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SIZE AT MATURITY OF FEMALE AMERICAN LOBSTERS FROM AN ESTUARINE AND COASTAL POPULATION

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ABSTRACT The size at which female lobsters reach sexual maturity was determined for two populations that inhabit waters along the coast of New Hampshire. One group was captured in the Great Bay estuary, where water temperatures in the summer typically average between 17°C and 20°C. The other group of lobsters resided in coastal waters, near the Isles of Shoals, where the water temperature was much colder during the summer (11–15°C). Maturity was assessed using criteria that included the following: ovarian classification; abdominal width/carapace length (CL) ratio; and the size frequency distribution of berried females. All the techniques yielded similar results and consistently demonstrated that female lobsters in the estuary matured at a smaller size than those in colder coastal waters. The smallest mature females from Great Bay were 72 mm in CL, with 50% reaching sexual maturity by 83 mm CL and all becoming mature by 89 mm CL. The smallest mature female from the Isles of Shoals area was 77 mm CL, with 50% mature by 86 mm CL and all mature by 93 mm CL. The difference in the proportion of mature lobsters in the estuarine versus coastal populations was much greater in the smaller size classes than in the larger size classes, suggesting a mixing of the two populations, most likely due to females from Great Bay migrating into coastal waters.

KEY WORDS: estuary, *Homarus americanus*, lobster, sexual maturity

INTRODUCTION

The American lobster, *Homarus americanus* (Milne-Edwards) is the most commercially valuable species harvested in the northwest Atlantic Ocean (NMFS 2002). Although lobsters are most abundant in coastal waters, estuarine populations are common and have been investigated from Canada to Massachusetts (Thomas 1968, Thomas & White 1969, Munro & Therriault 1983, Reynolds & Casterlin 1985, Jury et al. 1995; Howell et al. 1999; Watson et al. 1999). One population that has received considerable attention is located in the Great Bay estuary in New Hampshire. Howell et al. (1999) have demonstrated that, like the lobsters in the Iles-de-l-Madeleine in Canada (Munro & Therriault 1983), the sex ratio is skewed toward males throughout the estuary, with the greatest proportion of male lobsters found in the portions of the estuary furthest from the coast. It has been proposed that the skewed sex ratio in the estuary is the result of the differential seasonal migration of mature female lobsters out of the estuary (Watson et al. 1999).

To ensure that there are enough mature females in a given lobster population, a minimum legal size has been established. This allows a given proportion of the females to reach sexual maturity and reproduce at least once before they are landed. The size at which 50% of the females from an area are mature (50% maturity) is often used as a reference point because most models indicate that when the minimum size is set at this value sufficient recruits will be produced to sustain the fishery. Currently, the minimum size limit in the inshore waters of New Hampshire is 83 mm carapace length (CL).

There is a wide range of sizes over which female lobsters reach maturity. The smallest size at 50% maturity, 70 to 74 mm CL, is found in western Long Island Sound (Briggs & Mushacke 1979), and the largest size, 110 to 120 mm CL, is found in the Bay of Fundy (Templeman 1936, Groom 1977, Campbell 1983). It has been suggested that a number of different factors influence the size at which female lobsters mature, including nutrient availability (Lawton & Lavalli 1995), fishing pressure (Polovina 1989, Landers et al. 2001), and temperature (Templeman 1936, Templeman 1944, Aiken & Waddy 1980, 1986, Estrella & McKiernan 1989, Fogarty 1995). Increases in all, or any, of these factors results in a decrease in the size at which females reach sexual maturity.

Temperature is thought to be the most influential of these factors because it is known to directly affect the growth rates of lobsters, with development occurring more quickly with increased temperature (Aiken & Waddy 1976). The rate of ovarian development is primarily controlled by summer water temperature, with little development occurring throughout the winter months (Templeman 1936). Thus, in areas with warmer water in the summer, lobsters reach sexual maturity at smaller sizes.

Estuaries, such as the Great Bay estuary in New Hampshire, are characterized by large daily and seasonal fluctuations in temperature and salinity. In the Great Bay estuary, the water temperature in the summer is approximately 10°C higher than in New Hampshire coastal waters (Short 1992). Given the apparent influence of water temperature on the rate of maturation of female lobsters, we hypothesized that female lobsters in the Great Bay estuary would reach sexual maturity at a smaller size than those in coastal waters, such as near the Isles of Shoals, which are located 11 km away from where the Great Bay estuary empties into the Gulf of Maine (Fig. 1).

To test our hypothesis, we determined the size at maturity for 92 lobsters collected in the Great Bay estuary with 106 lobsters collected near the Isles of Shoals. A comparison of the results yielded by analyzing (1) the size distribution of berried females, (2) the size of female abdomens relative to their length, and (3) the stage of eggs removed from the ovaries yielded the same pattern. Female lobsters from the estuarine site matured at a smaller size than those from the coastal site, probably due to the influence of warmer summer water temperatures on their growth and development.

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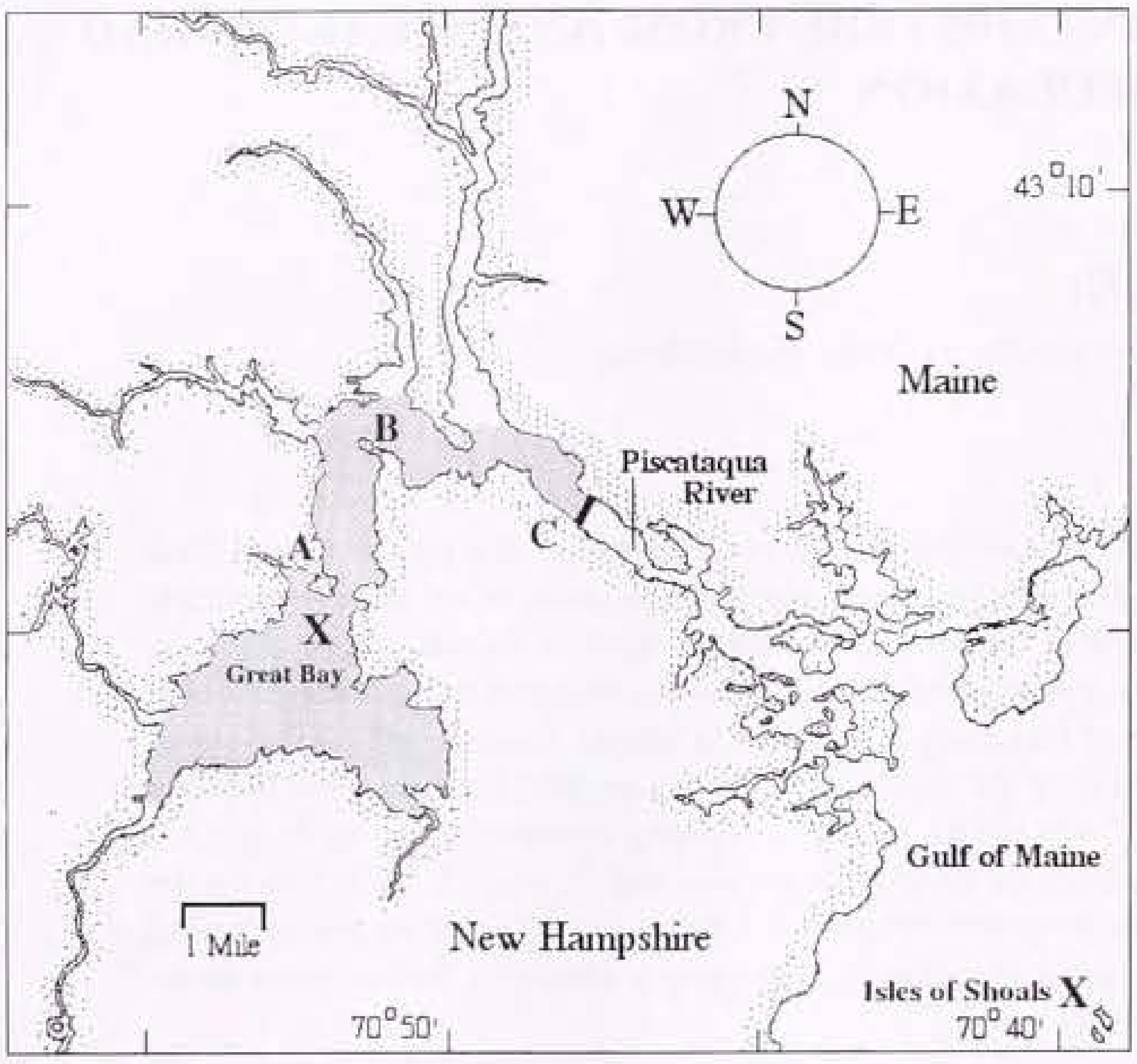

Figure 1. The two study sites are marked with an X [Great Bay Estuary and Isle of Shoals (11 km off the coast of New Hampshire)]. Sites of temperature data collection for the Great Bay Estuary are: A, Jackson Estuarine Laboratory; B, Fox Point; and C, Upper Piscataqua River. Lobsters were obtained from the Great Bay estuary within the area indicated by shading.

MATERIALS AND METHODS

Temperature

Bottom temperatures were collected in the waters surrounding the Isles of Shoals from 1997 to 2001 at depths of approximately 8 to 10 m using HOBOTemp temperature data loggers (Onset Computer, Falmouth, MA) that recorded water temperature at 2-h intervals for 5 to 6 mo at a time. Bottom temperature data for Great Bay was collected from 1997 to 2001 at three different locations that spanned the area where lobsters were collected (Fig. 1). The most consistent data set were obtained from a location near the University of New Hampshire Jackson Estuarine Laboratory, at a depth of approximately 3 to 5 m, using a YSI multiparameter 6600 datalogger (YSI Inc., Marion, MA) that recorded the water temperature every 30 min. Water temperature also was recorded near Fox Point and along the Piscataqua River in 1990 and 1993, using a YSI meter model 33 attached to a probe that was lowered to a point near the bottom. Data were obtained from these two sites approximately every other day while hauling some of the traps used to collect lobsters for this study. Data from all three sites were averaged from all available years to yield a temperature profile of the area from which lobsters were collected. The mean monthly temperature then was calculated, and the total annual degree-days >8°C were summed for each location by adding together the number of degrees that exceeded 8°C for each day of the year and summing them for the entire year.

