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A comparison of the size at maturity of female American lobsters (*Homarus americanus*) over three decades and across coastal areas of the Gulf of Maine using ovarian staging

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The carapace length (CL) at which American lobster (*Homarus americanus*) females reach maturity can be used to evaluate egg production, growth patterns, and the overall health of lobster stocks. The female maturity datasets used to represent Gulf of Maine (GOM) lobsters in the 2015 Atlantic States Marine Fisheries Commission American Lobster Stock Assessment were collected in the 1990s by the Maine Department of Marine Resources at two coastal sites. Many studies have demonstrated an inverse relationship between temperature and the size at maturity in female lobsters, and GOM waters have warmed significantly over this period. To update these GOM maturity datasets, we used ovarian staging to determine the maturity status of over 1200 females from fives sites over 3 years. Broad application of this methodology in tandem with key growth measurements on females 50–120 mm CL allowed us to characterize reproductive development and generate maturity ogives (proportion mature at a given CL). We observed a latitudinal gradient in the size at maturity across this coastal region of the GOM and quantified a decrease in this size over 25 years. These findings have implications for future stock assessment approaches and management measures implemented to sustain this valuable fishery.

Keywords: Gulf of Maine, L_{50}, lobster reproductive development, ovarian staging

Introduction

The American lobster (*Homarus americanus*) fishery is currently the most valuable single-species fishery in the United States with ex-vessel value exceeding $628 million in 2019 (NMFS, 2020). Over 80% of the US American lobster landings come from Maine commercial fishing vessels, underscoring the economic and cultural importance of the Gulf of Maine/Georges Bank (GOM/GBK) stock to Maine and the regional economy (ASMFC, 2020). As temperatures in the GOM continue to rise and the spatial distribution of fishing effort continues to expand, the success of lobster fishery management in the GOM/GBK stock will depend upon the availability of current and regionally specific biological datasets needed to best describe lobster biology and phenology across the oceanographically varied stock area. Datasets that describe the carapace length (CL) at which females reach sexual maturity can be incorporated into model-free indicators used to estimate reproductive capacity and growth in support of the length-based catch-at-length stock assessment model used by the Atlantic States Marine Fisheries Commission (ASMFC; Chen *et al.*, 2005). Females will moult annually or more frequently before the onset of sexual maturity but will slow their rate of somatic growth once mature to accommodate egg production and external brooding (Aiken and Waddy, 1976; Waddy *et al.*, 1995). Size at maturity datasets can inform estimates of female growth and spawning stock biomass (SSB) used to assess the reproductive potential of the females in each stock (GOM/GBK and Southern New England) (ASMFC, 2020). For the purposes of the assessment, each stock is then further divided and analysed as a function of National Marine Fisheries Service (NMFS) statistical areas.

The majority of the GOM/GBK size at maturity data used in the 2015 assessment was collected by Maine Department of Marine Resources (MEDMR) researchers from two nearshore (0–12 nautical miles, 0–22.2 km) locations along the Maine coast. These data were collected in Boothbay Harbor and Sorrento, Maine from 1994 to 1998 (Nutting, 1999; ASMFC, 2015). MEDMR researchers made maturity determinations using 227 females from Boothbay Harbor, and 247 females from Sorrento (65–110 mm CL) collected from commercial fishing traps (Nutting, 1999). These determinations were based on ovary colour and oocyte diameter, and MEDMR analysed these determinations in 5 mm CL size bins to generate size at maturity estimates (Nutting, 1999). The lack of more recent or broad-scale maturity work was noted in the 2015 assessment report since the region has undergone both significant changes in the fishery and rates of warming since these biological data were collected (Mills *et al.*, 2013; Pershing *et al.*, 2015; Thomas *et al.*, 2017; MEDMR, 2020a). Past size at maturity studies in the GOM/GBK show that warming temperatures are the likely driver of observed shifts in the size at maturity and the increasing number of relatively small ovigerous females over time (Pugh *et al.*, 2013; Le Bris *et al.*, 2017; Waller *et al.*, 2019).

Both anecdotal observations from lobster industry members and recent studies in the area suggest that female lobster reproductive development is changing in the GOM/GBK stock over the scale of decades. This inverse relationship between temperature and the size at maturity has also been confirmed across the lobsters' wider historical range with lobsters from relatively warm locations reaching maturity at a smaller size than lobsters in colder and deeper areas (Aiken and Waddy, 1976; Estrella and McKiernan, 1989; Little and Watson, 2003, 2005; Watson *et al.*, 2013; Gaudette *et al.*, 2014). The size at maturity may also be connected to the selective pressure associated with high fishing effort and conservation measures focused on the protection of reproductive females (Gaudette *et al.*, 2014; Le Bris *et al.*, 2017; Haarr *et al.*, 2018).

The size of the fishery and kilograms landed not only impacts the anthropological pressures exerted on the stock but also how the size at maturity is incorporated into this type of stock assessment process. Maturity ogives, the estimated proportion of mature females by CL, for each stock is weighted by the landings from each NMFS statistical area when calculating the maturity ogive for the broader stock (ASMFC, 2020). This means it is crucial to have current and reliable growth and maturity datasets readily available for the statistical areas with the highest landings. In recent years, there have been large shifts in fishery productivity in the NMFS statistical areas that line the coast of Maine (513, 512, 511, Figure 1). In 1995, 34.8% of Maine's lobster landings came from statistical area 513, the most western area (MEDMR, 2020a). At this time, the most eastern area, statistical area 511, accounted for only 6.8% (MEDMR, 2020a). In 2018, this eastern area of the coast was responsible for 19.2% of the state's landings with statistical area 513 now claiming 21.7% (MEDMR, 2020a). The two maturity ogives generated by MEDMR in the mid-1990s are only representative of females at this time from relatively

