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FEATURE ARTICLE

# American lobster and Jonah crab populations inside and outside the Northeast Canyons and Seamounts Marine National Monument, USA

**Stephen A. Arnott** | **Michael P. Long** | **Aubrey Ellertson** | **N. David Bethoney**

Commercial Fisheries Research Foundation, Saunderstown, Rhode Island, USA

**Correspondence**
N. David Bethoney
Email: dbethoney@cfrfoundation.org

**Present address**
Stephen A. Arnott, Northeast Fisheries Science Center, Milford Laboratory, Milford, Connecticut, USA

Aubrey Ellertson, Cape Cod Commercial Fishermen's Alliance, Chatham, Massachusetts, USA

**Abstract**

**Objective:** There is international pressure to increase the worldwide expanse of marine protected areas (MPAs). However, MPAs often lack preexisting long-term biological baselines, which are essential for assessing MPA effects and for refining the conservation and socioeconomic benefits they confer to society. Our study addresses this issue by establishing demographic baselines for two commercially important species prior to a proposed fishing ban inside the Northeast Canyons and Seamounts Marine National Monument, a recently established MPA on the continental shelf break approximately 200 km southeast of Cape Cod, Massachusetts.

**Methods:** Samples were obtained by the Commercial Fisheries Research Foundation's American Lobster and Jonah Crab Research Fleet, which is an industry-based, fishery-dependent data collection program. Specially trained participants recorded year-round biological data from their 2013 to 2021 commercial catches of American lobster *Homarus americanus* and Jonah crab *Cancer borealis*. Samples were taken from an area inside the MPA and from two areas outside the MPA, spanning 130 km to the east and west.

**Result:** American lobster sizes and sex ratios varied between areas, and their sizes, sex ratios, and proportion of ovigerous females differed between submarine canyons within areas. American lobster sizes, sex ratio, proportion of ovigerous females, and prevalence of shell disease were also affected by season and/or depth. Jonah crab parameters did not vary between areas, but sex ratio varied with season and depth, and the proportion of ovigerous females varied with depth.

**Conclusion:** These demographic baselines are the only data available, at a sufficient spatial and temporal resolution, for evaluating the effects of a proposed fishing ban in the MPA, and they fill important data gaps for stock assessments. To evaluate possible future population changes, it will be necessary to continue collecting data from inside and outside the MPA using comparable methods, and to account for the preexisting sources of variation that we have identified.

**KEYWORDS**
American lobster, fisheries, Jonah crab, marine protected areas, population dynamics

# INTRODUCTION

The use of marine protected areas (MPAs) as a form of ocean governance has become increasingly popular in recent years (Boonzaier and Pauly 2016; European Union 2017; Smith et al. 2017; Grorud-Colvert et al. 2019; Brander et al. 2020). A major goal of MPAs is to protect vulnerable habitat and species inside their boundaries and to enhance surrounding areas by the dispersal of protected species (Goñi et al. 2010; Cohen and Foale 2013; Barceló et al. 2021; Ohayon et al. 2021). The use of MPAs as a management tool is likely to increase worldwide as nations (currently over 100) sign on to the "30 by 30" approach, which aims to protect 30% of the Earth's land and ocean by 2030 (Dinerstein et al. 2019; Roberts et al. 2020; Sala et al. 2021). However, MPAs need to be carefully monitored to evaluate their conservation and socioeconomic benefits and to balance the potentially negative effects of displacing human activities into surrounding areas (Agardy et al. 2011; Hilborn and Kaiser 2022).

Political support for expanding the number and extent of MPAs is divided within the United States. In 2016, President Obama created the Northeast Canyons and Seamounts Marine National Monument (hereafter referred to as the "Monument") by presidential proclamation under the Antiquities Act of 1906 (Federal Register 2016). The Monument is the first of its kind to be established in U.S. Atlantic waters, although four others exist in the U.S. Pacific. It is situated approximately 200 km southeast of Cape Cod, Massachusetts, along the continental shelf break (Figure 1A), in an area with high biodiversity and sensitive deep-sea habitat (Brooke and Ross 2014; Auster et al. 2020). Areas inside the Monument have historically sustained a variety of economically important benthic and pelagic fisheries (Lynham 2022). Most of these fisheries were banned soon after the 2016 proclamation, which resulted in a series of lawsuits by the commercial fishing industry (U.S. District Court for the District of Columbia 2017). In 2020, President Trump reversed the commercial fishing ban, which resulted in new lawsuits, this time by conservation organizations (U.S. District Court for the District of Columbia 2020). In 2021, President Biden reimposed the commercial fishing ban. At present, all commercial fishing is banned inside the Monument, except for fixed-gear (trap) fisheries for American lobster *Homarus americanus* and deep-sea red crab *Chaceon quinquedens*, although these are scheduled to be banned in 2023. Jonah crab *Cancer borealis* is also harvested at present because they are regulated as part of the lobster fishery.

The controversy over the Monument, with its potential ecological benefits and economic impacts on stakeholders, underscores the need to properly evaluate the effects of restricting or eliminating commercial fishing within its boundaries (Lynham 2022). However, many studies that have attempted to evaluate ecological responses to MPAs lack rigor due to insufficient temporal coverage (both before and after MPA implementation) and/or insufficient spatial coverage (areas inside the MPA and reference areas outside its boundaries; Halpern 2003; Lester et al. 2009; Christie et al. 2020).

> **Impact statement**
>
> Marine protected areas (MPAs) need monitoring to evaluate their benefits to society. We characterized American lobster and Jonah crab populations inside and outside a newly created MPA while commercial harvest was still operating, thereby providing essential information needed for assessing future responses to planned fishing closures.

Data limitation is particularly problematic when evaluating impacts in remote, inaccessible areas. This is the case for American lobster and Jonah crab, which are targeted in the submarine canyons and intercanyon breaks in and around the Monument's Canyon Unit. American lobster is one of the most valuable fisheries in the United States (Zou et al. 2021), and the Jonah crab fishery has become increasingly important over the last two decades, with landings increasing fourfold during that time. American lobster is widely harvested along the northeastern coast and continental shelf of the USA, and although it is mostly a coastal fishery, fishing effort has shifted more offshore in recent years (Atlantic States Marine Fisheries Commission [ASMFC] 2020). The Jonah crab fishery occurs mostly within National Oceanic and Atmospheric Administration (NOAA) statistical area 537 (directly west of our study area), but 20% of landings originate from NOAA statistical areas 525 and 526 (ASMFC 2021), which encompass our study area (Figure 1A). The economic significance of the Monument to American lobster and Jonah crab commercial harvesters was exemplified by a clause in the 2016 proclamation that allowed lobster and crab fishing to continue inside the Monument for 7 years after its creation (i.e., until 2023).

