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DIFFERENCES IN THE SIZE AT MATURITY OF FEMALE AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, CAPTURED THROUGHOUT THE RANGE OF THE OFFSHORE FISHERY

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ABSTRACT

The purpose of this study was to determine whether female American lobsters (*Homarus americanus*) inhabiting different offshore areas reached sexual maturity at different sizes. We determined the sexual maturity of 734 lobsters captured in three different offshore locations (North: Georges Bank and offshore Gulf of Maine; Middle: southern New England shelf and slope and; South: offshore Rhode Island to New Jersey) using a combination of methods including abdominal width : carapace length ratios, cement gland examination, and ovarian staging. Lobsters that experienced the most degree-days > 8°C (dd) reached sexual maturity at smaller sizes. The size at which 50 percent of the lobsters were mature was 79 mm CL for the South (annual dd = 808), 82 mm CL for the Middle (999 dd), and 92 mm CL for the North (234 dd). This regional difference in size at maturity was also manifested in the average size, and range of sizes, of berried females captured in each location. These data will likely be of use when developing appropriate regulations for managing the offshore fishery.

The American lobster, *Homarus americanus*, is the most commercially valuable species harvested in the northwest Atlantic Ocean (National Marine Fisheries Service, 2002). Its range extends from Labrador to Cape Hatteras, North Carolina, and lobsters are found in depths of up to 700 meters. The fishery for lobsters is divided into inshore and offshore components for which different management regulations apply. The inshore fishery is defined as the area from the coast out to 19 km from shore. It represents the majority of the catch. It also has a long history of exploitation, and data collection from this area is extensive. The offshore fishery is defined as the area starting 19 km from shore and extending out to the continental shelf edge and slope. It contributes 15–20% of the annual catch in New England (Northeast Fisheries Science Center, 1996), yet relatively little data are available concerning the attributes of this lobster stock.

Management of the lobster fishery is based, to a large degree, upon maintaining enough mature females in the population for adequate egg production. This goal is accomplished, in part, through the establishment of a minimum legal size. The goal of scientists and managers is to set this value at the size at which 50% of the females in a population are mature. At the time of this study, the minimum size limit for the entire offshore fishery was 83 mm CL, but on July 1, 2004, it increased to 85.6 mm CL and by July of 2005, it will increase again to 86.4 mm CL.

That lobster development occurs more quickly in warmer waters and lobsters reach sexual maturity at a smaller size in warmer water is well accepted (Aiken and Waddy, 1976). For example, in western Long Island Sound, where the water temperature is high, 50% of the females are sexually mature between 70–74 mm CL (Briggs and Mushacke, 1980), whereas in the Bay of Fundy, where the water is very cold, the size at 50% maturity is not reached until between 110–120 mm CL (Templeman, 1936; Groom, 1977; Campbell and Robinson, 1983). This same relationship between temperature and size at maturity has even been demonstrated in areas that are in very close proximity, but differ markedly in temperature (Estrella and McKiernan, 1989; Little and Watson, 2003).

Despite the very large geographic range of the offshore lobster fishery, it is all managed as one unit (Area 3). Yet, given the range of temperatures experienced by lobsters inhabiting these offshore waters, it is likely that the size at maturity would differ with water temperature in the same manner demonstrated in inshore waters. However, there is little size-at-maturity data available for this region and none that demonstrate differences in size at maturity across the range of the fishery. Perkins and Skud (1966) looked at size at maturity in offshore waters from Corsair Canyon (Georges Bank) in the north to Hudson Canyon (New Jersey) in the south and found a combined average size at 50% maturity of 77 mm CL, but they did not make comparisons between the canyons. However, data from Skud and Perkins (1969) did show differences in the size ranges of egg-bearing females between the canyons, suggesting that differences in size at maturity may exist within the offshore fishery. In order to test the hypothesis that size at maturity varies between different regions of the offshore lobster fishery, we determined the size at maturity for a total of 734 lobsters captured from three offshore regions we designated as south, middle, and north. We found that lobsters that resided in the warmer south and middle areas matured at significantly smaller sizes that those that were captured in the colder northern waters.