Maturity Assessments

Dissections

Lobsters were collected from two areas (Fig. 1) by commercial fishermen and by University of New Hampshire personnel using standard traps. The first site consisted of the upper region of the Great Bay estuary (i.e., Great Bay, Little Bay, and the upper Piscataqua River), and the second site included waters near the Isles of Shoals.

Lobsters were collected in 1991, 1992, 1994, and 2002. The lobsters from each site were divided into 1-mm size classes ranging from 66 to 110 mm CL. A total of 92 lobsters were dissected from Great Bay, and a total of 106 from Isles of Shoals.

Female, nonovigerous, lobsters were examined, using multiple criteria, to determine whether they were sexually mature. For each animal, the CL and the width of the second abdominal segment were measured in millimeters, and the molt stage was recorded by examining the carapace and pleopods. One pair of pleopods then was removed for examination under a dissecting microscope to determine the cement gland stage (Aiken & Waddy 1982) and whether lobsters were in a premolt condition (Aiken 1973). A small circular incision then was made just behind the eye socket to access the anterior end of one of the ovaries. Several eggs were removed, and their size range and color were recorded. An egg stage was assigned to each lobster based on criteria established by Aiken and Waddy (1980).

Whether a female was sexually mature, or not, was determined using a combination of criteria, with ovarian stage as the primary tool. Any females with resorbed oocytes were considered to be mature, as these are an indication of prior spawning. Of the females without resorbed oocytes, those with ovaries that were at stage 4 and higher were also considered to be mature. The size range for stage 4 ovaries is different in the spring (stage 4b) than in the fall (stage 4a) due to the timing of development, and this was taken into account. Those females with ovaries at stage 2 and below were considered to be immature. To determine the maturity of those with stage 3 ovaries, we considered cement gland stage as well as egg stage. If a female lobster with stage 3 ovaries had cement glands that were at stage 3 or greater, then the lobster was considered to be mature.

To determine the size at which 50% of the females from each area were mature, a nonlinear regression of percent mature for each 1-mm CL size class was carried out using the statistical program, SYSTAT. The following equation was used:

$$p = (1/(1 + \exp(-b0^{*}(L-b1)))$$

where p is the proportion mature, b0 is the curve shape parameter, L is the carapace length, and b1 is the size at 50% maturity (estimated as a starting point for calculations by the user). The program estimated values of b0, based on the data set, until it found the best-fit curve. This resulted in sigmoid curve from which b1 could be calculated with a 95% confidence interval. A statistical comparison of the regression lines that resulted from each population of lobsters was made to determine whether they were significantly different from each other.

Sea Sampling Data

Sea-sampling data were obtained from University of New Hampshire research traps, and during trips on commercial lobster boats in 1990 to 1993 and 2002 at each location. The data collected included CL, width of the second abdominal segment, sex, and whether females were ovigerous. A total of 8199 lobsters were examined during these sea-sampling trips.

Abdominal Width

A ratio of abdomen width to CL (ABD/CL ratio) was calculated for each female, and these were averaged for each 1-mm CL size class. A plot then was made of CL versus this ratio for each size class. A nonlinear polynomial regression of these data was created for each site using SYSTAT. The following equation was used: ABD/CL = a + bx + cx^2 + dx^3, where x = CL. SYSTAT then estimated the values of a, b, c, and d to most closely fit the curve to the data. To determine the inflection point of the curve, which represents the point at which the rate of change in the ABD/CL ratio is greatest, and therefore approximates the size at which 50% of the females have reached maturity, the second derivative of the original equation, y = 2cx + 6dx, was calculated. That equation was then set to equal zero and was solved for x, yielding the equation x = −2c/6d. Then, the c and d values from SYSTAT were used to solve for x (the CL at 50% maturity) (Landers et al. 2001). The size at 50% maturity that was estimated by this method was compared with that obtained by dissection for the estuarine and coastal lobster populations to determine whether the abdominal width estimates fell within the 95% confidence intervals of the dissection estimates.

Berried Female Size Frequency Distributions

From the sea-sampling data, a size frequency distribution of berried females, as well as a plot of the overall size frequency distribution of the population was made for each area. The plots of overall size frequency were divided into the proportions that were male and female in each size class so that the proportion that was female at a given size class could be compared with the proportion of females that were berried at that same size class. For each plot the average size, the SEM, size range, and sex ratio were calculated for comparison. The size distributions for the overall population and for only berried females were compared between sites using a χ^2 test of independence.

RESULTS

A Comparison of Estuarine Versus Coastal Water Degree-Days

There was a large difference between the number of annual degree-days (>8°C) in the Great Bay estuary (1532) compared to those in the waters near the Isles of Shoals (738) (Fig. 2). The greatest difference in temperature occurred during the summer

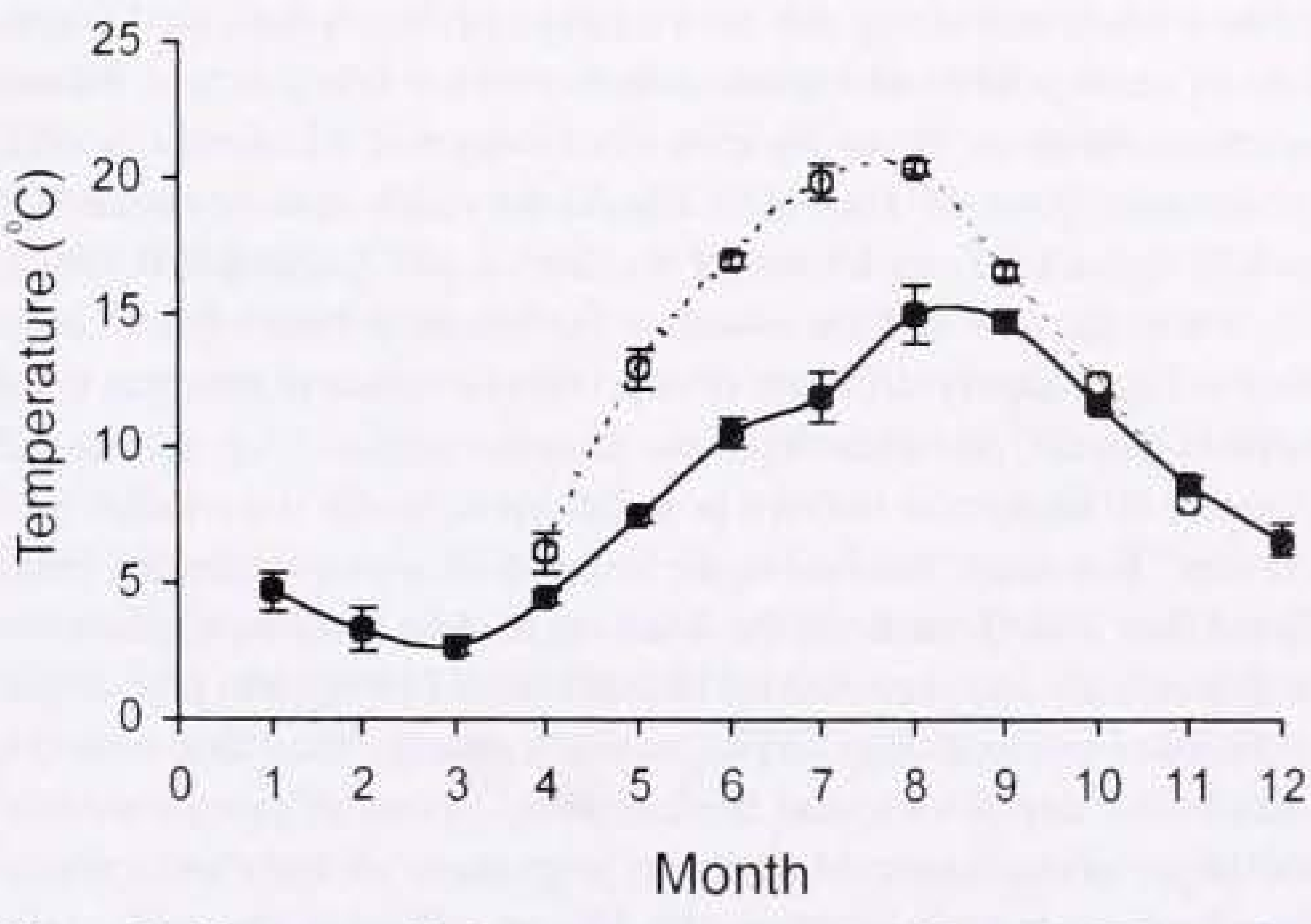

Figure 2. Mean monthly bottom temperatures (°C), with SE bars, for water in the Great Bay estuary (open circle) and near the Isles of Shoals (solid circles) (1997–2001). Water temperature for Great Bay is an average of three sites that encompass the area from which lobsters were collected.

months (June–August; Great Bay 995; Isles of Shoals 404). The difference in degree-days between the two sites for these 3 mo accounted for 75% of the difference in degree-days for the entire year. During this period, the mean water temperature averaged 12.5°C at Isles of Shoals and 19°C in Great Bay.