Large decapods such as American lobster and Jonah crab play an important role in structuring benthic ecosystems (Boudreau and Worm 2012), and their effects are thought to enhance the overall diversity within the canyons of the Monument (Auster et al. 2020). However, there is a lack of detailed fishery-independent data for assessing American lobster and Jonah crab populations in the vicinity of the Monument. The only consistent source of fishery-independent data in the region comes from the Northeast Fisheries Science Center bottom trawl survey (Politis et al. 2014), which conducts about one tow per 885 km$^2$ per year (ASMFC 2020) and

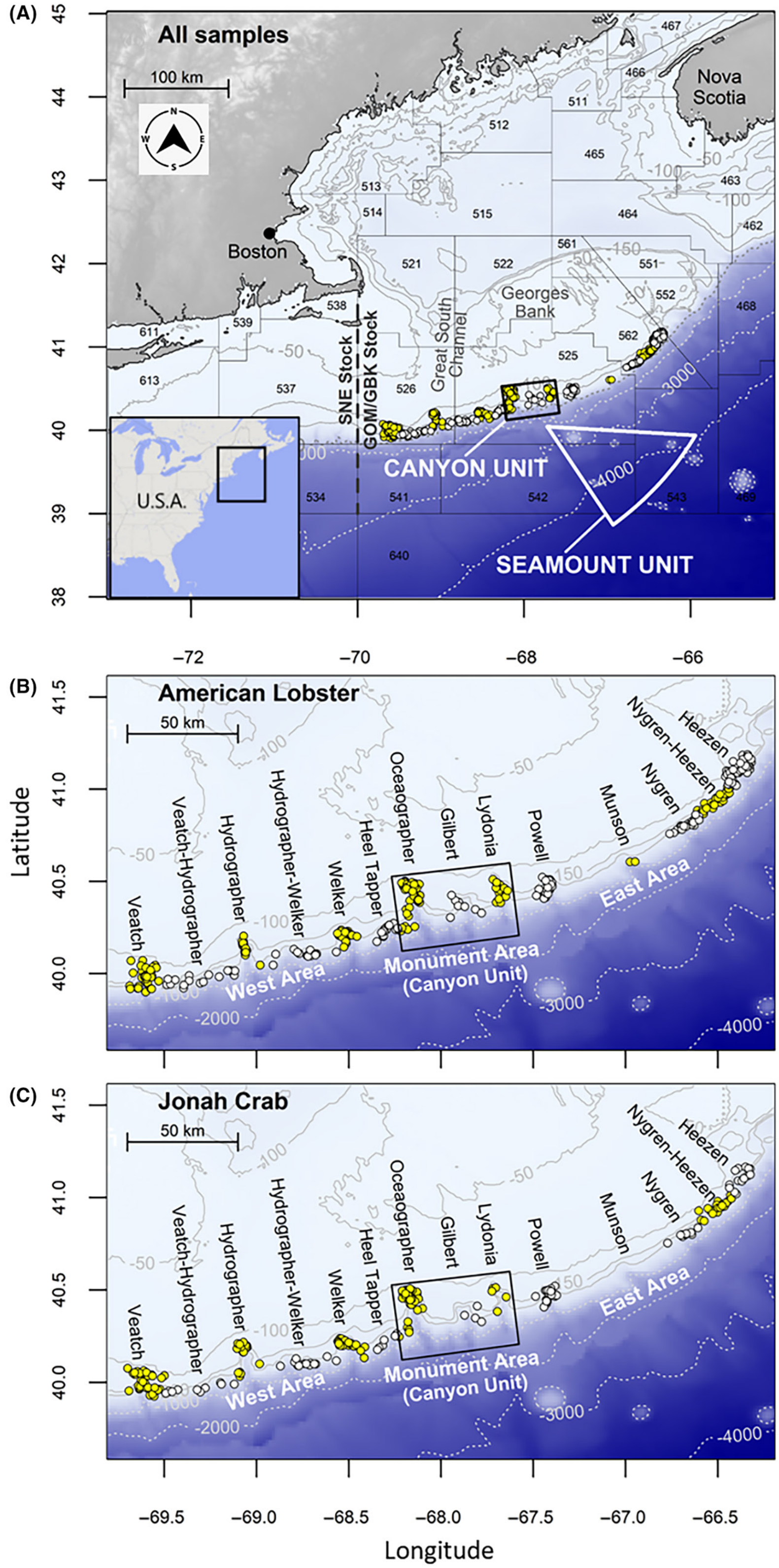


**FIGURE 1** American lobster and Jonah crab sampling sites, showing (A) a regional overview of all sampling sites in the vicinity of the Northeast Canyons and Seamounts Marine National Monument (comprising a Canyon Unit and a Seamount Unit). Numbered boxes are NOAA statistical areas. The vertical dashed line separates American lobster stocks (Southern New England; Gulf of Maine and Georges Bank). Panel (B) shows a detailed view of American lobster sampling sites inside the marine protected area (Monument Area) and outside its boundaries (West Area and East Area). Panel (C) shows a detailed view of Jonah crab sampling sites. In all panels, isobaths show depths in meters. Alternating groups of yellow and white circles distinguish between sampling sites of neighboring submarine canyons or intercanyon breaks (canyon names are shown in panels B and C; hyphenated names represent intercanyon breaks—i.e., shelf edge between two canyons).

typically catches less than 30 lobsters per year within the full latitudinal and longitudinal range of the areas we sampled in this study (ScienceBase 2022). Furthermore, the trawl survey is unable to sample structurally complex benthic habitats occupied by American lobster and Jonah crab.

The primary source of offshore data used in American lobster and Jonah crab stock assessments comes from the Commercial Fisheries Research Foundation's American Lobster and Jonah Crab Research Fleet (Mercer et al. 2018; ASMFC 2020, 2021; Ellertson et al. 2022). The Research Fleet leverages commercial fishing activity to scientifically collect fishing effort and fishery-dependent biological data. Part of the Research Fleet operates on the continental shelf break along the southern edge of Georges Bank, which includes submarine canyons in the vicinity of the Monument.

In this study, we used data from the Research Fleet to describe the demographics of American lobster and Jonah crab populations inside the Monument's Canyon Unit and two areas outside the Monument spanning 130 km to the east and west (Figure 1A). We analyzed data from 2013 to 2021, prior to the scheduled 2023 ban on commercial harvest. Our primary goal was to establish baseline information for a before-after–control-impact study (Seger et al. 2021). These reference data provide essential information needed for evaluating any future population changes and for identifying specific MPA effects from other, unrelated spatial and temporal signals. Our data also provide important biological information for stock assessment scientists, especially for Jonah crab, which is considered a data-poor species (ASMFC 2021).

