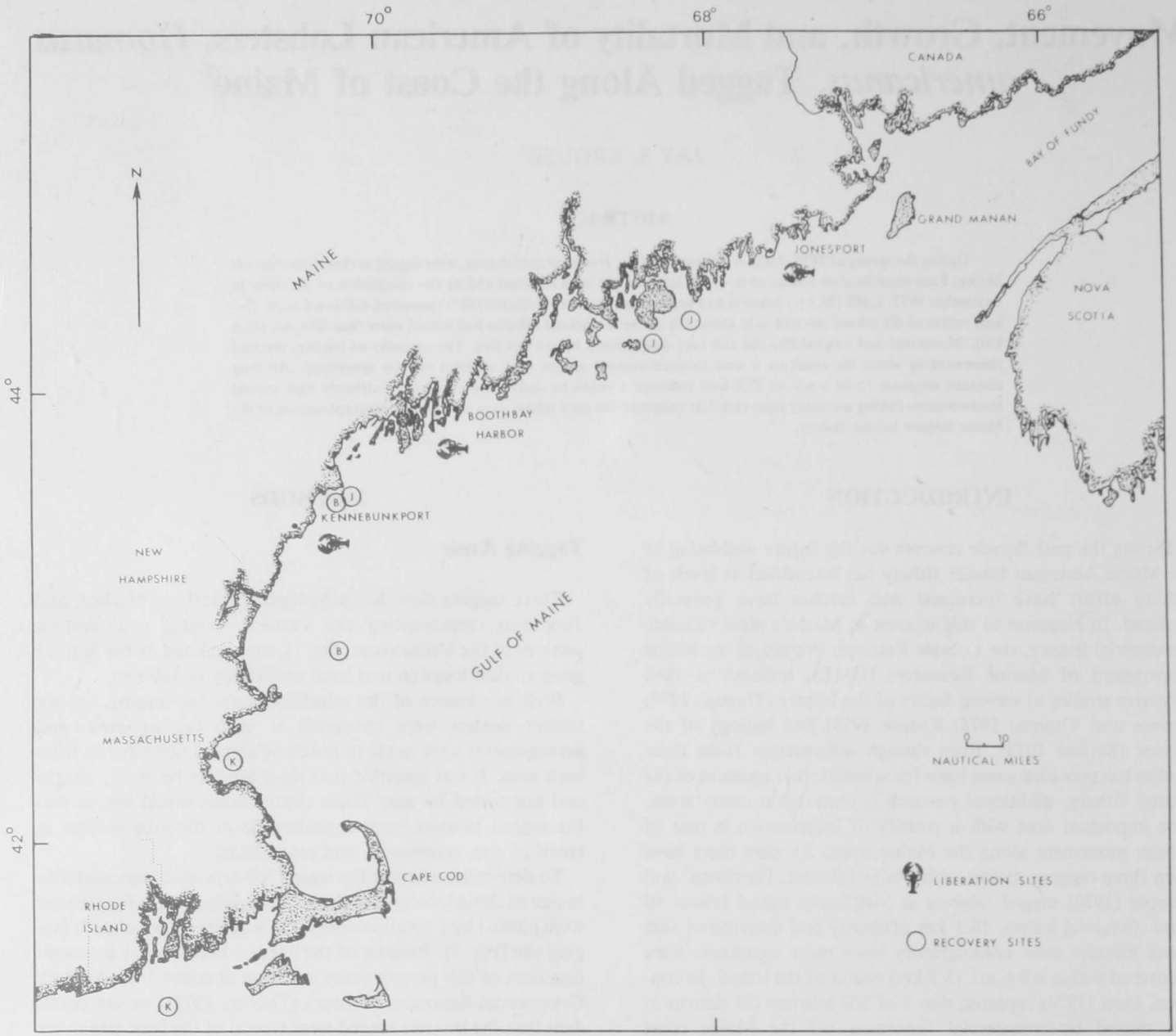

Figure 1.—Maine coast showing the three tagging areas and recovery points of American lobsters that moved ≥ 20 n.mi. (37.0 km). Lobsters released at Boothbay Harbor, Jonesport, and Kennebunkport, Maine, are denoted by B, J, and K in circles.

the rate of sphyrion tag loss. Experimentation with the nylon cinch-up tag revealed that this material expands upon immersion in water and consequently might slip off the claw. To minimize stretching, the tags were soaked in tepid water prior to application.

Publicity

To ensure that fishermen and dealers would be informed of the tagging program, posters advertising rewards for the return of tagged lobsters were distributed to almost all lobster dealers along the Maine coast. Cash rewards were $2.00 for return of only the tag and $5.00 for lobster with tag(s) intact. Throughout the study we strived to maintain the fishing community's interest and cooperation through periodic press releases on the progress of the tagging program and frequent contact with those dealers most likely to receive tagged lobsters.

Tagging commenced in late April 1975, which was the earliest that an adequate supply of lobsters could be guaranteed, yet early enough for sphyrion tags to become firmly encysted in advance of the peak molting period in August and September. Before each lobster was tagged, carapace length, weight, and sex were recorded along with the corresponding numbers of both tags. Immediately after the tags were attached, the lobster was placed in a partitioned fiber glass tray, where circulating seawater hastened blood coagulation. Following a short recovery period (½-1h) lobsters not displaying normal vigor were discarded while all others were transferred to individual sections of 10.2 cm diameter PVC pipe (23-28 cm long) contained in rectangular wire cages. These cages were hung over the side of the boat until all lobsters (about 1,000) for that area were tagged and could be released simultaneously. The holding period ranged from 1 to 5 d. This system of isolation eliminated the loss and mutilation of sphyrion tags which occurs when tag-

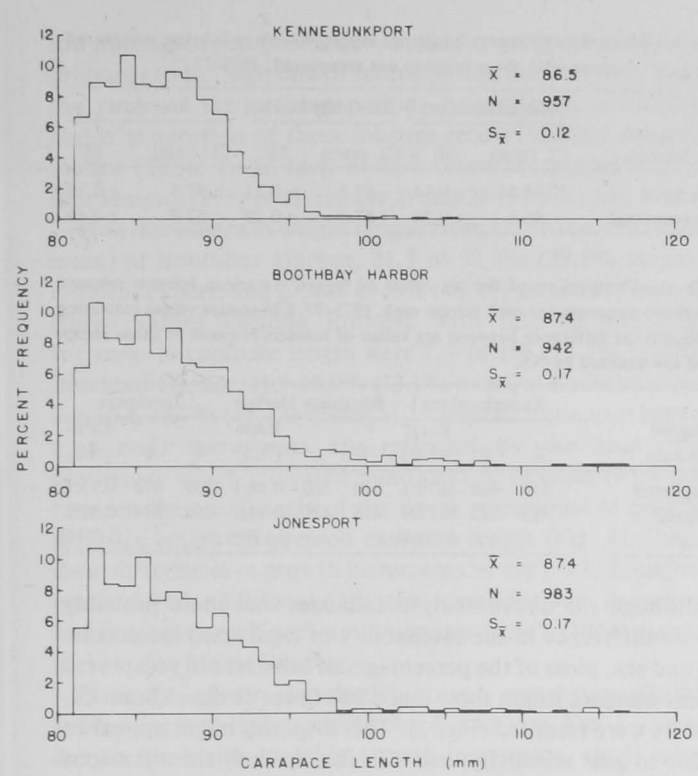

Figure 2.—Length-frequencies of American lobsters tagged and released at Kennebunkport (6 May 1975), Boothbay Harbor (17 May 1975), and Jonesport (30 May 1975), Maine.

ged lobsters are crowded together. Other advantages were: 1) reduction of postrelease tag mortality (most deaths attributable to this cause would occur prior to release); 2) opportunity for the sphyrion tag to become firmly attached during the lobster's quiescence in "solitary confinement"; and 3) considerable savings in boat-running time by eliminating daily excursions to release lobsters.