Materials and Methods

Regions of the Fishery

This project was carried out in collaboration with the Atlantic Offshore Lobstermen's Association. Because we were asking the participants to collect lobsters and data for us during the normal course of their fishing operations, data were obtained from areas where they typically set their traps. Therefore, the partitioning into three regions was not based on known

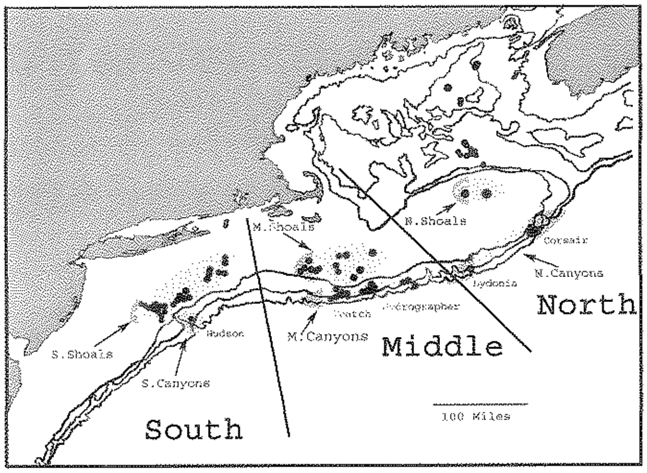

Fig. 1. Site map with lines delimiting the three major regions of the offshore lobster fishery: North, Middle, and South. Each dot represents the position of an experimental trap-trawl that was used to collect females used for dissection. Circled gray areas represent subregions: outermost areas are Canyons and midshelf areas are Shoals. Northern dots that are not circled represent the North Basin subregion. The three northern canyons where lobsters were trapped for this study (Nygren, Munson, and Powell) are all located between Corsair and Lydonia canyons.

or hypothesized stock areas, but rather upon clusters of fishermen in different areas. These clusters were geographically distinct, and were designated as: North–4 boats, Middle–4 boats, and South–2 boats (Fig. 1). The primary site of data collection for each region was the canyon area (240–400 meters in depth). In addition, when possible, data were also collected from the shallower shoals area of each region (60–80 meters in depth).

Dissections

Female lobsters (not berried and not V-notched) were collected from the three aforementioned offshore regions by commercial fishermen using standard lobster traps, and they were purchased for dissection at the dock. Lobsters were collected from each of three offshore canyon areas: North (Nygren, Munson, and Powell Canyons; $n = 144$), Middle (Veatch and Hydrographer; $n = 201$), and South (Hudson; $n = 200$). They were divided into 5-mm CL size classes ranging 50–135 mm CL (Table 1). Lobsters were also collected from three shoals sites: North Shoals ($n = 110$), Middle Shoals ($n = 34$), and South Shoals ($n = 45$). These lobsters were also divided into 5-mm CL size classes ranging 70–115 mm CL (Table 1). Dissections were done in the fall (Sept–Nov) and spring (April–June) months when maturity is easiest to determine.

The determination of whether individual lobsters were mature and the calculations of size at 50% maturity were carried out as described in Little and Watson (2003). For each animal, the carapace length and the outside width of the second abdominal somite were measured in millimeters, and the molt stage was determined by examining the carapace and pleopods. One pair of pleopods was then removed for examination under a dissecting microscope in order to determine the cement gland stage (Aiken and Waddy, 1982) and whether lobsters were in a premolt condition (Aiken, 1973). The presence or absence of a spermatophore was determined by extracting a small amount of fluid from the seminal receptacle and examining it under a compound microscope (× 400). A small circular incision was then made just behind the eye socket to access the anterior end of one of the ovaries. At least a dozen eggs were removed, and their size range and color were recorded. An egg stage was assigned to each lobster based on the criteria established by Aiken and Waddy (1982) (Table 2).

Determining Maturity

Ovarian stage was the primary tool used to determine sexual maturity. Any females with resorbed oocytes were considered mature, as these are an indication of a mature ovary (Aiken and Waddy, 1980). Of the females without resorbed oocytes, those with ovaries that were stage 4 and higher were considered to be mature. The size range for stage 4 ovaries is different in the spring (4b) than in the fall (4a) because of the timing of development, and this was taken into consideration. Those females with ovaries stage 2 and below were considered immature. In order to determine the maturity of those with stage 3 ovaries, we considered cement gland stage as well as ovarian stage. If a female with stage 3 ovaries had cement glands that were stage 3 or greater, then it was considered to be mature. For each group of lobsters in each 5 mm CL size class, the percentage of lobsters that were mature was then calculated, and this value was used, as described below, to develop a maturity ogive.

