

American Lobster Maturity Assessment

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Final Project Report

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BACKGROUND

The American lobster (*Homarus americanus*) supports the largest commercial fishery in North America (ASMFC; Le Bris *et al.*, 2017). In 2017, 136.7 million pounds of lobster were landed coastwide, representing \$566.4 million in ex-vessel value (ASMFC). The vast majority of these landings came from the Gulf of Maine/Georges Bank, where the stock is at record abundance. In contrast, lobster abundance in the Southern New England stock area has drastically declined since 1999 (Angell 2013; ASMFC 2015). Despite the economic and cultural importance of the lobster fishery, managers, research scientists and industry members agree that the datasets being used to assess these stocks lack sufficient spatial and temporal coverage, particularly in Southern New England (ASMFC 2010). Specifically, there is a mismatch between the location of primary lobster fishing grounds in this region (10-200 miles offshore) and the location where data are being collected (0-3 miles from shore).

Complicating the issue is the potential impact on the resource attributable to changing environmental factors, such as rising water temperatures. In the Southern New England stock, lobster abundance has drastically declined since the 1990's (Angell 2013; ASMFC 2015; Kavanaugh et al., 2017). At the same time, southern New England waters have experienced dramatic and widespread warming, suggesting an environmental mechanism for the lobster population downturn (Manning & Pelletier 2009; ASMFC 2010; Wahle et al., 2015). Projections of future bottom temperatures in the region suggest that there will be a significant number of days per year in which temperatures exceed 20°C, a temperature unsuitable for lobster habitat (Rheuban et al., 2017). Many inshore regions that were historically important for lobster habitat have been undergoing prolonged periods of time over 20°C for more than a decade now (ASMFC 2015), and the stock is currently depleted and experiencing recruitment failure due in part to changing ocean conditions (ASMFC 2015). It has been well-documented that female lobsters often migrate to avoid temperatures that could harm or delay egg development (Crossin et al., 1998, Cowan et al., 2007), influencing the distribution and concentration of ovigerous females (Jury et al., 2019; Carloni & Watson, 2018). Scientists have begun to theorize that female lobsters are moving out of their traditional sheltered bays to more open ocean environments in response to rising water temperatures, affecting juvenile lobster settlement (Glenn et al., 2011).

Temperature is perhaps the most significant environmental force in the American lobster life history and determinations of habitat suitability. Sea temperatures have been known to influence molting, growth (Waddy *et al.*, 1995), and reproductive development (Templeman 1936; Estrella & McKiernan 1989; Little & Watson 2005; LeBris *et al.*, 2017; Waller *et al.*, 2019). Female lobsters mature at a smaller size in warmer waters than those in colder waters (Aiken & Waddy, 1976). Research in inshore areas has shown a strong linkage between the timing of spring warming in Southern New England and the timing of the lobster molt (Groner *et al.*, 2018) with subsequent consequences to the prevalence of shell disease. Increases in water temperature in this region have likely resulted in changes in female lobster size at maturity and growth patterns, given that temperature has a strong influence on these vital processes.

The maturity datasets used in the 2015 American Lobster Benchmark Stock Assessment are more than 20 years old, making it probable that changes have occurred since these data were collected. As

a result, the Commercial Fisheries Research Foundation (CFRF) in partnership with the Massachusetts Division of Marine Fisheries(MA DMF), the Atlantic States Marine Fisheries Commission (ASMFC), and the Maine Department of Marine Resources (ME DMR), conducted an American lobster maturity study in the summer of 2019 to provide updated maturity information for the Southern New England and Georges Bank stocks. The objective of this work was to provide high quality biological datasets that could be used in the upcoming lobster stock assessment.

