



At-sea determination of female American lobster (*Homarus americanus*) mating activity: Patterns vs. expectations



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ABSTRACT

We examined female American lobsters (*Homarus americanus*) for evidence of mating activity in selected regions within Gulf of Maine (GOM) and Southern New England (SNE) waters. The presence of a spermatophore in their seminal receptacles was used as an indication of mating activity (spermatophore positive, “SP”). To determine if all presumably-mature females had mated, the proportion of females that were SP was compared to the size-at-maturity data used in the Atlantic States Marine Fisheries Commission (ASMFC) American Lobster Stock Assessment. A total of 1696 females were examined, and in all regions >75% of these females were SP. In most regions, more presumably-immature females (based on pre-existing maturity data) were SP than expected, while in the two SNE regions (Rhode Island) there were more presumably-mature females lacking sperm than expected. We suggest that due to the depleted condition of the SNE lobster stock, the discrepancy between expected maturity and mating activity in SNE females warrants further attention. Additionally, our data suggest that there is a need to re-examine lobster size-at-maturity throughout the GOM lobster stock. It appears as if either the maturity schedules have recently shifted, or sexually immature females are regularly mating in many regions.

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1. Introduction

Management of many decapod crustacean fisheries operates with the underlying assumption that sperm is not a limiting factor in the exploited population. Regulations protecting ovigerous females and setting minimum size limits have arisen based on the view that reproductive success depends primarily on female biology (e.g. size-at-maturity and size-based fecundity). As a result, decapod fisheries tend to preferentially remove males at harvestable sizes while allowing reproductive females to accumulate in the population (Cobb and Wang, 1985; Smith and Jamieson, 1991). This can ultimately limit the number of large males while simultaneously increasing the number of larger females in the population (Miller, 1976; Pollock, 1986; Smith and Jamieson, 1991;

Sainte-Marie and Hazel, 1992). In some species, fishing pressure has been shown to alter operational sex ratios (MacDiarmid and Sainte-Marie, 2006), disrupt reproduction in local populations by decreasing the frequency of encounters between potential mates (Gray and Powell, 1964; Powell et al., 1973; Ennis, 1980; Stephens et al., 1999; Gascoigne et al., 2009), and interfere with the process of sexual selection (Sato and Goshima, 2007). As a result of all of these factors, sperm limitation is a strong possibility in exploited populations (Miller, 1976; Pollock, 1986; Smith and Jamieson, 1991; Sainte-Marie and Hazel, 1992).

Recent work suggests that sperm limitation may occur in a number of commercially important marine decapod crustaceans including spiny lobsters (*Jasus edwardsii* and *Panulirus argus*, MacDiarmid and Butler, 1999), blue crabs (*Callinectes sapidus*, Jivoff, 1997, 2003; Kendall and Wolcott, 1999; Kendall et al., 2002; Hines et al., 2003), king crabs (*Paralithodes camtschaticus*, Powell et al., 1974), spiny king crabs (*Paralithodes brevipes*, Sato et al., 2005), and snow crabs (*Chionoecetes opilio*, Rondeau and Sainte-Marie, 2001). The manner by which sperm is limited for these species varies, but includes: (1) increased dependence on small males that have insufficient sperm supplies to fully inseminate larger females (Paul, 1992; Jivoff, 1997; Kendall et al., 2001; Robertson, 2001; Sato et al., 2005, 2006); (2) males depleting their sperm reserves over

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multiple matings due to female-skewed sex ratios (Dewsbury, 1982; Nakatsura and Kramer, 1982; Rutowski et al., 1987; Jivoff, 1997; Kendall and Wolcott, 1999; MacDiarmid and Butler, 1999; Sato and Goshima, 2007); (3) insufficient time between matings to fully restore sperm reserves (particularly for small males; Powell et al., 1974; Paul and Paul, 1989; Sainte-Marie et al., 1995; Kendall et al., 2001; Rondeau and Sainte-Marie, 2001; Sato and Goshima, 2006; Sato et al., 2005, 2006); and (4) males limiting the size of their spermatophores to allocate their resources among multiple females over a short time period (Pitnick, 1991; Pitnick and Markow, 1994; Warner et al., 1995; Preston et al., 2001; Rondeau and Sainte-Marie, 2001; Sato et al., 2005; Sato and Goshima, 2006).

Similar to other crustacean fisheries, the U.S. fishery for American lobster (*Homarus americanus*) is managed using biological controls that include minimum harvestable sizes (determined partly by female size-at-maturity) and protection of ovigerous females (see Miller, 1995 for review). An additional management tool is the conservation of females that are 'proven breeders' using the practice of V-notching (mandatory in the Gulf of Maine (GOM) stock), whereby a v-shaped notch is cut into the uropod of ovigerous females to protect them from harvest after their clutch has hatched (Kelly, 1992; Miller, 1995). These differential protections that female lobsters receive relative to males upon reaching harvestable size increases female survivorship and allows females to accumulate in the population, which increases the potential for sperm limitation.

Mating in the American lobster is generally focused around the female's molt (Templeman, 1934, reviewed in Atema, 1986). Pre-molt females seek out and cohabitate with the dominant males in their shelters just prior to molting and for several days afterwards (Stein et al., 1975; Atema et al., 1979; Atema, 1986; Karnofsky and Price, 1989; Cowan and Atema, 1990). Mating typically occurs within 24–48 h of the female molt (Templeman, 1934, 1936) and is accomplished when the male turns the female onto her back and inserts his modified pleopods into her seminal receptacle to deposit a spermatophore (Templeman, 1934; Atema et al., 1979), a portion of which subsequently hardens into a sperm plug (Templeman, 1934; Talbot and Helluy, 1995).

Some field data suggest that sperm limitation may be of concern in American lobster populations. Gosselin et al. (2003) examined the seminal receptacle loads in female American lobsters from the Gulf of St. Lawrence, Canada (Anticosti and Magdalen Islands), and their results suggest that small males are primarily responsible for mating with females in these areas. Complementary laboratory trials showed that small male lobsters contribute smaller spermatophores to females than larger males (Gosselin et al., 2003). While female size is positively correlated with fecundity (Aiken and Waddy, 1980; Attard and Hudon, 1987; Estrella and Cadrin, 1995), the evidence presented by Gosselin et al. (2003) may suggest that sperm limitation could prevent larger females from fertilizing their entire clutch when insufficient numbers of large males are available. In fact, subsequent work documented multiple paternity in heavily exploited locales (Grand Manan Island and Magdalen Islands vs. Anticosti) and the authors suggested that promiscuity by females was an attempt to avoid sperm limitation (Gosselin et al., 2005). Finally, recent tag/recapture data collected in New Hampshire waters indicated that approximately 15% of ovigerous females had dropped their clutches prematurely, which may indicate that those females lacked sufficient sperm reserves with which to fertilize their eggs (Goldstein, unpublished data).