On 6 May, 957 tagged lobsters were released 2 n.mi. (3.7 km) seaward of the mouth of the Kennebunk River. Next on 17 May, 942 lobsters were released 10 n.mi. (18.5 km) south of Boothbay Harbor. Finally on 30 May, 983 tagged lobsters were liberated about 12 n.mi. (22.2 km) southwest of Jonesport. Although immediate release points were virtually void of traps, substantial numbers of traps were within 1-5 n.mi (1.9-9.3 km).

Recovery

All recapture sites were identified and the latitude and longitude determined and plotted. The straight line distance between release and recapture points was measured and the number of days at liberty were calculated for each lobster. All data were coded and key punched for subsequent tabulation (Krouse 1978).[4]

RESULTS AND DISCUSSION

Recaptures

Of 2,882 American lobsters tagged during the spring of 1975, 75.9% were recaptured through September 1977 (Table 1). Returns by tagging area were 85.2% at Jonesport, 74.8% at Kennebunkport, and 67.4% at Boothbay Harbor. These different return rates may be explained, in part, by the proximity of

[4]Krouse, J. S. 1978. Listing of data for lobsters tagged and recaptured off the Maine coast (1975-77). Research Reference Document 78/8, 37 p. Maine Dep. Mar. Resour., W. Boothbay Harbor, ME 04575.

Table 1.—Monthly tag recoveries of American lobsters by release area off Maine, 1975-77. Numbers in parentheses refer to lobsters that molted.

	Kennebunkport			Boothbay Harbor			Jonesport			Total	
	Recaptured			Recaptured			Recaptured			Cumulative return	
		Cumulative			Cumulative			Cumulative			
Month	Number	Nos.	%	Number	Nos.	%	Number	Nos.	%	Nos.	%
1975											
May	136	136	14.2	18	18	1.9	—	—	—	154	5.3
June	244	380	39.7	176	194	20.6	315	315	32.0	889	30.9
July	119	499	52.1	160	354	37.6	285(1)	600	61.0	1,453	50.4
Aug.	132	631	65.9	145(1)	499	53.0	132(3)	732	74.5	1,862	64.6
Sept.	39(3)	670	70.0	58(4)	557	59.1	60(6)	792	80.6	2,019	70.1
Oct.	17	687	71.8	33(1)	590	62.6	29(7)	821	83.5	2,098	72.8
Nov.	11(3)	698	72.9	9(2)	599	63.6	9(5)	830	84.4	2,127	73.8
Dec.	5	703	73.5	10(2)	609	64.7	0			2,142	74.3
1976											
Jan.	3(1)	706	73.8	5(1)	614	65.2	0			2,150	74.6
Feb.	0			0			0				
Mar.	0			0			1(1)	831	84.5	2,151	74.6
Apr.	0			3	617	65.5	2(1)	833	84.7	2,156	74.8
May	1(1)	707	73.9	2(1)	619	65.7	2	835	84.9	2,161	75.0
June	2	709	74.1	1	620	65.8	0			2,164	75.1
July	1(1)	710	74.2	2(1)	622	66.0	1(1)	836	85.1	2,168	75.2
Aug.	1(1)	711	74.3	2(2)	624	66.2	0			2,171	75.3
Sept.	3(2)	714	74.6	6(6)	630	66.9	1(1)	837	85.2	2,181	75.7
Oct.	0			1(1)	631	67.0	0			2,182	75.7
Nov.	0			1(1)	632	67.1	0			2,183	75.8
Dec.	0			3(3)	635	67.4	0			2,186	75.9
1977											
Apr.	1(1)	715	74.7	0			0			2,187	75.9
May.	1(1)	716	74.8	0			0			2,188	75.9
Sept.	0			0			0				
Totals	(14)	716	74.8	(26)	635	67.4	(26)	837	85.2	2,188	75.9

release sites to zones of moderate to high fishing intensity. For instance, at Boothbay Harbor tagged lobsters were released more seaward than at the other areas and were therefore more removed from immediate fishing pressure. Also, based on our sightings of boats towing their nets near the release area shortly after liberating tagged lobsters and rumors of trawlers catching tagged lobsters but not reporting them (unlawful for trawlermen to land lobsters in Maine), there is reason to believe that perhaps several of the Boothbay Harbor releases were removed from the fishery by trawlers. In Jonesport, where returns were the highest, even though releases were in an area with very few traps, substantial concentrations of traps were only about 1 n.mi. (1.9 km) away in all directions; whereas, at Kennebunkport, where returns were intermediate to the other two areas, the proximity of the area's release site to the trap fields would be ranked between that of Jonesport and Boothbay Harbor.

Because differences in tag recoveries by area might be partially due to any variations in the tagging adeptness of the two biologists who applied the tags in this study, we evaluated this possibility by comparing the proportions of the number of lobsters returned with those tagged by biologists at each release site (Table 2). As there were no significant differences (chi-square test, $P>0.05$) between these proportions, it appears that the biologists applied the sphyrion tags with nearly equal skill; thus any major variations in returns from different areas could not be related to differences in numbers of lobsters marked by any one tagger.

Table 2.—Comparison of the proportions of American lobsters recaptured with those tagged by two biologists at each release area, 1975–77. Chi-square values indicating no significant difference ($P>0.05$) between proportions are denoted by NS.

	Kennebunkport		Boothbay Harbor		Jonesport		Total	
Tagger	Number tagged	% returned	Number tagged	% returned	Number tagged	% returned	Number tagged	% returned
A	560	79	514	70	490	85	1,564	78
B	394	69	428	64	493	84	1,315	73
χ^2	1.61 NS		0.58 NS		0.0001 NS		1.03 NS	

Four months after release, 53-81% (67% combined) of the tagged lobsters had been returned in each area, and after 1 yr 66-85% (75% combined) had been recaptured. These high rates of return, which corroborate the lobster fishery's high exploitation rate, have undoubtedly been reduced by tag loss, incomplete reporting of recaptures, and natural and tag induced mortality. Based on our observations of lobsters following tagging until time of release and our close familiarity with the fishing community, it appears that only a negligible number of lobsters died as a result of tagging or were captured and not reported (exclusive of Boothbay Harbor). Thus, in this study, tag loss and natural mortality (< 10% annually, Thomas 1973) were probably the most important sources of error.

The effect of size on catchability was examined by comparing the mean carapace length of lobsters recaptured at each release site with those tagged lobsters not recaptured before October 1977 (Table 3). The *t*-test ($P>0.05$) revealed no significant difference between the mean sizes of those lobsters caught with those still at large. Similarly, the chi-square test indicated no statistical differences ($P>0.05$) between sex ratios of lobsters returned to those liberated (Table 4).

Table 3.—Mean sizes (carapace length) of tagged American lobsters recaptured along with those lobsters not recaptured, 1975-77.

