MATURITY, SEX RATIO, AND SIZE COMPOSITION OF THE NATURAL POPULATION OF AMERICAN LOBSTER, *HOMARUS AMERICANUS*, ALONG THE MAINE COAST[1]

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ABSTRACT

From 1968 through 1970, American lobsters, *Homarus americanus*, were collected in coastal water near Boothbay Harbor, Maine. Length-frequency histograms graphically displayed the marked effects of high commercial exploitation on the natural lobster population. Sex ratios approximated a 1:1 relationship for sublegal lobsters (Maine minimum size is 81-mm carapace length). Length-weight relationship was determined for 454 lobsters. Shedding was observed to begin in spring and then peak in late summer.

On the basis of ovarian classification, presence of spermatophores in seminal receptacles, length-frequency distribution of berried females, and morphometric measurements, nearly all females above 100-mm carapace length were assumed to be mature, whereas only a few females between 81- to 90-mm carapace length were mature. Examination of male gonads suggested that male lobsters began maturing at relatively small sizes (50% mature at about 44-mm carapace length).

The American lobster, *Homarus americanus* Milne Edwards, is one of the most valuable and heavily exploited commercial species occurring along the Maine coast. Recognizing the urgent need for biological management of this inshore fishery, the Maine Department of Sea and Shore Fisheries initiated the Lobster Research Program in April 1966. The two primary phases of this program have encompassed: 1) probability sampling of the commercial lobster fishery along the entire Maine coast and 2) collection of prerecruit and legal-sized lobsters (minimum size in Maine is now 81-mm carapace length) near Boothbay Harbor, Maine (this phase began in March 1968). With data from these two independent sampling schemes, various population parameters have been calculated and then ultimately employed to estimate the minimum size limit for maximum sustainable yield (Thomas, 1971).[3]

The objectives of this paper, which are based upon data collections of the natural lobster population from Boothbay Harbor, are concerned with: 1) sex ratios; 2) incidence of molting; 3) length-weight relationship; 4) size composition of catch; and 5) the size at first sexual maturity for both sexes.

METHODS AND MATERIALS

Lobsters were collected in coastal waters near Boothbay Harbor, Maine, from April 1968 through December 1970. The following types of gear were used: (1) rectangular vinyl-coated lobster traps (1- × 2-inch and 1- × 1-inch mesh); (2) elliptical polyethylene lobster traps; (3) conventional wooden lobster traps; (4) a

[1] This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-14-R.

[2] Maine Department of Sea and Shore Fisheries, West Boothbay Harbor, ME 04575.

[3] Thomas, J. C. 1971. An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. Unpublished manuscript, 73 p. Maine Department of Sea and Shore Fisheries, Completion Report.

Manuscript accepted July 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

shrimp try trawl with a cod end of 1-inch stretch mesh; and (5) a variable mesh monofilament gill net (four 25-ft sections of 1-, 2-, 3-, and 4-inch mesh). SCUBA divers were also employed on a few occasions to collect small male lobsters from which supplemental data were obtained for our maturity studies.

Of the aforementioned types of gear, considerably more fishing effort has been expended with wire traps. This disproportion of effort resulted from early fishing success experienced with wire traps and their relative suitability for hauling from a 17-ft Boston Whaler.[4] Subsequently, only 67 (2.6%) of 2,582 lobsters were captured with the other types of gear.

Carapace length (distance measured along midline from posterodorsal edge of carapace to posterior margin of eye socket) and total length (distance measured dorsally from tip of rostrum to tip of telson) were determined to the nearest millimeter for all lobsters sampled. Wet weights were recorded to the nearest 10 g.

MATURITY STUDY— GONAD EXAMINATION

Males

The vas deferens and/or testes of 204 male lobsters (carapace lengths ranged from 36 to 95 mm) were examined for the presence or absence of spermatophores (Figures 1 and 2). Males having spermatophores were considered mature. Because it was economically objectionable to sacrifice large numbers of lobsters, a method whereby the internal sex organs could be probed or extracted without any detrimental effects to the lobster was desirable. Initially, I attempted to withdraw sperm samples through a blunt hypodermic needle inserted into the vas deferens via its valvular orifice on the fifth pair of pereiopods. This technique produced inconsistent results and had to be abandoned. I then discovered that both the vas deferens and testis could be extracted with a forceps introduced through a small incision at the base of the fifth pair of walking legs. This procedure yielded reliable results and had no noticeable deleterious effects upon lobster survival throughout a postoperative period of several months.