The overall goal of this study was to examine the mating activity of female American lobsters as a first step in understanding the potential for sperm limitation in portions of the U.S. fishery. We focused on regions throughout the inshore fishery where maturity data utilized in the American Lobster Stock Assessment could be used as an index of expected mating activity, and where additional

data from commercial trap sampling programs were available for examination of sex ratios. Most of the regions selected were in the Gulf of Maine (GOM) lobster stock, which is in "favorable condition" and where "overfishing is not occurring" (ASMFC, 2009b). We also selected two regions in the Southern New England (SNE) stock, which is in "poor condition" and for which "recruitment failure" was recently declared (ASMFC, 2009b, 2010). For each region, we compared the proportion of females in a given size class that were carrying spermatophores to the predicted proportion of females at that size that were sexually mature. Maturity data provided to the Atlantic States Marine Fisheries Commission (ASMFC) Lobster Stock Assessment (ASMFC, 2009a; personal communication R. Glenn, ASMFC Lobster Stock Assessment Committee Chair 2012) were used as the model to represent the proportion of females at a given length that should be sexually mature and thus reproducing. We hypothesized that the proportion of females in each size class that had mated (acquired a spermatophore) should match the proportion of females that were sexually mature, and that discrepancies between mating activity and expected maturity may indicate the data utilized in the assessment might not accurately represent current reproductive activity. Additionally, we examined the sex ratios in each region to determine if skewed sex ratios might influence mating activity.

2. Materials and methods

2.1. Study sites

This study targeted four regions in the Gulf of Maine (GOM): mid-coast Maine (Friendship), coastal New Hampshire, Massachusetts (inner and outer Boston Harbor), and two regions in Southern New England (SNE): Narragansett Bay, Rhode Island and Rhode Island Sound (Fig. 1). Sampling trips were conducted opportunistically aboard commercial lobster vessels during their normal operations. A total of 16 at-sea trips were completed during the fall of 2008 and summer and fall of 2009. Additional samples were obtained in the summer of 2010 from port (dealer) sampling, to increase the sample sizes of females from Narragansett Bay, RI. Preliminary analyses indicated no differences between seasons, so all time periods were combined for subsequent analyses.

2.2. Sampling procedure

During each sampling trip, we processed a haphazard sample of female lobsters ≥ 60 mm in carapace length (CL) that were captured in standard commercial lobster traps. Shell hardness was examined to determine molt stage (based on external criteria; Aiken, 1980) and the CL was measured to the nearest 1.0 mm using conventional calipers. The presence and stage (early, late, or recently hatched) of extruded ova were noted for all ovigerous females. A total of 1696 female lobsters were examined.

To determine if a given female had mated, the seminal receptacle was examined for evidence of a spermatophore (Goldstein et al., in press). When a male deposits a spermatophore into the female's seminal receptacle, a portion of it typically hardens into a sperm plug that blocks the entrance of the receptacle and protects the spermatozoa, which remain in gelatinous form near the bottom of the receptacle (Talbot and Helluy, 1995). Therefore, the presence of a sperm plug indicates a female has mated. To acquire a sample from the seminal receptacle, we inserted a blunt-tipped hypodermic needle (Monoject 18-G \times 2.5 cm, Webster Veterinary, Devens, MA, USA) into the receptacle and pushed it through the sperm plug (if present) to the bottom of the receptacle where the spermatozoa are stored (Fig. 2A–C). The needle acted as a mini-coring device, removing a tiny core of plug material and the associated spermatozoa.

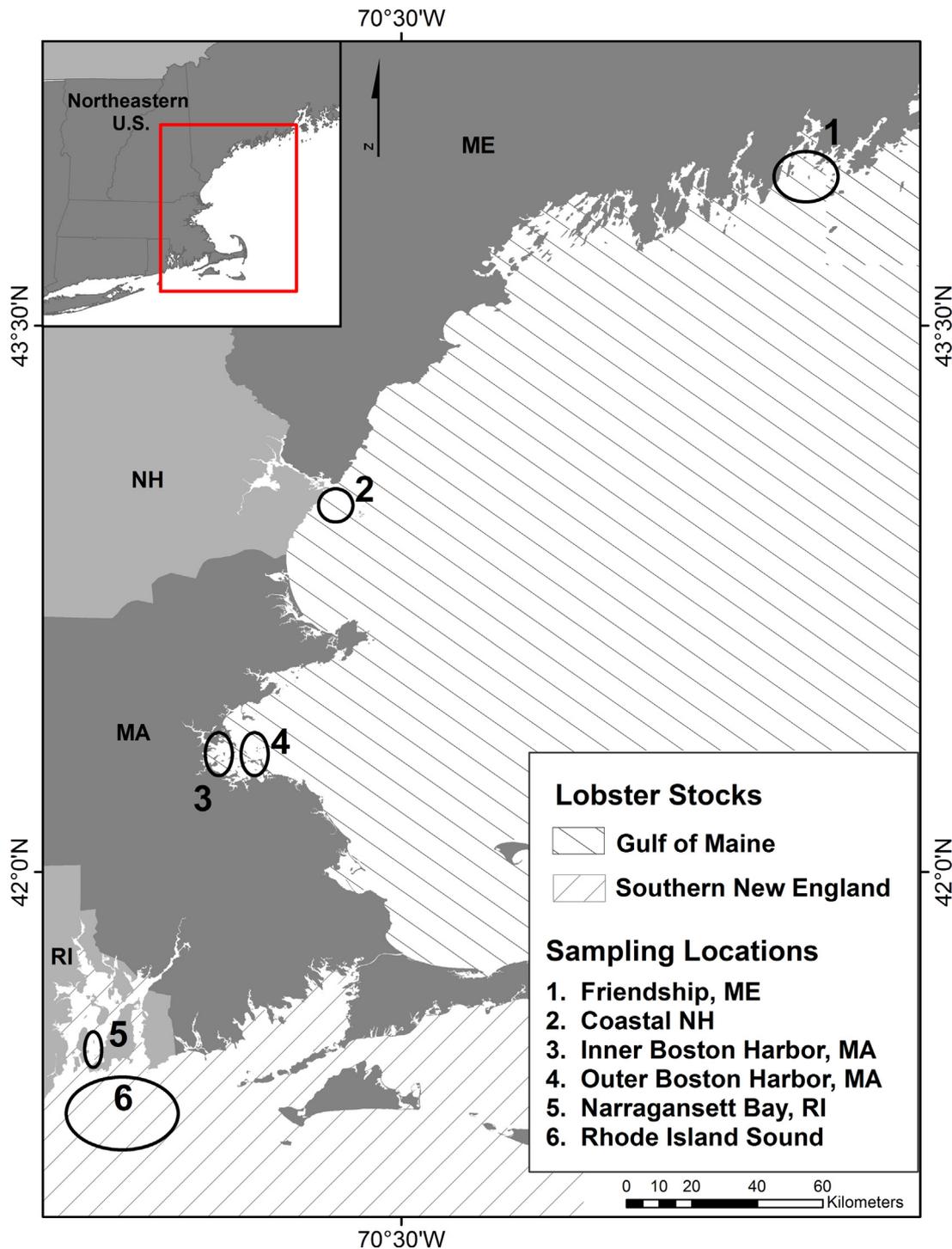


Fig. 1. Map of coastal New England showing the locations of the six at-sea sampling regions, as well as the Gulf of Maine (GOM) and Southern New England (SNE) lobster stock areas. Circles within each sampling region indicate the approximate areal extent from which commercial trap sampling data were used to calculate sex ratios.