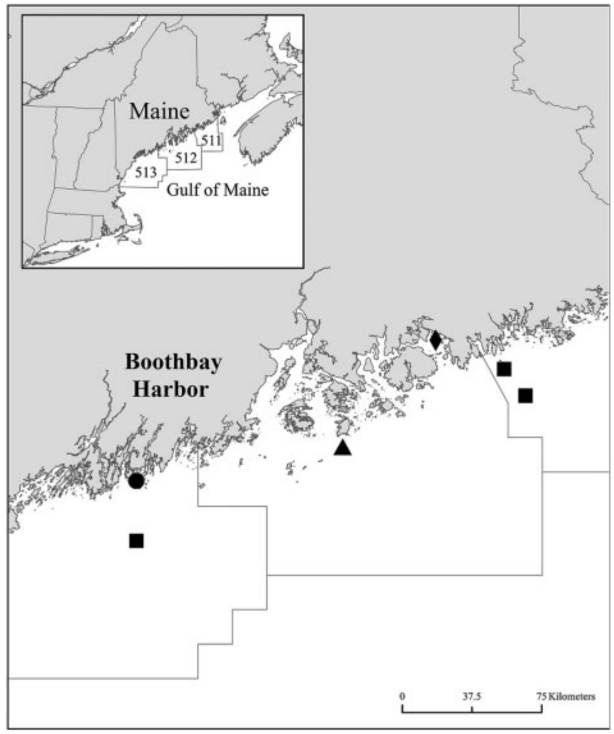

Figure 1. Map of female American lobster, *H. americanus*, collection sites in each NMFS statistical area in coastal Maine. Markers (circle-2018, squares-2019, triangle-2020) represent an average waypoint from collection trips in inshore and nearshore regions made by MEDMR samplers. The circle (Boothbay Harbor) and diamond (Sorrento) represent sampling ports for MEDMR studies conducted from 1994 to 1998. The exact locations of collections are not available for these historical MEDMR works.

limited sampling efforts at a site in statistical area 513 (Boothbay Harbor) and a site in statistical area 512 (Sorrento). These data should not be used in current GOM/GBK analyses in light of the well-documented changes in this nearshore environment and the distribution of fishery productivity. Both the lack of relevant data in what are now the most productive areas of the entire American lobster fishery and the age of available data across the GOM/GBK stock means that up to date female size at maturity studies and accompanying biological measurements are necessary for future assessment and management efforts.

Citing these factors, both female growth and size at maturity were highlighted as a research priority in the 2015 ASMFC American Lobster stock assessment report (Section 8.3, p. 100, ASMFC, 2015). In response to this priority data gap, MEDMR collected and examined 1273 females from five sites across the three NMFS statistical areas that line Maine's coast from 2018 to 2020. We used ovarian staging and key growth measurements to determine the maturity status of each female (Aiken and Waddy, 1982; ASMFC, 2020). To accompany this work, we also assess and review changes in sea surface temperature (SST) since MEDMR's research in the 1990s and across statistical areas. The goal of this study was to conduct an unprecedented, comprehensive assessment of female lobster reproductive development across coastal Maine and to provide insights into changes over the last three decades. Through this work, we were able to use ovarian staging to quantify a latitudinal gradient in the size at maturity across these productive GOM statistical areas and document a broad decrease over 25 years. The results of this work are already being used to better understand the current reproductive potential and population size structure of females in the GOM/GBK stock.

Material and methods

Female lobster collections

All non-ovigerous female lobsters were collected by MEDMR staff onboard commercial fishing vessels using commercial traps from 2018 to 2020 in NMFS statistical areas 513, 512, and 511 (Figure 1). MEDMR staff conducted each sampling trip for this work using a unique protocol developed in support of our objective to collect specimens that represent the population of females in each area across a broad size range. During each trip, samplers measured CL to the nearest mm and randomly retained females ranging in size from 50 to 120 mm CL (Figure 2). In recognition of the high rates of v-notching of ovigerous females in this region and the potential for females with natural mutilations to be considered notched, MEDMR staff aimed to collect an equal proportion of notched and non-notched females as a function of 5 mm CL size bins across the size range of females collected during each sampling trip. We selected this collection approach to best address the inherent biases associated with determining female size at maturity in a heavily fished region with multiple conservation measures to protect mature and ovigerous females from harvest. Lobster collections for this work were focused on sampling the lobster population across a range of sizes, but it is possible that sustained fishing effort in each area differentially removes immature females from the population. This bias cannot be fully remedied in commercially active areas, but MEDMR staff collected this broad size range of females to best represent the population and mitigate this potential source of bias.

The timing of lobster collections in each year and area was determined using trends from current and historical SST and MEDMR Lobster Sea Sampling data (MEDMR, 2020b, c; NERACOOS, 2020). These temperature data and observations were used to select a sampling period within a few weeks of the anticipated onset of the egg-hatching and moulting seasons in each statistical area (Waddy and Aiken, 2005). Seasonal timing is a crucial consideration in *H. americanus* maturity studies as females must be collected at distinctive points in their reproductive development in order to correctly apply and interpret all the ovarian staging criteria (Aiken and Waddy, 1982). Other considerations around the sampling timeframe included the timing needed to characterize the relatively rare occurrence of adult 1-b females, females who will moult and spawn in the same season (Waddy and Aiken, 2005).