In order to determine the size at which 50% of the females from each area were mature, a nonlinear regression of percent mature for each 5-mm CL size class was carried out using the statistical program SYSTAT. The following equation was used: $p = (1/(1 + e^{(-b0 * (L-b1))}))$, where p = proportion mature, $b0$ = curve shape parameter, L = carapace length, and $b1$ = size at 50% maturity ($b0$ and $b1$ were estimated as starting points for the iterative process that SYSTAT used to best fit the curve). We used $b0 = 0.3$ and $b1 = 83$ as starting values, based on values calculated by Angell and Olszewski (2000), in order to determine size at 50% maturity. SYSTAT then calculated a best-fit value for $b0$, the curve shape parameter, and a value for $b1$, size at 50% maturity, as well as a 95% confidence interval for the $b1$ value. Comparisons were made between the regression lines within each region to determine whether data from subregions could be combined. Comparisons were also done between each region (North, Middle, and South) to determine which groups were significantly different from each other. These comparisons between regressions were performed using the following equation to perform multiple comparisons among variances (Zar, 1998):

$$F = \frac{\frac{(SSE1\&2)-(SSE1+SSE2)}{(m+1)\cdot(k-1)}}{\frac{(SSE1+SSE2)}{(n1-m-1)+(n2-m-1)}}.$$

In this equation SSE1&2 = the residual sum-of-squares for the curve generated from the the data points from both data sets (1&2) being compared, SSE1 and SSE2 = the residual sum-of-squares for the curve generated for each data set independently, m = the number of parameters being calculated in the model (in this case there are two: b0 and b1), k = the number of lines being compared, and n1 and n2 = the number of data points for each data set. A P-value was then calculated from F, and the two regressions being compared were considered statistically different if the P-value was < 0.05.

Abdominal Width : Carapace Length Ratios

The primary purpose of using this method was to compare the results with those obtained using dissections. A ratio of abdomen width to carapace length (ABD/CL) was calculated for each female that was dissected, along with some additional females measured at the dock, and these were averaged for each 5-mm CL size class (North $n = 367$, Middle $n = 235$, South $n = 357$). A plot was then made of carapace length *versus* this ratio for each size class, and a nonlinear polynomial regression was created for

Table 1. Sample sizes of female lobsters (in 5-mm CL size classes) that were dissected from each subregion of the offshore fishery and used for maturity assessments.

Size class (mm CL)	North Canyons	North Shoals	Middle Canyons	Middle Shoals	South Canyons	South Shoals
51–55			2			
56–60			2			
61–65			5		15	
66–70	1		25		16	
71–75	2		20		24	2
76–80	10		19		19	3
81–85	10	9	25	10	22	13
86–90	21	32	20	10	24	7
91–95	20	28	22	8	22	12
96–100	20	21	21	6	23	8
101–105	20	6	13		22	
106–110	20	12	20		13	
111–115	20	2	2			
116–120			1			
121–125			1			
126–130			2			
131–135			1			
Totals	144	110	201	34	200	45

Table 3. Statistical significance of the comparisons of regressions that were generated from maturity data. Comparisons were made within each major region (North, Middle, and South) and between these regions.

Regions being compared	P-values
North Canyons v. Shoals	0.6888
Middle Canyons v. Shoals	0.0416
South Canyons v. Shoals	0.0860
North v. Middle	$7.97\ e^{-10}$
North v. South	$1.46\ e^{-7}$
Middle v. South	0.1283

Shoals were not used for the subsequent comparisons between the three major regions (Fig. 3).

Using the combined data (shoals and canyons in the north and south, just the canyons in the middle), maturity ogives were developed for each region and used to estimate the size at 50% maturity. In the North, the size at 50% maturity was 91.9 mm CL (with a 95% confidence interval of 91.4–92.5 mm, $n = 254$) (Fig. 3). Fifty percent of females from the Middle were mature at 82.3 mm CL (with a 95% confidence interval of 81.3–83.4 mm CL, $n = 201$), and from the South at 79 mm CL (with a 95% confidence interval of 77–81.1 mm CL, $n = 245$). A comparison of these three regressions (comparing multiple regression equations; Zar, 1998) showed that the females from the North matured at a significantly larger size than those from the Middle and South ($P < 0.001$). Females from the Middle and South did not mature at significantly different sizes ($P > 0.05$) (Table 3).

The smallest mature female was 82 mm CL in the North, 73 mm CL in the Middle, and 71 mm CL in the South. All females examined that were greater than 111 mm CL were mature in the North, while all those greater than 99 mm CL in the Middle or 98 mm CL in the South were mature.

Abdominal Width : Carapace Length Ratios

Nonlinear regressions of CL *versus* ABD/CL were fitted to the data, and these curves were used to estimate size at 50% maturity (Fig. 4). According to the ABD/CL ratio data, half of the females from the North were mature by 88.7 mm CL, from the Middle by 76 mm CL, and from the South by 77.8 mm CL. All these values were smaller than the size at 50% maturity as determined by dissections, although the estimate for the South did fall within the 95% confidence interval estimated by ovarian staging (76.8–80.4 mm CL).