During the January 2019 American Lobster Stock Assessment Workshop, the Stock Assessment Subcommittee discussed how to conduct an effective, updated American Lobster maturity study in NMFS statistical areas (stat areas) of commercial and ecological significance. Details of the sampling protocols were discussed, and this group agreed that future works should follow the methodologies described in Waller et al., (2019). This approach relies upon the collection of non-ovigerous females and maturity determinations using ovarian staging (Aiken & Waddy, 1982). The size range of females to be collected and analyzed (53-118 mm carapace length, grouped by 5 mm bins) was set to align with the current stock assessment size bins. This included a break at the minimum size limit to ensure adequate sampling at and above the minimum legal harvest size in these areas. Following Waller et al., (2019), the target sample size was set to 20 females per 5 mm carapace length (CL) size bin. During these discussions of sampling protocols, it was recommended that this work exclude egg-bearing female lobsters since they are known to be mature without having to retain and analyze ovaries. Due to the variability in v-notch definitions and interpretation, the group concluded that vnotched females should be included in this work.

Stock-wide maturity schedules (ogives) for the assessment are typically generated by weighting stat area-specific biological data by stat area-specific landings. Therefore, average annual female landings from 2015-2017 by stat area were compared to stat areas sampled by CFRF's Lobster and Jonah Crab Research Fleet to prioritize stat areas for sampling. The six Southern New England stat areas with the highest average landings from greatest to least were 537, 539, 611, 538, 612 and 616. Stat area 537 was broken into inshore and offshore sub-areas for sampling considerations. Additionally, offshore stat areas 561 and 562 in the Gulf of Maine/Georges Bank stock were noted as needing sampling. Stat area 562 averaged more annual female landings than stat area 561 from 2015-2017. As a result, stat areas 537 (offshore southwest corner), and 562 were identified as the highest priorities.

To make accurate determinations via ovarian staging, non-ovigerous female lobsters must be collected and analyzed before the onset of the egg-hatching and molting seasons (Waddy & Aiken, 2005). We were able to evaluate the proportion of ovigerous females in these stat areas during each month using recent datasets from CFRF. Proportions from stat areas 537 and 539 tended to decline from peaks in May to low values in July, suggesting hatching throughout June. Proportions from stat areas 561 and 562 were more variable but declined from peaks in June to low values in July during several years, suggesting slightly later hatching in these stat areas. Based on these data, sampling was conducted from mid-May to mid-June for stat area 537, and throughout June for stat area 562. During this time, Jesica Waller (ME DMR) would evaluate the newly collected data weekly to ensure all protocols were being applied correctly. After all data collection was completed (July 2019), all data analysis would be conducted by J. Waller.

METHODS

Lobster collection, lab and image analysis

Each fishing vessel participating in this project followed CFRF's Lobster and Jonah Crab Research Fleet sampling protocols. They would collect fishing effort and biological lobster data from a subset of randomly-selected commercial gear hauls. A gear haul consists of one string of lobster traps. To minimize sampling bias, fishermen either sampled the catch from all of the traps within a gear haul or the first 20 traps. Fishermen aimed to sample a minimum of 100 lobsters or 20 traps during each sampling session. For each sampling session, participant fishermen would use CFRF's On Deck Data application to record a suite of fishing effort data, including the depth and soak time of sampled traps, and the total number of traps sampled. The date, time, latitude, and longitude of each sampling session were automatically recorded via the tablet's internal clock and GPS. For biological data collection the On Deck Data application prompted Research Fleet participants to record the carapace length (CL), sex, shell disease severity, presence or absence of eggs and/or v-notch, and disposition for each individual lobster. Digital electronic calipers were used to measure CL to the nearest millimeter and fleet participants manually entered length data into the On Deck Data appl.