The initial sample was deposited into an Eppendorf tube, and then a small amount of seawater (<0.5 mL) was used to flush the receptacle. A second sample was collected after flushing and included the added seawater; this was placed in the same Eppendorf tube. In receptacles without a sperm plug, the needle encountered no resistance until reaching the bottom of the receptacle, where a sample of any material present was taken. Needles and syringes were thoroughly rinsed with seawater and wiped clean to remove any residual material after every sample; needles were replaced if clogged or if samplers believed they could not be cleared. Presence or absence of the sperm plug was noted and samples were stored

in individually labeled 1.5 mL Eppendorf tubes and kept cool. No mortality was noted with this sampling technique.

Samples were subsequently examined in the laboratory to determine the presence or absence of sperm. Approximately 50 µL of fluid was removed from each sample tube, placed under a cover slip on a glass slide, and viewed at 100× with a compound light microscope (Olympus BH System; Fig. 2D). Each sample was coded as sperm present (sparse or abundant was also noted) or absent. A female was considered “spermatophore positive” (SP) and to have successfully mated if a sperm plug or sperm were present in the seminal receptacle. Females that had no sperm plug but were

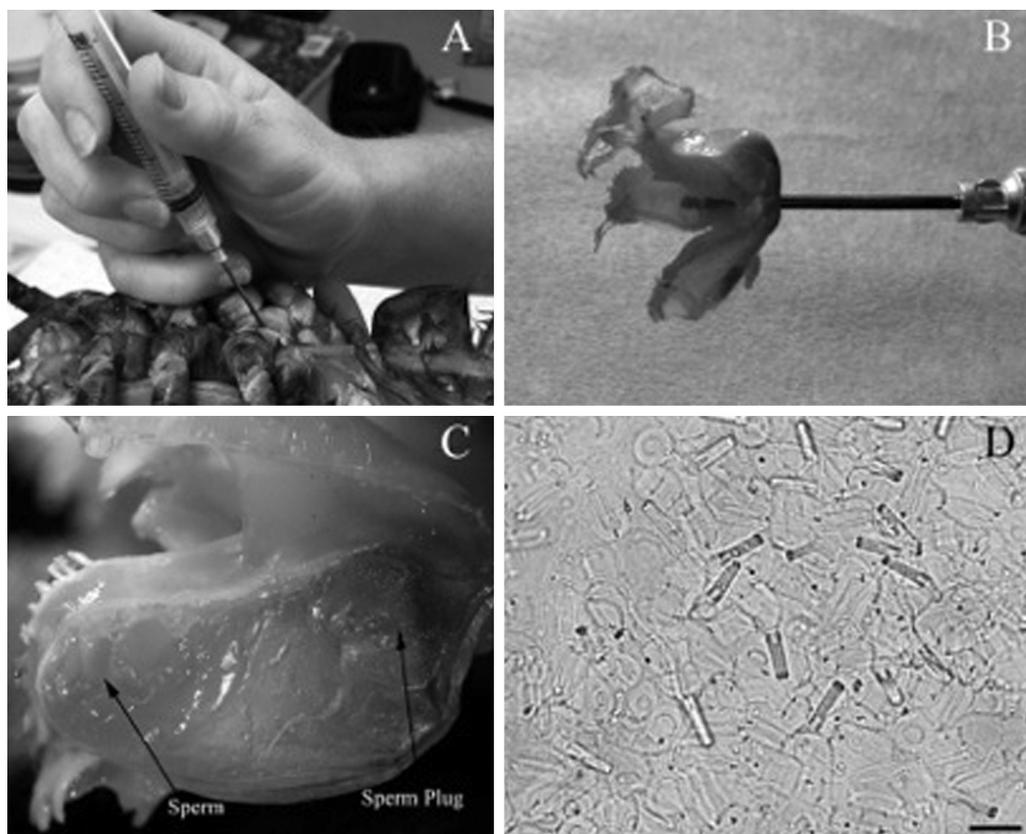


Fig. 2. Methods used to obtain sperm, as well as images of a seminal receptacle and sperm. (A) A blunt-tipped needle being inserted into the seminal receptacle of a female lobster. Needle was inserted at a slight angle, as shown, to both determine if a sperm plug was present and then to sample for sperm. (B) Dissected seminal receptacle showing penetration of needle into hardened portion (plug) of spermatophore. (C) An enlarged view of a bisected seminal receptacle with a spermatophore. Sperm cells typically are located at the bottom of the spermatophore (left side in this image), while the top portion hardens into plug. (D) Sperm cells from a sample of spermatophore taken from a female's seminal receptacle. Scale bar in $D = 50 \mu\text{m}$.

positive for sperm were excluded if only sparse amounts of sperm were detected, to avoid any potential questions of contamination. If no sperm plug or sperm cells were detected, that female was coded as not being SP.

To determine if there was a limitation in our ability to detect mating activity relative to the timing of the female's reproductive cycle, we included ovigerous females in our samples. If there was no evidence of a spermatophore in ovigerous females, then our technique would be unable to differentiate between a used spermatophore and lack of a spermatophore, limiting the time window in which this technique would be useful.

2.3. Sex ratio and maturity data

Raw data from the 2008 and 2009 commercial trap sampling programs conducted by the Maine Department of Marine Resources (MEDMR), New Hampshire Fish and Game Department (NHFG), Massachusetts Division of Marine Fisheries (MADMF), and Rhode Island Department of Environmental Management (RIDEM) were used to calculate the sex ratio in each sampling region. Since tagging studies indicate that inshore lobsters often move approximately 5–10 km from their release location (see reviews by Krouse, 1980; Haakonsen and Anorou, 1994; Lawton and Lavalli, 1995; Goldstein and Watson, unpublished data), only lobsters sampled from commercial trips that occurred within the vicinity of our sampling regions were included in the calculations of sex ratios (Fig. 1, circled regions). For each region, we calculated the sex ratio for each 5 mm CL size bin by including all lobsters one size bin above and below the given size bin (for example, the sex ratio for size bin 75–80 mm included all lobsters from 71 mm CL to 85 mm CL).

We reasoned that lobsters within a 15 mm CL size window were potential reproductive partners (e.g. Templeman, 1934; Gosselin et al., 2003; Pugh, unpublished data), making this an applicable sex ratio for our purposes.