	Kennebunkport		Boothbay Harbor		Jonesport	
Tagged lobsters	$\overline{CL}$ (mm)	SE	$\overline{CL}$ (mm)	SE	$\overline{CL}$ (mm)	SE
Recaptured	86.5	±0.14	87.5	±0.21	87.4	±0.19
Not recaptured	86.6	±0.24	87.0	±0.29	87.8	±0.40

Table 4.—Comparison of the sex ratios of tagged American lobsters released with those recaptured at each release area, 1975–77. Chi-square values indicating no significant difference between sex ratios of lobsters released to those recaptured are denoted by NS.

	Kennebunkport			Boothbay Harbor			Jonesport		
Tagged lobsters	♂	♀	Ratio (♂:♀)	♂	♀	Ratio (♂:♀)	♂	♀	Ratio (♂:♀)
Recaptured	316	400	0.79:1	314	320	0.98:1	359	478	0.75:1
Released	415	542	0.77:1	456	486	0.94:1	439	544	0.81:1
χ^2			0.07NS			0.15NS			0.05NS

Although the above analysis indicates that there probably was no difference in the catchability of legal-sized lobsters by size and sex, plots of the percentages of lobsters not recaptured against carapace length show that 4-9% fewer 81 than 82 mm CL lobsters were returned (Fig. 3). This disparity might appear to be due to gear selectivity, but is in fact unlikely since previous studies (Krouse 1973; Krouse and Thomas 1975) show that lobsters become fully vulnerable to conventional lobster pots at about 75 mm CL. Actually this lower than expected catch of small legal lobsters is due to the Maine fishermen's method of measurement and interpretation of what lobsters are legal to keep. The minimum legal size is 81 mm (3-3/16 in) CL in Maine; but the minimum size retained in practice is closer to 82-83 mm. This conclusion is further supported by length frequencies of Maine commercial lobster catches compiled by Thomas (1973) which showed marked deficiencies of the 81 mm group; in fact, even the 82 through 84 mm sizes were less numerous than expected.

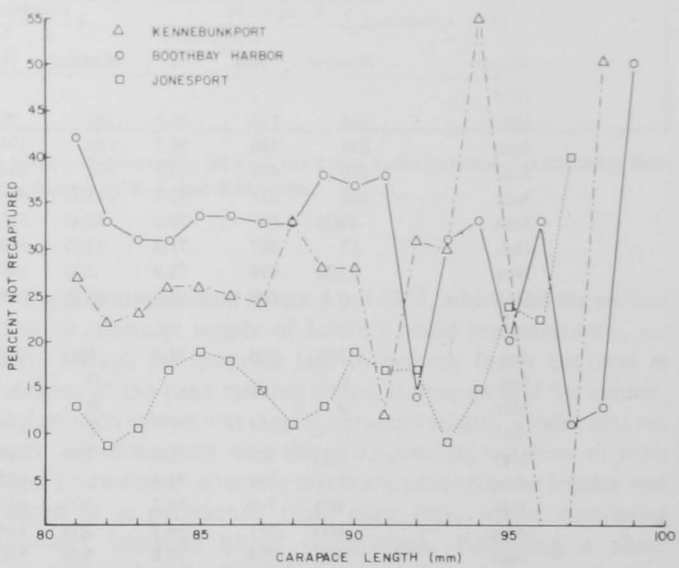

Figure 3.—Size distributions of tagged American lobsters still at large after September 1977 (about 28 mo since release) at each tagging area.

Growth

From July 1975 through May 1977, only 66 (3.0%) lobsters of 2,188 returns had molted prior to recapture. This extremely

low number of recaptured new-shell lobsters may be attributed primarily to the high rate of return during the first 3 mo before the peak of the molting period. Accordingly, a decidedly higher proportion of those lobsters recovered after 4 mo had molted (Table 1). In fact, of 46 lobsters recaptured after the first season (1975) at all release areas, 28 (60.9%) had molted.

Molt increments in weight ranged from 21.9 to 64.4% (40.9% mean) at Boothbay Harbor, 21.3 to 52.8% (39.8% mean) at Kennebunkport, and 27.3 to 67.5% (46.2% mean) at Jonesport (these values exclude lobsters with missing chelipeds). Increases in carapace length were 7.3-18.1% (12.7% mean) at Boothbay Harbor, 11.5-16.0% (13.1% mean) at Kennebunkport, and 10.6-18.5% (15.1% mean) at Jonesport. Variations between area molt increments are reflected by the analysis of covariance which indicated significant differences ($P = 0.05$) between the coefficients of the linear regressions of postmolt carapace length on premolt carapace length (Fig. 4). Despite these differences in growth increments by area, which might be resolved with additional data, the overall increase in carapace length (areas combined) approximates Dow's (1964) estimate of 14% for Maine lobsters.

Estimates of von Bertalanffy growth parameters (Gulland 1969) were not realistic (negative K and very low L_∞ values) due to the highly variable growth increments, small sample sizes, and the limited range of sizes and ages represented by the data.

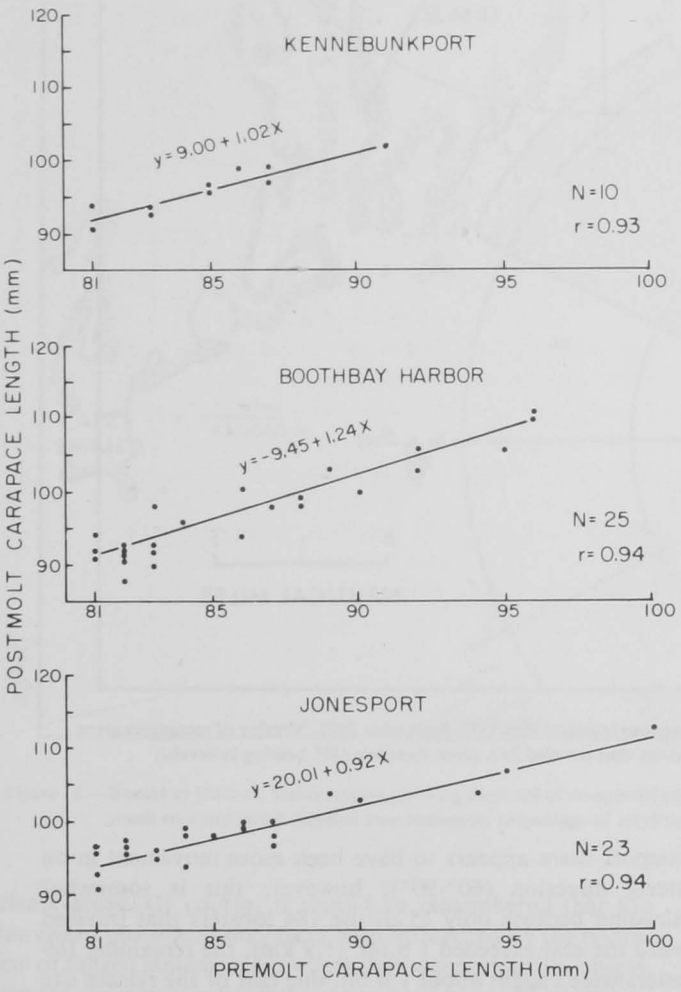

Figure 4.—Premolt-postmolt carapace length relations of recaptured tagged American lobsters that molted at each release site.