To best represent lobsters across each statistical area, female lobster collections took place in two regions within each statistical area. We grouped female lobsters collected within three nautical miles (5.56 km) of shore representing the boundary line for Maine state waters together as "inshore" collections, and we grouped specimens collected farther offshore than this point as "nearshore" collections (Figure 1). These terms are used for broad categorization and grouping within a statistical area and should not be interpreted as a reflection of the oceanography or bathymetry at these locations. All trips for each region in each statistical area were conducted with the same industry captain to ensure consistent sampling over the specified region. MEDMR samplers in coordination with industry boats collected female lobsters from nearshore 513 on 16 and 23 May 2019. Collections made in the inshore region of 513 during 2018 were described in Waller *et al.* (2019). Female lobster collections in statistical area 511 took place on 28 May and 3 June 2019 in the inshore region and on 19 and 28 June 2019 in the nearshore region. Collections in 512 only

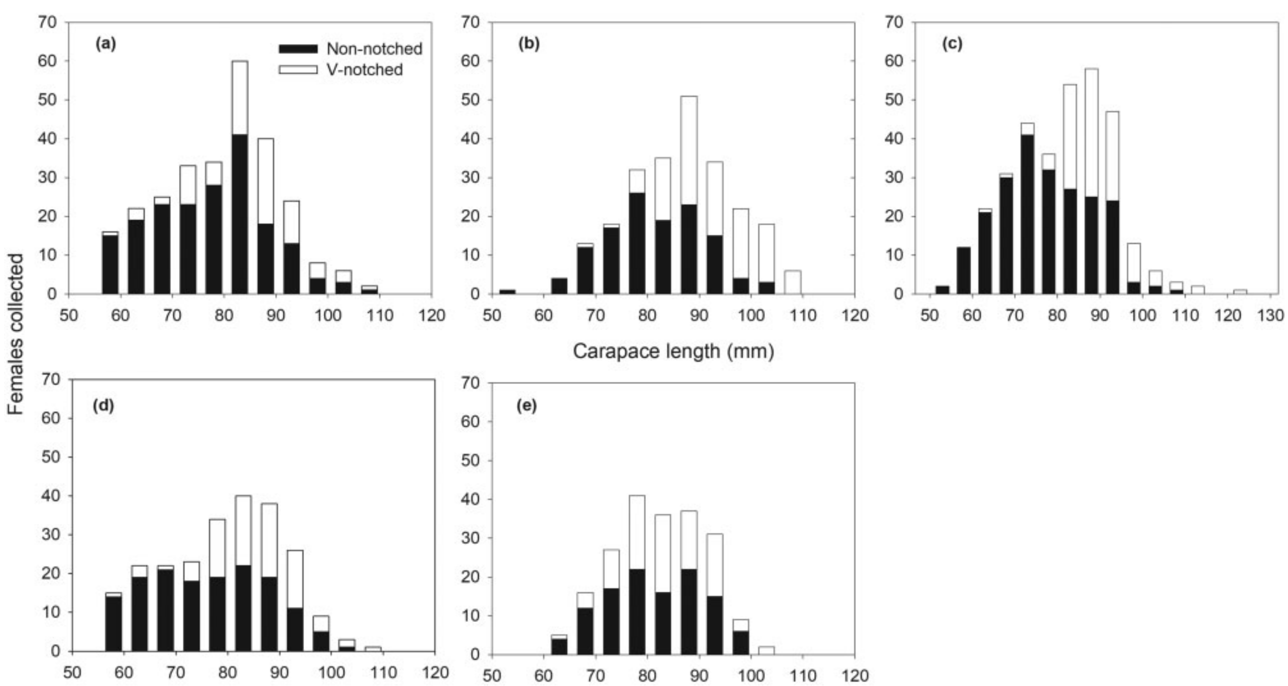

Figure 2. The number of non-ovigerous female *H. americanus* collected and analysed in each 5 mm CL size bin in inshore NMFS statistical area 513 (a), nearshore statistical area 513 (b), statistical area 512 (c), inshore statistical area 511 (d), and nearshore statistical area 511 (e).

occurred in the inshore region and took place on 14 and 26 May 2020. Over the course of 3 years, MEDMR staff collected 1273 non-ovigerous female lobsters representing a total of 504 females from statistical area 513, 331 from statistical area 512, and 438 from statistical area 511 (Figure 2).

Lab holding and processing

All lobster holding, measurements, and lab dissections followed the protocols established in Waller *et al.* (2019). Although there are no regulations that pertain to the American lobster, lab procedures were made in consultation with the University of Maine's Institutional Animal Care and Use Committee office. Lobsters were banded and kept communally in flow-through tanks at MEDMR in West Boothbay Harbor, ME. All lobsters were analysed within 10 d of collection to reduce exposure to high densities and lab conditions. The CL to the nearest 0.5 mm, shell hardness (hard or soft), and whole-body wet weight were recorded on each lobster. A pair of pleopods was removed from each female and examined under a dissecting microscope to determine setogenic stage (Aiken, 1973). A female at setogenic stage 3.0 or higher was assumed to be in an active premoult condition meaning that moulting is imminent, and no further ovary development would have occurred at the current size (Waddy and Aiken, 1992).

To record all the parameters needed to appropriately apply the ovarian staging criteria, each female was dissected after external measurements were completed. Prior to dissection, females were kept individually in a freezer for a minimum of 15 min in order to sedate and euthanize each lobster. Using forceps, staff removed the carapace of the lobster to record the colour of the ovary and the oviducts. We also recorded any indications of previous spawning events and ovary resorption including residual oocytes in the lobes of the ovary. The ovary was removed and weighed and a minimum of 50 oocytes were removed from the centre of the ovary and carefully moved onto a microscope slide. Oocytes from each female were photographed using a dissecting microscope equipped with an Olympus DP73 and the diameter was measured in NIH Image J (Schneider *et al.*, 2012).

Maturity ogives and associated analyses

Final maturity determinations were made without knowledge of CL and v-notch status to avoid bias in these determinations. Consistent with Waller *et al.* (2019), females that met the criteria for stage 4b or higher were designated as mature. Females identified as stage 4b have dark green ovaries, an ovary factor exceeding 200, and oocytes ranging in diameter from 0.8 to 1.6 mm (Aiken and Waddy, 1982). To generate maturity ogives, each female was assigned an ovarian stage and then a value of 0 (immature) or 1 (mature) to represent a final maturity determination. Females in each region were grouped into 5 mm CL size bins and logistic regression (binomial distribution, logit link) was fit to these data using the generalized linear model (GLM) function in R (R Core Team, 2020; RStudio Team, 2020). Model parameters and the 95% confidence limits were obtained from logistic regressions and used to generate maturity ogives (fit to the function below) for each region and then statistical area.