Maturity Assessments

Dissections

Nonlinear regressions of CL versus percent mature, as determined by dissections, were used to calculate the size at 50% maturity for each site (Fig. 3a). The size at 50% maturity for females obtained from waters near the Isles of Shoals was 85.9 mm CL (95% confidence interval 85.3–86.5; n = 106). Fifty percent of females from Great Bay were mature at 83 mm CL (95% confidence interval 80.6–85.4 mm; n = 92). A comparison of the two regressions showed that they were significantly different from each other ($P < 0.001$). The smallest mature female captured near

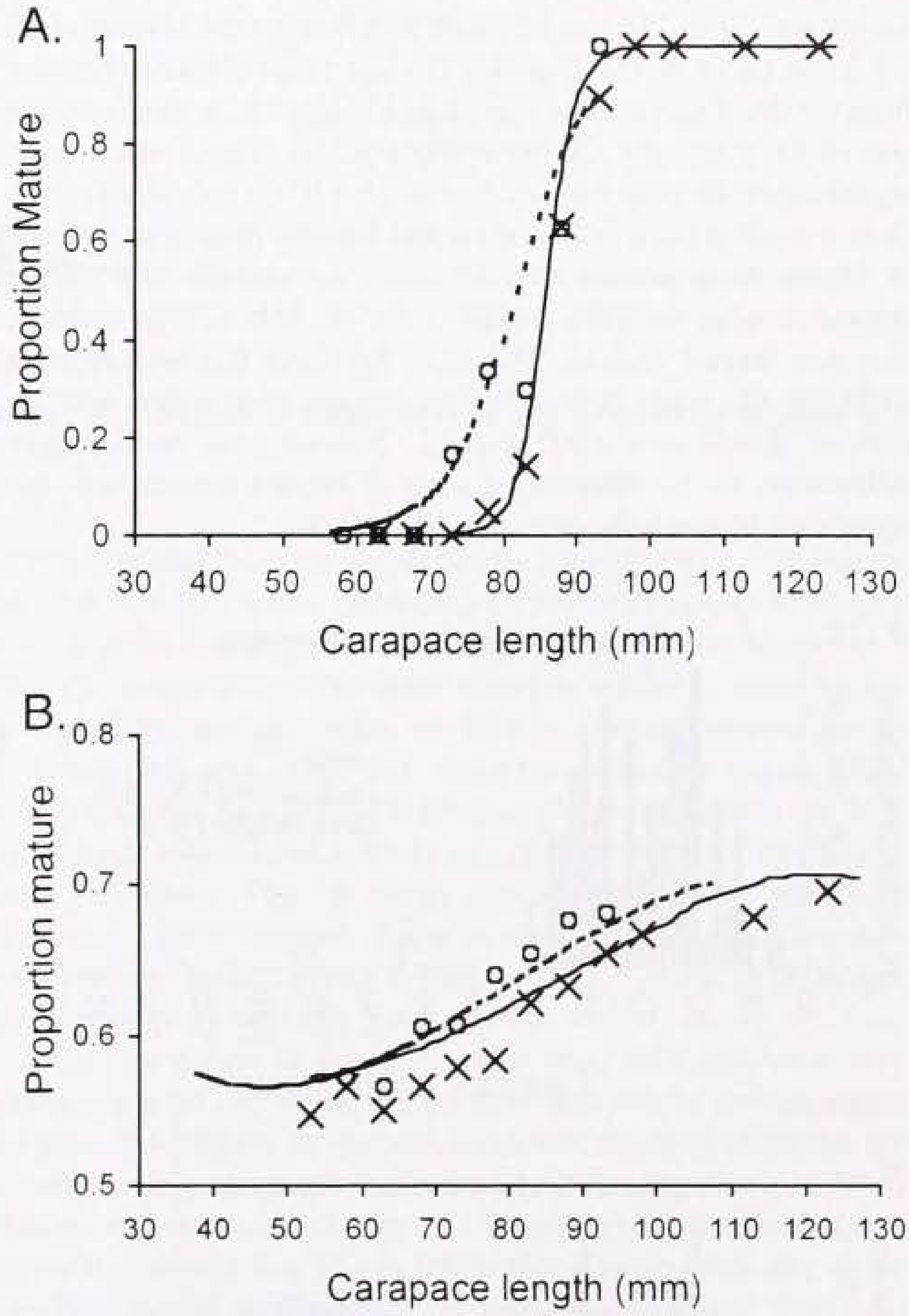

Figure 3. (A) Maturity ogives estimated by nonlinear regressions based on dissection data from 1-mm size classes from Great Bay (dashed line) and Isles of Shoals (solid line): Great Bay 50% maturity = 83 mm CL (95% confidence interval 80.6–85.4; n = 92); Isles of Shoals 50% maturity = 85.9 mm CL (95% confidence interval 85.3–86.5; n = 106). Actual values are plotted for each 5-mm size class. (B) Polynomial regression estimated from abdominal width measurements for 1-mm size classes from Great Bay (dashed line) and Isles of Shoals (solid line): Great Bay 50% maturity = 81.5 mm CL (n = 1613); Isles of Shoals 50% maturity = 86.9 (n = 1699). Actual values are plotted for each 5-mm size class.

the Isles of Shoals was 80 mm CL, while in the estuary a 72-mm CL mature female was captured. All females were mature by 93 mm CL at the Isles of Shoals study site, and by 89 mm CL in the Great Bay estuary.

Abdominal width: CL ratios

Nonlinear regressions of ABD/CL ratios were fitted to the data to calculate size at 50% maturity (Fig. 3b). The resulting curves indicated that half the females from Isles of Shoals were mature by 86.9 mm (n = 1699), while the size at 50% mature for lobsters captured in the estuary was 81.5 mm (n = 1613). The estimate for the Isles of Shoals lobsters did not fall within the 95% confidence interval generated from the dissection data (85.3–86.5), but was very close. The estimate for the Great Bay estuary lobsters fell within the 95% confidence interval (80.6–85.4).

Size frequency distributions

The size range of berried females collected near the Isles of Shoals was 77 to 138 mm CL, with an average (±SEM) size of 92 ± 1.0 mm CL (n = 152; Fig. 4b). The size range of berried females from the Great Bay estuary was 72 to 107 mm CL, with an average size of 85 ± 0.6 mm CL (n = 98; Fig. 4a). These means were significantly different from each other ($P < 0.001$ two-tailed t test). Only a small portion (30%) of berried females from near the Isles of Shoals were smaller than 85 mm CL, whereas 50% of the berried females from the estuary were <85 mm CL. In contrast, very few berried females (1%) from the Great Bay estuary were >100 mm CL, while 20% of berried females from waters near the Isles of Shoals were >100 mm CL. Nevertheless, despite these differences, the distribution of sizes of berried females was not significant between the two sites (P = 0.067).

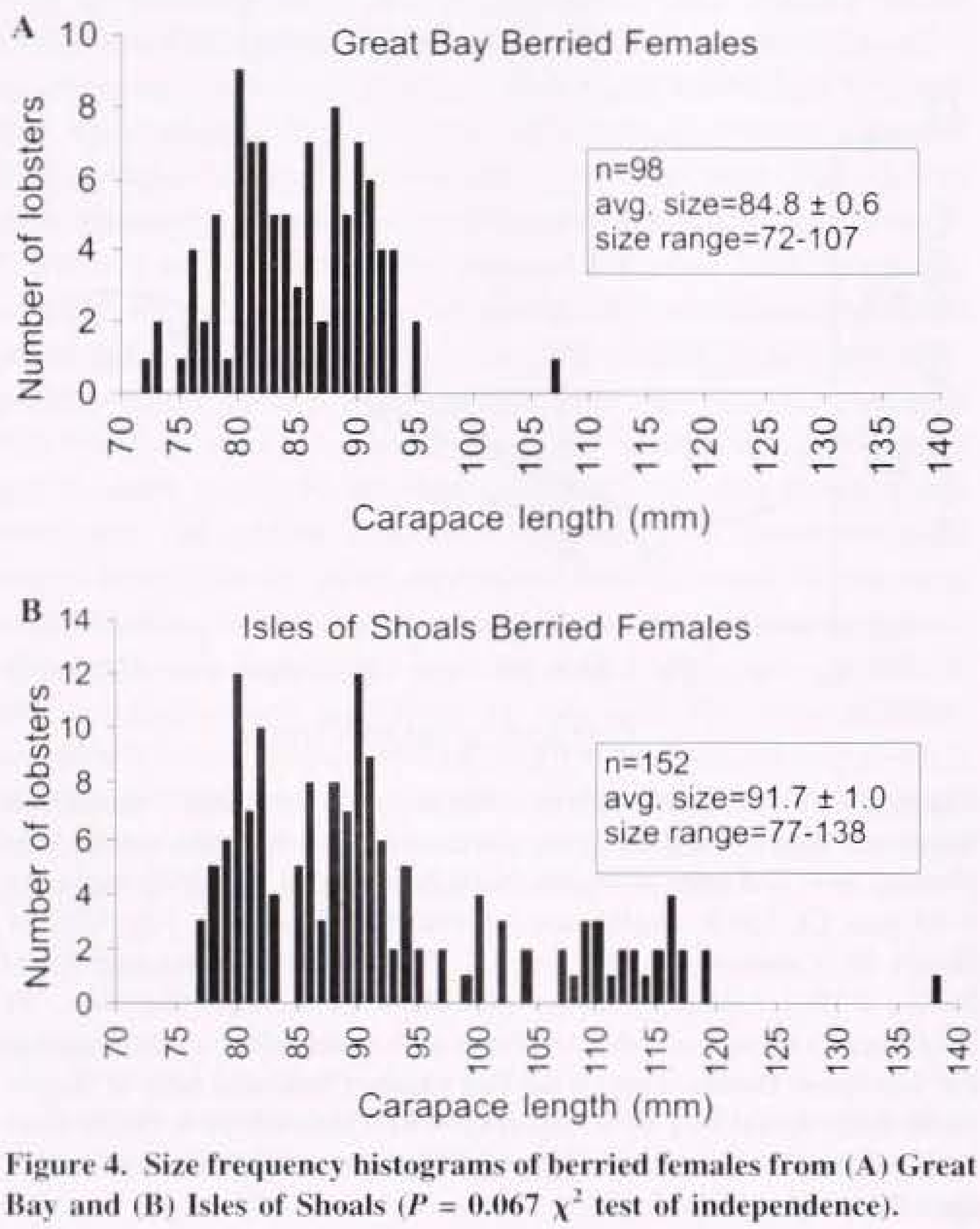

Figure 4. Size frequency histograms of berried females from (A) Great Bay and (B) Isles of Shoals (P = 0.067 χ^2 test of independence).