Movement

Before movement trends of recaptured tagged lobsters can be thoroughly analyzed, it is necessary to consider the intensity, distribution, and seasonality of fishing effort at each release site. Unfortunately, sufficient data were not available to quantify effort by area; however, in view of catch and effort information of the Maine commercial lobster fishery collected coastwise by DMR's Lobster Research Project personnel, it was apparent that fishing pressure was extremely intense at all tagging areas. Seasonal changes in fishing intensity and location of lobster trap fields are well-known occurrences along the Maine coast (Dow 1961; Thomas 1973; Cooper et al. 1975). During the summer-fall period when the most intense fishing activity occurs, most traps are rather uniformly distributed along the shores of the mainland, around islands and ledge outcroppings where usually rough, rocky substrates provide ideal lobster habitat. In winter and spring when fishing effort is minimal, most traps are moved to deeper water (>30 m) (Cooper et al. 1975) where 1) traps are less apt to be damaged or lost due to severe winter storms, 2) warmer water temperatures cause lobsters to be more active and subsequently more catchable, and 3) lobsters are now more abundant due to the fact that most traps are fished in shoaler water (<30 m) during the warmer months.

Another factor which should be considered when assessing movement trends of this study was the release of tagged lobsters at locations differing from those of original capture. Nevertheless, as mentioned previously, all lobsters tagged and released at a certain site were caught within that general area.

Movement patterns were initially assessed by plotting the points of recapture at each release site (Figs. 5-7). Of the Kennebunkport releases (Fig. 5), most lobsters were recaptured in close proximity to shore within a 5 n.mi. (9.3 km) radius of the release site. Only 14 recaptures traveled >5 n.mi. and 10 of these lobsters moved in a southerly direction. The most notable movements were by a male (90 mm CL) which was at large 369 d and traveled 63 n.mi. (116.7 km) to Boston and a female (88 mm CL) which was allegedly caught near Tiverton, R.I. (185 n.mi., 342.6 km), 199 d after release.

At Boothbay Harbor (Fig. 6), most lobsters were recovered between the mouths of the Kennebec and Damariscotta Rivers. Only one lobster was recaptured in the Damariscotta River, while none was reported from the Kennebec River. By contrast, numerous tagged lobsters were returned from the Sheepscot River estuary. Twelve lobsters traveled ≥ 10 n.mi. (18.5 km) up this estuary. Significant easterly and southerly movement was limited to a female (87 mm CL), at large 23 d, that traveled 14 n.mi (25.9 km) to Monhegan Island; a male (107 mm CL), at large 88 d, which moved 42 n.mi. (77.8 km) to Cape Porpoise; and a female (99 mm CL) caught at Jeffreys Ledge (61 n.mi., 113.0 km) after 197 d at liberty.

In comparison with other areas, directional movement of Jonesport recaptures appeared to be less restricted (Fig. 7). Although several lobsters were recaptured seaward of the release locations, most were taken inshore. The greatest movements (≥ 20 n.mi., 37.0 km) were by three lobsters that traveled southwesterly. The farthest distance moved was 134 n.mi. (248.2 km) (to Kennebunkport) by an 89 mm CL male at large 405 d, followed by a 29 n.mi. (53.7 km) trek to Great Duck Island by a small male (81 mm CL) at large 49 d, and a

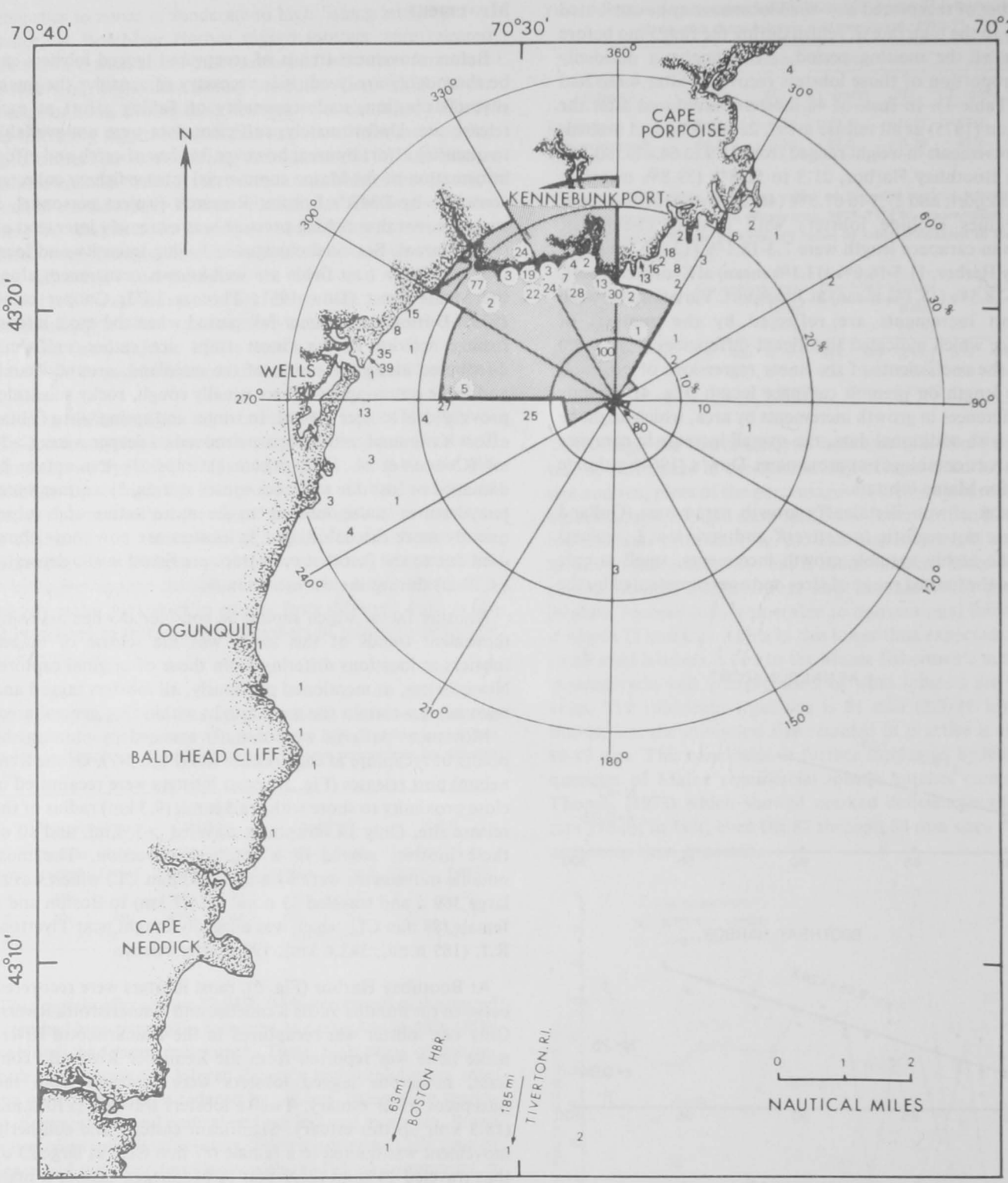

Figure 5.—Kennebunkport, Maine, region showing dispersal of recaptured tagged American lobsters, May 1975–September 1977. Number of recaptures given at each recovery point. Shaded area represents percentage of recaptured lobsters that traveled in a given direction (30° bearing intervals).

20 n.mi. (37.0 km) movement to Schoodic Head by a 96 mm CL female at large 327 d.