$$p = 1/1 + e^{(\alpha+\beta * CL)}$$

In alignment with the ASMFC stock assessment ogives, p is the proportion of mature females at a specified CL and both α and β are fitted parameters (ASMFC, 2020). We derived the CL at which 50% of females reach maturity (L_{50}) from the fitted parameters of each ogive ($-\beta/\alpha$). Model fits were evaluated for each logistic regression using a goodness-of-fit test, a pseudo-R^2 from the descr package, and by inspecting residuals (Faraway, 2006; Watson *et al.*, 2017). The error associated with L_{50} was estimated using the "p.dose" command in the MASS package. Representations of each maturity ogive were generated using the recommendations presented in McBride (2016) and by the ASMFC American Lobster Technical Committee. Logistic regressions were also used to test for significant differences between the intercepts of maturity ogives generated by region within a statistical area, by statistical areas, and by MEDMR year of collection (Ogle, 2016). We evaluated maturity predictor variables (CL, region, statistical area, year) and selected models using the "aictab" function of the AICcmodavg package (Mazerolle, 2020). To evaluate potential biases, we also generated a maturity ogive for each statistical area based on determinations only on females below legal harvest size (82.55 mm) and compared the L_{50} and fitted parameters to those derived from the full ogive in each area. Analysis of variance (ANOVA), linear models, and GLMs were used to test for significant differences in biological parameters across statistical areas and over time once all assumptions were met for each test and dataset.

SST and degree days

We used SST data extracted from NOAA's optimum interpolation sea surface temperature (OISST) AVHRR-2 dataset (https://www.ncdc.noaa.gov/oisst) to examine temperatures changes in these NMFS statistical areas over the last 25 years. SST is more reliably and easily accessible compared to bottom temperatures, and recent work has shown that SST is equally effective when using temperatures to examine estimated changes in maturity ogives over time (Le Bris *et al.*, 2017). All extracted values were grouped by statistical area and an average daily SST was calculated for each area from 1995 to 2019 resulting in a single value for each day of the year in each area. Total annual degree days were calculated for each area by summing the number of degrees that exceed 5°C for each day's average temperature and then summing them for each year examined.

Results

Maturity determinations and ogives

After conducting individual maturity determinations for each female collected and analysed, females were grouped into 5 mm CL size bins and logistic regressions were used to generate maturity ogives for inshore and nearshore regions in each statistical area. The maturity ogive for inshore 513 was generated from a new analysis of the maturity determinations described in Waller *et al.* (2019). In both statistical 511 and 513, our model selection based on AICc revealed that a model with CL as the only predictor of maturity was best suited to these data (Table 1). In both 511 and 513, logistic regression revealed no significant differences between the intercepts of ogives generated for inshore and nearshore regions within each area ($p > 0.05$, Figure 3). Using the same approach, these data were then combined to represent a single ogive for each statistical area. We evaluated the maturity ogives generated only from females below 83 mm CL and found that all L_{50} and curve shape parameters aligned closely with the full ogive in each statistical area and fell within the 95% *CI*s. These results

Table 1. The results of the AICc model selection for maturity determinations generated by region in 2018–2020.

	AIC_C	Δ	W_i
Predictors statistical area 513			
CL	462.57	0.00	0.63
CL+ Region	464.52	1.95	0.24
CL* Region	465.59	3.01	0.14
Region	681.69	219.12	0.00
Predictors statistical area 511			
CL	348.82	0.00	0.66
CL+ Region	350.85	2.02	0.24
CL* Region	352.53	3.71	0.10
Region	546.36	197.54	0.00

The response variable was the maturity determinations for female *H. americanus*. Predictor variables were CL by 5 mm CL size bin and collection region (inshore/nearshore) within NMFS statistical areas 513 and 511. Delta (Δ) is the difference from the best model. W_i is the probability that the model is the most appropriate (Akaike weight).

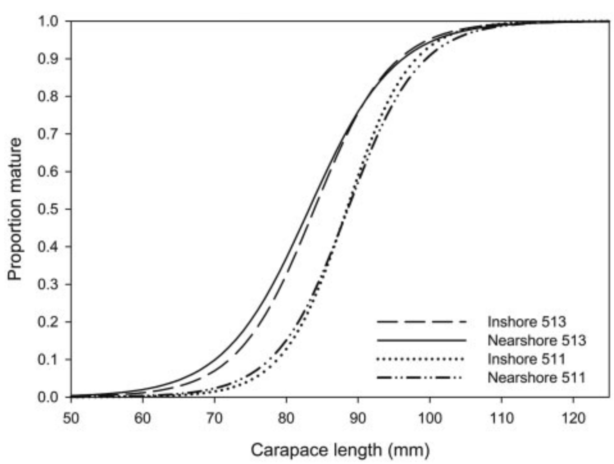

Figure 3. Logistic regressions showing the predicted proportion of mature female *H. americanus* from two regions within NMFS statistical areas 511 and 513 as a function of CL. There were no differences in the proportion mature by CL between regions within each area (logistic regression, $p > 0.05$).

indicate that our collection approach was sufficient to reduce the bias introduced by fishing exploitation and conservation measures, and it was appropriate to proceed with the ogives derived from females 50–120 mm CL in each area.

Of the 438 females collected in NMFS statistical area 511, 32.4% were classified as mature using ovarian and setal staging. The smallest mature female was observed at 73 mm CL, and all females were mature at 97 mm CL. A logistic regression fit to the observed proportion mature in each size bin was used to estimate a predicted maturity curve as a function of CL [$\alpha = 18.898$ (UCI: 22.195, LCI: 15.931), $\beta = -0.213$ (UCI: −0.179, LCI: −0.251, Figure 4a] and subsequent tests revealed a suitable fit to these data ($\chi^2 = 4.10$, $p = 0.77$, $R^2 = 0.52$). These determinations and accompanying analyses represent the first maturity ogive generated for female lobsters in this statistical area. Using this predicted maturity curve, L_{50} was estimated at 88.6 mm CL (UCI: 89.9, LCI: 87.3) in this area.