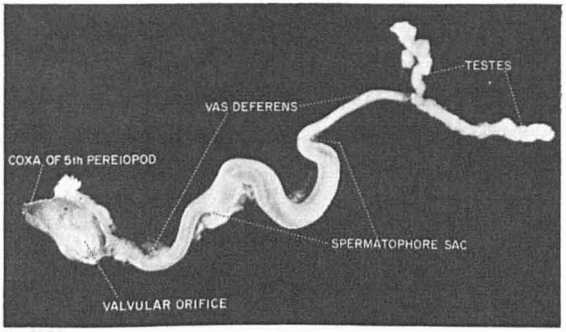

FIGURE 1.—Reproductive system dissected from a male lobster.

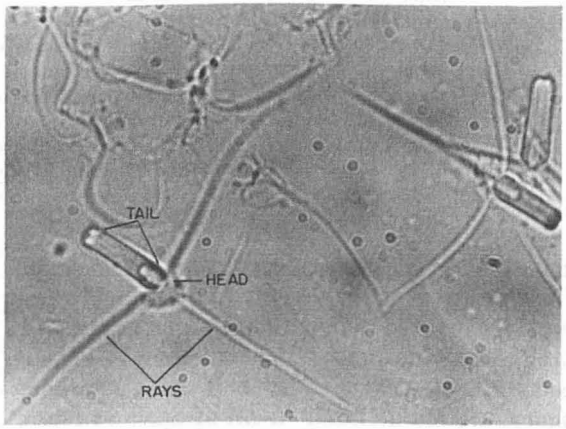

FIGURE 2.—Lobster sperm cells photographed under oil immersion at 970×.

Females

Ovaries were dissected from 158 female lobsters and then ovarian color and ova diameter (to nearest 0.1 mm) were recorded. Egg diameters were based on the average of a random sample of 10 eggs (distorted eggs were rejected) from each ovary. Using the criteria of ovarian color and ova diameter, ovaries were assigned to one of the following stages of development:

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Stage of development	*Ovary color*	*Egg diameter (mm)*
immature	translucent white	$\leqslant$ 0.4
developing	yellow-orange	0.5-0.7
mature	dark green	$\geqslant$ 0.8

Two additional determinations were made for each female: 1) width of the second abdominal segment (distance between deepest part of pleura on ventral surface) and 2) examination of the seminal receptacle (structure where sperm is stored upon copulation until egg extrusion) for the presence of sperm. As a check on my technique for detecting spermatophores, I examined 31 berried lobsters from Canada and found sperm in all of them.

In conjunction with the annual berried female program, during which the State of Maine purchases from the pound owners lobsters that have become ovigerous while in captivity, carapace lengths were recorded for 1,150 berried females.[5] These data were obtained during the period 1966 through 1970.

RESULTS AND DISCUSSION

SEX RATIOS

Sex ratios were analyzed by assigning lobsters from catches during the period 1968 through 1970 to 5-mm carapace length size groups by sex. Midpoints of each size increment were then plotted against the number of lobsters in each of the respective size groups (Figure 3). Although differences did exist between the proportion of males to females within various size classes, these differences were not consistent from year to year, suggesting that they may have been artifacts of sampling. In 1969 and 1970 when the catches were relatively large (greater than 1,000 lobsters), the overall percentages of females were 48.1 and 50.3, respectively. While the sex ratio approached 1:1 in 1969 and 1970, in 1968, when the sample size was half that of the other two years, the proportion of females was 56.4%. This disparity may best be attributed to the smaller sample size in 1968.

[5] Maine law prohibits the possession or sale of egg-bearing female lobsters.