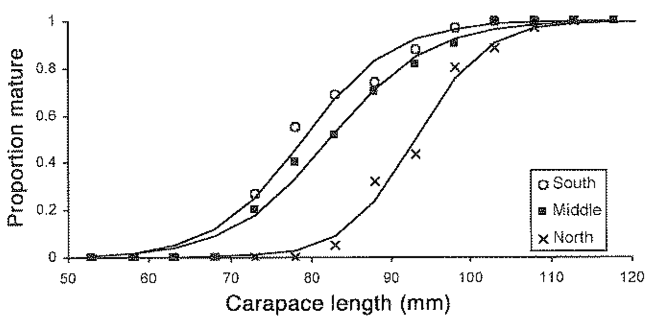

Fig. 3. Percentage of female lobsters that are mature in each size class ranging 50–120 mm CL, in 5-mm CL increments. The nonlinear regressions were fit to each data set using SYSTAT. Sample sizes are as follows: North = 254, Middle = 201, and South = 245.

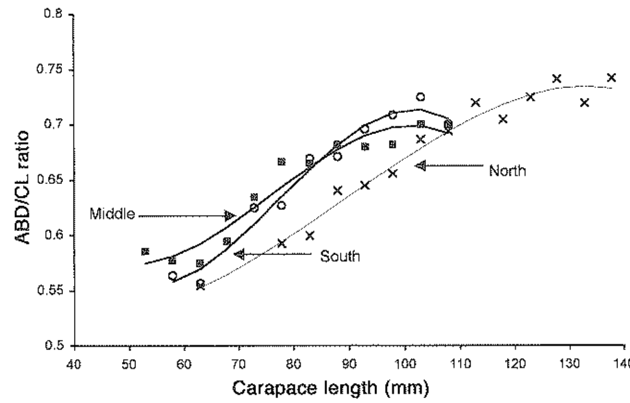

Fig. 4. Abdominal width : carapace length ratios for lobsters in each 5-mm CL size class from 50 mm to 140 mm CL. The equation used to fit the curves to the data is described in the methods. Sample sizes are as follows: North (X) = 367, Middle (filled square) = 235, South (o) = 357.

Size Frequency Distributions of Ovigerous Females

The ovigerous females from the North tended to be larger (112.0 ± 0.8 mm CL), than those from the Middle (98.0 ± 0.7 mm CL) and the South (92.0 ± 0.8 mm CL), and all three means were significantly different from each other ($P < 0.001$; Kruskal-Wallis one-way ANOVA, with Tukey's post-test). Moreover, a multiple comparison among variances indicated that the variances from the three regions were all statistically significantly different from each other (Fig. 5; $P < 0.001$). In general, the size ranges and average sizes of ovigerous females from each region were consistent with the size at maturity estimates calculated for lobsters from the same areas and were larger than estimates obtained using the other methods.

Temperature Profiles of Study Sites

Monthly temperature profiles for the canyon areas are shown for the three regions of interest in Fig. 6. Whether examined in terms of monthly mean temperatures or annual degree-days, the Middle and South offshore regions were warmer than the North. The annual degree-days greater than 8°C offshore were considerably higher in the Middle and South than in the North (Table 4). Moreover, offshore temperatures in the North were as low as 4°C, whereas in the Middle and South they were no lower than 7°C or 6°C, respectively. If the well-documented movements of lobsters are taken into account, the annual temperatures experienced by the northern lobsters are probably even colder.

Discussion

All three methods that we used to assess the size at maturity of female American lobsters (ovarian stage, ABD/CL ratios, and ovigerous female size-frequency distributions) indicated that female lobsters from the North mature at a larger size than those from the Middle and South. There was no significant difference in the size at 50% maturity between lobsters captured from the Middle and South, most likely because: 1) the two populations experience considerable mixing, especially along the continental shelf (Cooper and Uzmann, 1971; Uzmann *et al.*, 1977); and 2) lobsters in these two regions are under the influence of very similar

Table 2. Criteria established by Aiken and Waddy (1982) (adapted from Aiken and Waddy, 1980) for determining categories of ovarian development in female American lobsters.