This analysis was repeated on maturity determinations in statistical area 512 with maturity first observed at 74 mm CL and 36.6% of all sampled females classified as mature. The logistic regression fit to these data ($\chi^2 = 11.81$, $p = 0.16$, $R^2 = 0.44$) generated a predicted maturity ogive for this area [$\alpha = 15.092$ (UCI: 18.111, LCI: 12.401), $\beta = -0.174$ (UCI: −0.142, LCI: −0.209), Figure 4b] and was used to estimate L_{50} for females in this area (86.7 mm, UCI: 88.4, LCI: 85.0). Maturity determinations for lobsters collected in statistical area 513 revealed that 48.2% of females collected were classified as mature with the smallest mature female observed at 68 mm CL. Logistic regression was used to represent the proportion mature in this statistical area as a function of CL, and all model tests indicated a good fit to these data ($\chi^2 = 5.90$, $p = 0.66$, $R^2 = 0.50$). The resulting ogive [$\alpha = 14.841$ (UCI: 17.191, LCI: 12.695), $\beta = -0.178$ (UCI: −0.152, LCI: −0.206, Figure 4c] was used to estimate that L_{50} occurs at 83.4 mm (UCI: 84.7, LCI: 82.1) in this statistical area. When all 2018–2020 determinations were evaluated together, our model selection showed that CL + statistical area was the most suitable model for further analysis (Table 2). Logistic regression was also used to examine these three maturity ogives using the model selected and revealed a latitudinal gradient in the predicted size at maturity with females reaching maturity at the smallest sizes in statistical area 513 and the largest in 511 ($p < 0.05$, Figure 5).

Measures of size, reproductive development, and changes over time

To make these maturity determinations and best characterize the size at maturity in these areas, this work also included key measures of growth and reproductive development. In all areas sampled, the average oocyte diameter of each female increased as a function of CL (Figure 6). A GLM fit to log-transformed oocyte diameters and subsequent analysis to test for differences in intercepts revealed that both CL and statistical area of origin had a significant effect on oocyte diameter with females from 513 having significantly larger oocytes compared to females from other areas [ANOVA, $F_{(2,\ 1260)} = 30.84$, $p < 0.001$]. Working under the assumption that females of all sizes would be expected to extrude eggs at the same time in a season, we found that 70 mm CL females had a mean oocyte diameter of 0.37 mm (± 0.12 *SD*) in statistical area 511, 0.36 mm (± 0.09 *SD*) in 512 and 0.32 mm (± 0.04 *SD*) in 513. At 95 mm CL, a size representing a high proportion of mature females in all areas, females in 513 had the largest mean oocyte diameter (1.25 mm, ± 0.29 *SD*) while we observed mean oocyte diameters of 1.02 (± 0.30 *SD*) and 1.08 (± 0.33 *SD*) in 512 and 511, respectively.

In the females collected from coastal Maine in 2018–2020, wet weight increased significantly as a function of CL, but an ANOVA on log-transformed data revealed no significant differences by statistical area of collection [$F_{(2,\ 1266)} = 2.52$, $p = 0.81$]. We can also compare this measurement to historical work to evaluate changes or consistencies across areas and over time. In past works, MEDMR researchers have measured whole-body wet weight and derived a length–weight relationship from females in Boothbay Harbor (Krouse, 1973). The stock assessment uses datasets from the NMFS trawl survey to define a length–weight relationship for females across the stock beginning in 1982 (ASMFC, 2020). The wet weights as a function of CL recorded for the 1273 females examined here closely followed the relationship

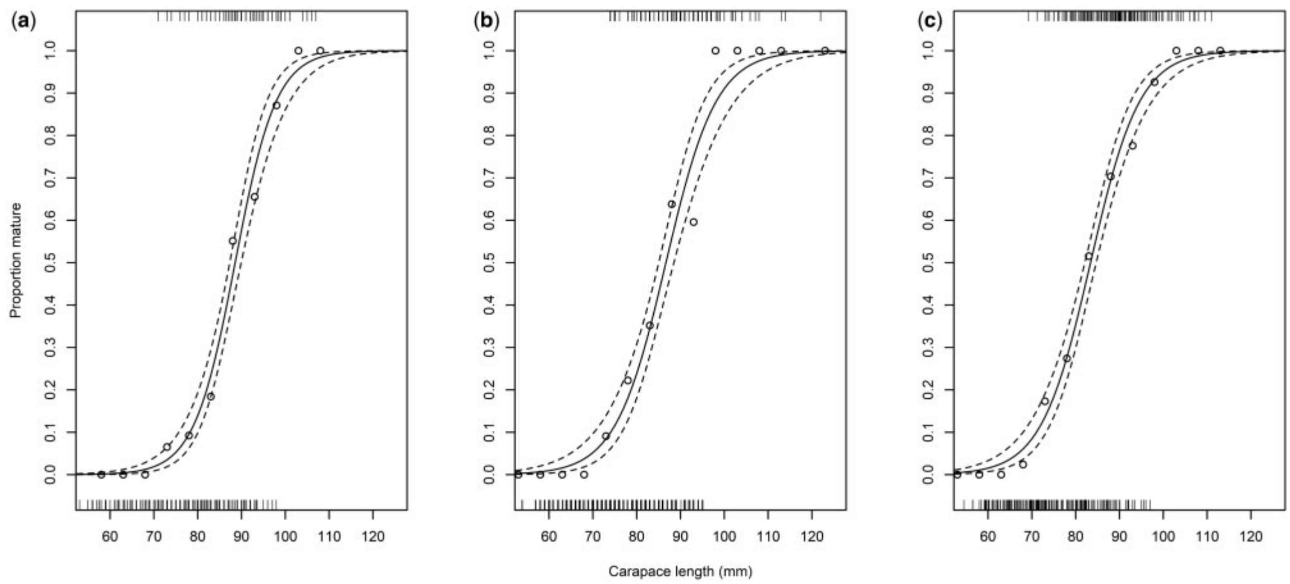

Figure 4. Female *H. americanus* maturity determinations fit with a logistic regression showing the proportion mature as a function of CL in NMFS statistical area 511 (a), 512 (b), and 513 (c). Open circles represent the proportion mature in each 5 mm CL size bin and the solid line represents the predicted proportion mature. The dashed lines are the associated 95% confidence limit. Each tick mark on the lower axis (0) represents an individual female classified as immature. Each tick mark on the upper axis (1) represents an individual female classified as mature. Tick marks are jittered to reduce overlap.