Non-ovigerous female lobsters were collected by CFRF's Lobster and Jonah Crab Research Fleet participants from May 24th to June 23rd, 2019. Sample collection occurred in offshore NMFS statistical area 537 and NMFS statistical area 562 (Figure 1). The timing of lobster collections was determined with ASMFC's American Lobster Technical Committee members by evaluating CFRF's Lobster and Jonah Crab Research Fleet sea sampling data. These data were used to select a sampling timeframe within a few weeks of the onset of the expected egg-hatching and molting seasons (Waddy & Aiken, 2005). The timeframe was selected so that all female lobsters would be at distinct points of ovarian development during this time (Aiken & Waddy, 1982). The CFRF worked with three fishing vessels in CFRF's Lobster and Jonah Crab Research Fleet (F/V Lady Clare, F/V Excalibur, F/V Direction) to target 20 female lobsters from each 5 mm size bin for stat areas 537 and 562 (Table 1). A target of 240 female lobsters (20 from each size bin) were anticipated for stat area 537 and 240 female lobsters for stat area 562. F/V Lady Clare and F/V Excalibur collected female lobsters from offshore stat area 537, and F/V Direction collected female lobsters from stat area 562.

Before collecting lobsters CFRF staff participated in a two-day training in New Bedford, MA on May 1st and 2nd with Tracy Pugh (MA DMF) and Jesica Waller (ME DMR). The goal of this training was for CFRF staff to learn proper lobster dissection protocols and how to photograph oocytes and pleopods for maturity staging. After this training there were some unexpected delays in lobster collection efforts. During May several fishing vessels participating in this summer study underwent spring vessel maintenance and were not actively fishing until late May/early June. As a result, the first lobsters collected for this study began on May 24th, 2019 for stat area 537, and June 12th, 2019 for stat area 562. Fishermen involved in this maturity study collected 10 females on May 24th, 30 females on June 7th, 55 females on June 8th, 92 females on June 12th, 15 females on June 18th, 45 females on June 19th, and 61 females on June 23rd, 2019.

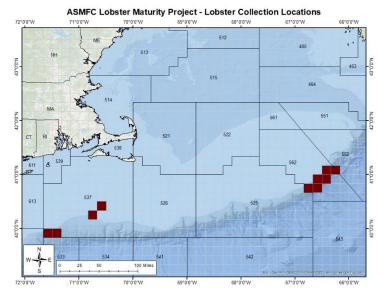


Figure 1. National Marine Fisheries Service statistical areas and locations of female lobster collection trips by CFRF's Lobster and Jonah Crab Research Fleet participants.

Table 1. American Lobster (*Homarus americanus*) target carapace length size bins for each NMFS stat area studied.

Carapace Length Size Bins (mm)
53- 58 mm
58-63 mm
63-68 mm
68-73 mm
73-78 mm
78-83 mm
83-88 mm
88-93 mm
93-98 mm
98-103 mm
103-108 mm
108-113 mm
113-118 mm
>118 mm

Lobsters were banded and kept communally in flow-through tanks at the University of Massachusetts Dartmouth School for Marine Science and Technology (SMAST) in New Bedford, MA. Lobsters were put in four different tanks depending on collection date and stat area to prioritize dissections and processing efficiency. For each lobster a suite of collection and biological data was collected and recorded before lab processing. These data included vessel ID, lobster lab ID number, stat area, date of capture, processing date, sex, carapace length (mm), width of the second abdominal segment (mm), presence or absence of eggs, cull status, shell disease severity, presence or absence of v-notch, weight of whole body (g), and weight of body with no claws (g). Each female was also examined for the presence of a sperm plug in the seminal receptacle. This was done by inserting a blunt tip needle into the seminal receptacle. If there was resistance before reaching the bottom of the receptacle, it was assumed that a sperm plug was present (Goldstein *et al.*, 2014).

Females were kept in a freezer for 15-20 minutes prior to dissection. The carapace of the lobster was then removed to determine the color of the ovary (Appendix 1). The ovary was then weighed (g) and at least 10 oocytes were removed and photographed under a dissecting microscope. The diameter (mm) of each oocyte was measured in NIH ImageJ. Next, a pleopod from the second pair on the right side when holding the lobster (ventral side up) was removed from each female and examined under a dissecting microscope to determine the setogenic stage (Aiken, 1973; Appendix 2). If the pleopod was missing or damaged, we took the third pleopod on the top right-hand side. A female with a pleopod at setogenic stage 3.0 or higher was assumed to be in active pre-molt condition (Waddy & Aiken, 1992). If in active pre-molt, it was assumed that the lobster would have molted in the coming weeks/months and the ovaries would have suspended development until that molt occurs. A female with a pleopod at setogenic stage of 2.5 or less was assumed to be in intermolt/premolt stage. This means lobsters in these stages are unlikely to molt soon and ovary development can occur during these stages. Finally, the pleopod was then examined under a dissecting microscope and photographed to record cement gland stage (Appendix 3). Females at cement gland stage 2 or higher can be classified as mature using this approach (Aiken & Waddy, 1982).