The size range of the overall lobster population at the Isles of Shoals site was 48 to 144 mm with a mean size of 81 ± 0.1 mm CL (n = 3337; Fig. 5b), while the size range of the population from the Great Bay site was 38 to 113 mm CL, with an average size of 78 ± 0.1 mm CL (n = 4862; Fig. 5a). The size frequency distribution of all lobsters was significantly different between the two sites ($P < 0.05$). The Great Bay population includes more small lobsters <65 mm CL (6%) than the Isles of Shoals population (3%), and the Isles of Shoals site has more legal lobsters >83 mm CL (27%) than the Great Bay estuary (18%), particularly those >100 mm CL (2% at Isles of Shoals, <1% at Great Bay). The most striking difference between these sites is the sex ratio, as reported by Howell and Watson (1999). The overall proportion of females at the Isles of Shoals site (64%) was much larger than that in the Great Bay estuary population (35%), and this was increasingly true at larger sizes. The percentage of females in the Great Bay estuary fluctuated between 30% and 40% but dropped to <30% at sizes >82 mm CL, and no females >96 mm CL were captured in the Great Bay estuary. In contrast, the proportion of females near the Isles of Shoals increased with size class, so that 80% of the lobsters >96 mm CL were female.

DISCUSSION

All three methods used to assess the size at maturity of female American lobsters (i.e., egg stage, ABD/CL ratios, and berried female size frequency distributions) indicate that female lobsters from the Isles of Shoals mature at a larger size (50% = 85.9 mm CL) than those from the Great Bay estuary (50% = 83 mm CL), even though the two populations are <14 km apart. One of the major differences between these two locations is water temperature. The Great Bay estuary (1532 annual degree-days) is significantly warmer than the Isles of Shoals study site (738 degree-days), with the greatest difference in temperature (74% of the total difference in degree-days) occurring in the summer months. We conclude that this increased temperature accelerates the rate of development of females in the Great Bay estuary, thereby causing them to reach sexual maturity at a smaller size. This finding once again supports the theory first put forth by Templeman (1936) that summer water temperatures determine size at maturity. The small difference in size at maturity reported is similar to a larger scale pattern observed along the entire range of the American lobster. For example, 50% of female lobsters from Long Island Sound reach maturity at 70 to 74 mm CL (Briggs & Mushacke 1979), while those from the Bay of Fundy do not reach maturity until 110 to 120 mm CL (Templeman 1936, Groom 1977, Campbell 1983).

While the size at 50% maturity for female lobsters from Great Bay is significantly different ($P < 0.001$) than that of females from Isles of Shoals, it is clear from the maturity ogives (Fig. 3) that the greatest difference in the two populations exists in the smaller size classes. This may be due to the mixing of mature females from Great Bay with those from the coast, as mature females migrate out of the estuary. As reported by Howell et al. (1999), the proportion of females in Great Bay (35%) is much smaller than that near the Isles of Shoals (64%), and this difference is most pronounced in the larger size classes. In fact, the proportion of females in Great Bay begins to decline above the 82-mm CL size class (Fig. 4), which is approximately the size at which lobsters are reaching maturity. As proposed by Watson et al. (1999) and Howell et al. (1999), it would be advantageous for females to move out of the estuary for optimal egg development and survival of larvae. While

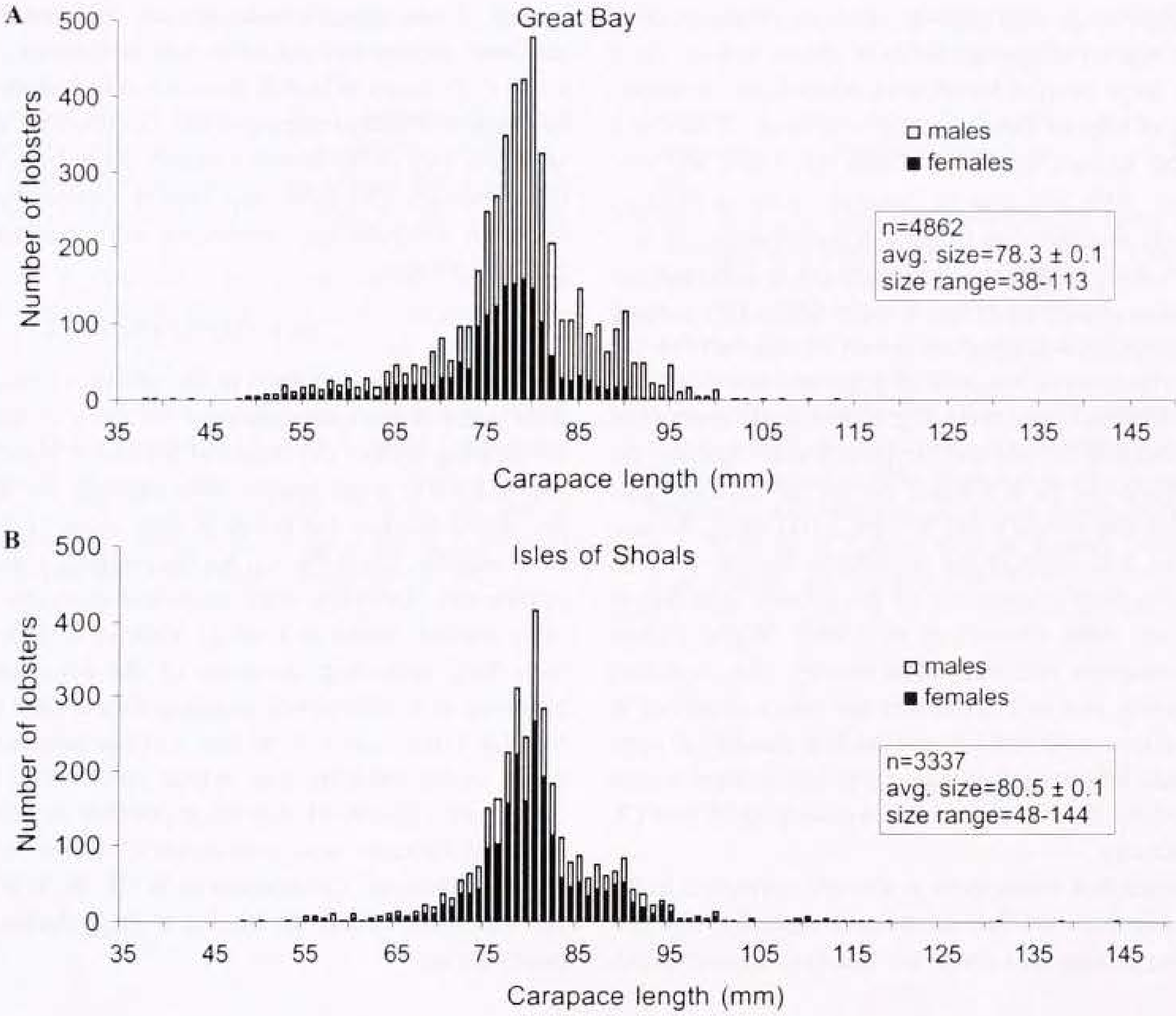

Figure 5. Size frequency histograms of the overall catch from (A) Great Bay and (B) Isles of Shoals, divided into proportions of males and females ($P < 0.05$ χ^2 test of independence).

there is a greater tendency for lobsters to leave the estuary, a number of coastal lobsters also move into the estuary, especially in the summer, presumably to take advantage of the warmer temperatures (Watson et al. 1999). Therefore, while there is a clear difference in the size at maturity of female lobsters from the two populations, the mixing of the coastal and estuarine lobsters due to seasonal migrations may be responsible for making this difference less evident, especially in the larger size classes.

Although warmer summer water temperature appears to be the most likely factor causing lobsters in the estuary to mature at a smaller size than New Hampshire coastal lobsters, another possibility is that berried females from offshore waters migrate inshore to the waters near Isles of Shoals and skew the size frequency of berried females there toward larger sizes. Berried females often migrate inshore to complete their reproductive cycle because the warm temperature inshore speeds their development (Cooper & Uzmann 1971, Uzmann et al. 1977, Cooper & Uzmann 1980, Fogarty et al. 1980, Campbell et al. 1984, Campbell & Stasko 1986). Seasonal concentrations of large berried females in inshore areas off Cape Cod, MA (Estrella & McKiernan 1989), and Long Island, NY (Briggs & Mushacke 1979), are thought to be the result of berried females from offshore migrating shoreward. Berried females from offshore in both of these areas are larger than those inshore, and thus the mixing of offshore berried females with the local inshore populations would distort the apparent size frequencies. This remains a viable explanation for the size at maturity differences that we have observed.

Analyses of both egg stage data and ABD/CL ratios yielded similar results, in terms of size at maturity. Based in egg stages, 50% of females from the waters off the Isles of Shoals were mature at 85.9 mm CL, while, according to ABD/CL ratios, 50% were mature at 86.9 mm CL. In Great Bay, the values were 83 and 81.5 mm CL, respectively. The value based on ABD/CL ratios for the estuarine lobsters fell within the 95% confidence interval generated from egg stage data, and, while the estimate based on ABD/CL ratios from Isles of Shoals lobsters did not fall within the 95% confidence interval (85.3–86.5) generated from dissection data, it was very close. Thus, it seems that ABD/CL ratios provide a reasonably good estimate of size at maturity, as indicated in several previous studies (Skud & Perkins 1969, Krouse 1973, Briggs & Mushacke 1979, 1980, Ennis 1980).