Table 2. The results of the AICc model selection with maturity ogives for female *H. americanus* as the response variable.

Predictors 2018–2020	**AIC_C**	**Δ**	**W_i**
CL + Stat. area	1101.47	0.00	0.55
CL * Stat. area	1101.84	0.37	0.45
CL	1133.66	32.19	0.00
Stat. area	1686.67	585.21	0.00
Predictors 1994–1998 and 2018–2020			
CL+ Stat. area + Year	70.13	0.00	0.78
CL + Year	73.22	3.09	0.17
CL * Stat. area *Year	76.46	6.32	0.03
CL + Stat. area	78.71	8.57	0.01

For the 2018–2020 models, the predictor variables were CL by 5 mm size bin and statistical area. For the 1994–1998 and 2018–2020 models, the predictor variables were CL , statistical area, and year of collection. Only models with a W_i above 0.00 are reported in the lower table.

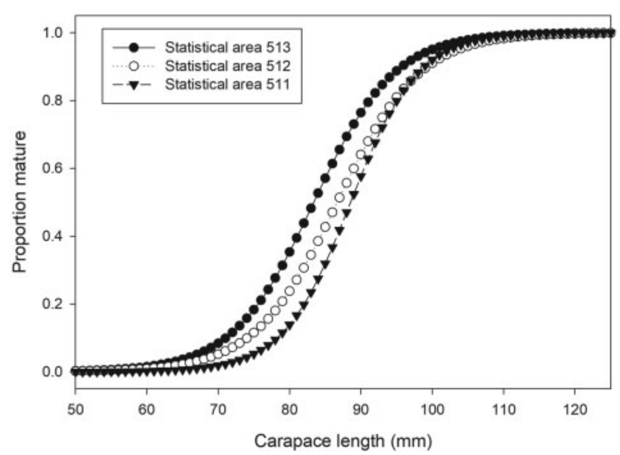

Figure 5. Logistic regressions showing the predicted proportion of mature female *H. americanus* from each NMFS statistical area in coastal Maine as a function of CL.

predicted in these historical works as did the length–weight equation generated from these data ($y = 0.0018x^{2.81}$, $R^2 = 0.93$, Figure 7). A linear model fit to the datasets from these three relationships showed the expected significant effect of CL (Multiple $R^2 = 0.96$, $p < 0.001$), but also revealed no significant difference in intercepts between MEDMR and NMFS data sources ($p > 0.05$).

The maturity results can also be contrasted to the size at maturity work conducted by MEDMR researchers in the 1990s. The estimated L_{50} value for each MEDMR sampling effort and statistical area shows that females across the Maine coast are reaching maturity at smaller sizes over time (Table 3). In statistical areas 513 and 512, L_{50} decreased an estimated 5.6 and 6.7 mm, respectively, over this period. The results presented here are compared against historical MEDMR work that was conducted in a more eastern area of 512, so differences in sampling locations within a statistical area may account for some aspects of this result (Figure 1). MEDMR did not sample in statistical area 511 during these past efforts, so this historical work in eastern statistical area 512 is the best available point of comparison for this purpose. This comparison shows that L_{50} in this area likely decreased by 4.8 mm since the mid-1990s (Table 3). The estimated curve shape parameters derived from modelling the proportion mature as a function of CL also reflect that lobsters collected from each area are reaching maturity at relatively smaller sizes (Table 3). A logistic regression fit to each ogive and sampling

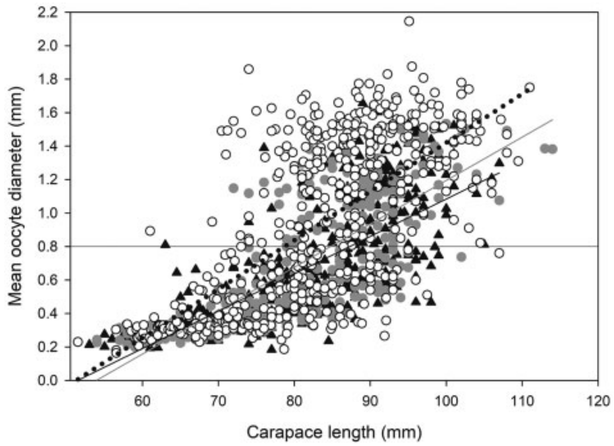

Figure 6. Average oocyte diameter of female *H. americanus* collected across coastal Maine statistical areas from 2018 to 2020. Triangles represent females from NMFS statistical area 511, filled circles represent females from 512, and open circles represent females from 513. The line at 0.8 mm oocyte diameter represents the maturity oocyte threshold value from Aiken and Waddy, 1982. The fitted models are represented for females collected from NMFS statistical areas 513 (dotted), 512 (grey), and 511 (black).

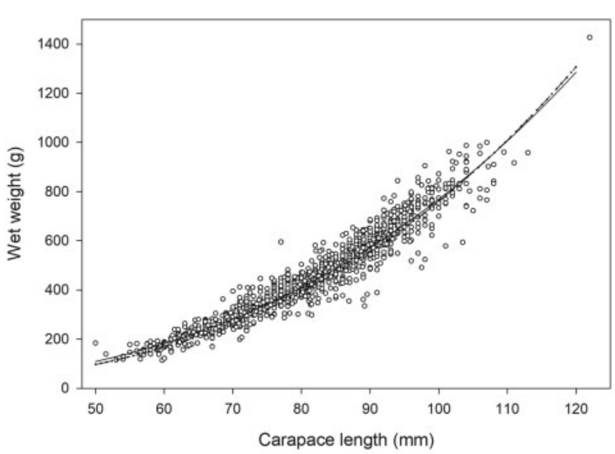

Figure 7. Observed and calculated length–weight relationships for female *H. americanus*. The circles depict the weight of individual females measured in this effort. The calculated relationships are represented by the solid (this study), the dashed (Krouse, 1973), and the dotted (ASMFC, 2020) lines.

periodshowed decreases in the predicted size at maturity over this 25-year period in each area ($p < 0.05$).