Additionally, data from the MADMF commercial trap sampling program (the longest available time series, sampled annually May–November from 1981 to 2011) were examined for any changes in the long-term trends of ovigerous females by size class. For this analysis, all trips within National Marine Fisheries Service (NMFS) Statistical Area 514 (Cape Cod Bay north to the NH border; see <http://www.nero.noaa.gov/nero/fishermen/charts/stat1.html> accessed 6/17/13) were included.

Maturity data (ogives) were obtained from the ASMFC American Lobster Stock Assessment Subcommittee, and these data were originally collected as noted in Table 1. These data represent the maturity information incorporated into the ASMFC Lobster Stock Assessment; thus we used them here to represent the expected proportion of females within each size category that should be reproductively active. The purpose of this comparison was to determine whether mating activity corresponded to the size-at-maturity data used in the stock assessment. Specifically, we were testing the hypothesis that the proportion of females in a given size class that were SP would match the proportion that the maturity data indicated were sexually mature.

2.4. Data analysis

To test the aforementioned hypothesis, the proportions of SP females for each 5 mm CL size bin were calculated and compared to the proportion of mature females based on the existing maturity

Table 1

Field sampling locations where SP data were collected, and the sources (location, data collection agency, approx. time period) and analysis techniques for the representative maturity data, utilized in the ASMFC American Lobster Stock Assessment.

| Field sampling location | ASMFC Stock Assessment Maturity Data | |
|---|--|---------------------------------|
| | Location (source) | Technique |
| Friendship, ME | Boothbay Harbor, ME (MEDMR, ~1994–1998) | Ova diameter |
| NH coast | Cape Porpoise, ME (MEDMR, ~1994–1998) | Ova diameter |
| Boston Harbor (Inner and Outer) | NMFS Area 514 ^a (MADMF: Estrella and McKiernan, 1989) | Cement gland and ova diameter |
| Rhode Island coast and Narragansett Bay | NMFS Area 539 ^a (RIDEM, ~1990–1995) | Ova color, external examination |

^a Please refer to <http://www.nero.noaa.gov/nero/fishermen/charts/stat1.html> for map of National Marine Fisheries Service Northeastern Statistical Areas (accessed 6/16/13).

data from each region. Either the chi-square goodness of fit test or, for those size bins with expected frequencies ≤ 5 , the binomial test for goodness of fit was used to detect statistically significant differences (Zar, 1999).

We also examined the sex ratios for each size bin in relation to the proportion of females that were SP, with the expectation that if the proportion SP was lower than the expected proportion mature, the sex ratio would be female-skewed, suggesting that available males were a limited resource.

3. Results

3.1. Mating activity

Overall, most of the females sampled in the six regions were SP, indicating that they had mated (low 78.5% in Maine, high 97.1% in RI Sound; Table 2 and Fig. 3). Within each region the proportion of SP females generally increased with increasing lobster size (Table 2 and Fig. 3). However, in nearly every region, there were surprisingly high proportions of SP females in size classes that were, according to available maturity data, predominantly immature. In Maine and coastal NH, females from 76 mm through 90 mm CL had mated significantly more than expected based on maturity information (Table 2a and b, Fig. 3A and B). In the two Boston Harbor regions, females as small as 71 mm (Inner Harbor, Table 2c and Fig. 3C) and even down to 61 mm CL (Outer Harbor, Table 2d and Fig. 3D), had mated more often than expected, and this trend extended up to the 91–95 mm CL size class in both regions. Sample sizes of lobsters smaller than the 81–85 mm CL size class were limited due to larger escape vents in the two Rhode Island regions; however we had sufficient data to determine that females in the 81–85 mm CL size class in Rhode Island Sound had mated significantly more than expected (Table 2e and Fig. 3E).

In none of the four GOM locations did we observe significantly lower proportions of SP females than expected based on the maturity information. However, in the two Rhode Island (SNE) regions, there were some larger females that should have been mature that were not SP. In Rhode Island Sound, significantly fewer females in the 91–95 mm CL size class had mated than expected based on available maturity information (Table 2e and Fig. 3E). In Narragansett Bay, there were three size classes that had significantly lower proportions of SP females than expected: those in the 86–90, 91–95, and 96–100 mm CL size classes (Table 2f and Fig. 3F).

In the four GOM regions combined, 172 of the females sampled had fertile egg clutches (detectable eye spots), and 98.8% of these females were SP. Only 32 ovigerous females (fertile clutches) were sampled in the two RI regions, 90.6% of which were SP. These data provide evidence that the sperm plug does persist post-fertilization, and demonstrate that use of this sampling technique is not limited to new-shelled females in the period between mating and spawning.

3.2. Sex ratios

Data from the various state-run commercial trap sampling programs generally indicated that sex ratios became more female-skewed at larger sizes, particularly above the minimum legal sizes (83 mm CL in GOM regions, 86 mm CL in the two RI regions; Table 2). There were two exceptions to this pattern: Boston Inner Harbor was generally male-skewed (Table 2c) and Narragansett Bay varied from male to female-skewed (Table 2f). Small sample sizes in the largest size classes make the sex ratio data difficult to interpret, although our SP data were similarly limited by small sample sizes in the larger size classes. The truncated size distribution of the lobsters in both GOM and SNE inshore stocks makes obtaining data on larger lobsters difficult, as there are relatively few available.

In those size ranges where the bulk of our SP samples were obtained, sex ratios were relatively balanced to slightly female-skewed (except in Boston Inner Harbor and Narragansett Bay). Sex ratios within a region were relatively consistent from 2008 to 2009, except in those size categories with lower sample sizes (Table 2). One size class in Narragansett Bay and one in Rhode Island Sound had female-skewed sex ratios and SP levels significantly lower than the expected proportion mature (Table 2e: Rhode Island Sound 91–95 mm CL, 88% SP, 65–85% female; Table 2f: Narragansett Bay 86–90 mm CL, 87% SP, 73–77% female).

3.3. Reproductive activity in small females

The preponderance of smaller, presumably immature females that were SP in the four GOM regions presented a surprisingly large discrepancy between the maturity data and our SP data indicating mating activity. To determine if there was additional evidence that smaller females in GOM areas were more reproductively active than in the past, we calculated the percentage of females that were ovigerous in each size class from the MADMF commercial trap sampling data. Since 1981 there has been an increase in the percentage of females with eggs in multiple size classes (Fig. 4A and B). However, for those size classes affected by the fishery and by increases in minimum legal size over time (Fig. 4B), it is difficult to separate conservation-related effects (i.e. allowing more females to reproduce by increasing minimum legal size) from changes in reproductive activity. Lobsters ≤ 80 mm CL have never been harvestable, and there has been an increase from <3% to 10–15% of females with eggs in the 76–80 mm CL size class, and a less dramatic increase (<1–5%) in the 71–75 mm CL size class over time (Fig. 4A). This suggests that smaller females have become increasingly reproductively active in recent years, and that size at maturity may have shifted to smaller sizes since it was last examined in the mid-1980s (Estrella and McKiernan, 1989).