# METHODS

## Study site

Information about the Northeast Canyons and Seamounts National Monument is available from NOAA (NOAA 2022). The Monument is located approximately 200 km southeast of Cape Cod, Massachusetts. It was enacted in 2016 as the first U.S. National Monument in Atlantic waters and comprises two distinct areas: a Canyon Unit (approximate center at 40.4°N, 67.9°W), which spans a 2437 $km^2$ section of the continental shelf break to the south of Georges Bank, and a Seamount Unit (39.6°N, 66.9°W), which covers a 12,725 $km^2$ area further offshore, beyond the shelf break. Both units are highly biodiverse and harbor deep shelf fauna that includes invertebrates, fishes, sea corals, sponges, chemosynthetic communities, cetaceans, sea turtles, and seabirds (Brooke and Ross 2014; Auster et al. 2020). Historically, the Monument has supported commercial fisheries targeting American lobster (ASMFC 2020), Jonah crab (ASMFC 2021), longfin squid *Doryteuthis pealeii*, and a range of finfish including Butterfish *Peprilus triacanthus*, Atlantic Mackerel *Scomber scombrus*, Swordfish *Xiphias gladius*, and five species of tuna *Thunnus* spp. (Lynham 2022).

This study focuses on the Canyon Unit and areas to its west and east (Figure 1A), where a commercial fishery for American lobster began in the early 1900s and expanded after the 1950s (Schroeder 1959; Skud 1969). Jonah crab was primarily a bycatch species before 2000 but it has developed into a targeted fishery in more recent years (ASMFC 2021).

We acquired American lobster and Jonah crab sample data from submarine canyons and intercanyon breaks along the edge of the continental shelf, both inside the Monument boundaries (Monument area), as well as 130 km to the west (West area) and 130 km to the east (East area) of the Monument boundaries (Figure 1B,C). The West and East areas were chosen as reference sites for a before-after–control-impact study (Seger et al. 2021) designed to assess the effects of fishing closures inside the Monument. Samples from inside the Monument area came from Oceanographer Canyon, Gilbert Canyon, and Lydonia Canyon. Samples from the West area came from Veatch Canyon, Veatch–Hydrographer Break (shelf edge between canyons), Hydrographer Canyon, Hydrographer–Welker Break, Welker Canyon, and Heel Tapper Canyon. Samples from the East area came from Powell Canyon, Munson Canyon, Nygren Canyon, Heezen–Nygren Break, and Heezen Canyon.

## Sampling

The American Lobster and Jonah Crab Research Fleet was established by the Commercial Fisheries Research Foundation (Rhode Island) in 2013 to provide biological data for stock assessments and management plans (Ellertson et al. 2022). Details of the methods used are provided by Mercer et al. (2018). In brief, participating commercial fishers used a specialized computer tablet application and digital calipers to record in situ information about American lobster and Jonah crab specimens caught using commercial traps during routine commercial fishing operations. Each sampling session consisted of data collected by a single vessel on a single day and from a single submarine canyon or canyon break (shelf edge between two neighboring canyons; Figure 1). Variables recorded for each session included the following: latitude, longitude, NOAA Fisheries statistical area, date, time, and depth. Variables recorded from each specimen included the following: sex (based on anatomy of the first pair of pleopods for American lobster or abdomen shape for Jonah crab), size to the nearest millimeter (carapace length for American lobster, carapace width for Jonah crab), female egg status (ovigerous or nonovigerous, based on the presence of eggs attached to pleopods), and shell softness (hard or soft, the latter implying a recent molt). For American lobster, shell disease status (Castro et al. 2006) was also assessed (1 = diseased, 0 = not diseased, based on the presence or absence of shell lesions and/or erosions).

## Analysis of fishing session depths

Fishing session depths were compared between areas and seasons using linear mixed-effect models, implemented with the lmer function in the lme4 R package (Bates et al. 2015). Area, season, and their interaction term were entered as fixed factors, and fishing vessel was entered as a random factor. Seasons were categorized as winter (January–March), spring (April–June), summer (July–September), and fall (October–December).

In the analyses of specimen data (presented below), depth was categorized into two depth zones: a depth zone ≤250 m and a depth zone >250 m, based on a roughly equal split in the data (for American lobster, 250 m was the 51st percentile of session depths; for Jonah crab, 250 m was the 62nd percentile).

## Analysis of body size data

To compare body size data, linear mixed-effect models were implemented using the lmer function in the lme4 R package (Bates et al. 2015). Separate analyses were performed at two spatial scales: (1) a broad-scale comparison between areas (West, Monument, and East) and (2) a fine-scale comparison between canyons (and intercanyons breaks). When comparing areas, the mixed-model fixed factors included area, sex, season, and depth zone. Two-way interactions between the fixed factors were also included. Fishing vessel, fishing session, and canyon were entered as random factors. When comparing canyons, area was replaced by canyon as a fixed factor (and canyon was removed as a random factor). Data from Munson Canyon were excluded from the canyon models because it was poorly sampled (Figure 1B,C), and the canyon × season interaction term was not tested due to insufficient data.

The initial version of each model was simplified by backward elimination of nonsignificant terms, evaluation of Akaike information criteria (AIC), and chi-square model comparisons. Pairwise differences between fixed factors retained in the final models were evaluated using the emmeans function in the emmeans R package (Lenth 2022), with the implementation of a Bonferroni correction factor. To assess the partial effect size of fixed factors, Cohen's *F* was calculated using the cohens_f function of the effectsize R package (Ben-Shachar et al. 2020), adopting the convention that terms with a Cohens *F*-value ≥0.10 had a small partial effect size, those ≥0.25 had a medium partial effect size, and those ≥0.40 had a large partial effect size (Cohen 1988).

## Analysis of binary data

Binary response variables included sex ratio (female = 1, male = 0), shell softness (soft = 1, hard = 0), shell disease (diseased = 1, nondiseased = 0; lobsters only), and female egg status (ovigerous, with eggs attached to pleopods = 1, nonovigerous = 0). Results from the analyses of each variable are reported as percentages (i.e., percent females, percent with soft shells, etc.).

Binary variables were analyzed using the generalized linear mixed-effects models (glmer) function of lme4 package (Bates et al. 2015). To test whether proportions varied across a broad spatial scale, area, season, and depth zone were entered as fixed factors (interactions terms were not included because they caused model convergence issues). Fishing vessel, fishing session, and canyon were entered as random factors. When analyzing proportions of ovigerous females, male data were excluded from the model. When analyzing shell softness and shell disease, an explanatory variable with combined sex and egg condition was included as a fixed factor (i.e., each individual categorized as either a male, an ovigerous female, or a nonovigerous female).