To evaluate directional movement more objectively, compass bearings were assigned to all recapture coordinates and grouped by 30° increments (Figs. 5-7). At Kennebunkport and Boothbay Harbor most lobsters were recovered at bearings 1°-30° and 270°-360° from the release areas while only 8.5% of the returns from both areas traveled in other directions. At Jonesport there appears to have been more movement in an easterly direction (60°-90°); however, this is somewhat misleading because only 15 of the 184 lobsters that traveled toward the east exceeded 1 n.mi. (1.9 km), the remaining 169 lobsters were caught about 1 n.mi. due east of the release site near Nashes Island (Fig. 7).

In view of the information presented herein, it can be seen that the majority of recaptured lobsters moved inshore at all

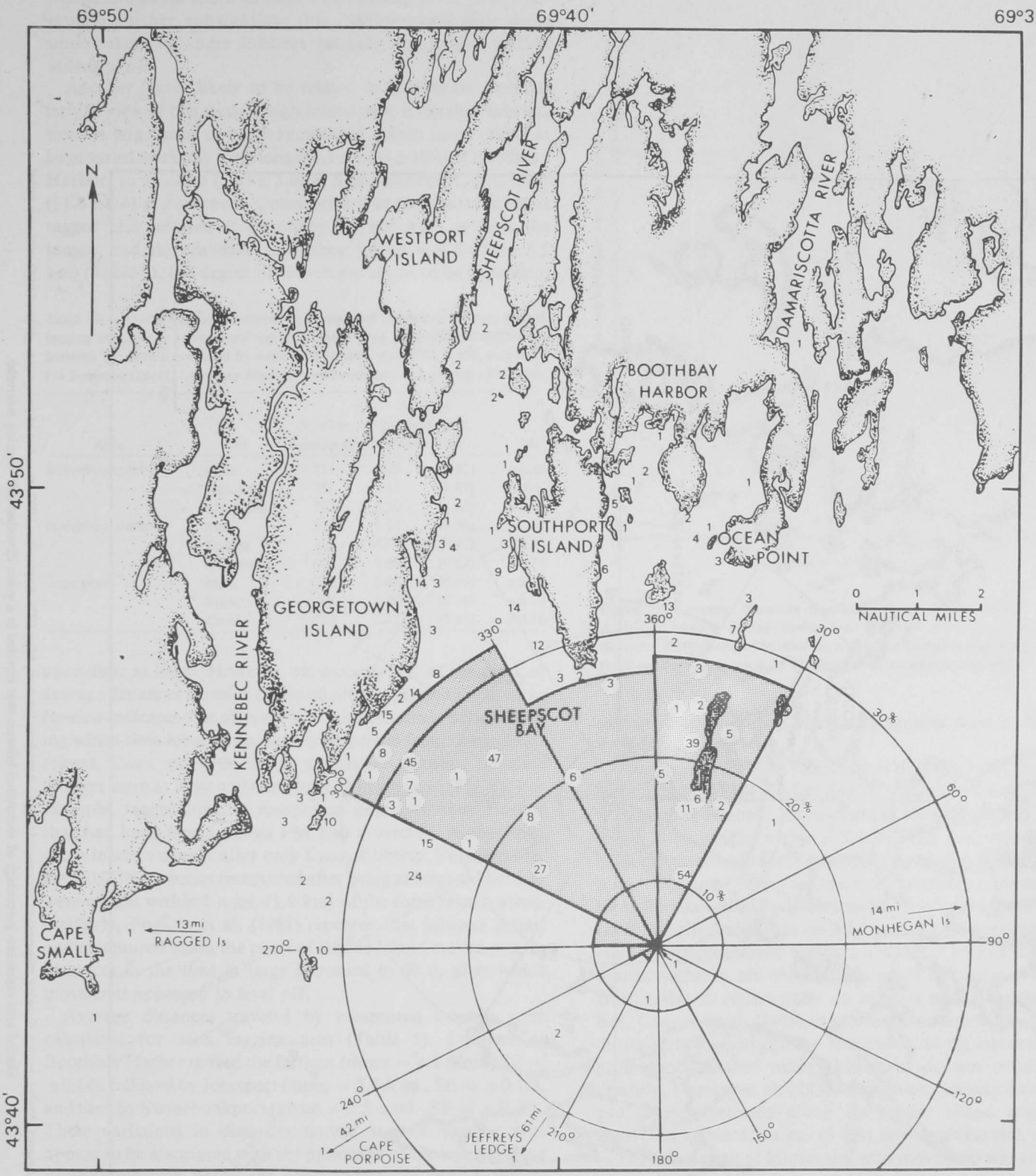

Figure 6.—Boothbay Harbor, Maine, region showing dispersal of recaptured tagged American lobsters, May 1975–September 1977. Number of recaptures given at each recovery point. Shaded area represents percentage of recaptured lobsters that traveled in a given direction (30° bearing intervals).

release areas. Of course, it should be remembered that this shoreward movement may have been influenced by the relocation of tagged animals from where they were originally caught. Limited movement toward the east, which was particularly evident at Boothbay Harbor, might be the result of the counterclockwise current along the Maine coast. Accordingly, all long distance migrants (≥20 n.mi., 37.0 km) of this study appeared to travel in the direction of the prevailing south to southwesterly coastal currents (Fig. 1). Likewise, the major migrants of Dow's (1974) tagging study followed a south by southwesterly course as they moved from Maine coastal waters toward New Hampshire and Massachusetts. Moreover, recent returns of several tagged Canadian lobsters (released off Grand Manan Island, N.B. (Fig. 1)) from various locations in