4. Discussion

Overall, mating success was relatively high in all six sampling regions, particularly considering that the size range we

Table 2
Summary of data for each region and size class. For each 5 mm CL bin the following data are presented: the number of females sampled, the number SP, the number of females excluded from analysis (these females had no detectable plug and sparse sperm), the proportion of females that were SP, the proportion of females that were expected to be mature (based on existing maturity data), the statistical result comparing the proportion SP to the expected proportion mature (χ^2 statistic or binomial *p*-value, refer to text), and the sex ratio (and total sample size) from 2008 to 2009 commercial trap sampling programs (refer to Table 1 for data source). "ID" = insufficient data to perform statistical analysis. Statistical significance at $\alpha = 0.05$ (*) or 0.01 (**) is noted.

| CL size bin | N sampled | N SP | N excluded | Proportion SP | Expected proportion mature | χ^2 or (binomial p) | % Female (N) – commercial sampling | |
|--------------------------------|-----------|------|------------|---------------|----------------------------|--------------------------|------------------------------------|---------------|
| | | | | | | | 2008 | 2009 |
| a – Friendship, ME | | | | | | | | |
| 51–55 | 1 | 0 | | 0.000 | 0.000 | ID | | |
| 56–60 | 1 | 0 | | 0.000 | 0.000 | ID | 50 (1843) | 49.1 (2422) |
| 61–65 | 0 | | | | 0.001 | | 51.3 (2355) | 49.6 (2812) |
| 66–70 | 1 | 1 | | 1.000 | 0.005 | ID | 53.6 (2977) | 50.9 (3493) |
| 71–75 | 2 | 1 | | 0.500 | 0.019 | ID | 58.9 (5358) | 59.2 (6399) |
| 76–80 | 28 | 21 | 1 | 0.778 | 0.067 | (0.000)** | 62.1 (9423) | 61.1 (10,724) |
| 81–85 | 69 | 49 | 2 | 0.731 | 0.209 | 110.71** | 62.2 (11,617) | 61.3 (12,927) |
| 86–90 | 40 | 33 | 1 | 0.846 | 0.487 | 20.09** | 61.2 (11,154) | 57.5 (11,884) |
| 91–95 | 17 | 14 | 1 | 0.875 | 0.774 | (0.443) | 57.6 (6891) | 53.8 (7156) |
| 96–100 | 1 | 1 | | 1.000 | 0.926 | ID | 57.1 (3756) | 50.9 (3683) |
| 101–105 | 4 | 4 | | 1.000 | 0.979 | ID | 60.3 (1231) | 58.9 (940) |
| 106–110 | 0 | | | | 0.994 | | 80.2 (585) | 79.6 (324) |
| 111–115 | 3 | 3 | | 1.000 | 0.998 | ID | 80.6 (340) | 75.2 (149) |
| 116–120 | 1 | 1 | | 1.000 | 1.000 | ID | 68.5 (314) | 68.3 (104) |
| Totals | 168 | 128 | 5 | 0.785 | | | | |
| b – Coastal NH | | | | | | | | |
| 51–55 | 1 | 0 | | 0.000 | 0.003 | ID | | |
| 56–60 | 1 | 0 | | 0.000 | 0.008 | ID | 50.5 (679) | 51.1 (904) |
| 61–65 | 1 | 0 | | 0.000 | 0.020 | ID | 51.8 (884) | 51 (1147) |
| 66–70 | 3 | 0 | | 0.000 | 0.045 | ID | 52.6 (1041) | 54 (1350) |
| 71–75 | 8 | 2 | | 0.250 | 0.101 | ID | 65 (2211) | 63.1 (2841) |
| 76–80 | 37 | 32 | 1 | 0.889 | 0.211 | 99.57** | 68.1 (3443) | 66.3 (4054) |
| 81–85 | 54 | 46 | 2 | 0.885 | 0.386 | 54.42** | 70.1 (3727) | 67.6 (4186) |
| 86–90 | 45 | 41 | 2 | 0.953 | 0.597 | 22.68** | 68.7 (2520) | 66.9 (2596) |
| 91–95 | 18 | 15 | | 0.833 | 0.778 | (0.410) | 68.1 (977) | 65.4 (998) |
| 96–100 | 7 | 7 | | 1.000 | 0.892 | ID | 61.7 (300) | 59.9 (319) |
| 101–105 | 3 | 3 | | 1.000 | 0.952 | ID | 85.7 (77) | 84.8 (66) |
| 106–110 | 2 | 1 | 1 | | 0.979 | | 96 (50) | 97.1 (34) |
| 111–115 | 2 | 2 | | 1.000 | 0.991 | ID | 100 (28) | 100 (23) |
| 116–120 | 0 | | | | 0.996 | | 96 (25) | 100 (20) |
| Totals | 182 | 149 | 6 | 0.847 | | | | |
| c – Boston Inner Harbor | | | | | | | | |
| 51–55 | 0 | | | | 0.004 | | | |
| 56–60 | 7 | 0 | | 0.000 | 0.008 | ID | 52.6 (114) | 53.5 (172) |
| 61–65 | 11 | 2 | 1 | 0.200 | 0.017 | (0.012)* | 42 (150) | 49.2 (258) |
| 66–70 | 10 | 0 | | 0.000 | 0.038 | (0.679) | 32.7 (223) | 40.9 (345) |
| 71–75 | 11 | 7 | | 0.636 | 0.079 | (0.000)** | 41 (466) | 37.3 (603) |
| 76–80 | 77 | 71 | | 0.922 | 0.159 | 334.64** | 40.8 (831) | 35.3 (873) |
| 81–85 | 119 | 109 | | 0.916 | 0.294 | 222.35** | 39.6 (1054) | 34 (990) |
| 86–90 | 56 | 51 | | 0.911 | 0.476 | 42.40** | 33.9 (906) | 27.3 (847) |
| 91–95 | 36 | 33 | | 0.917 | 0.665 | 10.21** | 29.4 (493) | 20 (519) |
| 96–100 | 4 | 3 | | 0.750 | 0.813 | ID | 21.7 (166) | 11.7 (274) |
| 101–105 | 2 | 2 | | 1.000 | 0.905 | ID | 42.3 (26) | 9.2 (76) |
| 106–110 | 1 | 1 | | 1.000 | 0.955 | ID | 75 (8) | 8.7 (23) |
| 111–115 | 0 | | | | 0.979 | | 80 (5) | 8.3 (12) |
| 116–120 | 1 | 1 | | 1.000 | 0.990 | ID | | 12.5 (8) |
| Totals | 335 | 280 | 1 | 0.838 | | | | |