Immature ovary	Developing ovary	Gravid ovary	Spent/Resorbing ovary
Category 1- Ovary white Oocytes <0.5 mm Ovary factor* <100 Category 2- Yellow, beige, pale green Oocytes <0.8 mm Ovary factor <100	Category 3- Light to medium green Oocytes <1.0 mm Ovary factor <200 Category 4a (autumn)- Medium to dark green Oocytes 0.1–1.6 mm Ovary factor <200 Category 4b (spring)- Medium to dark green Oocytes 0.8–1.6 mm Ovary factor 200–235 Category 5- Ovary dark green Oocytes 1.0–1.6 mm Ovary factor>325	Category 6- Dark green Oocytes 1.4–1.6 mm Ovary factor>400 Category 6a- Postovulation Oocytes free in ovary	Category 7- Ovary large, flaccid, white or yellow. May have residual green oocytes

* Ovary factor = Ovary wet weight (mg)/Carapace length (cm) 3 × 10.

each site, using SYSTAT, and following the approach used by Landers *et al.* (2001). The following equation was used: $ABD/CL = a + bx + cx^2 + dx^3$, where x = carapace length. SYSTAT then estimated the values of *a*, *b*, *c*, and *d* in order to most closely fit the curve to the data. In order to determine the inflection point of the curve, which represents the point at which the rate of change in ABD/CL is greatest and therefore approximates the size at which 50% of the females have reached maturity, we took the second derivative of the original equation, which is $y = 2cx + 6dx$. That equation is then set to equal zero in order to solve for x, yielding the equation $x = -2c/6d$. Then, we inserted the *c* and *d* values from SYSTAT and solved for x (the carapace length at 50% maturity) (Landers *et al.*, 2001). The size at 50% maturity that was estimated by this method was then compared to that obtained by dissection for the lobster populations from each area in order to see whether the ABD/CL curve estimates fell within the 95% confidence intervals of the dissection curve estimates.

Size Frequency Distributions of Ovigerous Females

A Thistle Marine electronic data logger (Thistle box) was installed on commercial offshore fishing boats so that lobstermen could record information about all of the lobsters captured from one forty-trap trawl per vessel. Ten traps of this trawl were designated as "experimental traps," and specific data were recorded for each lobster caught in these traps, including size, sex, presence of eggs, egg stage (1–4), presence of a V-notch, and shell disease stage (0–5). Data were obtained from a total of 55,895 lobsters during September 2001–April 2003. Size-frequency profiles of a total of 933 ovigerous females captured in each area were generated from these data, and the average size (± SE standard error) and size range were also calculated for each region. The average size of berried females was compared between regions using a Kruskal-Wallis one-way ANOVA, followed by Tukey's multiple comparison on ranks. The size distributions of the berried females from each region were compared using a multiple comparison among variances.

Temperature Profiles of Study Sites

Bottom temperature data were collected from each site so that the potential impact of temperature on the size at which females reach sexual maturity could be assessed. Offshore temperatures were measured with HOBOTemp temperature data loggers (Onset Computer; Falmouth, Massachusetts). These were placed on lobster traps from all collection sites to record bottom temperatures at one-minute intervals throughout the year. Data collected from similar depths in each area were combined and averaged for each month of the year. Where year-round data were not available, bottom temperature data from Tidbits were supplemented by data from the TempEst program (David Mountain, NOAA). This program calculates the predicted bottom temperature for a give location using data from the nearest locations for which actual data were collected through the MARMAP sampling program (NOAA, 1989). The mean monthly temperature was calculated for each area, and the total annual degree-days were calculated by adding together the number of degrees that exceeded 8°C for each day of the year and then summing them for the entire year. The 8°C threshold was based upon physiological and behavioral responses of lobsters to temperatures below 8°C, which include decreased developmental rate (Cooper and Uzmann, 1971; Aiken and Waddy, 1989; Waddy *et al.*, 1995) and locomotion (Jury, 1999).

Results

Dissections

Nonlinear regressions of carapace length *versus* percent mature were used to determine whether there were differences in the size at maturity between subregions in each area (Fig. 2). The regressions were not statistically significantly different between the North and South subregions ($P > 0.05$), but were significantly different in the Middle (Table 3). We believe the main reason for the differences observed in the Middle was that we were unable to obtain sublegal lobsters from the Middle Shoals (Table 1). As a result, it was difficult to generate a curve that accurately represented the probable distribution of the animals in this region because there were only four points with which to determine a regression and no size classes at the low end of the curve. Therefore, the low end of the curve never reached zero like the other curves. For this reason, data from the Middle

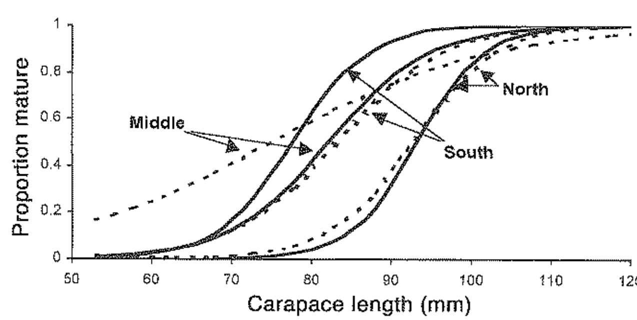

Fig. 2. Percentage of female lobsters that are mature in each size class ranging 50–120 mm CL, in 5-mm CL increments, for each subregion studied. Dashed lines are Shoals subregions and solid lines are Canyon subregions for the North, Middle, and South.