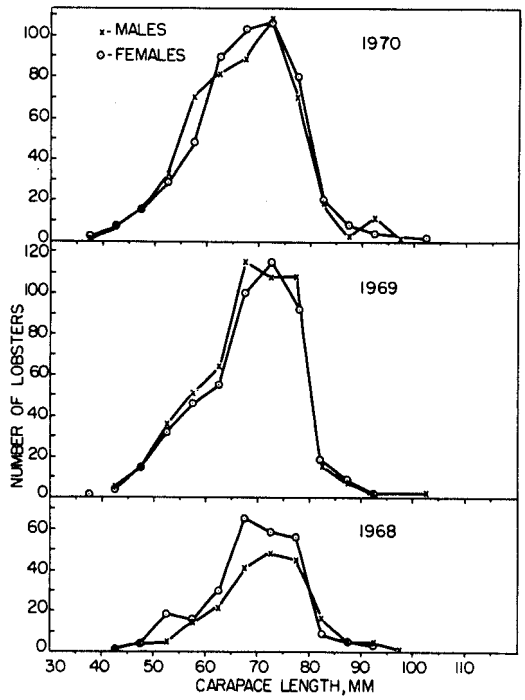

FIGURE 3.—Number of male and female lobsters grouped by 5-mm size classes from Boothbay Harbor, 1968 through 1970.

As the samples were predominantly composed of sublegal lobsters, our estimate of approximately a 1:1 sex ratio suggests that immature female and mature male lobsters have similar molting frequencies and increments of growth. In contrast to this, Herrick (1911), Templeman (1939), and Wilder (1953) have demonstrated that most sexually mature males molt annually and mature females every other year. In a tagging study conducted off Monhegan Island, Maine, Cooper (1970) found no significant differences in growth increments of male and female lobsters (average carapace length of 90 mm). Unlike the Maine findings, studies by Wilder (1963) in Egmont Bay, Prince Edward Island, and Squires (1970) and Ennis (1972) off Newfoundland revealed larger increments of growth for males than females for sizes above about 65-mm carapace length. Based on the maturity work of Templeman (1944), female lobsters from the aforementioned Canadian

study areas attain maturity at smaller sizes (50% mature between 70- to 80-mm carapace length) than Maine females as indicated by results of this present study; thus, I believe this explains why Canadian lobsters exhibited a differential growth rate between sexes, while Maine lobsters (our samples were markedly deficient of mature females) appeared to grow at the same rate regardless of sex.

MOLTING

Lobsters were classified as shedders (recently molted) when their carapace and/or chelipeds were soft to the touch (lacked normal rigidity). Because molting was observed to be concurrent for males and females, shedding data were combined for sexes (Table 1). While a few lobsters were observed to molt in spring, shedding did not reach a peak until September in 1968 and August in 1969 and 1970.

TABLE 1.—Percentage of soft-shelled lobsters in monthly samples from Boothbay Harbor, 1968 through 1970.

Month	1968	1969	1970
January	--[1]	0	--[1]
February	--[1]	--[1]	0
March	--[1]	0	0
April	0	0	4
May	0	0	1
June	0	3	4
July	2	6	19
August	1	10	24
September	16	1	18
October	10	0	17
November	1	--[1]	7
December	0	0	0

[1] No sample collected.

LENGTH-WEIGHT RELATIONSHIP

The regression of total wet weight on carapace length was calculated for 454 lobsters (206 males and 248 females) collected from April 1968 through March 1969. The equation used was $W = aL^b$, where W = wet weight in grams, L = carapace length in millimeters, and a and b are constants. The regression was fitted by the method of least squares using the logarithmic transformation $\log_{10}W = \log_{10}a + b \log_{10}L$.

Analysis of covariance on the regression coefficients as described by Steel and Torrie (1960) revealed no significant difference between sexes, so data from all lobsters were combined. The calculated regression equation was $\log W = -2.9052 + 2.9013 \log L$. This mathematical relationship is represented by the curve in Figure 4.

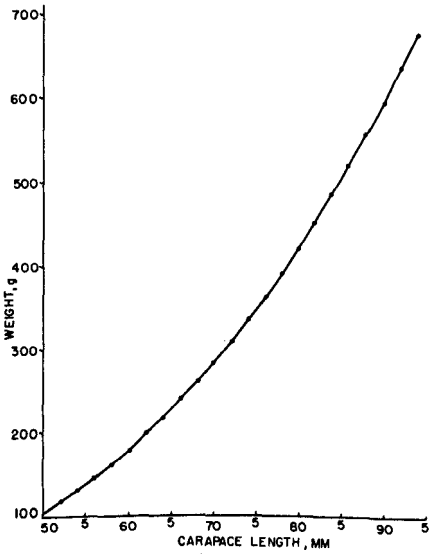

FIGURE 4.—Calculated length-weight relationship for 454 lobsters from Boothbay Harbor. The regression equation is $\log W = -2.9052 + 2.9013 \log L$.