Final maturity determinations and data analysis

All measurements and data were shared with the Maine Department of Marine Resources (ME DMR), so that the maturity status of each female lobster could be determined using ovarian staging. This method assigns ovary development stages to a non-ovigerous female based on the color of the ovary, the range of oocyte diameters, and the relative ovary weight (ovary factor). A female that met the criteria for stage 4b or higher was classified as mature (Aiken & Waddy, 1982). Females at this stage or higher have medium to dark green ovaries, an ovary factor of at least 200 and oocytes that ranged from 0.8-1.6mm in diameter (Aiken & Waddy, 1982). All biological data and collection meta-data was collected, entered and organized by A. Ellertson and shared with Jesica Waller (ME DMR) on a weekly basis. Final maturity determinations were conducted by J. Waller at ME DMR.

Ovarian staging was used as the primary maturity determination method, but cement gland staging and the abdomen width to carapace length ratio were considered when the results of ovarian staging were inconclusive or if key data parameters were missing. These secondary maturity metrics were used to evaluate the maturity status of 26 females collected from stat area 537. Ovarian staging could not be applied to these females for a suite of reasons ranging from timing of collections to missing data. After careful consideration and consultation with MA DMF, final maturity determinations were made for all females. J. Waller also relied on all images and lab notes provided by CFRF to perform quality control checks and validate initial maturity determinations.

Each female was assigned an ovarian stage (Aiken & Waddy, 1982) and then a value of 0 (immature) or 1 (mature) to represent the final maturity determination. For each stat area, females were grouped into the appropriate 5 mm carapace length (CL) size bins and a logistic regression (binomial

distribution, logit link) was fit to these data using the GLM function in RStudio (RStudio Team, 2015). Model fit was assessed for each logistic regression using a goodness-of-fit test, a pseudo-R2 from the "descr" package and inspection of the residuals (Faraway, 2006). The CL at which 50% of females in a population are mature (L50) was calculated using the "p.dose" feature in the MASS package in RStudio. This produces an estimated value and a standard error at a set proportion. The model parameters and 95% confidence intervals were derived from each logistic regression and used to generate maturity ogives for each stat area sampled. All figures were generated in RStudio.

RESULTS

Lobster collections and sample sizes by NMFS statistical area

From May 24th, 2019 to June 23rd, 2019, a total of 315 lobsters were collected (308 females, and 7 males) from all stat areas sampled. The males, however, were not used as part of this project, and were collected by accident from participating fishermen who mistook v-notched males for female lobsters. 155 female lobsters were collected from offshore stat area 537 (Table 2), and 153 were collected from stat area 562 (Table 3). On June 28th, A. Ellertson reached out to Tracy Pugh (MA DMF) and Jesica Waller (ME DMR) to share recent photos of ovigerous females observed by lobstermen involved in the project . It was determined that the eggs were close to hatching and sample collection would need to cease in the next week or so. A Ellertson was away on vacation July 1-8th, 2019 and as a result collection of lobsters had to stop at the end of June.

For stat area 537, two fishing vessels collected female lobsters for this maturity study (F/V Lady Clare and F/V Excalibur). During the time of lobster collection, both fishing vessels were primarily targeting Jonah crab. Any of the legal-sized lobsters they caught they wanted to give to their dealer despite CFRF offering to compensate them. As a result, A. Ellertson was often given undersized female lobsters and or v-notched legal females, which created a skew in the number of individual lobsters in each size bin (Table 2). Of the 155 female lobsters sampled in stat area 537, 23 of them were v-notched, and 13 of the v-notched females were over 90 mm. Size bin 83-88 mm had the most individual females per size bin, with 78-83 mm, and 88-93 mm in second and third place.