Table 2 (Continued)

| | | | | | | | | | |
|--------------------------|-----|-----|----|-------|-------|-----------|-------------|--|---------------|
| d – Boston Outer Harbor | | | | | | | | | |
| 51–55 | 0 | | | | 0.004 | | | | |
| 56–60 | 4 | 0 | | 0.000 | 0.008 | ID | 55.2 (569) | | 52.3 (610) |
| 61–65 | 15 | 3 | | 0.200 | 0.017 | (0.002)** | 55.1 (853) | | 51.9 (902) |
| 66–70 | 23 | 15 | 1 | 0.682 | 0.038 | (0.000)** | 50.5 (1253) | | 51.9 (1234) |
| 71–75 | 25 | 23 | | 0.920 | 0.079 | (0.000)** | 60.2 (2452) | | 60.8 (2346) |
| 76–80 | 141 | 137 | 1 | 0.979 | 0.159 | 701.90** | 65 (3942) | | 66.1 (3439) |
| 81–85 | 278 | 274 | | 0.986 | 0.294 | 642.18** | 68 (4228) | | 70.1 (3646) |
| 86–90 | 128 | 126 | 1 | 0.992 | 0.476 | 135.55** | 68.1 (2950) | | 72.2 (2390) |
| 91–95 | 25 | 25 | | 1.000 | 0.665 | 12.58** | 66.5 (1119) | | 75.7 (904) |
| 96–100 | 4 | 4 | | 1.000 | 0.813 | ID | 62.4 (287) | | 70.6 (177) |
| 101–105 | 5 | 5 | | 1.000 | 0.905 | ID | 78.9 (71) | | 96.2 (26) |
| 106–110 | 5 | 4 | | | 0.955 | | 83.8 (37) | | 100 (18) |
| 111–115 | 1 | 1 | | | 0.979 | | 85.7 (28) | | 100 (10) |
| 116–120 | 0 | | | | 0.990 | | 92.6 (27) | | 100 (7) |
| Totals | 654 | 617 | 3 | 0.948 | | | | | |
| e – Rhode Island Sound | | | | | | | | | |
| 51–55 | | | | | 0.004 | | | | |
| 56–60 | 1 | 0 | | 0.000 | 0.016 | ID | 42.1 (19) | | 59.9 (137) |
| 61–65 | | | | | 0.055 | | 46.2 (39) | | 55.2 (201) |
| 66–70 | 1 | 1 | | 1.000 | 0.173 | ID | 52.1 (71) | | 61.4 (339) |
| 71–75 | | | | | 0.425 | | 62.8 (183) | | 71.7 (703) |
| 76–80 | 6 | 6 | | 1.000 | 0.722 | ID | 79.2 (879) | | 84.9 (3199) |
| 81–85 | 50 | 50 | | 1.000 | 0.903 | (0.006)** | 75.8 (1217) | | 86.1 (4171) |
| 86–90 | 87 | 84 | 2 | 0.988 | 0.971 | (0.290) | 74.3 (1250) | | 86.5 (4241) |
| 91–95 | 25 | 22 | | 0.880 | 0.992 | (0.001)** | 64.5 (569) | | 84.8 (1755) |
| 96–100 | 1 | 1 | | 1.000 | 0.998 | ID | 64 (203) | | 82.1 (637) |
| 101–105 | 1 | 1 | | 1.000 | 0.999 | ID | 80.8 (52) | | 81 (153) |
| 106–110 | | | | | 1.000 | | 92.3 (13) | | 96.1 (51) |
| 111–115 | | | | | 1.000 | | | | 100 (18) |
| 116–120 | 1 | 1 | | 1.000 | 1.000 | ID | | | 100 (6) |
| Totals | 173 | 166 | 2 | 0.971 | | | | | |
| f – Narragansett Bay, RI | | | | | | | | | |
| 51–55 | | | | | 0.004 | | | | |
| 56–60 | | | | | 0.016 | | 48.1 (135) | | 53.6 (194) |
| 61–65 | | | | | 0.055 | | 45.8 (168) | | 47.1 (276) |
| 66–70 | | | | | 0.173 | | 45.2 (263) | | 54 (498) |
| 71–75 | | | | | 0.425 | | 67.2 (747) | | 71.8 (1643) |
| 76–80 | 3 | 1 | 2 | 1.000 | 0.722 | ID | 78.7 (4045) | | 80.4 (11,349) |
| 81–85 | 43 | 37 | 2 | 0.902 | 0.903 | (0.572) | 76.2 (4722) | | 79.1 (12,838) |
| 86–90 | 58 | 45 | 6 | 0.865 | 0.971 | (0.001)** | 72.6 (4732) | | 76.8 (12,521) |
| 91–95 | 42 | 37 | 1 | 0.902 | 0.992 | (0.000)** | 51.2 (1522) | | 57.1 (2896) |
| 96–100 | 25 | 22 | | 0.880 | 0.998 | (0.000)** | 42.4 (726) | | 41 (1149) |
| 101–105 | 11 | 11 | | 1.000 | 0.999 | (0.989) | 37.7 (175) | | 26.2 (256) |
| 106–110 | 1 | 1 | | 1.000 | 1.000 | ID | 75 (24) | | 66 (47) |
| 111–115 | 1 | 1 | | 1.000 | 1.000 | ID | 100 (5) | | 84.6 (13) |
| 116–120 | | | | | 1.000 | | | | 100 (5) |
| Totals | 184 | 155 | 11 | 0.896 | | | | | |