SIZE COMPOSITION OF CATCH

I compiled length-frequency histograms of lobsters collected with wire traps in 1968, 1969, and 1970 (Figure 5). The effects of availability (term encompassing both vulnerability and accessibility) and the high rate of exploitation by the commercial fishery on our annual catches are manifested by the histograms.

The stepwise increase in numbers of lobsters with size up to approximately 70-mm carapace length led me to assume that this mode represented the size at which lobsters were fully vulnerable to our gear. Reduced vulnerability of lobsters smaller than 70-mm carapace length in our samples might best be attributed to the effects of gear selectivity and, possibly, the more seclusive behavior of small lobsters. In ecological studies of the lobster being conducted

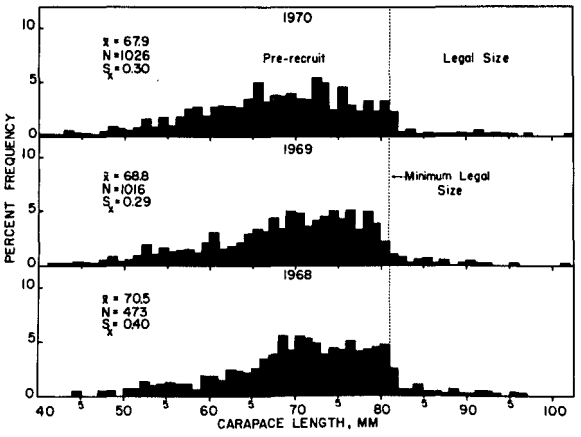

FIGURE 5.—Annual length-frequency distributions of lobsters sampled near Boothbay Harbor, 1968 through 1970.

in the Boothbay Harbor area, SCUBA divers have observed lobsters of less than 40-mm carapace length to be virtually inactive during nocturnal periods and apparently passing most of their early life within subterranean burrows (Richard A. Cooper, pers. comm.).

Sharp reductions in the number of lobsters above the minimum legal size (81-mm carapace length) reflected the influence of commercial exploitation. The legal-sized lobsters composed only 6 to 9% by number of the three annual catches.

For each annual length-frequency distribution, I attempted to select, on an objective basis, modes representative of assumed age or molt groups by analyzing the polymodal frequency distributions graphically with probability paper (Harding, 1949). Unfortunately, I discovered that I could not pick meaningful age or molt group modes due primarily to the limited size range (70- to 80-mm carapace length) over which our samples were considered to be representative of the natural lobster population. Since the increment of a lobster's growth was assumed to be about a 13 to 14% increase in carapace length (Wilder, 1953), it became apparent that our representative size range of 70- to 80-mm carapace length contained, at best, only one mode or possibly more if an age class experienced differential growth.

SIZE AT MATURITY

Males

In the Boothbay Harbor area, 50% of the male lobsters sampled were sexually mature at about 44-mm carapace length (Figure 6). The smallest mature male was 41-mm carapace length. Although sample size was limited for lobsters smaller than 45-mm carapace length, I do not believe that this significantly affected our conclusions.

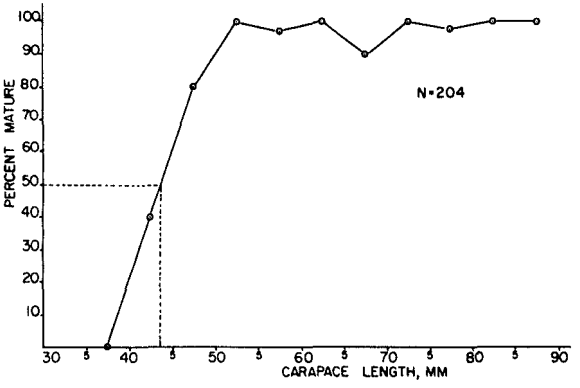

FIGURE 6.—Percentage frequency of mature male lobsters by 5-mm size classes.