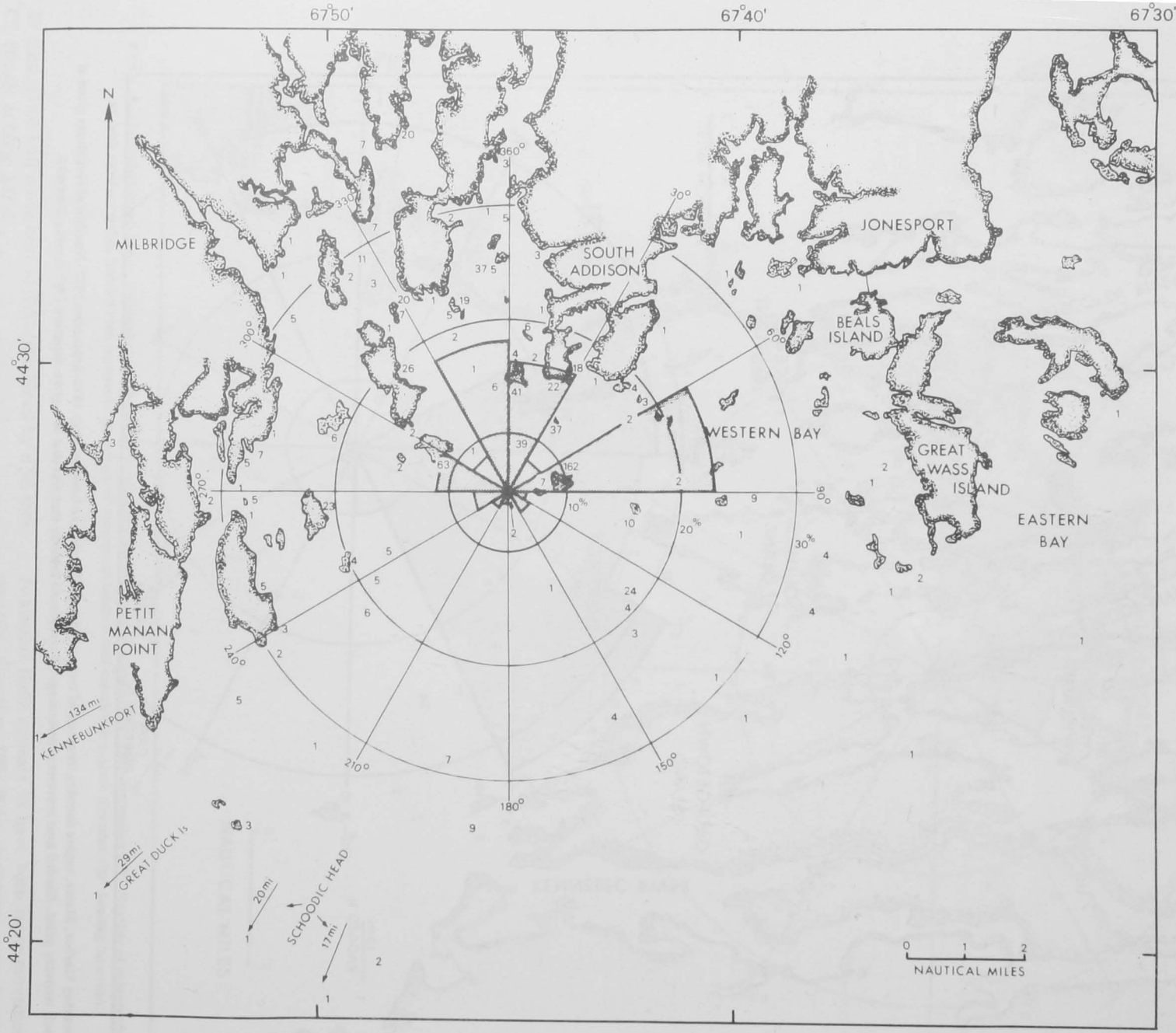

Figure 7.—Jonesport, Maine, region showing dispersal of recaptured tagged American lobsters, May 1975–September 1977. Number of recaptures given at each recovery point. Shaded area represents percentage of recaptured lobsters that traveled in a given direction (30° bearing intervals).

Maine and as far south as Cape Cod (Groom 1978, pers. commun.[5]) further substantiate this southwesterly movement undertaken by some lobsters (usually the larger mature individuals).

Another factor likely to be related to movement, particularly in view of this study's high return rate, is the time lobsters were at large prior to being recaptured. Mean times (days) at large varied markedly from long (86.1 ± 3.4) ($\pm$1SE) at Boothbay Harbor, to medium (70.5 ± 2.6) at Kennebunkport, and short (51.8 ± 1.4) at Jonesport. Considering that recaptured lobsters tagged and released at Boothbay Harbor were at large the longest and also traveled the farthest (mean = 4.6 n.mi., 8.5 km) (Table 5), the degree of movement seems to be dependent

Table 5.—Average distances moved by recaptured American lobsters at each tagging area. Sexes were combined since there were no statistical differences between the distances moved by males and females ($t = 0.594$, 0.301, and 0.677 for Kennebunkport, Boothbay Harbor, and Jonesport, respectively; $P > 0.05$).

Area	Sex	Number recaptured	Average nautical miles moved	(km)	SE
Kennebunkport	Male	314	2.33	(4.32)	±0.21
	Female	398	2.63	(4.87)	±0.47
	Combined	712	2.50	(4.63)	±0.28
Boothbay Harbor	Male	307	4.62	(8.56)	±0.17
	Female	317	4.54	(8.41)	±0.21
	Combined	624	4.60	(8.52)	±0.14
Jonesport	Male	351	3.07	(5.69)	±0.39
	Female	468	2.80	(5.19)	±0.10
	Combined	819	2.92	(5.41)	±0.18

upon time at large. However, an examination of the plots of average distances traveled (nautical miles) against time at large (weeks) indicates that after an 8-10 wk postrelease period, during which time lobsters apparently dispersed from the point of release, there was little if any association between the time lobsters were at large and the extent of movement (Fig. 8). For example, tagged lobsters recaptured near Boothbay Harbor that had been free 6 mo to 1 yr had moved no farther than those lobsters caught after only 2 mo of liberty. Furthermore, 8 of 30 (27%) lobsters recaptured after being at large at least 1 yr were caught within 1 n.mi. (1.9 km) of the three release areas. Similarly, Fogarty et al. (1981) reported that lobsters tagged and recaptured along the coast of Rhode Island moved greater distances as the time at large increased to 90 d, after which movement appeared to level off.

Average distances traveled by recaptured lobsters were calculated for each tagging area (Table 5). Lobsters at Boothbay Harbor moved the farthest (mean = 4.6 n.mi., SE = ±0.14), followed by Jonesport (mean = 2.9 n.mi., SE = ±0.18), and then by Kennebunkport (mean = 2.5 n.mi., SE = ±0.28). These variations in distances moved at each tagging area appear to be associated with the proximity of the release site to neighboring trap fields, the configuration of the immediate coastline, and, possibly, to where the lobsters were originally caught. For instance, at Boothbay Harbor where lobster movement was the most extensive, the liberation area was not only farther from shore relative to the other areas, but also more removed from zones of moderate to intense fishing pressure. Of course these factors, particularly the latter, also

[5]W. Groom, Fishery Biologist, New Brunswick Department of Fisheries, Fredericton, New Brunswick, Canada, pers. commun. March 1980.

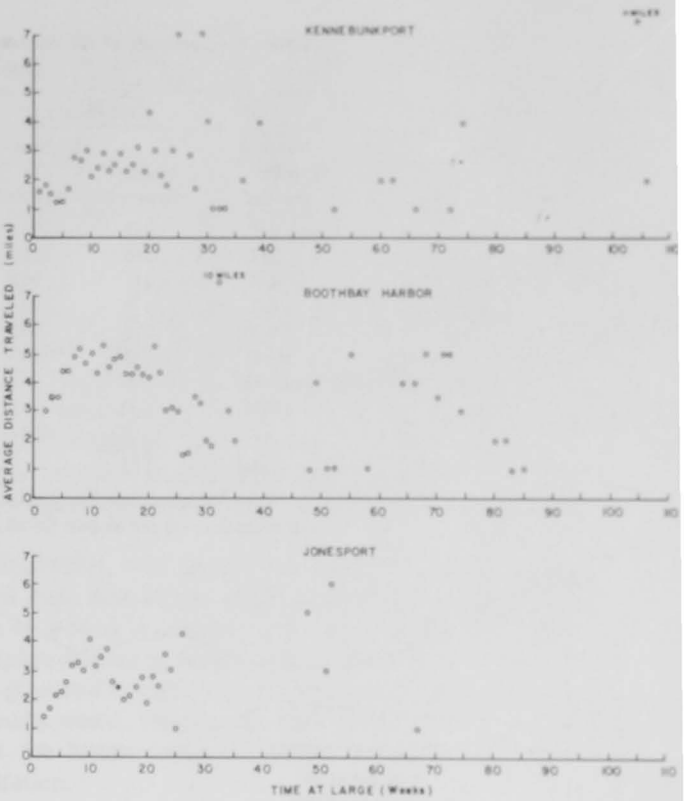

Figure 8.—Average distances (nautical miles, 1.9 km) traveled by tagged American lobsters during weekly time intervals prior to recapture. Mean distances were calculated by dividing total miles moved by tagged lobsters recaptured during a given week by the number of recaptures that week.

explain why Boothbay Harbor recaptures were at large the longest.