The size ranges of berried females from both sites were very similar to what one would predict from analyses of the egg stages of dissected lobsters. In the population near the Isles of Shoals, the smallest mature female was 80 mm CL, while the smallest berried female captured was 77 mm CL. Likewise, the smallest mature Great Bay female was 72 mm CL, which was the same size as the smallest berried female observed while sea sampling. This suggests that it might be possible to construct a fairly accurate maturity ogive using a combination of two noninvasive methods: the size range of berried females and ABD/CL ratios. Measurements of berried females are useful in defining the size range of mature females in a population and can serve as a good indication of the size at which the smallest females become mature. However, these measurements do not indicate what proportion of the females at a given size are mature, and these data could be derived from measurements of the ABD/CL ratios over a range of relevant size classes.

While the size frequency distributions of berried females from the two sites were not significantly different ($P = 0.067$), there were clearly more large berried females near the Isles of Shoals (20% >100 mm CL at Isles of Shoals vs. 1% >100 mm CL in Great Bay) and more small berried females in Great Bay (50% <85 mm CL in Great Bay vs. 70% >85 mm CL near the Isles of Shoals). Therefore, it is likely that the size frequency distributions of berried females in both study sites were not significantly different due to the low sample size of berried females in the Great Bay estuary ($n = 98$). This assumption is supported, in part, by the fact that the size frequency distributions of the overall populations ($n = 4862$ for the estuary) at the two sites were significantly different ($P < 0.05$). As with the berried female size frequency distributions, the bulk of this difference can be accounted for by the lack of large lobsters in the Great Bay estuary (<1% were >100 mm). As discussed earlier, these data support the hypothesis that as lobsters reach sexual maturity they migrate out of the estuary into deeper water (Watson et al. 1999, Howell et al. 1999). While mature females probably undergo this migration shortly after reaching sexual maturity, giving rise to the skewed sex ratios observed in the estuary in size classes >80 mm CL and the low number of large berried females, male lobsters eventually move into coastal waters as well, as indicated by the scarcity of any lobsters >100 mm CL in the Great Bay estuary.

Our results indicate that while there is a small difference in the size at which females from the two sites reach maturity, that difference is small, suggesting that these are not two distinct populations. There appears to be mixing between the two areas, particularly among the sexually mature lobsters. Thus, despite the small differences in size at maturity, it is probably not necessary to implement different management measures for each area. The size at which half of the females mature from both sites approximates the minimum size limit, and thus it appears to be appropriate to maintain adequate egg production and recruitment to satisfy the F10 requirement.

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LITERATURE CITED

Aiken, D. E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). *J. Fish. Res. Board Can.* 30:1337–1344.

Aiken, D. E. & S. L. Waddy. 1976. Controlling growth and reproduction in the American lobster. *Proc. World Maricult. Soc.* 7:415–430.

Aiken, D. E. & S. L. Waddy. 1980. Reproductive biology. In: J. S. Cobb & B. F. Phillips, editors. The biology and management of lobsters, vol. 1. New York: Academic Press, pp. 215–276.

Aiken, D. E. & S. L. Waddy. 1982. Cement gland development, ovary maturation, and reproductive cycles in the american lobster *Homarus americanus*. *J. Crustacean Biol.* 2:315–327.

Aiken, D. E. & S. L. Waddy. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. *Can. J. Fish. Aquat. Sci.* 43:2258–2270.

Briggs, P. & F. Mushacke. 1979. The American lobster in western Long Island sound. *N. Y. Fish Game J.* 26:59–86.

Briggs, P. T. & F. M. Mushacke. 1980. The American lobster and the pot fishery in the inshore waters off the south shore of Long Island, New York. *N. Y. Fish Game J.* 27:156–178.

Campbell, A. 1983. Growth of tagged lobsters (*Homarus americanus*) off Port Maitland, Nova Scotia 1948–1980. *Can. Tech. Rep. Fish. And Aquat. Sci.* 1232:1–10.

Campbell, A., D. E. Graham, H. J. MacNichol & A. M. Williamson. 1984. Movements of tagged lobsters released on the continental shelf from Georges Bank to Baccaro Bank 1971–73. *Can. Tech. Rep. Fish. And Aquat. Sci.* 1288:1–16.

Campbell, A. & A. Stasko. 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Marine Biol.* 92:393–404.

Cooper, R. & J. Uzmann. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science 171:288–290.

Cooper, R. & J. Uzmann. 1980. Ecology of juvenile and adult Homarus. In: J. S. Cobb & B. F. Phillips, editors. The biology and management of lobsters, vol. 2. New York: Academic Press, pp. 97–142.

Ennis, G. P. 1980. Size-maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 37:945–956.

Estrella, B. T. & D. J. McKiernan. 1989. Catch-per-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: Description and trends. Washington, DC: U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Report NMFS SSRF 81.

Fogarty, M. J. 1995. Populations, fisheries and management. In: J. Factor, editor. Biology of the lobster, *Homarus americanus*. New York: Academic Press, pp. 111–137.

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

Groom, W. 1977. Lobster project, 1977, Grand Manan Island: Fish'N'Ships, notice to Bay of Fundy Fishermen. New Brunswick Department of Fishing Information, Fredericton, New Brunswick, pp. 1–10.

Howell, W. H., W. H. Watson, III & S. H. Jury. 1999. Skewed sex ratio in an estuarine lobster (*Homarus americanus*) population. *J. Shellfish Res.* 18:193–201.

Jury, S. H., W. H. Howell & W. H. Watson, III. 1995. Lobster movements in response to a hurricane. *Mar. Col. Prog. Ser.* 119:305–310.

Krouse, J. 1973. Maturity, sex ratio, and size composition of the natural population of american lobster, *Homarus americanus*, along the Maine coast. *Fishery Bull.* 71:165–172.

Landers, D. F., Jr., M. Keser & S. B. Saila. 2001. Changes in female lobster (*Homarus americanus*) size at maturity and implications for the lobster resource in Long Island Sound, Connecticut. *Marine Freshwater Res.* 52:1283–1290.

Lawton, P. & K. L. Lavalli. 1995. Postlarval, juvenile, adolescent and adult ecology. In: J. R. Factor, editor. Biology of the lobster, *Homarus americanus*. New York: Academic Press, pp. 47–88.

Munro, J. & J. C. Therriault. 1983. Migrations saisonnieres du homard (*Homarus americanus*) entre la cote et les lagunes des Iles-de-la-Madeleine. *Can. J. Fish. Aquat. Sci.* 40:905–918.

National Marine Fisheries Service (NMFS). 2002. Available at: http://www.st.nmfs.gov/pls/webpls/MF_ANNUAL_LANDINGS.RESULTS

Polovina, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. *Can. J. Fish. Aquat. Sci.* 46:660–665.

Reynolds, W. W. & M. E. Casterlin. 1985. Vagile macrofauna and the hydrographic environment of the Saco River Estuary and adjacent waters of the Gulf of Maine. *Hydrobiologia* 128:207–215.

Short, F. T., editor. 1992. The ecology of the Great Bay Estuary, New Hampshire and Maine: an estuarine profile and bibliography. Washington, DC: Coastal Ocean Program Publication, National Oceanic and Atmospheric Administration, 222 pp.

Skud, B. & H. Perkins. 1969. Size composition, sex ratio, and size at maturity of offshore northern lobsters. Washington, DC: U.S. Fish and Wildlife Service Special Scientific Report—Fisheries No. 598.

Templeman, W. 1936. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime Provinces of Canada. *J. Biol. Bd. Can.* 2:41–88.

Templeman, W. 1944. Abdominal width and sexual maturity of female lobsters on the Canadian Atlantic coast. *J. Fish. Res. Bd. Can.* 6:281–290.

Thomas, M. L. H. 1968. Overwintering of american lobster, *Homarus americanus*, in burrows in Bideford River, Prince Edward Island. *J. Fish. Res. Board. Can.* 25:2725–2727.

Thomas, M. L. H. & G. N. White. 1969. Mass mortality of estuarine fauna at Bideford P.E.I. associated with abnormally low salinities. *J. Fish. Res. Board Can.* 26:701–704.

Uzmann, J. R., R. Cooper & K. Pecci. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. Washington, DC: National Oceanic and Atmospheric Administration Technical Report NMFS SSRF-705.

Watson, W. H. III, A. Vetrovs & W. H. Howell. 1999. Lobster movements in an estuary. *Marine Biol.* 134:65–75.

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SIZE AT MATURITY OF FEMALE AMERICAN LOBSTERS FROM AN ESTUARINE AND

COASTAL POPULATION

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ABSTRACT The size at which female lobsters reach sexual maturity was determined for two populations that inhabit waters along

the coast of New Hampshire. One group was captured in the Great Bay estuary, where water temperatures in the summer typically

average between 1 7°C and 20°C. The other group of lobsters resided in coastal waters, near the Isles of Shoals, where the water

temperature was much colder during the summer (1 1-15"C). Maturity was assessed using criteria that included the following: ovarian

classification; abdominal width/carapace length (CL) ratio; and the size frequency distribution of berried females. All the techniques

yielded similar results and consistently demonstrated that female lobsters in the estuary matured at a smaller size than those in colder

coastal waters. The smallest mature females from Great Bay were 72 mm in CL. with iWr reaching se.xual maturity by 83 mm CL

and all beconung mature by 89 mm CL. The smallest mature female from the Isles of Shoals area was 77 mm CL, with 50% mature

by 86 mm CL and all mature by 93 mm CL. The difference in the proportion of mature lobsters in the estuarine versus coastal

populations was much greater in the smaller size classes than in the larger size classes, suggesting a mi.xing of the two populations,

most likely due to females from Great Bay migrating into coastal waters.