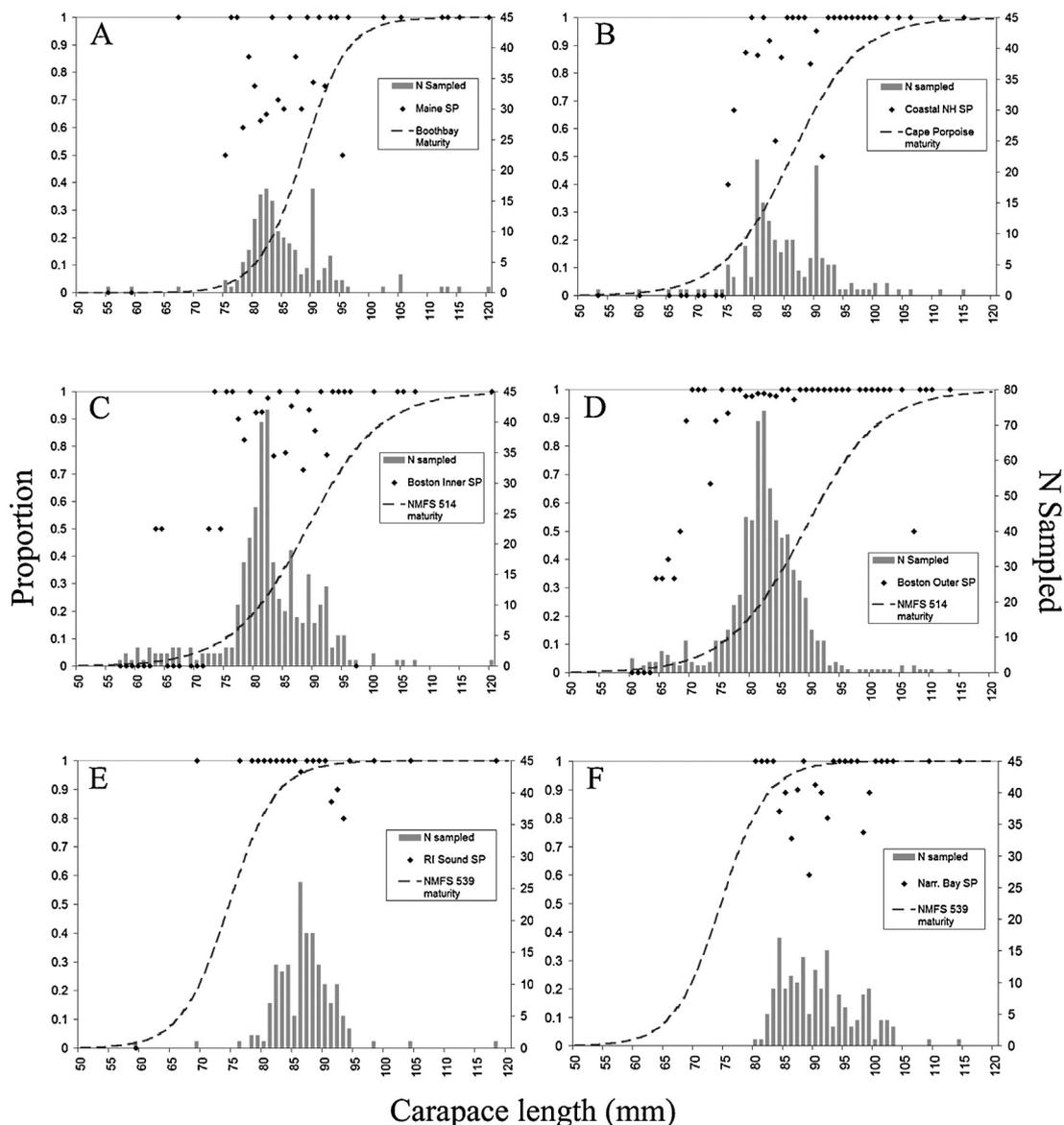


Fig. 3. The proportion of females in each 1 mm CL size class that successfully mated (presence of a spermatophore, “SP”) in each of the six sampling regions: (A) Friendship, ME; (B) coastal NH; (C) Boston Inner Harbor, MA; (D) Boston Outer Harbor, MA; (E) RI Sound; (F) Narragansett Bay, RI. The number of females sampled in each 1 mm CL size class is indicated by the gray bars (right axis). Diamonds indicate the proportion of the females in each size class that were SP (left axis). The dashed line is the maturity ogive, representing the expected proportion of females that were mature in each size class (see Table 1 for data source; left axis). Note that, if diamonds fall above the dashed line, it indicates that more females than expected had mated in that size class.

sampled encompassed many presumably immature lobsters. In the four GOM sampling regions, there was no indication that mature females were failing to mate. In fact, in these areas, the unexpectedly high occurrence of smaller females with spermatophores suggests that there may be more mating activity than anticipated based on existing maturity data. In the SNE sampling regions, represented by the two Rhode Island regions, there were some presumably mature females that were not SP, particularly in the Narragansett Bay region.

4.1. Rhode Island females

One size class of females in Rhode Island Sound region and three size classes in Narragansett Bay had lower proportions of SP females than expected based on available maturity information. For those Rhode Island females that were not SP (had empty receptacles), there are several possible explanations including: (1) they were immature, (2) they failed to mate, or (3) the sperm plugs had

deteriorated past the level of detection, either due to poor initial quality or from previous use.

While it is possible that these non-SP females were immature, two of these females had mature ovaries upon subsequent examination (the remainder were not available for ovary examination), and three others were carrying fertilized egg clutches. In addition, the females without sperm had abdomen width to CL ratios (an indicator of maturity; Krouse, 1973; Aiken and Waddy, 1980) comparable to those of SP females (Pugh et al., unpublished data). Thus, while it seems unlikely that these particular females (>86 mm CL) were immature, future sampling to document mating activity may benefit from combining our sperm sampling technique with observations of ovary condition, cement gland stage, or both (see Waddy and Aiken, 2005) to clarify any maturity-related concerns.

The most likely explanation for the lack of a spermatophore in these Rhode Island females is that they either did not mate, or they mated but received a low quality spermatophore from their partner. Female-skewed sex ratios, especially in the larger size classes,

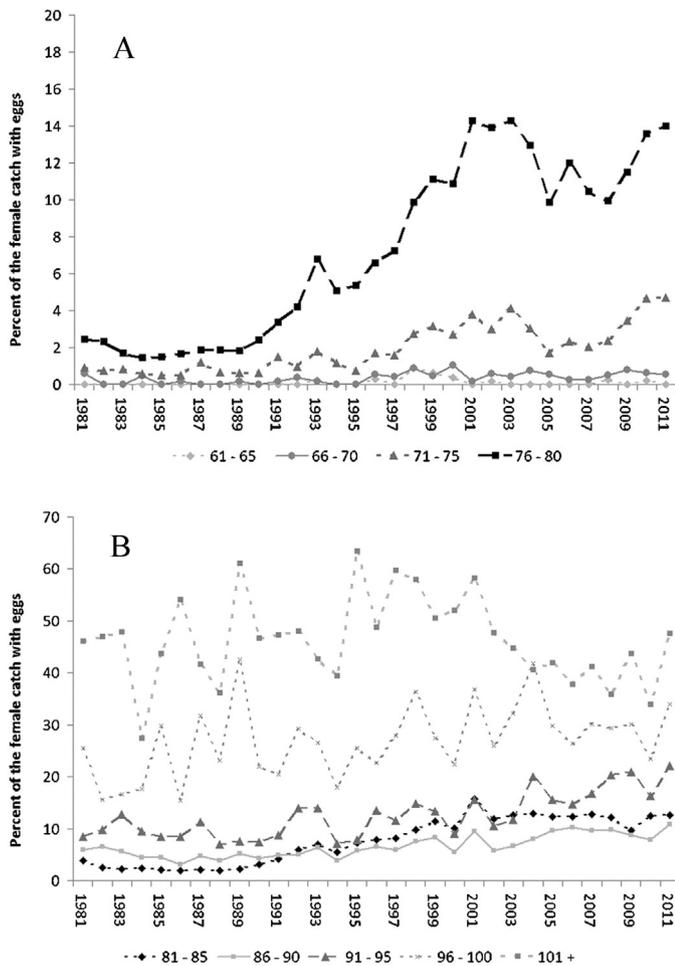


Fig. 4. Percent of female lobsters by size category (5 mm CL size bins) that were ovigerous, 1981–2011 (May–November annually) MADMF commercial trap sampling data in NMFS Statistical Area 514. (A) Unexploited size classes (61–65 mm, 66–70 mm, 71–75 mm, 76–80 mm) and (B) exploited size classes (81–85 mm, 86–90 mm, 91–95 mm, 96–100 mm, 101+ mm). Please refer to <http://www.nero.noaa.gov/nero/fishermen/charts/stat1.html> for map of National Marine Fisheries Service Northeastern Statistical Areas (accessed 6/16/13).

could prevent some females from finding an appropriate male with which to mate, resulting in either a failure to mate or a sub-optimal spermatophore. There are no restrictions against landing males within the window between minimum and maximum legal size (86 mm CL to 133 mm CL in Lobster Conservation Management Area 2), which can produce female-skewed sex ratios in the legal-sized range in some portions of SNE (Glenn et al., 2007; MADMF unpublished data).