Changes in SST between statistical areas and across decades

Modelled SST data can be used to describe changes in key temperatures in these coastal areas since MEDMR's historical sampling efforts. We selected 5°C as the degree days value for this analysis as reproductive development is typically suspended at temperatures below this point (Waddy and Aiken, 1995). The number of degree days increased in each statistical area from 1995 to 2019, and a linear model fit to these degree day data showed significant differences over time and between statistical areas (Multiple $R^2 = 0.66$, $p < 0.001$), with the greatest increase in degree days, rising from 1698 to 1992, occurring in statistical area 513 (Figure 8).

Discussion

Differences in reproductive development over space and time

This work provides a snapshot of the growth and reproductive development of female lobsters across the three NFMS statistical areas that line Maine's coast, representing the most productive

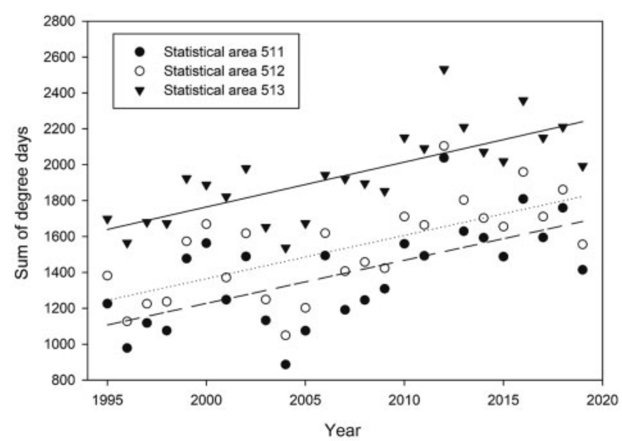

Figure 8. Cumulative degree days greater than 5°C in each NMFS statistical area from 1995 to 2019. The black line represents the linear fit to data from statistical area 513 ($m = 25.0$, $R^2 = 0.55$), the dotted represents statistical area 512 ($m = 24.1$, $R^2 = 0.44$), and the dashed represents the linear fit to statistical area 511 ($m = 24.0$, $R^2 = 0.45$).

Table 3. The estimated length at which 50% of female *H. americanus* (L_{50}) reach maturity and the maturity ogive curve shape parameters by statistical area from MEDMR research during 1994–1998 and 2018–2020.

NMFS Statistical area	L_{50} 1994–1998	L_{50} 2018–2020	α, β 1994–1998	α, β 2018–2020
511	93.4 mm*	88.6 mm	29.920, −0.320*	18.898, −0.213
512	93.4 mm	86.7 mm	29.920, −0.320	15.092, −0.174
513	89.0 mm	83.4 mm	23.191, −0.261	14.841, −0.178

Historic curve shape parameters were provided by the ASMFC American Lobster Technical Committee. Confidence intervals for ogive parameters and L_{50} can be found in the Results section.

*No research was done from 1994 to 1998 in statistical area 511, so the 512 values are displayed as a point of comparison.

American lobster fishing grounds in the world. We used ovarian staging, the method recommended by the ASMFC American Lobster Stock Assessment, to determine the maturity status of over 1273 females over a 3-year period. Applying this methodology on females at this sample size and from 50 to 120 mm CL allowed us to estimate the size at maturity in each area and provide updated maturity ogives to the ASMFC American Lobster Technical Committee for use in assessment analyses. These updated ogives showed differences in the size at maturity across the coast with females from western areas reaching maturity at a smaller size compared to females from eastern areas. When compared to historical MEDMR research, we also saw a decrease in L_{50} over the last three decades in each area with L_{50} shifting 4.8–6.7 mm CL over time. Finally, we also recorded significant differences by statistical area in average oocyte diameter and no differences in the length–weight relationship of females across these areas and over time.

Given the well-studied and observed relationship between temperature and female lobster reproductive development, we also examined changes in SST over the last 25 years using modelled temperature data from NOAA's OISST AVHRR-2 dataset. The total number of degree days increased significantly in each statistical area over this period with the greatest rate of increase occurring in the most western area, statistical area 513. Ovary development in this species is dependent upon a balance of days below and above key temperatures in each season during the 3 years preceding the onset of maturity with exposure to these temperatures also influencing somatic growth (Aiken and Waddy, 1980, 1982; Waddy and Aiken, 1995; Waddy and Aiken, 2005). We used ovarian staging as the maturity determination method in this work to examine the developmental stage of each female over this key 3-year period or to determine if a female had already undergone vitellogenesis and reached maturity.

Vitellogenesis occurs in the years preceding spawning (egg extrusion) during which researchers have observed gradual increases in ovary size before the female will enter a temperature-driven diapause in the winter months (Aiken and Waddy, 1980; Comeau and Benhalima, 2018). The degree days analysis presented here is an indicator that there is an increasing period in each year when temperatures are high enough to sustain the development of the ovary though lobster exposure to these temperatures will vary by habitat and with seasonal migration patterns (Waddy *et al*., 1995; Waddy and Aiken, 2005). Haarr *et al.* (2020) proposed a similar mechanism when making connections between warming fall temperatures and changes in the reproductive development and timing of egg hatching in the southern Gulf of Saint Lawrence. These temperature increases may also present a mechanism for the average oocyte diameter result by statistical area. Females from statistical area 513 had significantly larger oocytes compared to their counterparts from other areas, and this area also experienced the highest number of degree days during the years when the females studied here would be undergoing vitellogenesis, allowing for longer periods of oocyte development and shorter periods of diapause. All temperature links to these biological results should be considered in the context of the prevailing conditions driven by the heavily mixed Eastern Maine Coastal Current and the highly stratified Western Maine Coastal Current (Pettigrew *et al*., 2005).