To test for differences at a smaller spatial scale, canyon was entered as a fixed factor (instead of area), and fishing vessel and fishing session were entered as random factors. Munson Canyon was excluded due to insufficient sampling (see Figure 1B,C).

Analyses of the binary response variables were more problematic than the size data because singular fit or model convergence issues sometimes occurred. In some cases, it was possible to negate these issues by adjusting the complexity of the analysis (e.g., dropping poorly sampled canyons; such cases are reported in the results), but in other instances, rigorous conclusions could not be drawn. Binary variables that were not analyzed include the following: canyon-level models of American lobster shell softness and

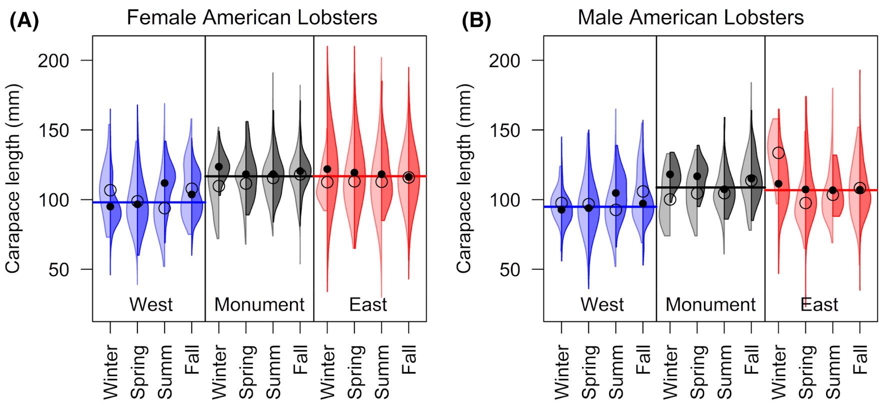


**FIGURE 2** Plots showing smoothed size distributions of (A) female and (B) male American lobster carapace lengths, grouped by area, season, and depth zone. Within each season, the left distribution (lighter shade) represents depths ≤250 m (open circle = mean), and the right distribution (darker shade) represents depths >250 m (filled circle = mean). Colored horizontal lines represent the overall mean within each area. Data were pooled across vessels, sampling sessions, and years. Colors denote sampling area (West = blue, Monument = gray, and East = red).

shell disease, the area-level model of Jonah crab shell softness, and all Jonah crab canyon-level models.

# RESULTS

## Samples

### American lobster

A total of 16,364 American lobsters were sampled from 2013 to 2021 by nine vessels that performed 388 sampling sessions (Tables S1 and S2 available in the Supplement separately online). Mean sampling depths of the American lobster sessions were 257 m (range = 108–439 m), 203 m (77–357 m), and 366 m (91–487 m) in the West, Monument, and East areas, respectively. Mean sampling depth varied significantly between areas ($p < 0.001$) and seasons ($p < 0.001$), with a significant interaction between area × season ($p < 0.001$; Figure S1A available in the Supplement separately online).

### Jonah crab

A total of 14,620 Jonah crab specimens were sampled from 2014 to 2021 by nine vessels that performed 242 sampling sessions (Tables S3 and S4). Mean sampling depths of Jonah crab sessions were 210 m (range = 108–375 m), 174 m (110–320 m), and 304 m (91–461 m) in the West, Monument, and East areas, respectively. Mean sampling depth varied significantly between areas ($p < 0.001$) and seasons ($p < 0.001$), with a significant interaction between area × season ($p < 0.001$; Figure S1B).

## American lobster variation between areas

### American lobster sizes

Plots of the American lobster carapace length data, pooled across vessels, sampling sessions, and years, showed that lobsters from the West area were generally smaller than those from the Monument and East areas (Figure 2).

Results from the mixed model found significant effects of sex ($p < 0.001$), depth zone ($p < 0.01$), and season ($p = 0.02$). Area, by itself, was not significant ($p = 0.06$), but there was a significant interaction between area × sex ($p < 0.001$). Area had a large partial effect size in the model (Cohen's $F = 0.66$) compared with the other fixed-factor terms, which had small partial effect sizes (Cohen's $F$ ranging from 0.10 to 0.17). Female lobsters were significantly larger than male lobsters ($p < 0.001$) when averaged across factors other than sex. Pairwise comparisons between areas revealed that female lobsters in the West area were smaller than those in the Monument area ($p = 0.01$) and East area ($p < 0.01$). Lobsters collected from deeper than 250 m were generally larger than those from shallower depths ($p < 0.01$), and lobsters in the winter and fall were generally larger than those in the summer ($p = 0.04$).

A separate model fit to just the male lobster data (to simplify the model complexity) detected a significant effect of area ($p = 0.02$), as well as depth zone ($p < 0.001$), season ($p < 0.001$), depth zone × area ($p < 0.001$), and depth zone × season ($p < 0.01$). Averaging across other factors, male lobsters from the West area were significantly smaller than those from the Monument area ($p = 0.02$) and East area ($p = 0.05$). Males from depths >250 m were also larger than males from depths ≤250 m ($p < 0.001$), and males in the fall were larger than males in the spring ($p < 0.001$) and summer ($p < 0.01$). The significant interaction terms were caused by the area differences and seasonal differences being significant in the deeper zone (>250 m) but not in the shallower zone (≤250 m). Area had a large partial effect size in the male model (Cohen's $F = 0.84$), whereas the other terms had small partial effect sizes (range of Cohen's $F = 0.19$–$0.23$).

### American lobster sex ratios

The overall proportion of female lobsters was 70.5% (11,531/16,364). By area, the proportions were 51.4% in the West area (3113/6056 specimens), 72.6% in the Monument area (1717/2365), and 84.4% in the East area (6701/7943), with the West area having a significantly lower proportion of females than the Monument area ($p < 0.01$) and the East area ($p < 0.001$). Seasonally, the proportion of females was significantly lower in the fall compared with the spring when averaged across areas ($p = 0.04$; Figure 3A).

### American lobster ovigerous females

The smallest ovigerous female lobster was 75 mm. Among female lobsters ≥75 mm, 30.6% were ovigerous (3487/11,403), with 20.9% in the West area (629/3012), 38.7% in the Monument area (661/1709), and 32.9% in the East area (2197/6682). There was no significant difference between areas ($p > 0.9$), but there was a significantly greater proportion of ovigerous females in the shallower depth zone (≤250 m) compared with deeper depth zone ($p < 0.001$). Seasonally, the proportion of ovigerous females peaked in spring (spring vs. summer, $p < 0.001$; spring vs. fall, $p = 0.01$) and declined to a minimum in summer (summer vs. all other seasons, $p < 0.01$; Figure 3B).