We had originally hypothesized that female-skewed sex ratios could lead to mating failure. One size class of Rhode Island Sound females and one size class of Narragansett Bay females did have SP levels significantly lower than the expected proportion mature and female-skewed sex ratios. While the Narragansett Bay sex ratio in larger size classes varied from male to female-skewed, in Rhode Island Sound it was consistently female-skewed at larger sizes. Unfortunately our small sample sizes in the larger size classes preclude further testing of this hypothesis with the existing data. However, these results, while not providing strong evidence that sex ratios may affect mating, support the need for additional work to examine the potential relationship.

Exploitation that removes large males may alter the male mating pool so that only smaller and/or depleted males are available, potentially resulting in reduced male contributions (smaller or poor

quality spermatophores; see MacDiarmid and Butler, 1999; Kendall et al., 2001; Rondeau and Sainte-Marie, 2001; Sainte-Marie et al., 2002; Gosselin et al., 2003; Hines et al., 2003; Sato et al., 2005; Wolcott et al., 2005). Additionally, males stressed by the elevated inshore water temperatures in SNE, which have been linked to other negative physiological effects (Powers et al., 2004; Dove et al., 2005; Glenn and Pugh, 2006; Homerding et al., 2012), may produce poor quality spermatophores (see Talbot et al., 1983; Aiken et al., 1984). Comeau and Benhalima (2009) documented damaged reproductive organs in male lobsters with shell disease, which is prevalent in SNE (Castro et al., 2005; Glenn and Pugh, 2006; Castro and Somers, 2012). Smaller or lower quality spermatophores may not function well as a sperm storage device and may produce a negative result in our sampling procedure, as well as sub-optimal fertilization results if sperm are not well protected between mating and spawning.

Finally, the depleted stock conditions in Rhode Island (part of the Southern New England lobster stock; ASMFC, 2009a, 2010) may reduce encounter rates between pre-molt females and available males, leaving some females unmated. If mating success in this species is density-dependent (e.g. mate-finding Allee effects, see Stephens et al., 1999; Gascoigne et al., 2009), the relatively low abundance in Southern New England could be negatively impacting female reproductive success, which will further complicate attempts to rebuild the stock.

4.2. Mating activity in small GOM females

We observed higher than expected frequencies of small SP females, particularly in the GOM sampling locations. This suggests that either large numbers of immature females are mating, or that females are maturing at smaller sizes than existing data indicate. It has been documented that males will mate with immature females (Krouse, 1973 (but see Waddy and Aiken, 2005 for critique of maturity definition); Waddy and Aiken, 1990; Watson: 12/66 females with immature ovaries had mated, unpublished data). However, this is considered to be a rare occurrence (Waddy et al., 1995) and males are apparently capable of distinguishing female ovary stage (Waddy and Aiken, 1990). Males of the shrimp *Penaeus vannamei* perform the first three stages of mating behavior with immature females, but do not actually inseminate females unless they have ripe ovaries (Yano et al., 1988). Mature spiders (*Anelosimus studiosus*) also appear to “practice” mating in a similar manner, which benefits them in subsequent encounters with mature females; however, they also do not actually transfer sperm to the immature females (Pruitt and Riechert, 2011). While “practice” may similarly benefit a male lobster by attracting other females to his shelter (Atema, 1986), it would be a waste of potentially costly sperm to actually pass a spermatophore to an immature female (Dewsbury, 1982). In contrast, it would benefit an immature female to molt, mate, and then receive protection from a male while her shell hardened.

It is possible that there have been shifts in maturity schedules since the time when the original maturity data were collected (see Table 1), and that female lobsters are now maturing at smaller sizes. The increase in ovigerous females in several un-exploited size classes since 1981 (Fig. 4) supports this hypothesis of shifts toward smaller sizes at maturity. Fishery-induced selection for early maturity, resulting from persistent high levels of exploitation over the past several decades, may be a contributing factor. Additionally, sea surface temperature data suggest warming trends in New England coastal areas (Nixon et al., 2004; Oviatt, 2004), which could also drive shifts to smaller sizes at maturity since temperature is a key determinant of this life history parameter in lobsters (Waddy et al., 1995). Landers et al. (2001) documented a reduction in the size-at-maturity over the course of approximately 20 years in female

lobsters from eastern Long Island Sound, and suggested warming temperatures and fishing-induced selection as potential causal factors. The bulk of the maturity data used for comparison to our SP results were derived from studies conducted in the 1980s and early 1990s (see Table 1), so exploitation levels and environmental conditions have had multiple generations on which to impose selective forces. The discrepancies between our SP data and existing maturity data suggest the need for a systematic revision of lobster maturity (see Waddy and Aiken, 2005) to provide updated data for stock assessment models.

5. Conclusions

In this study we documented mating activity in female lobsters, based on evidence of a spermatophore in the seminal receptacle, throughout portions of the Gulf of Maine (GOM) and Southern New England (SNE) lobster stocks. We made no effort to quantify sperm, so our data only indicate whether a female has mated, not whether there were sufficient sperm delivered to fertilize all the eggs. Spermatophores appear to vary in quality (Talbot et al., 1983; Aiken et al., 1984), and partial fertilization of female clutches has been documented (Johnson et al., 2011); however, there are no publications describing the sperm:egg ratios necessary for fertilization success in this species. Determination of these sperm:egg ratios and development of techniques to quantify sperm delivered by a male are necessary steps to understand sperm limitation in American lobster. The first step in successful reproduction for a female is to acquire a spermatophore from a male, and this is where our data are informative.

Mating activity was higher than expected in most of our sampling regions. Only in the two Rhode Island sampling regions was there evidence of presumably mature females without spermatophores, probably due to either a failure to mate or to low quality spermatophores. Reduced mating success coupled with low abundance in this region (ASMFC, 2009a) may have a negative impact on reproductive output, and warrants further scrutiny. When designing rebuilding efforts for this stock, management should ensure that both sexes are targeted for rebuilding efforts, not just females.

The results of this study also suggest the need for a re-examination of lobster size at maturity, particularly in the Gulf of Maine stock where many more small lobsters were SP than expected based on existing maturity information. The observed increase in ovigerous females over time in the MADMF sea sampling program supports this conclusion. Updated maturity indices are vital to the stock assessment processes of estimating growth, spawning stock biomass, and egg production.

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