In this study, maturity was solely based upon the criterion of presence or absence of sperm cells. Therefore, even though a lobster might appear to be physically mature (possessed sperm cells), this particular individual might be incapable of successfully copulating with a female. In mating experiments, Templeman (1934) observed that male lobsters were unable to mate with considerably larger females. In fact, the success of mating was greatest when the males were slightly larger than the females. As most females in the Boothbay Harbor area mature above the minimum legal size of 81-mm carapace length (discussed in following section), it appears that prerecruit males seldom contribute reproductively to the natural population.

Females

Size-frequency polygons of the three ovarian stages of development indicated that immature ovaries occurred in females from 51- to 89-mm carapace length; developing ovaries in females from 69- to 94-mm carapace length; and mature ovaries in females from 77- to 100-mm carapace length (Figure 7). Although the size ranges of the various ovarian stages overlapped considerably, the following trends are apparent: 1) immature ovaries predominated in females with carapace lengths less than 75 mm; 2) developing ovaries were most common at intermediate sizes (75- to 90-mm carapace length); and 3) mature ovaries gradually increased in frequency at sizes greater than 85-mm carapace length. Unfortunately, owing to difficulty in procuring legal-sized lobsters, the sample size of individuals between 85 and 100 mm in carapace length was limited to 47 lobsters; thus the task of determining size where approximately half the female lobsters became mature was confounded. However, the data indicated that a few females matured between 80- and 90-mm carapace length, but the onset of maturity for most females was at carapace lengths greater than 90 mm. This conclusion is further substantiated and expanded by the following facets of the maturity investigation.

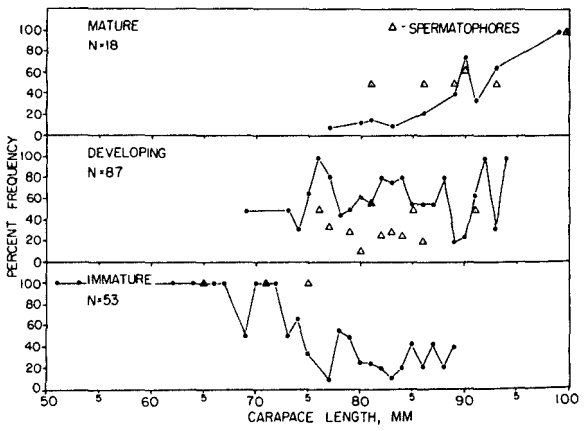

FIGURE 7.—Percentage frequency of the three ovarian stages of development and the occurrence of spermatophores (triangles) in the seminal receptacles.

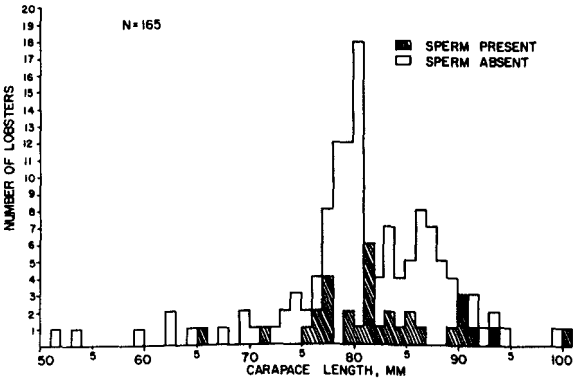

FIGURE 8.—Number of female lobsters with spermatophores in their seminal receptacles.

Spermatophores, the presence of which was another criterion for maturity, were detected more frequently in the seminal receptacles of mature females, particularly those females larger than 90 mm carapace length (Figures 7 and 8). Only 2 females with carapace lengths less than 75 mm had sperm cells, whereas 7 of 18 (39%) lobsters larger than 89-mm carapace length had spermatophores. From mating experiments, Templeman (1932, 1934) concluded that females had to be soft-shelled for mating to be accomplished successfully. Thus, females without spermatophores, even though their ovaries were classified as mature or well developed, would not be capable of spawning until they had undergone at least another molt and then, while soft-shelled, had copulated with a male. The absence of spermatophores in many females, which were observed to have developing or mature ovaries, suggested that these lobsters would not spawn until they advanced to the next molt class. Thus only 5 of 84 (6%) females from 80- to 90-mm carapace length were considered to be fully mature (possessed mature ovaries along with spermatophores), whereas the remaining 79 lobsters would not spawn until they attained carapace lengths of about 91 to 102 mm (assuming a 14% growth increment).