### American lobster soft shells

The proportion of soft-shell individuals among the total catch of American lobster was 2.2% (368/16,364). Soft shells were less common among ovigerous females (0.1%, 5/3483) compared with nonovigerous females ($p < 0.001$; 2.0%, 162/7881) and males ($p < 0.001$; 4.2%, 201/4632), but there was no difference between nonovigerous female and male lobsters ($p = 0.37$; Figure 4). There was no significant difference between areas ($p \geq 0.623$), seasons ($p \geq 0.593$), or depth zones ($p > 0.20$).

### American lobster shell disease

The proportion of all lobsters with shell disease was 1.8% (294/16,364). Prevalence was 4.0% in ovigerous females (138/3488), 1.6% in nonovigerous females (129/8043), and 0.6% in males (27/4833), with each group differing significantly from each other ($p < 0.001$; Figure 5A). There was no significant difference between areas ($p > 0.9$), but shell disease was less prevalent in fall compared with spring ($p < 0.001$) and summer ($p = 0.03$; Figure 5B).

## American lobster variation between canyons

### American lobster sizes

Plots of the American lobster carapace length data by canyon revealed that the smaller mean carapace lengths in the West area (reported above) were mainly attributable to the two westernmost canyons (Veatch and Hydrographer) and their neighboring intercanyon breaks (Figure 6A,B).

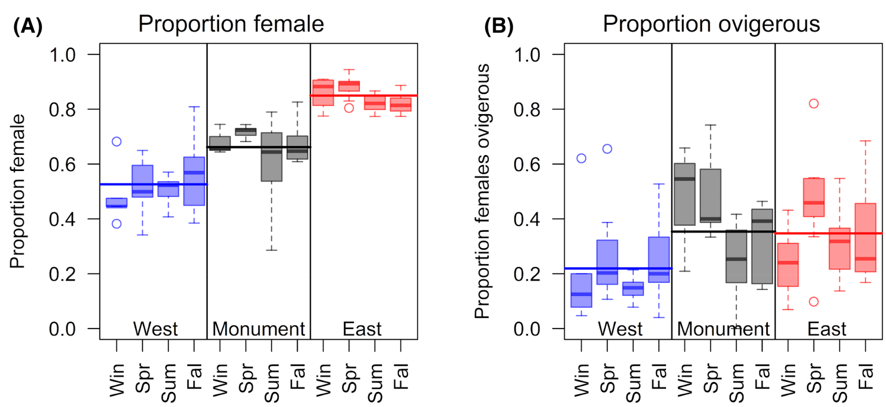


**FIGURE 3** The proportion of American lobsters sampled that were (A) female and (B) the proportion of female lobsters that were ovigerous. Box plots show variation in annual proportions by area and season, where the horizontal line in each box represents the median, the box spans the interquartile range (IQR), the upper whisker extends to the upper observed value lying within 1.5× the IQR above the 75th percentile, the lower whisker extends to the lower observed value lying within 1.5× the IQR below the 25th percentile, and circles show values that outside the whisker range. Wide horizontal lines represent the mean of each area. Colors denote sampling area (West = blue, Monument = gray, and East = red).

The model exploring canyon effects on lobster carapace length showed significant effects of canyon ($p<0.01$), sex ($p<0.001$), depth zone ($p<0.01$), and season ($p<0.01$), as well as significant effects of all the two-way interaction terms ($p \leq 0.03$), except for depth × sex ($p=0.78$) and canyon × season (not tested due to insufficient data). Canyon had a large partial effect size in the model (Cohen's $F=3.48$), canyon × depth had a medium partial size effect (Cohen's $F=0.33$), and the remaining terms had small partial effect sizes (Cohen's $F=0.02$–$0.23$).

Within the West area, pairwise comparisons between canyons showed that lobster sizes decreased significantly towards its western boundary: sizes were significantly smaller in Veatch Canyon and Veatch–Hydrographer Break compared with the more easterly Hydrographer–Welker Break, Welker Canyon, and Heel Tapper Canyon ($p \leq 0.01$; differences were detected in both sexes, in both depth zones, and across multiple seasons). Female lobsters deeper than 250 m were also significantly smaller in Hydrographer Canyon compared with the more easterly Welker and Heel Tapper Canyons.

Within the Monument area, no significant pairwise differences were detected between canyons. Within the East area, lobster sizes were generally similar among canyons, except females from deeper than 250 m were smaller in Powell Canyon compared with those in Heezeen–Nygrene Break ($p<0.01$).

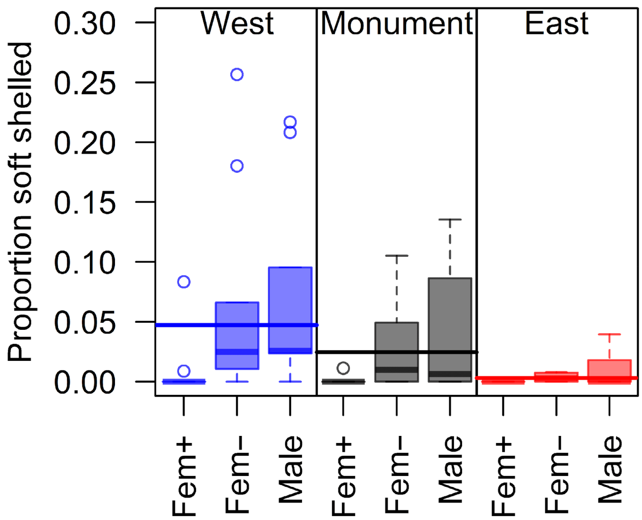


**FIGURE 4** Proportion of American lobsters with soft shells, grouped by area, sex, and egg status (Fem+ and Fem− represent ovigerous and nonovigerous females, respectively). Box plots show variation in annual proportions by group, where the horizontal line in each box represents the median, the box spans the interquartile range (IQR), the upper whisker extends to the upper observed value lying within 1.5× the IQR above the 75th percentile, the lower whisker extends to the lower observed value lying within 1.5× the IQR below the 25th percentile, and circles show observed values outside the whiskers. Wide horizontal lines represent the mean of each area.