Recent work has presented differing broad trends of warming in these currents with increased surface warming in western portions of the coast since the 1980s while bottom temperatures warmed faster in the east (Goode *et al*., 2019). This study also highlighted the variation driven by currents and bathymetry in each area such as the steep temperature gradient at shallow depths (0–25 m) in western portions of the coast where the warmest temperatures occur (Goode *et al*., 2019). The range of our collection sites and the thermal conditions within and across these statistical areas should be considered carefully alongside the results presented here at the scale of the statistical area. In addition to the thermal range of these areas, researchers in the western statistical area have documented the seasonal movements of female lobsters to avoid cold conditions and seek relatively warm, shallow habitat (Watson *et al*., 1999; Goldstein and Watson, 2015). These systems are complex and vary significantly by depth within a statistical area, so more information on the seasonal migrations of lobsters in coastal Maine waters is needed to more fully examine how long-term warming in each current and statistical area has impacted exposure to these thermal trends and dictated female reproductive development.

Temperature is also known to significantly impact lobster growth by influencing moult probability (Waddy *et al*., 1995; Tremblay and Eagles, 1997; Comeau and Savoie, 2001). It has been proposed that lobsters in relatively warm areas undergo short intervals between moults at the expense of the increment of relative growth per moult (Waddy *et al*., 1995; Landers *et al*., 2001). Moulting is also interconnected with egg production in females, and both the moult frequency and interval shift once a female reaches maturity with mature females generally alternating between annual egg production and growth (Waddy and Aiken, 2005). Growth as a proportion of premoult size occurs linearly until a female reaches maturity at which point the female begins to divert significant resources to reproductive success (Waddy *et al*., 1995; Bergeron, 2011). The similarities between length–weight relationships over time in Maine coastal waters and a stock-wide relationship indicate that changes in moult frequency and increment driven by decreases in the size at maturity may be offset by other changes in body volume and weight (development of reproductive tissues, widening of abdomen width in preparation for oviposition) resulting in no discernable change in length–weight relationships over time and across areas. Greater sample sizes may be needed to elucidate subtle differences over space and time in this key metric.

After examining the effect of temperature on individual measures of growth and oocyte development in tandem with the broad warming trends presented here, the findings from this study can be compiled to support the notion that temperature is the likely driver of the downward shifts in maturity ogives across these areas and over the scale of recent decades. These findings align with comparable works that show the effect of temperature on individual aspects of female development and the estimated size at maturity (Waddy and Aiken, 1995; Landers *et al*., 2001; Little and Watson, 2005; Waller *et al*., 2019). This work highlights the need to update historical maturity datasets as these measures of lobster development and growth are integral to evaluations of the size-based regulatory tools used in the management of the American lobster fishery.

Implications for management and future stock assessments

The objective of this work was to provide updated maturity parameters to accurately reflect the reproductive development of females in these statistical areas and the GOM/GBK stock. These parameters can be incorporated into multiple aspects of the stock assessment process including estimates of SSB and estimated moult probabilities for the growth transition matrix (ASMFC, 2020). Fecundity is not currently included in the catch-at-length stock assessment model, so SSB is used as a key model-free indicator to examine the reproductive potential of the females in each stock. A growth transition matrix is used to describe the size structure of each stock by calculating the probability that an individual lobster will moult from one 5 mm CL size bin to another within a year (ASMFC, 2009; Cronin-Fine and Punt, 2020). Since maturity reduces the probability of a female moulting, shifts in the proportion mature by length have significant implications for the model's ability to describe the current growth of females in the stock. This research was focused on generating maturity ogives that can be used to determine the probability that a female is mature at a given size, but these estimates may not represent the proportion of females within this population that are mature inclusive of ovigerous females. These metrics should be interpreted and applied in different ways, and the primary objective of this research was to provide ogives for fishery management processes.

Our work quantifies and describes differences in the reproductive development of female lobsters over the scale of decades and across coastal areas of Maine. In its current form, the stock assessment model does not have the capability to account for changes in key biological parameters over time (ASMFC, 2020). This presents challenges both in stock assessment model development and interpretations of current results. This also highlights the need for time-varying growth transition matrices or other ways to compensate for changes within a stock. In past stock assessments, the GOM/GBK stock was compared to a reference period from 1982 to 2003. As of 2020, the status of the GOM/GBK stock is now compared to a reference period based on a regime shift analysis to identify high, medium, and low productivity time periods (ASMFC, 2020). These updates will improve future assessments and other works that account for these biological and abiotic changes in the stock over recent decades.

The findings presented here can be used in Maine and regionally to support management decision-making as the fishery and conditions in the GOM/GBK stock continue to change. The ASMFC Interstate Fishery Management Plan for American Lobster established minimum legal harvest size as a foundational management measure across the species US range (ASMFC, 1997). One consideration behind the current minimum legal harvest size (82.55 mm CL) was that the size should be below the anticipated size at maturity to allow reproductive females to remain in the stock, particularly first-time spawners, to ensure the long-term success of the stock (ASMFC, 1997; MEDMR, 2020b). After decades of warming in the GOM and changing fishery dynamics, our work shows that L_{50} in coastal Maine waters has shifted closer or nearly to the existing minimum size without any changes to this management measure over the last 25 years. The results of this work have already been shared and incorporated into stock assessment and management efforts and provide specific insights into the growth and maturation of females in the Northwest Atlantic's most valuable fishery.

Data availability

All data are available upon request through the Maine Department of Marine Resources (jesica.d.waller@maine.gov).

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Author contributions

JDW, KMR, ELS, and CJW designed and conceived of this study. BPJ performed at-sea specimen and data collection onboard commercial vessels. JDW, BJP, and SEC performed all laboratory work and image analysis. All authors contributed to data analysis and interpretation. JDW drafted the manuscript. All authors contributed to manuscript editing.

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