KEY WORDS: cslu.irv. Hoiiniiiis itmericiiniis. lobster, sexual maturitv

INTRODUCTION

The American lobster. Hoinunts anicncanus (Milne-Edwards) is the most commercially valuable species harvested in the northwest Atlantic Ocean (NMFS 2002). Although lobsters are most abundant in coastal waters, estuarine populations are common and have been investigated from Canada to Massachusetts (Thomas iy6S. Thomas & White 1969. Munro & Theriiaull 19S-3. Reynolds & Casterlin 1985. Jury et al. 1995: Howell et al. 1999; Watson et al. 1999). One population that has received considerable attention is located in the Great Bay estuary in New Hampshire. Howell et al. (1999) have demonstrated that, like the lobsters in the Iles-de-l-Madeleine in Canada (Munro & Therriault 19S.3). the sex ratio is skewed toward males throughout the estuary, with the greatest proportion of male lobsters found in the portions of the estuary furthest from the coast. It has been proposed that the skewed sex ratio in the estuary is the result of the differential seasonal migration of mature female lobsters out of the estuary (Watson et al. 1999).

To ensure that there are enough mature females in a given lobster population, a minimum legal size has been established. This allows a given proportion of the females to reach sexual maturity and reproduce at least once befoi-e they are landed. The size at which 50% of the females from an area are mature (50% maturity) is often used as a reference point because most models indicate that when the minimum size is set at this value sufficient recruits will be produced to sustain the fishery. Currently, the minimum size limit in the inshore waters of New Hampshire is 83 mm carapace length (CL).

There is a wide range of sizes over which female lobsters reach maturity. The smallest size at 50% maturity. 70 to 74 mm CL. is found in western Long Island Sound (Briggs & Mushacke 1979), and the largest size. 110 to 120 mm CL. is found in the Bay of Fundy (Templeman 1936. Groom 1977. Campbell 1983). It has been suggested that a number of different factors infiuence the size

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at which female lobsters mature, including nutrient availability (Lawton & Lavalli 1995). fishing pressure (Polovina 1989. Landers et al. 2001). and temperature (Templeman 1936. Templeman 1944. Aiken & Waddy 1980. 1986. Estrella & McKiernan 1989. Fogarty 1995). Increases in all. or any, of these factors results in a decrease in the size at which females reach sexual maturity.

Temperature is thought to be the most influential of these factors because it is known to directly affect the growth rates of lobsters, with development occurring more quickly with increased temperature (Aiken & Waddy 1976). The rate of ovarian development is primarily controlled by summer water temperature, with little development occurring throughout the winter months (Templeman 1936). Thus, in areas with warmer water in the summer, lobsters reach sexual maturity at smaller sizes.

Estuaries, such as the Great Bay estuary in New Hampshire, are characterized by large daily and seasonal fluctuations in temperature and salinity. In the Great Bay estuary, the water temperature in the summer is approximately IO°C higher than in New Hampshire coastal waters (Short 1992). Given the apparent influence of water temperature on the rate of inaturation of female lobsters, we hypothesized that female lobsters in the Great Bay estuary would reach sexual maturity at a smaller size than those in coastal waters, such as near the Isles of Shoals, which are located 1 1 km away from where the Great Bay estuary empties into the Gulf of Maine (Fig. 1).

To test our hypothesis, we determined the size at maturity for 92 lobsters collected in the Great Bay estuary with 106 lobsters collected near the Isles of Shoals. A comparison of the results yielded by analyzing (1) the size distribution of berried females, (2) the size of female abdomens relative to their length, and (3) the stage of eggs removed from the ovaries yielded the same pattern. Female lobsters from the estuarine site matured at a smaller size than those from the coastal site, probably due to the influence of warmer summer water temperatures on their growth and development.

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Figure 1. The two study sites are marl\ed witli an X [Great Bay Estuary and Isleof Slioals (II l<m off liie iitast of New Hampsiiirel]. Sites of temperature data collection for the (ireal Bay Estuary are: A, Jackson Estuarine Laboratory; B, Fox Point; and C. Upper Piscataqua River. Lobsters were obtained from the Great Bay estuary within the area indicated by shading.

MATERIALS AND METHODS

Temperature

Bottom temperatures were collected in the waters surrounding the Isles of Shoals from 1997 to 2001 at depths of approximately 8 to 10 m using HOBOTemp temperature data loggers (Onset Computer. Falmouth. MA) thai recorded water temperature at 2-h intervals for 5 to 6 mo at a time. Bottom temperature data for Great

Bay was collected from 1997 to 2001 at three different locations that spanned the area where lobsters were collected (Fig. 1). The most consistent data set were obtained from a location near the University of New Hampshire Jackson Estuarine Laboratory, at a depth of approximately 3 to 5 m. using a YSI multiparameter 6600 datalogger (YSI Inc.. Marion. MA) that recorded the water temperature every 30 min. Water temperature also was recorded near Fox Point and along the Piscataqua River in 1990 and 1993. using a YSI meter model 33 attached to a probe that was lowered to a point near the bottom. Data were obtained from these two sites approximately every other day while hauling some of the traps used to collect lobsters for this study. Data from all three sites were averaged from all available years to yield a temperature profile of the area from which lobsters were collected. The mean monthly temperature then was calculated, and the total annual degree-days >8°C were summed for each location by adding together the number of degrees that exceeded S' C for each day of the year and summing them for the entire year.

Maturity Assessments

Dissections

Lobsters were collected from two areas (Fig. i) by commercial fishermen and by University of New Hampshire personnel using standard traps. The first site consisted of the upper region of the

Great Bay estuary (i.e.. Great Bay. Little Bay. and the upper Piscataqua River), and the second site included waters near the Isles of Shoals.

Lobsters were collected in 1991. 1992. 1994. and 2002. The lobsters from each site were divided into l-mm size classes ranging from 66 to 110 mm CL. A total of 92 lobsters were dissected from Great Bay. and a total of 106 from Isles of Shoals.

Female, nonovigerous. lobsters were examined, using multiple criteria, to determine whether they were sexually mature. For each animal, the CL and the width of the second abdominal segment were measured in millimeters, and the molt stage was recorded by examining the carapace and pleopods. One pair of pleopods then was removed for examination under a dissecting microscope to determine the cement gland stage (Aiken & Waddy 1982) and whether lobsters were in a premolt condition (Aiken 1973). A small circular incision then was made just behind the eye socket to access the anterior end of one of the ovaries. Several eggs were removed, and their size range and color were recorded. An egg stage was assigned to each lobster based on criteria established by Aiken and Waddy (1980).

Whether a female was sexually mature, or not. was determined using a combination of criteria, with ovarian stage as the primary tool. Any females with resorbed oocytes were considered to be mature, as these are an indication of prior spawning. Of the females without resorbed oocytes, those with ovaries that were at stage 4 and higher were also considered to be mature. The size range for stage 4 ovaries is different in the spring (stage 4b) than in the fall (stage 4a) due to the timing of development, and this was taken into account. Those females with ovaries at stage 2 and below were considered to be immature. To determine the maturity of those with stage 3 ovaries, we considered cement gland stage as well as egg stage. If a female lobster with stage 3 ovaries had cement glands that were at stage 3 or greater, then the lobster was considered to be mature.

To determine the size at which SC/c of the females from each area were mature, a nonlinear regression of percent mature for each l-mm CL size class was carried out using the statistical program, SYSTAT. The following equation was used:

p = (1/(1 -I- exp(-bO*(L-hl)))

where p is the proportion mature, bO is the curve shape parameter, L is the carapace length, and bl is the size at 50% maturity (estimated as a starting point for calculations by the user). The program estimated values of bO, based on the data set. until it found the best-fit curve. This resulted in sigmoid curve from which bl could be calculated with a 95% confidence interval. A statistical comparison of the regression lines that resulted from each population of lobsters was made to determine whether they were significantly different from each other.

Sea Sampling Data

Sea-sampling data were obtained from LIniversity of New Hampshire research traps, and during trips on commercial lobster boats in 1990 to 1993 and 2002 at each location. The data collected included CL. width of the second abdominal segment, sex. and whether females were ovigerous. A total of 8199 lobsters were examined during these sea-sampling trips.

Abdominal Width

A ratio of abdomen width to CL (ABD/CL ratio) was calcu-lated for each female, and these were averaged for each l-mm CL

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size class. A plot then was made of CL versus this ratio for each size class. A nonlinear polynomial regression of these data was created for each site using SYSTAT. The following equation was used: ABD/CL = a + bx + cx'^2 + d\'^3. where x = CL. SYSTAT then estimated the values of a. b. c. and d to most closely fit the curve to the data. To determine the inflection point of the curve, which represents the point at which the rate of change in the ABD/CL ratio is greatest, and therefore approximates the size at which SO'/c of the feinales have reached maturity, the second de-rivative of the original equation, y = 2cx + 6dx. was calculated. That equation was then set to equal zero and was solved for x. yielding the equation x = -2c/6d. Then, the c and d values from

SYSTAT were used to solve for x (the CL at 50% maturity) (Landers et al. 2001). The size at 50% maturity that was estimated by this method was compared with that obtained by dissection for the estuarine and coastal lobster populations to determine whether the abdominal width estimates fell within the 95% confidence intervals of the dissection estimates.

months (June-August; Great Bay 995; Isles of Shoals 404). The difference in degree-days between the two sites for these 3 mo accounted for 75% of the difference in degree-days for the entire year. During this period, the mean water temperature averaged 12.5°C at Isles of Shoals and 19=C in Great Bay.