## American lobster sex ratios

The proportion of female lobsters varied significantly among canyons. There was a general transition from lower female proportions in the west (about 50%) to higher female proportions in the east (about 85%). The canyons and intercanyon breaks fell into three main groups: a westerly group from Veatch Canyon to Hydrographer–Welker Break, a central group from Welker Canyon to Oceanographer Canyon, and an easterly group from Gilbert Canyon to Heezen Canyon (Figure 6C). These groupings spanned the boundaries separating the Monument area from the West and East areas. Within each group, canyons or intercanyon breaks did

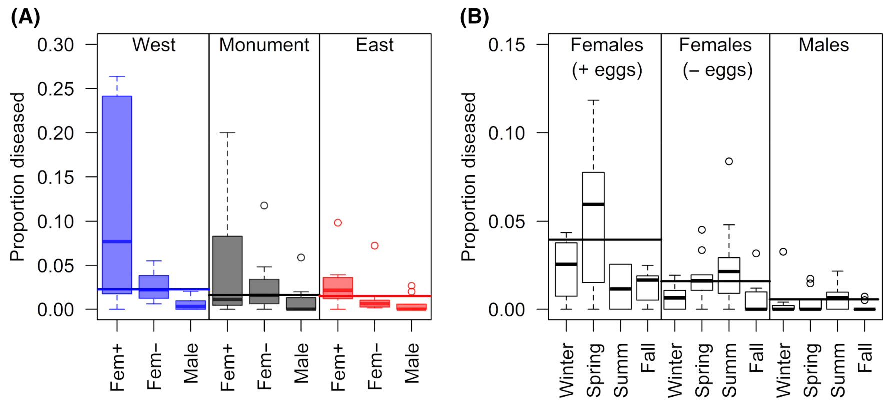


**FIGURE 5** Proportion of American lobsters with shell disease, plotted (A) by area and (B) by season. Lobsters were grouped by sex and egg status (Fem+ and Fem− represent ovigerous and nonovigerous females, respectively). Box plots show variation in annual proportions by group, where the horizontal line in each box represents the median, the box spans the interquartile range (IQR), the upper whisker extends to the upper observed value lying within 1.5× the IQR above the 75th percentile, the lower whisker extends to the lower observed value lying within 1.5× the IQR below the 25th percentile, and circles show observed values outside the whiskers. Wide horizontal lines represent the mean of each area.

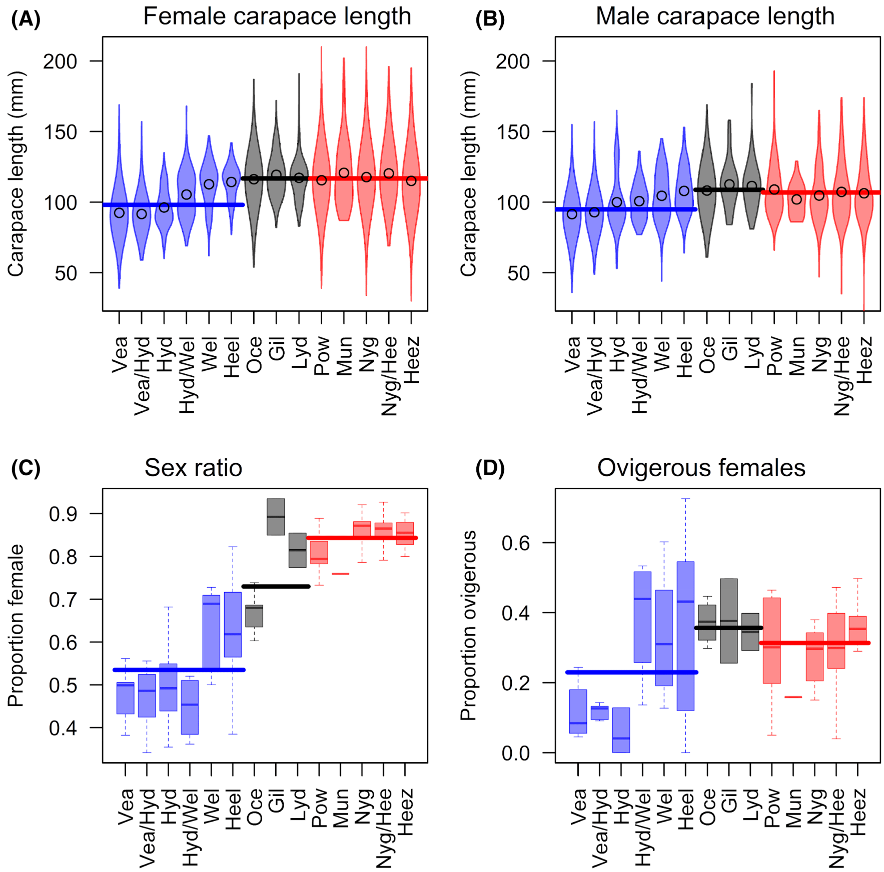


**FIGURE 6** Variation in American lobster traits between canyons, showing (A) size distribution of females, (B) size distribution of males, (C) sex ratio, and (D) proportion of female lobsters that were ovigerous. Plots of carapace length (panels A and B) show smoothed size distributions of data pooled across seasons and depth zones; circles represent mean values. Box plots of sex ratio and ovigerous data show variation in annual proportions by group, where the horizontal line in each box represents the median, the box spans the interquartile range (IQR), the upper whisker extends to the upper observed value lying within 1.5× the IQR above the 75th percentile, the lower whisker extends to the lower observed value lying within 1.5× the IQR below the 25th percentile, and circles show observed values outside the whiskers. Canyons and intercanyon breaks are ordered from west to east along the *x*-axis (see Figure 1 for full names). Wide horizontal lines represent the mean of each area, pooled across canyons and intercanyon breaks (West = blue, Monument = gray, and East = red).

not differ significantly from one another (pairwise comparisons, $p \geq 0.396$; Powell Canyon vs. Nygren Canyon was an exception, $p = 0.04$), but they differed significantly from the canyons and intercanyon breaks elsewhere ($p < 0.01$; Heel Tapper Canyon vs. Powell Canyon was an exception, $p = 0.07$).

### American lobster ovigerous females

The proportion of female lobsters that were ovigerous differed significantly among canyons and intercanyon breaks and were split into two main groups (Figure 6D). The first group, at the western end of the study area, had a lower proportion of ovigerous females and included Veatch Canyon, Veatch–Hydrographer Break, and Hydrographer Canyon. None of these three locations differed significantly from one another ($p \geq 0.9$). The second group, which had a higher proportion of ovigerous females, spanned Hydrographer–Welker Break through Heezen Canyon, and none of these locations differed from one another ($p \geq 0.9$). There was a sharp transition between Hydrographer Canyon and Hydrographer–Welker Break, with a significant difference between these two adjacent locations ($p < 0.001$). Other locations within the more westerly group also had significantly lower proportions than the more easterly Gilbert Canyon, Lydonia Canyon, Powell Canyon, Heezen–Nygren Break, and Heezen Canyon (*p*-values ranging from 0.05 to <0.001).

## Jonah crab variation between areas

### Jonah crab sizes

Initial analyses of the Jonah crab data showed that most of the specimens were male (12,609/14,020) and that mean carapace width was significantly larger ($p < 0.001$) in male crabs (136.0 mm) than female crabs (108.9 mm). Significant interactions occurred between sex and depth zone ($p<0.001$), sex and area ($p<0.001$), and sex and season ($p<0.001$). To simplify the analyses, male and female data were modeled separately.