Most tagged lobsters remained in the vicinity of the release areas as indicated by the fact that 74, 92, and 98% of the returns at Boothbay Harbor, Jonesport, and Kennebunkport, respectively, were caught within a 5 n.mi. (9.3 km) radius of the release site and only about 1% of the recaptures wandered >10 n.mi. (18.5 km) (Table 6). Even more restricted movement patterns were observed by Harriman (see footnote 3) and Cooper (1970) who reported that most lobsters tagged near Monhegan Island were recaptured within 2 n.mi. (3.7 km) of the island. Similarly, based on observations made by scuba divers and from research submersibles on lobsters near Boothbay Harbor, Cooper et al. (1975) concluded that large-scale seasonal movements on and off the shallow (<24 m) inshore fishing grounds (notion of many fishermen) do not occur. More recently, Fogarty et al. (1981) noted that the majority of tagged lobsters released along the Rhode Island coast were recovered within 3.2 n.mi. (6 km) of the release site.

The association of lobster size with movement was evaluated by averaging the miles moved by lobsters in 5 mm CL increments and then plotting these values against carapace length (Fig. 9). Although there appears to be no relationship between size and movement, it should be noted that only 2.2% of the lobsters tagged in this study were >100 mm CL, and according to the studies of Dow (1974) and Groom (see footnote 5) the majority of major migrants along the Maine coast exceeded 100 mm CL. Aside from the fact that relatively few large lobsters (>100 mm CL) were tagged in this study, it should also be mentioned that only 19 (34.5%) of 55 recaptures >100 mm CL were at large more than 3 mo and only 4 (7.3%)

Table 6.—Summary of the distances traveled by recaptured tagged American lobsters at each tagging area, 1975-77.

Nautical miles traveled	Kennebunkport Number returned	Kennebunkport Cumulative % returned	Boothbay Harbor Number returned	Boothbay Harbor Cumulative % returned	Jonesport Number returned	Jonesport Cumulative % returned
0–1	219	30.8	56	10.0	311	38.0
2–3	368	82.4	112	26.9	264	70.2
4–5	111	98.0	291	73.6	174	91.5
6–7	8	99.2	140	96.0	58	98.5
8–9	1	99.3	12	97.9	3	98.9
10–11	3	99.7	7	99.0	1	99.0
12–13	0		2	99.4	4	99.5
14–15	0		2	99.7	0	
>15	2	100.0	2	100.0	4	100.0
Total[1]	712		624		819	

[1]These values are less than total number of recaptures reported in Table 1 because location of recapture was not known for all returns.

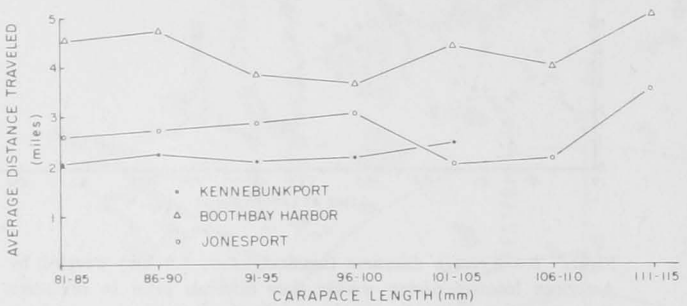

Figure 9.—Distances moved by recaptured American lobsters of various sizes tagged and released at Kennebunkport, Boothbay Harbor, and Jonesport, Maine.

lobsters were free longer than 1 yr prior to being caught. Perhaps, at least for the larger lobsters, reductions in times at large may have curtailed movement.

Mortality

Mortality rates were estimated from a linear regression of the number of tagged lobsters recaptured on the time at large. Regression coefficients were substituted into Gulland's (1969) equation (6.3):

$$\log_e n_r = -(F+M)\, r\, T + \log_e \left[\frac{FN_0}{F+M} \left(1 - e^{-(F+M)}\right) \right]$$

where the

$$\text{intercept (a)} = \log_e \left[\frac{FN_0}{F+M} \left(1 - e^{-(F+M)T}\right) \right]$$

$$\text{slope (b)} = -(F+M)\, r\, T$$

n_r = number of recaptures during interval r,

where r = 0, 1, 2, 3 ... weekly, biweekly, or monthly period following release

T = length of interval of time (r)

N_0 = number of tagged lobsters released.

Because an estimate of total mortality, derived with tagging data along, is the sum of fishing mortality (F) plus not only natural mortality (M), but also all other causes of reductions in the number of tagged animals, the value "X" (all sources of tag loss plus natural mortality) should replace M in the equations.

The number of recaptures plotted over time indicated that return rates increased during the first 4-8 wk, then leveled off for a brief period and eventually began to decrease (Fig. 10).

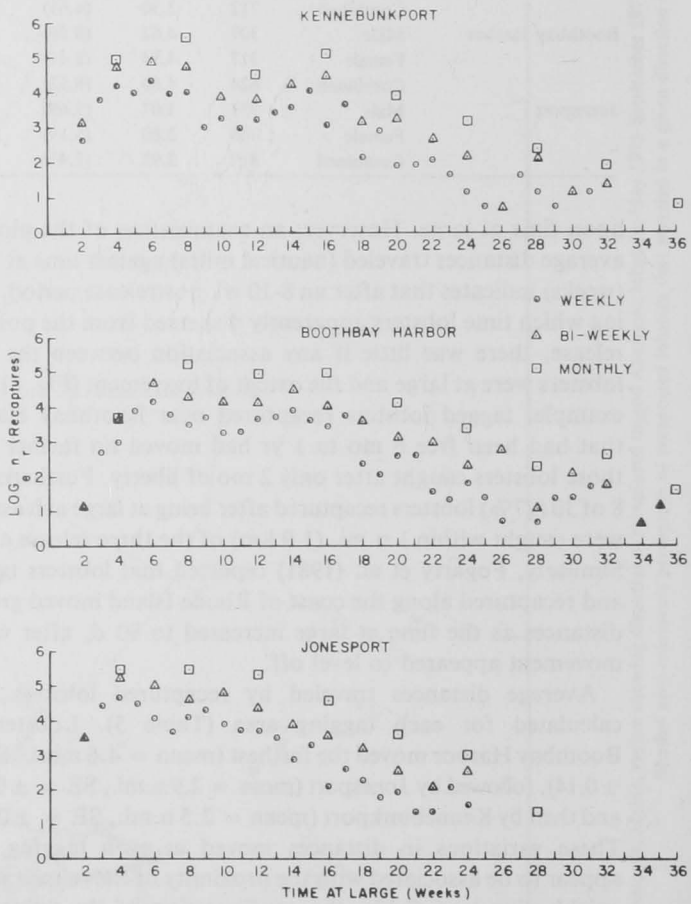

Figure 10.—Recaptures ($\log_e$ scale) of tagged American lobsters as related to time at large at each tagging area.

Increases in the number of recaptures during the first few successive weeks following release may be attributed to slow mixing of tagged animals with the fishable population in association with spatial variations in fishing intensity. Accordingly, mortality estimates were calculated from return data exclusive of those initial recovery intervals (2-4 wk) when mixing of tagged and untagged individuals was considered to be incomplete.