Maturity Assessments

Dissections

Nonlinear regressions of CL versus percent mature, as determined by dissections, were used to calculate the size at 50% maturity for each site (Fig. 3a). The size at 50% maturity for females obtained from waters near the Isles of Shoals was 85.9 mm CL (95% confidence interval 85.3-86.5; n = 106). Fifty percent of females from Great Bay were mature at 83 mm CL (95% confidence interval 80.6-85.4 mm; ;; = 92). A comparison of the two regressions showed that they were significantly different from each other ($P < 0.001$). The smallest mature female captured near

Berried Female Size Frequency Distributions

From the sea-sampling data, a size frequency distribution of berried females, as well as a plot of the overall size frequency distribution of the population was made for each area. The plots of overall size frequency were divided into the proportions that were male and female in each size class so that the proportion that was female at a given size class could be compared with the proportion of females that were berried at that same size class. For each plot the average size, the SEM. size range, and sex ratio were calculated for comparison. The size distributions for the overall population and for only berried females were compared between sites using a x" test of independence.

RESULTS

A Comparison oj tlsluarine Versus Coastal Water Degree-Days

There was a large difference between the number of annual degree-days (>8°C) in the Great Bay estuary (1532) compared to those in the waters near the Isles of Shoals (738) (Fig. 2). The greatest difference in temperature occun'ed during the summer

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Month

Figure 2. Mean monthly bottom temperatures (°C), with SE bars, for

water in the (Ireat Bay estuary (open circlel and near the Isles of

Shoals (solid circles! (1^97-2(1(11). W a(er temperature for (ireat Bay is

an average of three sites that encompass the area from w hich lobsters

were collected.

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Carapace length (mm)

30 40 50 60 70 80 90 100 110 120 130

Carapace length (mm)

Figure 3. (A) Maturity ogiyes estimated by nonlinear regressions based on dissection data from 1-mm size classes from Great Bay (dashed line! and Isles of Shoals (solid line): CJreat Bay 50% maturity = S3 mm CL (95% confidence interyal 8(1.6-85.4: n = 92l; Isles of Shoals 5(1% maturity = 85.9 mm CL (95'/^ confidence interval 85.3-86.5: n = 106). .\ctual values are plotted for each 5-mm size class. (B) Polynomial regression estimated from abdominal width measurements for I-nim size classes from (Jreat Bay (dashed line) and Isles of Shoals (solid line): (;reat Bay •^tt"(maturity = 81.5 mm CL (h = 1613): Isles of Shoals 50% maturity = 86.9 {n = 1699). Actual values are plotted for each 5-mm size class.

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the Isles of Shoals was 80 mm CL. while in the estuary a 72-mm CL mature female was captured. All females were mature by 93 mm CL at the Isles of Shoals study site, and by 89 mm CL in the Great Bay estuary.

Abdominal width: CL ratios

Nonlinear regressions of ABD/CL ratios were fitted to the data to calculate size at 50% maturity (Fig. 3b). The resulting curves indicated that half the females from Isles of Shoals were mature by 86.9 mm (/; = 1699), while the size at 50% mature for lobsters captured in the estuary was 81 .5 mm (/; = 1613). The estimate for the Isles of Shoals lobsters did not fall within the 95% confidence interval generated from the dissection data (85.3-86.5). but was very close. The estimate for the Great Bay estuary lobsters fell within the 95% confidence interval (80.6-85.4).

Size frequency distributions

The size range of berried females collected near the Isles of Shoals was 77 to 138 mm CL. with an average (±SEM) size of 92 ± 1.0 mm CL (« = 152; Fig. 4b). The size range of berried females from the Great Bay estuary was 72 to 107 mm CL, with an average size of 85 ± 0.6 mm CL {n = 98; Fig. 4a). These means were significantly different from each other (P < 0.001 two-tailed / test). Only a small portion (30%) of berried females from near the Isles of Shoals were smaller than 85 mm CL, whereas 50% of the berried females from the estuary were <85 mm CL. In contrast, very few berried females (1%) from the Great Bay estuary were >100 mm CL, while 20% of berried females from waters near the Isles of Shoals were >100 mm CL. Nevertheless, despite these differences, the distribution of sizes of berried females was not sianificant between the two sites (P = 0.067).

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Great Bay Berried Females

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n=98

avg. slze=84.8 ± 0.6

size range=72-107

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Carapace length (mm)

Isles of Shoals Berried Females

n=152

avg. size=91.7 ±1.0

size range=77-138

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Carapace length (mm)

Figure 4. Size frequency histoHranis of berried females from (A) Great

Bay and (B) Isles of Shoals (/' = 0.1)67 x" test of independence).

The size range of the overall lobster population at the Isles of Shoals site was 48 to 144 mm with a mean size of 8 1 ± 0. 1 mm CL in = 3337; Fig. 5b). while the size range of the population from the Great Bay site was 38 to 1 13 mm CL, with an average size of 78 ± 0.1 mm CL (;; = 4862; Fig. 5a). The size frequency distribution of all lobsters was significantly different between the two sites ($P < 0.05$). The Great Bay population includes more small lobsters <65 mm CL (6%) than the Isles of Shoals population (3%), and the Isles of Shoals site has more legal lobsters >83 mm CL (277(1) than the Great Bay estuary (18%), particularly those >I00 mm CL (2% at Isles of Shoals, <1% at Great Bay). The most striking difference between these sites is the sex ratio, as reported by Howell and Watson (1999). The overall proportion of females at the Isles of Shoals site (64 ^c) was much larger than that in the Great Bay estuary population (35%), and this was increasingly true at larger sizes. The percentage of females in the Great Bay estuary fluctuated between 30% and 40% but dropped to <30% at sizes >82 mm CL, and no females >96 mm CL were captured in the Great Bay estuary. In contrast, the proportion of females near the Isles of Shoals increased with size class, so that 80% of the lobsters >96 mm CL were female.

DISCUSSION

All three methods used to assess the size at maturity of female American lobsters (i.e., egg stage, ABD/CL ratios, and benied female size frequency distributions) indicate that female lobsters from the Isles of Shoals mature at a larger size (50% = 85.9 mm CL) than those from the Great Bay estuary (50% = 83 mm CL).

even though the two populations are <14 km apart. One of the major differences between these two locations is water temperature. The Great Bay estuary (1532 annual degree-days) is significantly warmer than the Isles of Shoals study site (738 degree-days), with the greatest difference in temperature (74% of the total difference in degree-days) occurring in the summer months. We conclude that this increased temperature accelerates the rate of development of females in the Great Bay estuary, thereby causing them to reach sexual maturity at a smaller size. This finding once again supports the theory first put forth by Templeman (1936) that summer water temperatures determine size at maturity. The small difference in size at maturity reported is similar to a larger scale pattern observed along the entire range of the American lobster. For example, 50%' of female lobsters from Long Island Sound reach maturity at 70 to 74 mm CL (Briggs & Mushacke 1979), while those from the Bay of Fundy do not reach maturity until 1 10 to 120 mm CL (Templeman 1936, Groom 1977, Campbell 1983).

While the size at 50% maturity for female lobsters from Great Bay is significantly different ($P < 0.001$) than that of females from Isles of Shoals, it is clear from the maturity ogives (Fig. 3) that the greatest difference in the two populations exists in the smaller size classes. This may be due to the mixing of mature females from Great Bay with those from the coast, as mature females migrate out of the estuary. As reported by Howell et al. (1999), the proportion of females in Great Bay (35%) is much smaller than that near the Isles of Shoals (64%), and this difference is most pronounced in the larger size classes. In fact, the proportion of females in Great

Bay begins to decline above the 82-mm CL size class (Fig. 4), which is approximately the size at which lobsters are reaching maturity. As proposed by Watson et al. (1999) and Howell et al. (1999), it would be advantageous for females to move out of the estuary for optimal egg development and survival of larvae. While

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Great Bay

45

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65

D males

females

n=4862

avg. slze=78.3 ± 0.1

size range=38-113

75 85 95 105 115

Carapace length (mm)

Isles of Shoals

125

135

145

D males

females

n=3337

javg. slze=80.5±0.1

size range=48-144

35 45 55 65 75 85 95 105 115 125 135 145

Carapace length (mm)

Figure 5. Sizt frequency histograms of the overall catch from (A) Great Bay and (B) Isles of Shoals, divided into proportions of males and

females (f < 0.05 \' test of independence).

there is a greater tendency for lobsters to leave the estuary, a number of coastal lobsters also move into the estuary, especially in the summer, presumably to take advantage of the warmer temperatures (Watson et al. 1999). Therefore, while there is a clear difference in the size at maturity of female lobsters from the two populations, the mixing of the coastal and estuarine lobsters due to seasonal migrations may be responsible for making this difference less evident, especially in the larger size classes.

Although warmer summer water temperature appears to be the most likely factor causing lobsters in the estuary to mature at a smaller size than New Hampshire coastal lobsters, another possibility is that berried females from offshore waters migrate inshore to the waters near Isles of Shoals and skew the size frequency of berried females there toward larger sizes. Berried females often migrate inshore to complete their reproductive cycle because the warm temperature inshore speeds their development (Cooper & L'zmann 1971. Uzmann et al. 1977. Cooper & Uzmann l9Sf), Fogaity et al. 1980, Campbell et al. 1984. Campbell & Stasko 1986). Seasonal concentrations of large berried females in inshore areas off Cape Cod. MA (Estrella & McKieman 1989), and Long Island, NY (Briggs & Mushacke 1979). are thought to be the result of berried females from offshore migrating shoreward. Berried females from offshore in both of these areas are larger than those inshore, and thus the mixing of offshore berried females with the local inshore populations would distort the apparent size frequencies. This remains a viable explanation for the size at maturity differences that we have observed.

Analyses of both egg stage data and ABD/CL ratios yielded similar results, in ternis of size at maturity. Based in egg stages.

50% of females from the waters off the Isles of Shoals were mature at 85.9 mm CL. while, according to ABD/CL ratios, 50% were mature at 86.9 mm CL. In Great Bay. the values were 83 and 81.5 mm CL. respectively. The value based on ABD/CL ratios for the estuarine lobsters fell within the 95% confidence interval generated from egg stage data, and, while the estimate based on ABD/

CL ratios from Isles of Shoals lobsters did not fall within the 95% confidence interval (85.3-86.5) generated from dissection data, it was very close. Thus, it seems that ABD/CL ratios provide a reasonably good estimate of size at maturity, as indicated in several previous studies (Skud & Perkins 1969, Krouse 1973, Briggs & Mushacke 1979, 1980, Ennis 1980).