inshore Rhode Island, with slightly cooler temperatures, reach 50% maturity by 81 mm CL (Angell and Olszewski, 2000); those from the southern Gulf of Maine, with still cooler temperatures, reach 50% maturity by 87 mm CL, and those from the northern Gulf of Maine, with even cooler temperatures, by 90 mm CL (Estrella and McKiernan, 1989). This pattern is illustrated in Fig. 5, which shows how the size at which 50% of females are mature from multiple locations varies according to the average water temperature in each area.

While this relationship between temperature and size at maturity appears to be well established, the mechanism by which temperature affects developmental rate has not been fully explained. What is not obvious is why lobsters in warmer waters not only reach maturity in fewer years, but also at a smaller size. It would seem logical that all lobsters would reach maturity at a given size, but that those in warmer waters would reach that size at a younger age because they grow faster. However, this is not the case. There are two possible explanations that might explain this situation. First, temperature may influence somatic and developmental growth rates differently, as has been found in zooplankton development (McLaren, 1963). For example, in copepods the temperature coefficient for growth rate is smaller than that for developmental rate (Runge and Myers, 1986), resulting in a smaller size at maturity for those raised in warmer temperatures. A second possibility is related to a suggestion put forth by Pollack (1993) to explain differences in size at maturity of spiny lobsters (*Jasus lalandii*). His models indicate that *J. lalandii* reached sexual maturity after 15 molts (Pollack, 1987), that females with a large growth increment per molt reach maturity at a larger size, and that females with small growth increments reach maturity at a smaller size (Pollack, 1991). In order for the hypothesis that lobsters in warmer water mature at smaller sizes to be correct, lobsters in warmer water would have to experience a smaller growth per molt. This has been found in freshwater crayfish where growth increment decreased at warmer temperatures (Verhoef *et al.*, 1998). A decrease in growth increment per molt due to increasing water temperature was also one explanation for the decrease in size at maturity in female lobsters in the Long Island Sound between 1981 and the present (Landers *et al.*, 2001). In summary, there is strong correlative evidence indicating that water temperature is a major determinant of size at maturity in lobsters. However, additional studies are necessary in order to determine the underlying mechanisms that produce this effect.

Other potential explanations for the observed differences in size at maturity have also been considered. Fishing pressure over time may exert an evolutionary pressure for lobsters to mature at smaller sizes in order to have a greater chance of reproducing before they are removed from the fishery. This hypothesis has been tested in inshore Massachusetts waters by looking at samples of ovigerous females taken one hundred years apart, and this comparison showed that there was no change in the size of the smallest ovigerous female over time (Estrella and Cadrin, 1995). A study in Long Island Sound, New York, found a decrease in the mean carapace length of ovigerous females from 82.6 mm CL in 1981–1986 to 69.5 mm CL in 1993–1999, and the authors suggested that this decrease is the result of increased exploitation rates, though it could also have been the result of warming water temperatures (Landers *et al.*, 2001). A comparison of the current size range of ovigerous females offshore with data collected during 1965–1967 by Skud and Perkins (1969) shows a slight decrease in the size of ovigerous females, but the differences between North and Middle and South in their data set are similar to the pattern we observed. At the time these data were collected, landings had exceeded 1000 metric tons for only four years, so the population had not been heavily fished for a long period. Their data showed that the size ranges of ovigerous females from two Northern Canyons were 100–200 mm CL and 90–190 mm CL. Those from the Middle Canyons ranged 90–170 mm CL, and those from the Southern Canyons ranged 80–140 mm CL. Our current data showed that North Canyon ovigerous females range 90–180 mm CL; Middle Canyons, 76–155 mm CL; and South Canyons, 75–125 mm CL. Therefore, while it is possible that fishing pressure may act to reduce size at maturity over time, the difference in the size of reproductive females between regions of the offshore fishery apparently preceded the period of heavy fishing pressure, and thus is most likely attributable to other causes.