Templeman (1944) related the onset of sexual maturity of Canadian female lobsters with the relative increase in width of the second abdominal segment to total length. This morpho-

metric relationship was based on Templeman's (1935) observation that the female's abdomen markedly increases in width during maturation. I applied Templeman's method to my data on 482 females from inshore Boothbay Harbor (1968-71) and 31 berried Canadian lobsters (1970) as well as data on 217 females from inshore Boothbay Harbor collected in 1966 by Herbert C. Perkins of the National Marine Fisheries Service, West Boothbay Harbor, Maine. Carapace lengths were grouped by 5-mm size groups, and then abdominal widths of each size group were averaged. Ratios of abdominal width to carapace length were plotted against carapace length, and resulting curves were fitted by eye (Figure 9). Inflection points, which indicated size where maturity began, occurred at approximately 80-mm carapace length for both sets of Boothbay Harbor data. For the offshore population of American lobsters, Skud and Perkins (1969) reported an inflection point of 77 mm. Asymptotes, which denoted the size where all lobsters were assumed to be mature, appeared at about 115 mm for Perkins' Boothbay Harbor data, while an asymptote was not reached for my Boothbay Harbor data. I believe the asymptote at 115 mm was probably deceptively higher

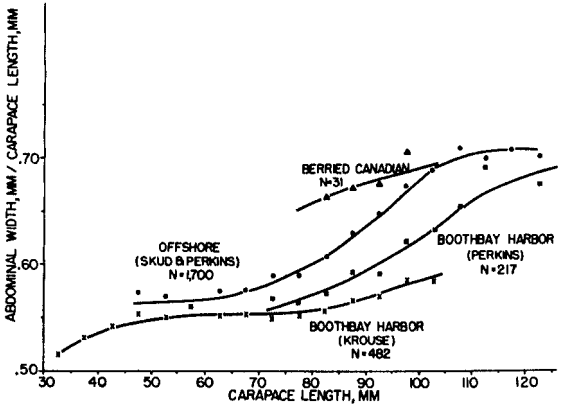

FIGURE 9.—Ratio of abdominal width to carapace length plotted against carapace length for Boothbay Harbor female data collected by Krouse and Perkins, berried Canadian female data, and Skud's and Perkins' study, 1969.

because of an insufficient number of lobsters sampled for sizes above 105 mm, which constituted less than 5% of the total sample. This conclusion was maintained both by Skud's and Perkins' (1969) data that demonstrated an asymptote at 100 mm and by the following section on length frequencies of ovigerous females from Maine. The relatively early maturity of Canadian females, particularly those inhabiting warm water of the southern part of the Gulf of St. Lawrence (Templeman, 1944), is demonstrated in Figure 9.

The length-frequency distribution of berried females taken along the Maine coast (Figure 10) disclosed that a few females began extruding

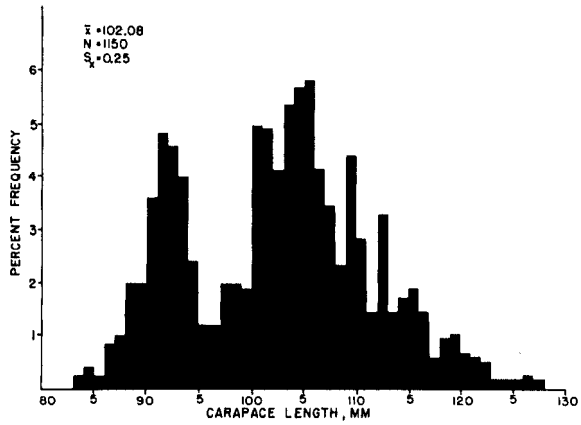

FIGURE 10.—Length-frequency distribution of native Maine berried females, 1966 through 1970.

eggs at 83-mm carapace length while the percentage of ovigerous females gradually increased to the first peak at 91 mm. The most pronounced mode occurred at about 105 mm, which was considered to be the size when nearly all females were mature. It should be mentioned that the modes at 91 and 105 mm corresponded with assumed age or molt class modes determined by Thomas (1971, see footnote 3) from commercial catch data.