Carapace Length Size Bins (mm)	Number of Individuals per Size Bin		
53- 58 mm	0		
58-63 mm	5		
63-68 mm	1		
68-73 mm	5		
73-78 mm	13		
78-83 mm	35		
83-88 mm	50		
88-93 mm	32		
93-98 mm	4		
98-103 mm	5		
103-108 mm	2		
108-113 mm	1		
113-118 mm	0		
>118 mm	2		

 Table 2. Number of female lobsters collected per size bin from NMFS statistical area 537.

For stat area 562, F/V Direction collected individual female lobsters for dissection. When comparing stat area 537 and 562, stat area 562 had a more even distribution of individuals per 5 mm CL size bin (Table 3). Nine of the bins had 10 or more individual lobsters collected. The most female lobsters collected were in the 98-103 mm size bin.

Carapace Length Size Bins (mm)	Number of Individuals per Size Bin
53- 58 mm	1
58-63 mm	1
63-68 mm	5
68-73 mm	11
73-78 mm	19
78-83 mm	12
83-88 mm	18
88-93 mm	14
93-98 mm	13
98-103 mm	23
103-108 mm	12
108-113 mm	16
113-118 mm	7
>118 mm	1

Table 3. Number of female lobsters per size bin from NMFS statistical area 562.

Maturity ogive for NMFS statistical area 537

Of the 154 females collected and analyzed from stat area 537, 103 were classified as sexually mature using the maturity criteria discussed above. The smallest mature female occurred at 71 mm CL and all females were mature after 90 mm CL. A logistic regression was fit to these data to evaluate the relationship between CL and maturity and provide a maturity ogive (Figure 2). All model diagnostics indicated a suitable fit to these data (GOF tests: X-squared = 0.544, df = 8, p-value = 0.999; pseudo-R2: McFadden's R2=0.899). Large 95% confidence intervals were observed at points in the curve. This can likely be attributed to small samples sizes at the extremes of the CLs collected and analyzed. The L50 in this area in 2019 was estimated to occur at 78.5 mm CL(LCI:75.58, UCI: 81.42).

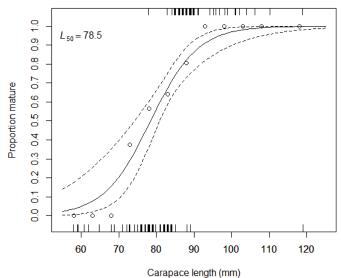


Figure 2. Logistic regression (solid line, $\alpha = 12.589$, $\beta = -0.160$) showing the predicted proportion of mature female *Homarus americanus* from offshore NMFS statistical area 537 as a function of carapace length and associated 95% confidence intervals (dashed lines). Open circles represent the calculated proportion mature by 5 mm carapace length size bin. Tick marks represent the binary (0=immature, 1=mature) maturity determination for each female analyzed. The estimated L50 is also represented on this plot.

Maturity ogive for NMFS statistical area 562

A logistic regression was also used to generate a maturity ogive for female lobsters collected from stat area 562 in 2019 (Figure 3). All model tests and evaluations indicated a good fit to these data (GOF tests: X-squared = 0.684, df = 8, p-value = 0.996; pseudo-R2: McFadden's R2=0.934). A total of 153 females were collected from this stat area, and 47 % were classified as mature. Compared to the females collected from stat area 537, maturity seemed to occur over a narrow range of CLs and at a larger size in general. One female at 76 mm CL was classified as mature but the onset of maturity appeared more widely at 85 mm and above. All females were classified as mature by 105 mm. The L50 in this area in 2019 was estimated to occur at 92.2 mm CL (LCI:90.15, UCI: 94.25).