A comparison of the three major methods used to assess the maturity of females suggests that none of the methods, taken alone, provides all the information necessary to assess the fishery. First, while the ogives developed from egg staging indicated that lobsters in the North, Middle, and South began to become mature at ~ 83, 70, and 70 mm CL, respectively, the smallest ovigerous females captured in each location were 90, 76, and 75 mm CL. This discrepancy between the smallest female considered mature by dissections and the smallest ovigerous female found in the same area supports the hypothesis that there may be a delay between physiological and functional maturity. Thus, some of the smallest females with mature eggs cannot really be considered to be part of the reproductive population, and the size at which 50% of females are mature, according to dissections, may be too small. Likewise, while the increase in abdomen width has been correlated with the onset of maturity (Templeman, 1935, 1944), the exact timing of the widening of the abdomen relative to the completion of development to sexual maturity is not known. Our results suggest that abdominal widening slightly precedes the onset of maturity, so that some females with widened abdomens are not yet fully mature. Aiken and Waddy (1980) found that in some females the increase in abdomen width began a few molts before egg extrusion, thus underestimating size at first maturity. However, while the ABD/CL ratio calculations underestimated the size at 50% maturity in comparison with dissections, the resulting values (North = 88.7, Middle = 76.0, South = 77.8) were very close to the size of the smallest berried females found in each area. Perhaps by combining information about the size range of berried females from a given area, with extensive measurements of the ABD/CL ratios, an accurate, noninvasive, method for measuring the size at "functional" maturity can be developed.

The most important regulation influencing the lobster fishery is the legal size limit. As described above, it is important to set the legal size at the size at which 50% of the

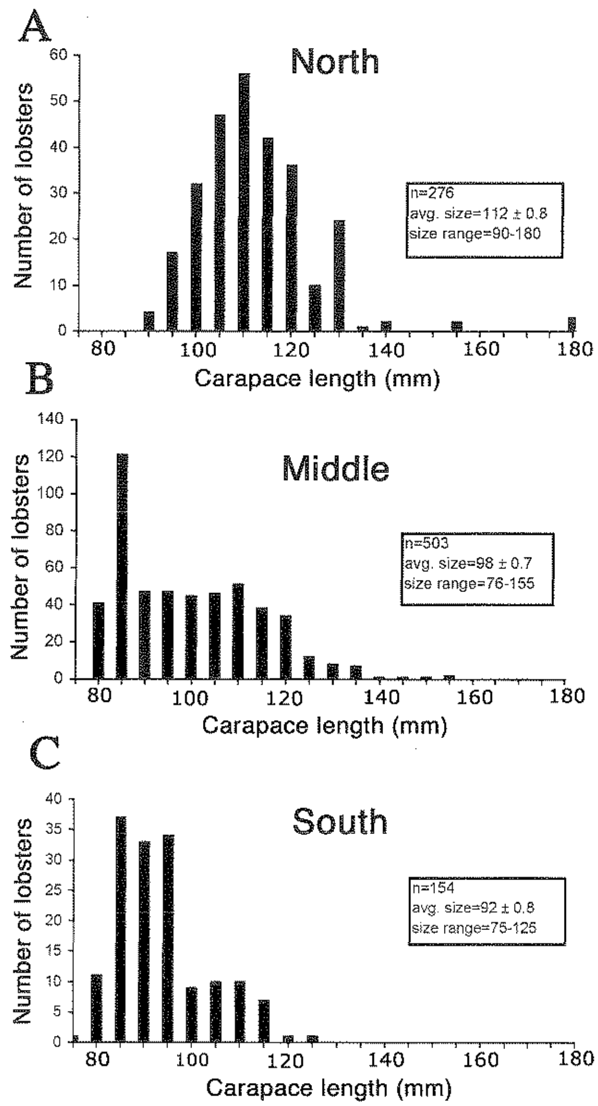

Fig. 5. Size-frequency distributions of ovigerous females plotted in 5-mm CL bins from the three offshore regions. A, North ($n = 276$); B, Middle ($n = 503$); C, South ($n = 154$).

environmental conditions, especially water temperatures. Given the strong influence of temperature on the rate of development and size at maturation (Aiken and Waddy, 1986), it is likely that the female lobsters in the middle and southern regions experience similar thermal histories and, as a result, reach sexual maturity at similar sizes.