Female carapace width did not vary between areas ($p=0.43$), seasons ($p=0.06$), or depth zones ($p=0.60$), and none of the two-way interaction terms were significant (Figure 7A). Similarly, male carapace width did not differ between areas ($p=0.68$), and there was no significant effect of season ($p=0.83$), depth zone ($p=0.06$), or any of the two-way interaction terms ($p\geq0.27$; Figure 7B).

### Jonah crab sex ratios

The proportion of females among the total Jonah crab catch was 13.8% (2011/14,620), with 14.7% occurring in the West area (1115/7610), 16.8% in the Monument area (536/3188), and 9.4% in the East area (360/3822; Figure 8A). There was no difference between areas ($p\geq0.13$), but the proportion of female crabs was significantly greater in the shallow zone (≤250 m) versus the deep zone (>250 m; 17.0% vs. 9.0%, respectively, $p<0.001$), and seasonal variation occurred (fall peak of 18.2% vs. spring low of 10.1%, $p=0.02$).

### Jonah crab ovigerous females

The smallest ovigerous female Jonah crab had a carapace width of 75 mm. Among females ≥75 mm, 4.9% were ovigerous (98/1983), with 5.3% occurring in the West area (59/1101), 7.4% in the Monument area (39/525), and 0.0% in the East area (0/357; Figure 8B). Seasonally, the proportion of ovigerous females peaked in spring (12.1%), declined in summer (2.8%; spring vs. summer, $p<0.01$), and no ovigerous females were observed during fall. The effects of area and depth zone were not tested (models failed to converge).

### Jonah crab soft shells

The proportion of soft-shell individuals among the total Jonah crab catch was 0.8% (110/14,620), with 0.7% in the West area (54/7556), 1.3% in the Monument area (43/3145), and 0.3% in the East area (13/3809). Percentages by sex and egg status were 1.8% in nonovigerous females (35/1912), 0.0% in ovigerous females (0/99), and 0.6% males (75/12,609; Figure 8C). Models comparing the effects of area, season, and depth zone were inconclusive (models failed due to the sparsity of soft-shelled crabs).

## Jonah crab variation between canyons

### Johan crab sizes

Female Jonah crab carapace width did not differ between canyons ($p=0.24$), seasons ($p=0.11$), or depth zones ($p=0.82$; Figure 9A). Similarly, male Jonah crab carapace width did not differ significantly between canyons ($p=0.18$), and there were no significant effects of season ($p=0.99$) or depth zone ($p=0.06$; Figure 9B).

## DISCUSSION

This study established baseline biological conditions for American lobster and Jonah crab populations in the relatively inaccessible waters of the Northeast Canyons and Seamounts Marine National Monument, located more than 200 km offshore along the continental shelf break of the northeastern United States. A key finding is that

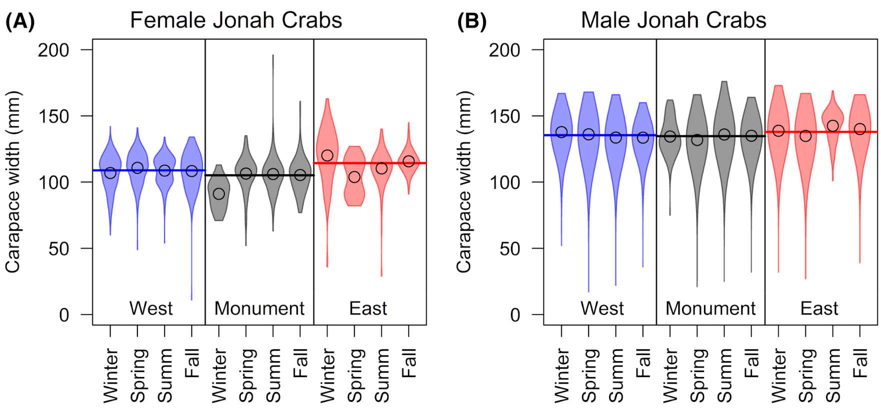


**FIGURE 7** Smoothed size distributions of (A) female and (B) male Jonah crab carapace width, grouped by area and season. Plotted data were pooled across vessels, sampling sessions, and years. Circles represent mean values. Colored horizontal lines represent the overall mean within each area (West = blue, Monument = gray, and East = red).