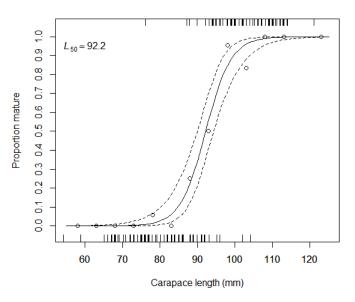


Figure 3. Logistic regression (solid line, $\alpha = 27.273$, $\beta = -0.296$) showing the predicted proportion of mature female *Homarus americanus* from NMFS statistical area 562 as a function of carapace length and associated 95% confidence intervals (dashed lines). Open circles represent the calculated proportion mature by 5 mm carapace length size bin. Tick marks represent the binary (0=immature, 1=mature) maturity determination for each female analyzed. The estimated L50 for this area is also represented on this plot.

Changes in female carapace length at maturity over time

The length at which 50% of females reach maturity in a population (L50) is a ready point of comparison between studies. Comparisons of this value also make it possible to examine changes in the size at maturity in female lobsters in a specific region over time (Table 4). Two studies conducted in the 1970's and 1980's estimated L50 to occur at 100 mm CL in females from stat area 562 and Georges Bank (Cooper & Uzmann, 1977; Fogarty & Idoine, 1988). We see by examining the results of the work presented in this report that L50 has shifted to 92.2 mm CL in this region. This value is also similar to preliminary work conducted by MA DMF in this region in 2016 and

2017. A downward shift in L50 over time was also observed in female lobsters collected from stat area 537. This value was estimated to occur at 82 mm CL in the early 2000s while more recent work in the area, including this study, estimated L50 between 76-78 mm CL.

Table 4. The estimated carapace length at which 50% of female *Homarus americanus* are mature (L50) in NMFS statistical areas 562 and 537. The historical studies listed below included females from other surrounding NMFS statistical areas, but these studies represent the most appropriate point of historical comparison. When possible, upper and lower 95% confidence limits are listed in parentheses below each L50 estimate. Values attributed to MA DMF are preliminary and were acquired through personal communication with Tracy Pugh (MA DMF). The values calculated during this work are attributed to ASMFC (2019).

Data source (NMFS statistical area 562)	L50	Data source (NMFS statistical area 537)	L50
Cooper ぐ Uzmann, 1977 Fogarty ぐ Idoine, 1988	100 mm	Little & Watson (2005)	82 mm (81.3, 83.4)
MA DMF (2016-2017)	87 mm	MA DMF (2017-2018)	76.1 mm (74.7, 77.5)
ASMFC (2019)	92.2 mm (90.2, 94.3)	ASMFC (2019)	78.5 mm (75.6, 81.4)

CONCLUSIONS

Aubrey Ellertson (CFRF) and Jesica Waller (ME DMR) presented the full results of this work to the ASMFC American Lobster Stock Assessment Technical Committee via webinar on October 10th, 2019. A. Ellertson presented the results of CFRF's collection efforts and the methodology used for laboratory and image analysis. J. Waller shared the data analysis, full results and comparisons to historical work described above. This committee agreed that these data were of value to future American lobster stock assessment efforts and should be incorporated into aspects of the current stock assessment model. J. Waller submitted all maturity determinations and data analysis to Jeff Kipp (ASMFC) on October 11th, 2019 in order to conclude this project and ensure that the ASMFC American Lobster Stock Assessment Technical Committee has access to this work.

This study provided detailed female *Homarus americanus* size at maturity datasets for two NMFS statistical areas (562, 537). A comparison of this work to historical studies conducted in these areas supports the notion that the size at maturity has decreased over time. This downward trend aligns with recent size at maturity work that recorded similar decreases over the span of the last several decades (Le Bris *et al.*, 2017; Waller *et al.*, 2019). Key results of this study also aligned closely with recent preliminary work conducted from 2016-2018 in these areas (T. Pugh, MA DMF, per. comm). Taken together these comparisons bolster confidence in the work described here and the maturity ogives generated for each stat area sampled. The results described in this report will be used by the ASMFC American Lobster Stock Assessment Technical Committee to update key parameters in the

stock assessment model related to female growth, egg production and stock determination (ASMFC 2015).