While there are definitely differences between the offshore bottom temperatures in the North, Middle, and South (Table 4; Fig. 6), the variability between regions may not be sufficient to cause the differences in size at maturity observed. Although the process of recruitment in offshore regions is not fully understood, based on catch data (Watson and Little, unpublished data), modeling of larval drift (Incze and Naimie, 2000), and observations with submersibles (Steneck, personal communication), many offshore lobsters probably develop to maturity inshore or on the continental shelf and then migrate into the deeper canyons. In this case, the temperature in the location where the lobsters experi-

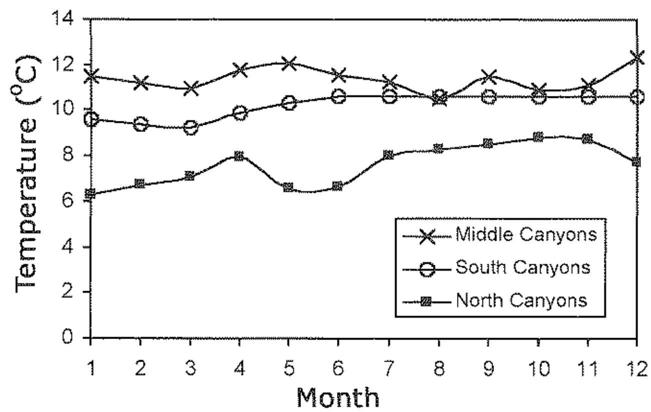

Fig. 6. Mean monthly temperature exposure (°C) of lobsters from the canyons of each region (North, Middle, and South).

enced most of their growth would have the greatest influence on the size at which they become mature, and the degree-days experienced by southern and middle lobsters would likely be even greater than northern lobsters. Lobsters are also very mobile and, while local movements are most common, a certain percentage of lobsters carry out long-distance migrations that tend to be in the offshore direction in the winter and inshore in the summer (reviewed by Krouse, 1980; Cooper and Uzmann, 1980; Haakonsen and Anoruo, 1994; Lawton and Lavalli, 1995). These migrations are thought to serve as a mechanism for enhancing their growth and development by keeping them at the warmest temperatures available during a given season. In general, lobsters in the Southern and Middle regions have a greater tendency to make these migrations, probably because in these areas the inshore waters are much warmer in the summer and therefore they have the most to gain from such movements. If these migrations are taken into account, then the number of degree-days experienced by the Middle and Southern lobsters is much greater than lobsters would experience in the North, and therefore these movements may contribute to the size at maturity differences we have observed.

Templeman (1936) first pointed out the relationship between temperature and maturity when he observed that females from the Gulf of St. Lawrence, an area with high summer water temperatures, matured at a smaller size than they did in Grand Manan, an area with low summer water temperatures. Several other subsequent studies from different areas of the fishery, both inshore and offshore, have shown that lobsters mature at smaller sizes in warmer water. Females in western Long Island Sound, an area of warm water temperature, reach 50% maturity between 70 mm and 74 mm CL (Briggs and Mushacke, 1980); those from

Table 4. Average total annual degree-days greater than 8°C and overall temperature range (°C) for each offshore region.

Location	Degree-days > 8°C	Temperature range
North	234	4–14
Middle	999	7–14
South	808	6–14

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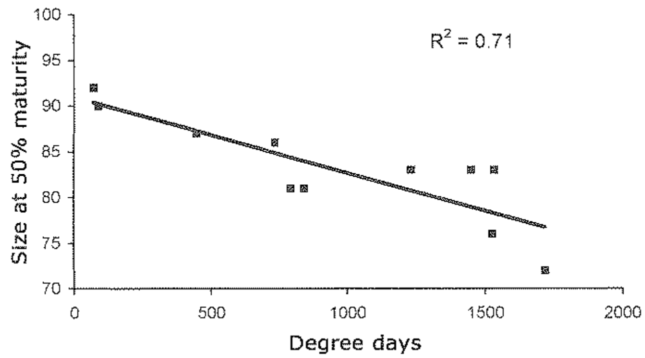

Fig. 7. Size at which 50% of females are sexually mature from areas of different temperature exposure (in terms of degree-days >8°C). Left to right: North Offshore; coastal Maine (Krouse, 1973), Southern Gulf of Maine (Estrella and McKiernan, 1989); coastal New Hampshire (Little and Watson, 2003); South Offshore; Rhode Island Sound (Angell and Olszewski, 2000); Middle Offshore; Eastern Long Island Sound (Landers *et al.*, 2001); Buzzards Bay, Massachusetts (Estrella and McKiernan, 1989); Great Bay, New Hampshire (Little and Watson, 2003); Western Long Island Sound (Briggs and Mushacke, 1980).

female lobsters reach sexual maturity. Unfortunately, this value varies considerably, both over the wide range of the American lobster fishery, as indicated by Fig. 7, and over small distances when large temperature gradients exist (Estrella and McKiernan, 1989; Little and Watson, 2003). Therefore, while it would be appropriate to adjust the legal size limit to match the size at maturity for all areas of the fishery, given the large variations in size at maturity that have been documented, and the ability of lobsters to move large distances, in practice this goal is difficult to achieve.

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