The length-frequency distribution of berried females becomes particularly meaningful when compared with percent frequencies of female

lobsters from the commercial catch in the following size classes:

Carapace length	Percentage of total catch	
	Commercial	Berried females
81-90 mm	80	11
91-100 mm	17	29
>100 mm	3	60

Because lobsters ranging in carapace length from 81 to 90 mm constituted approximately 80% of the commercial catch and only 11% of the berried female sample, it is apparent that only a very small percentage of females mature below 90-mm carapace length. Certainly the most marked disparity in size composition was for carapace lengths greater than 100 mm (3% commercial and 60% berried females). This would seem to validate the previous conclusion that most females above 100-mm carapace length are mature.

SUMMARY

This study which is concerned with the analyses of data collected from 1968 through 1970 on the natural population of American lobsters along the Maine coast has yielded the following information:

1. Sex ratio was 1:1, thus suggesting that differences in growth rate and molting frequency do not exist between mature males and immature females.

2. Molting was concurrent for males and females, with shedding reaching a peak in late summer.

3. The length-weight relationship for sexes combined was $\log W = -2.9052 + 2.9013 \log L$.

4. Length-frequency histograms revealed the high rate of exploitation by the commercial fishery and an increase in unavailability of lobsters progressively smaller than 70-mm carapace length.

5. Male lobsters begin maturing at relatively small sizes (50% mature at about 44-mm carapace length); however, because native Maine females rarely mature below the minimum legal size of 81-mm carapace length and males must approximate females' size to successfully mate, it is doubtful that prerecruit males contribute reproductively to the natural population.

6. Female maturity was assessed by the following methods: 1) classification of ovaries by color and ovum diameter to three stages of development; 2) examination of seminal receptacles for spermatophores; 3) morphometric relationship of abdominal width:carapace length ratio to carapace length; and 4) length-frequency distribution of native Maine berried females. From estimates by these four independent methods, I concluded that females seldom become sexually mature at a size less than 81-mm carapace length, and then only a small fraction of those females between 81 and 90 mm attain maturity, whereas, at carapace lengths greater than 100 mm, nearly all females are assumed to be mature. Bearing in mind the minimum legal size regulation of 81-mm carapace length, I demonstrated in this study that the majority of females are harvested commercially prior to their first opportunity to spawn. An obvious change in management suggested by the results of this study would be to increase the minimum size limit to insure successful spawning by a sizeable portion of the population. Based on results of this study and those from the commercial sampling phase of the Maine lobsters project, Thomas (1971, see footnote 3) deals specifically with minimum size limit increases as a means to achieve a maximum sustainable yield.

ACKNOWLEDGMENTS

I am indebted to James C. Thomas for his guidance and support throughout the course of this study and his review of the manuscript. Richard Hanley, Gerald Brackett, Robert Nunan, Stephen Ham, and Andrew Dolloff assisted with field collections and data compilations. Gareth Coffin of the Northeast Fisheries Center, National Marine Fisheries Service, West Boothbay Harbor, Maine, performed the photographic work.

LITERATURE CITED

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.

ENNIS, G. P.
1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. J. Fish. Res. Board Can. 29:143-148.

HARDING, J. P.
1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141-153.

HERRICK, F. H.
1911. Natural history of the American lobster. Bull. [U.S.] Bur. Fish. 29:149-408.

SKUD, B. E., AND H. C. PERKINS.
1969. Size composition, sex ratio, and size at maturity of offshore northern lobsters. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 598, 10 p.

SQUIRES, H. J.
1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. Proc. Natl. Shellfish. Assoc. 60:22-39.

STEEL, R. G. D., AND J. H. TORRIE.
1960. Principles and procedures of statistics with special references to the biological sciences. McGraw-Hill, N.Y., 481 p.

TEMPLEMAN, W.
1932. Investigator's summaries. Biol. Board Can., Annu. Rep., p. 38-41.
1934. Mating in the American lobster. Contrib. Can. Biol. Fish., New Ser. 8:421-432.
1935. Local differences in the body proportions of the lobsters, *Homarus americanus*. Biol. Board Can. J. 1:213-226.
1939. Investigations into the life history of the lobster (*Homarus americanus*) on the west coast of Newfoundland, 1938. Newfoundland Dep. Nat. Resour., Res. Bull. (Fish.) 7, 52 p.
1944. Abdominal width and sexual maturity of female lobsters on Canadian Atlantic coast. J. Fish. Res. Board Can. 6:281-290.

WILDER, D. G.
1953. The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10:371-412.
1963. Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20:305-318.