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REFERENCES

- Aiken, D.E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). Journal of the Fisheries Board of Canada, 30: 1337–1344.
- Aiken, D.E. & Waddy, S.L. 1982. Cement gland development, ovary maturation, and reproductive cycles in the American lobsters *Homarus americanus*. Journal of Crustacean Biology, 2: 315– 327.
- Atlantic Coastal Cooperative Statistics Program (ACCSP). 2019. ACCSP Data Warehouse, Arlington, VA. Available at <u>http://www.accsp.org/dataware.htm</u>.
- Atlantic States Marine Fisheries Commission (ASMFC). 2010. Recruitment failure in the Southern New England lobster stock. Prepared by the American Lobster Technical Committee, Atlantic State Marine Fisheries Commission, 58 pp.
- Atlantic States Marine Fisheries Commission (ASMFC). 2015. American lobster stock assessment report for peer review. Atlantic States Marine Fisheries Commission, Washington, D.C. <u>http://www.asmfc.org/uploads/file//55d61d73AmLobsterStockAssmt_PeerReviewReport_Aug2015_red2.pdf</u>
- Angell. Thomas E. 2013. ASMFC/Rhode Island 2006 2012 American Lobster Regional Ventless Trap Survey Report. RIDEM, Division of Fish and Wildlife, Marine Fisheries.
- Carloni, J.T. and W. H. Watson III. 2018. Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. Bull Mar Sci, 94(3): 555-570.
- Cooper, R.A. and J.R. Uzmann. 1971. Migrations and growth of deep-sea lobster, *Homarus americanus*. Science, 171: 288-290
- Cowan, D. F., W. H. Watson III, A. R. Solow, and A. M. Mountcastle. 2007. Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. Mar. Biol., 150: 463 470.
- Crossin, G. T., S. A. Al-Ayoub, S. H. Jury, W. H. Howell, and W. H. Watson III. 1998. Behavioral thermoregulation in the American lobster *Homarus americanus*. J. Exp. Biol., 201: 365 374.
- Estrella, B.T. and D. J. McKiernan. 1989. Catch-per-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: description and trends. NOAA Tech. Rep. NMFS 81.
- Faraway, J.J. 2006. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Taylor & Francis Group, Boca Raton, FL.
- Fogarty, M.J. and Idoine, J.S. 1988. Application of a yield and egg production model based on size to an offshore American lobster population. Trans. Am. Fish. Soc. 117:350-362.
- Glenn, Robert. 2011. "Examining Settlement Dynamics of Postlarval American Lobster in LMA 2", CFRF funded project, SNECRI Research program, Final report.
- Goldstein, J.S., Pugh, T.L., Dubofsky, E.A., Lavalli, K.L., Clancy, M. & Watson, W.H. III. 2014. A noninvasive method for in situ determination for mating success in female American lobsters (*Homarus americanus*). Journal of Visualized Experimentation, 84: e50498 [doi:10.3791/50498].