The size ranges of berried females from both sites were very similar to what one would predict from analyses of the egg stages of dissected lobsters. In the population near the Isles of Shoals, the smallest mature female was 80 mm CL. while the smallest berried female captured was 77 mm CL. Likewise, the smallest mature Great Bay female was 72 mm CL. which was the same size as the smallest berried female observed while sea sampling. This suggests that it might be possible to construct a fairly accurate maturity ogive using a combination of two noninvasive methods: the size range of berried females and ABD/CL ratios. Measurements of berried females are useful in defining the size range of mature females in a population and can serve as a good indication of the size at which the smallest females become mature. However, these measurements do not indicate what proportion of the females at a given size are mature, and these data could be derived from measurements of the ABD/CL ratios over a range of relevant size classes.

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While the size frequency distributions of berried females from the two sites were not significantly different (P = 0.067). there were clearly more large beri'ied females near the Isles of Shoals (20% > 1 00 mm CL at Isles of Shoals vs. 1 % > 1 00 mm CL in Great Bay) and more small berried females in Great Bay (SOVr <85 mm CL in Great Bay vs. 10% >85 mm CL near the Isles of Shoals). Therefore, it is likely that the size frequency distributions of berried females in both study sites were not significantly different due to the low sample size of berried females in the Great Bay estuary {J! = 98). This assumption is supported, in part, by the fact that the size frequency distributions of the overall populations (;; = 4862 for the estuary) at the two sites were significantly different (P < 0.05). As with the berried female size frequency distributions, the bulk of this difference can be accounted for by the lack of large lobsters in the Great Bay estuary (<l% were >100 mm). As discussed earlier, these data support the hypothesis that as lobsters reach se.xual maturity they migrate out of the estuary into deeper water (Watson et al. 1999, Howell et al. 1999). While mature females probably undergo this migration shortly after reaching sexual maturity, giving rise to the skewed sex ratios observed in the estuary in size classes >80 mm CL and the low number of large berried females, male lobsters eventually move into coastal waters as well, as indicated by the scarcity of any lobsters >I00 mm CL in the Great Bay estuary.

Our results indicate that while there is a small difference in the size at which females from the two sites reach maturity, that difference is small, suggesting that these are not two distinct populations. There appears to be mixing between the two areas, particularly among the sexually mature lobsters. Thus, despite the small differences in size at maturity, it is probably not necessary to implement different management measures for each area. The size at which half of the females mature from both sites approximates the minimum size limit, and thus it appears to be appropriate to maintain adequate egg production and recruitment to satisfy the FIO requirement.

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LITERATURE CITED

Aiken. D. E. 1973. Proecdysis, setal development, and molt prediction in the American lobster [Homanis americcvuis). J. Fish. Res. Board Can. 30:1337-1344.

Aiken, D. E. & S. L. Waddy. 1976. Controlling growth and reproduction in the American lobster. Proc. World Maricidl. Soc. 7:415-430.

Aiken, D. E. & S. L. Waddy. 1980. Reproductive biology. In: J. S. Cobb & B. F. Phillips, editors. The biology and management of lobsters, vol. I. New York: Academic Press, pp. 215-276.

Aiken. D. E. & S. L. Waddy. 1982. Cement gland development, ovary maturation, and reproductive cycles in the american lobster Homarus americaiuts. J. Crustacean Biol. 2:315-327.

Aiken. D. E. & S. L. Waddy. 1986. Environmental mduence on recruitment of the American lobster. Homarus americanus: a perspective. Can. J. Fislh Aqua!. Sci. 43:2258-2270.

Briggs, P. & F. Mushacke. 1979. The American lobster in western Long Island sound. N. Y. Fish Game J. 26:59-86.

Briggs. P. T. & F. M. Mushacke. 1980. The American lobster and the pot fishery in the inshore waters off the south shore of Long Island. New York. N. y. Fi.^h Game J. 27:156-178.

Campbell. A. 1983. Growth of tagged lobsters {Homarus americanus) off Port Maitland. Nova Scotia 1948-1980. Can. Tech. Rep. Fish. And Aqtuii. Sci. 1232:1-10.

Campbell, A., D. E. Graham, H. J. MacNichol & A. M. Williamson. 1984. Movements of tagged lobsters released on the continental shelf from Georges Bank to Baccaro Bank 1971-73. Can. Tech. Rep. Fisli. And Aqual. Sci. 1288:1-16.

Campbell. A. & A. Stasko. 1986. Movements of lobsters {Homarus americanus) tagged in the Bay of Fundy, Canada. Marine Biol. 92:393—404.

Cooper. R. & J. U/mann. 1971. Migrations and growth of deep-sea lobsters, Homarus americanus. Science 171:288-290.

Cooper, R. & J. Uzmann. 1980. Ecology of juvenile and adult Homarus. In: J. S. Cobb & B. F. Phillips, editors. The biology and management of lobsters, vol. 2. New York: Academic Press, pp. 97-142.

Ennis, G. P. 1980. Size-maturity relationships and related observations in Newfoundland populations of the lobster (Homarus americanus). Can. J. Fish. Aquat. Sci. 37:945-956.

Estrella. B. T. & D. J. McKieman. 1989. Catch-per-unit-eftort and biological parameters from the Massachusetts coastal lobster {Homarus americanus) resource: Description and trends. Washington. DC: U.S. Department of Commerce. National Oceanic and Atmospheric Administration Technical Report NMFS SSRF 81.

Fogarty, M. J. 1995. Populations, fisheries and management. In: J. Factor, editor. Biology of the lobster, Homarus americanus. New York: Academic Press, pp. 1 1 1-137.

Fogarty, M. J.. D. V. D. Borden & H. J. Russell. 1480. Movements of tagged american lobster. Homarus americanus. off Rhode Island. Fisheiy Bull. 78:771-780.

Groom. W. 1977. Lobster project, 1977, Grand Manan Island: Fish'N'Ships, notice to Bay of Fundy Fishermen. New Brunswick Department of Fishing Information, Fredericton. New Brunswick, pp. 1-10.

Howell. W. H.. W. H. Watson. Ill & S. H. Jury. 1999. Skewed sex ratio in an estuarine lobster {Homarus americanus) population. J. Shellfish Res. 18:193-201.

Jury. S. H., W. H. Howell & W. H. Watson, HI. 1995. Lobster movements in response to a hurricane. Mar. Col. Prog. Ser. 119:305-310.

Krouse. J. 1973. Maturity, sex ratio, and size composition of the natural population of american lobster, Homarus americanus. along the Maine coast. Fisheiy Bull. 71:165-172.

Landers. D. F., Jr., M. Ke.ser & S. B. Saila. 2001 . Changes m female lobster

{Homarus americanus) size at maturity and implications for the lobster resource in Long Island Sound, Connecticut. Marine Freshwater Res. 52:1283-1290.

Law ton. P. cS: K. L. Lavalli. 1995. Postlarval. juvenile, adolescent and adult ecology. In: J. R. Factor, editor. Biology of the lobster. Homarus americanus. New York: Academic Press, pp. 47-88.

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Munro. J. & J. C. Therriault. 1983. Migrations saisonnieres du homarii {Homurus cimericuiuis) entre la cote et les lagunes cjes Iles-de-la-Madelelne. Can. J. Fish. .Aqucil. Sci. 40:905-918.

National Marine Fisheries Service (NMFS). 2002. Available at: littp:// www.st.nnifs.gov/plsAvebpK/MF_ANNUAL_LANDlNGS.RESLILTS

Polovina. J. J. 1989. Density dependence in spiny lobster, Fainiliriis mar-ginatus. in the Northwestern Hawaiian Islands. Can. J. Fi.sli. Aqiiat. Scl. 46:660-665.

Reynolds. W. W. & M. E. Casterlin. 19S5. Vagile niacrotauna and the hydrographic environment of the Saco River Estuary and adjacent v\ a-ters of the Gulf of Maine. Hyclrobiologia 128:207-215.

Short. F. T.. editor. 1992. The ecology of the Great Bay Esluary. New Hampshire and Maine: an estuarine profile and bibliography. Washington. DC: Coastal Ocean Program Publication. National Oceanic and Atmospheric Administration. 222 pp.

Skud. B. & H. Perkins. 1969. Size composition, sex ratio, and size at maturity of offshore northern lobsters. Washington, DC: U.S. Fish and Wildlife Service Special Scientific Report — Fisheries No. 598.

Templeman, W. 1936. Local differences in the life history of the lobster {Honuiru.'i americaniis) on the coast of the Maritime Provinces of Canada. J. Biol. B,i. Can. 2:41-88.

Templeman. W. 1944. Abdominal width and sexual maturity of female lobsters on the Canadian Atlantic coast. J. Fisli. Re\. Bd. Can. 6:281-290.

Thomas, M. L. H. |9(iS. Overwintering of american lobster. Hoinanis americaniis. in burrows in Bideford River, Prince Edward Island. / F/.s7i. Res. Board. Can. 25:2725-2727.

Thomas. M. L. H. & G. N. White. 1969. Mass mortality of estuarine fauna at Bideford P.E.I, associated with abnormally low salinities. / Fish. Res. Board Can. 26:701-704.

U/niann. J. R.. R. Cooper & K. Pecci. 1977. Migration and dispersion of tagged American lobsters. Honuirus americaniis. on the southern New

England continental shelf Washington. DC: National Oceanic and Atmospheric Administration Technical Report NMFS SSRF-705.

Watson. W. H. III. A. Vetrovs & W. H. Howell. 1999. Lobster movements in an estuary. Marine Biol. 134:65-75.

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