Annual instantaneous rates of fishing mortality (F) and apparent total mortality (Z') which ranged from 4.14 to 7.31 and 5.89 to 8.73 (Table 7), respectively, were extremely high as

Table 7.—Annual instantaneous rates of apparent total (Z') and fishing (F) mortality on American lobsters estimated from returns grouped by different time intervals. Annual mortality rates expressed as percentages are in parentheses.

Time interval	Kennebunkport		Boothbay Harbor		Jonesport	
	Z'	F	Z'	F	Z'	F
Weekly	7.10	4.14	6.36	4.13	8.73	7.22
	(99.9)	(98.4)	(99.8)	(98.4)	(99.9)	(99.9)
Biweekly	7.08	4.89	6.16	4.11	8.39	7.31
	(99.9)	(99.2)	(99.8)	(98.4)	(99.9)	(99.9)
Monthly	7.12	4.93	5.89	3.98	8.72	7.27
	(99.9)	(99.3)	(99.7)	(98.1)	(99.9)	(99.9)

the result of the actual return rates which were, I believe, not fully representative of general conditions; the fact that annual mortality rates were calculated from tag return data collected when the catches of the seasonal lobster fishery were highest, and systematic errors inherent in most tagging studies. Gulland (1969) has classified these errors according to their effects on the various estimates. Types A and B errors result from tag loss and systematically bias mortality rates causing an underestimate of fishing mortality and an overestimate of the true total mortality (Z), respectively. Type A error, which is caused by death of fish shortly after tagging and incomplete reporting of recaptures, affects F but not Z. Type A errors appeared minimal except at Boothbay Harbor where trawlers were suspected of unreported catches of tagged lobsters. In fact, the relatively lower estimates of F at Boothbay Harbor may be attributable, in part, to this error. Of the Type B errors, which include natural mortality, emigration, and tag detachment, only the latter was of significant magnitude in this study to warrant consideration.

Quantitative estimates of tag loss were obtained by following Gulland's (1963) methodology for estimating tag retention rates with data from double tagging experiments. Due to problems that we encountered initially with this procedure, Russell (1980) analyzed this method and corrected some of Gulland's basic equations.

In all cases, estimated losses of the sphyrion tag were higher than those of the cinch tag (Table 8). Considering differences in modes of attachment, higher losses of sphyrion tags were expected; however, cinch tag losses were greater than anticipated. Evidently some of the cinch tags became loose and subsequently slipped off the chela (claw). In retrospect, this type of loss would have been minimized had the tag been secured around the carpus (section proximal to the propodus) of the pincer claw.

A comparison of the relatively high annual loss rates of individual tags (range of 39.4-51.5%) with those of both tags (range of 15.0-24.0%) clearly indicates how tag returns would have been reduced if only one tag rather than two had been used. Nevertheless, in view of these estimates, we feel that tag loss was of sufficient magnitude to bias mortality estimates. This error, termed Type B, is an additional cause of mortality ("X") and results in an overestimate of Z but has no effect on F. Unfortunately, if we convert the highest annual tag loss rates (39.4-51.5%) (Table 8) to instantaneous rates (0.50-0.72) and then subtract these values from estimates of Z' (5.89-8.73) (Table 7), this only results in an insignificant reduction in Z'. Thus it is apparent that other factors besides tag loss have caused overestimates of Z. When these errors are operative only F is estimated from tagging data; thus Z is derived from some independent estimate and M is the difference between F and Z.

Undoubtedly, the most meaningful mortality estimates derived from data of this study are those of F and even these values as well as estimates of Z are inflated as the result of incomplete mixing of tagged lobsters with the untagged population [Gulland's (1969) Type C error] along with other factors previously stated. Despite this bias, estimates of F do indeed reflect the Maine lobster fishery's extremely high rate of exploitation.

SUMMARY

1. Of 2,882 lobsters tagged in the spring of 1975, 2,188 (75.9%) were recaptured through September 1977. Lobsters released at Jonesport had the highest return (85.2%) followed by Kennebunkport (74.8%) and Boothbay Harbor (67.4%).
2. Catchability of legal-sized lobsters did not vary by sex nor size.
3. Twenty-four ovigerous females ranging from 82 to 109 mm CL were recaptured.
4. Sixty-six (3.0%) of the lobsters recaptured had molted while at large. Percentage of increases in carapace length varied from 7.3 to 18.1% (12.7% mean) at Boothbay Harbor, 11.5 to 16.0% (13.1% mean) at Kennebunkport, and 10.6 to 18.5% (15.1% mean) at Jonesport.
5. The majority of returns from Kennebunkport (98.0%), Boothbay Harbor (73.6%), and Jonesport (91.5%) were caught within a 5 n.mi. (9.3 km) radius of the release sites. Recaptured lobsters moved on the average more at Boothbay Harbor (4.45 n.mi., 8.2 km) and less at Kennebunkport (2.16 n.mi., 4.0 km). Only about 1% of the returns wandered >10 n.mi. (18.5 km).
6. Most movement was shoreward with a westerly drift from the point of release. Few lobsters traveled in an easterly

Table 8.—Estimated percentage of tag loss after various time intervals for American lobsters released at Kennebunkport, Boothbay Harbor, and Jonesport, Maine.

Week	Kennebunkport			Boothbay Harbor			Jonesport		
	Sphyrion	Cinch	Both tags	Sphyrion	Cinch	Both tags	Sphyrion	Cinch	Both tags
1	2.0	1.6	0.03	1.2	1.2	0.01	1.8	1.2	0.02
4	7.6	6.3	0.5	4.8	4.5	0.2	6.7	4.9	0.3
16	24.7	21.1	5.2	16.7	16.0	2.7	22.3	17.0	3.8
52	51.5	46.5	24.0	39.4	38.2	15.0	48.3	39.9	19.3

direction. All long distance migrants (≥20 n.mi., 37.0 km) followed a south to southwesterly course.

7. Male and female lobsters exhibited no differences in movement. There was no apparent relationship between a lobster's size (98% of the tagged lobsters ranged from 81 to 100 mm CL) and the distance moved.
8. Except for an initial period of about 8 wk, which we consider unrepresentative, there was no association between the time lobsters were at large and the distance traveled. Therefore, even if the recovery rate had been lower there is no reason to believe that the movement patterns would have deviated from those observed.
9. Annual instantaneous fishing mortality rates, which were calculated from return data grouped at weekly, biweekly, and monthly intervals, were 4.14 (98.4%) to 4.93 (99.3%) at Kennebunkport, 3.98 (98.1%) to 4.13 (98.4%) at Boothbay Harbor, and 7.22 (99.9%) to 7.31 (99.9%) at Jonesport. Although the accuracy of these values has been biased by errors associated with tagging, the magnitude of these F's still reveals the lobster fishery's precariously high level of exploitation.

ACKNOWLEDGMENTS

I thank David Libby for his assistance with all phases of this study; Paul DeRocher and Donald Card (crew of the RV *Duchess*) for their invaluable help during the entire tagging operation. Thanks are also extended to Clarence Burke, David Parkhurst, and Gary Robinson who provided assistance with tagging. I am appreciative for the guidance offered by James Thomas. I thank those lobster dealers and fishermen who, often at an inconvenience to themselves, supported our program by reporting returns and furnishing pertinent information. An anonymous reviewer critically reviewed the manuscript and offered many valuable suggestions.

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