- Goldstein, J.S. and W.H. Watson III. 2015. Influence of natural inshore and offshore thermal regimes on egg development and time of hatch in American lobsters, *Homarus americanus*. Biol. Bull. 228: 1-12
- Groner, M.L, J.D. Shields, D.F. Landers Jr., J. Swenarton, and J.M. Hoenig. 2018. Rising temperatures, molting phenology, and epizootics shell disease in the American lobster. Am. Nat. 192(5) DOI: 10.1086/699478
- Jury, S.H., T.L. Pugh, H. Henninger, J.T. Carloni, and W.H. Watson. 2019. Patterns and possible causes of skewed sex ratios in American lobster (*Homarus americanus*) populations. Invertebrate Reproduction and Development, 63. DOI: 10.1080/07924259.2019.1595184
- Kavanaugh, M.T., Rheuban, J.E., Luis, K.M.A., & Doney, S.C. 2017. Thirty-three years of ocean benthic warming along the U.S. Northeast Continental Shelf and Slope: Patterns, drives, and ecological consequences. Journal of Geophysical Research: Oceans, 122, 9399-9414.
- LeBris, A., A.J. Pershing, J. Gaudette, T.L. Pugh, and K.M. Reardon. 2017. Multi-scale quantification of the effects of temperature on size at maturity in the American lobster (*Homarus americanus*). Fish. Res., 186: 397-406
- Little, S.A. and W.H. Watson III. 2005. Difference in the size at maturity of female American lobsters. *Homarus americanus*, captured throughout the range of the offshore fishery. J. Crust. Biol., 25: 585-592.
- Manning, J.P. and E. Pelletier. 2009. Environmental Monitors on Lobster Traps: long term temperature observations from New England's bottom waters. Jour. of Operational Oceanography. Vol 2-1, p.25-33.
- Rheuban, J. E., Kavanaugh, M. T., & Doney, S. C. 2017. Implications of future Northwest Atlantic bottom temperatures on the American Lobster (*Homarus Americanus*) fishery. Journal of Geophysical Research: Oceans, 122(12), 9387-9398.
- RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.
- 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.
- Waddy, S. L. and D. E. Aiken. 1976. Controlling Growth and Reproduction in the American Lobster. Journal of World Aquaculture Society. Vol7, Issue 1-4. p 415-430.
- Waddy, S.L. & D.E. Aiken. 1992. Environmental intervention in the reproductive process of the American lobster, *Homarus americanus*. Invertebrate Reproduction and Development, 22: 245–252.
- Waddy, S. L. and D. E. Aiken. 1995. Temperature regulation of reproduction in female American lobsters (*Homarus americanus*). ICES Mar. Sci. Symp., 199: 54 – 60.
- Waddy, S. L., & Aiken, D. E. 2005. Impact of invalid biological assumptions and misapplication of maturity criteria on size-at-maturity estimates for American lobster. Transactions of the American Fisheries Society, 134(5), 1075-1090.

- Wahle, R. A., Dellinger, L., Olszewski, S., & Jekielek, P. 2015. American lobster nurseries of southern New England receding in the face of climate change. ICES Journal of Marine Science, 72(suppl_1), i69-i78.
- Waller, J. D., Reardon, K. M., Caron, S. E., Masters, H. M., Summers, E. L., & Wilson, C. J. 2019. Decrease in size at maturity of female American lobsters *Homarus americanus* (H. Milne Edwards, 1837)(Decapoda: Astacidea: Nephropidae) over a 50-year period in Maine, USA. Journal of Crustacean Biology, 39(4): 509–515, <u>https://doi.org/10.1093/jcbiol/ruz021</u>.

Appendix 1: Ovary Color Guide



Ovary Stage 1: white



Ovary Stage 3: light to medium green

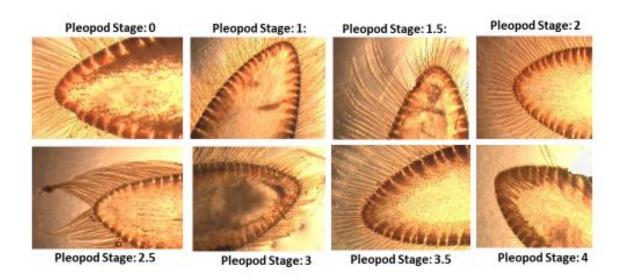


Ovary Stage 2: yellow, orange, beige



Ovary Stage 4: medium to dark green

Ovary Stage 5: dark green



Appendix 2: Pleopod Staging

Criteria used was from Factor Jr, ed. Biology of the lobster Homarus americanus. San Diego: Academic Press, 1995: p. 225. Pictures taken by A. Ellertson and F. Hart during dissection.

Appendix 3: Cement Gland Staging

Cement Gland Stage 0