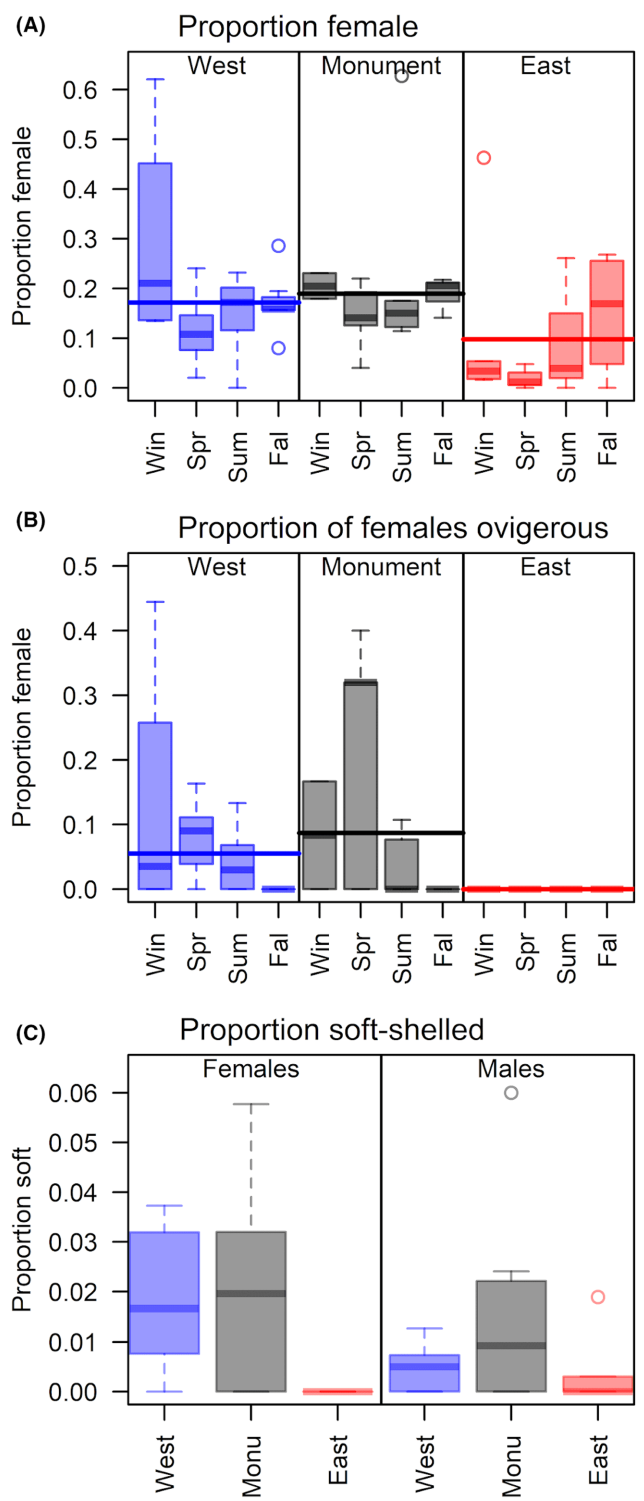


**FIGURE 8** Jonah crab proportion data, including (A) sex ratio (proportion of females), (B) the proportion of female crabs that were ovigerous, and (C) the proportion of crabs with soft shells. Box plots show the variation in annual proportions by group, where the horizontal line in each box represents the median, the box spans the interquartile range (IQR), the upper whisker extends to the upper observed value lying within 1.5× the IQR above the 75th percentile, the lower whisker extends to the lower observed value lying within 1.5× the IQR below the 25th percentile, and circles show observed values outside the whiskers. Wide horizontal lines in panels (A) and (B) represent the mean of each area (West = blue, Monument = gray, and East = red).

American lobster populations varied significantly between our three focal areas (i.e., the West, Monument, and East areas) and that the American lobster and Jonah crab populations varied with season and depth zone or a combination of these two factors (summarized Table 1). With American lobster, there was also evidence of spatial variation at a smaller scale, since differences were detected between canyons and intercanyon breaks. Future studies designed to evaluate the effects of the MPA will need to account for these sources of preexisting variation among populations.

## American lobster sizes

Lobster sizes varied between canyons and areas but also by sex, depth zone, and season. The spatial factors had bigger partial effects in the mixed models than the other factors, indicating that they were responsible for most of the variation in size.

Lobster sizes were generally smaller in the West area compared to the Monument and East areas, with the latter two being relatively similar to one another. The small sizes in the West area were mainly attributable to specimens caught in the two most westerly canyons, Veatch and Hydrographer, and their adjacent intercanyon breaks.

Skud (1969) noted a similar east-to-west decrease in American lobster sizes among canyons along the shelf break, which he attributed to higher fishing pressure in the west. He also found that sizes were smaller during the 1960s compared to the 1950s (McRae 1960), when fishing pressure was lower. In addition, environmental factors may play a role in the east-to-west shift in sizes. Hydrographer and Veatch canyons are situated to the western side of the Great South Channel (Figure 1A), which acts as a partial barrier to lobster migration (Cooper and Uzmann 1971; Uzmann et al. 1977; Estrella and Morrissey 1997), and they are close to the divide between the Southern New England and Gulf of Maine–Georges Bank stocks (Figure 1A).

Female lobsters were generally larger than males, which may be associated with several factors. For example, fishing pressure tends to modify the natural age, size, and sex composition of lobster populations because mature females are often released alive to support egg production. Mature females therefore incur a lower fishing mortality, which allows them to live longer and grow larger than mature males, despite growing slower than them (Chang et al. 2012). In addition, adult American lobsters often migrate seasonally, and different movement patterns by lobsters of different

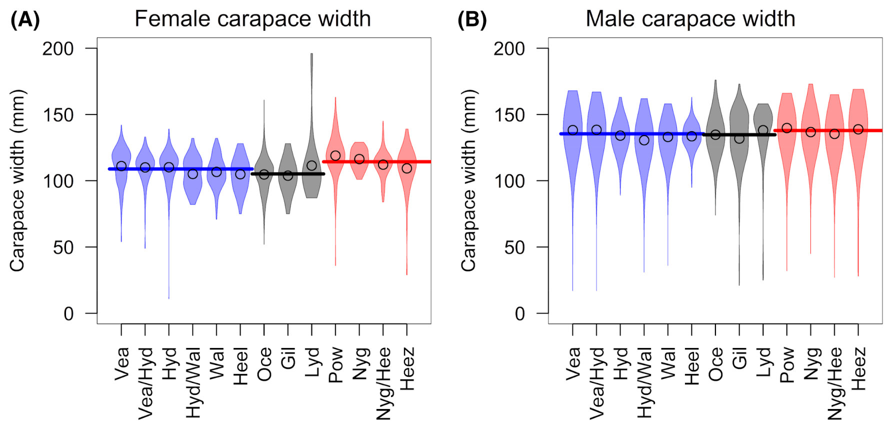


**FIGURE 9** Plots showing size distribution of (A) female and (B) male Jonah crab carapace widths, grouped by canyon and intercanyon breaks (ordered from west to east; see Figure 1 for full names). Plotted data are pooled across vessels, sampling sessions, years, and depths. Circles represent group mean values. Colored horizontal lines represent area mean values. Colors denote sampling areas (West = blue, Monument = gray, and East = red).

**TABLE 1** Summary of factors affecting American lobster and Jonah crab demographic parameters. Yes = significant effect detected, No = no significant effect detected, na = not applicable, and a dash = factor not tested (model limitations). An asterisk indicates that sex and female eggs status were categorized into a single factor with three levels (male, nonovigerous female, ovigerous female). Jonah crab shell disease was not quantified.

| | | Factors | | | | |
|---|---|---|---|---|---|---|
| **Species** | **Parameter** | **Sex** | **Area** | **Season** | **Depth** | **Canyon** |
| American lobster | Size | Yes | Yes | Yes | Yes | Yes |
| | Sex ratio | na | Yes | Yes | No | Yes |
| | Ovigerous females | na | No | Yes | Yes | Yes |
| | Soft shelled | Yes* | No | No | No | – |
| | Shell disease | Yes* | No | Yes | No | – |
| Jonah crab | Size | Yes | No | No | No | No |
| | Sex ratio | na | No | Yes | Yes | – |
| | Ovigerous females | na | – | Yes | – | – |
| | Soft shelled | – | – | – | – | – |

sizes and sexes can result in spatially heterogeneous size and sex distributions (Cooper and Uzmann 1971).

We found that American lobsters were generally larger in the deep zone (>250 m) compared with the shallower zone, as found by Skud (1969). They were also generally larger in winter and fall compared with summer, which matches the reported migration patterns of mature American lobsters on the continental slope (Cooper and Uzmann 1971; Campbell et al. 1984; Campbell and Stasko 1985; Campbell 1986).

## American lobster sex ratios

American lobster sex ratio varied between areas, increasing from approximately 50% females in the West area to more than 80% females in the East area. As with the size data, there was a steep transition in sex ratios across canyons within the West area, with changes occurring in a stepwise manner. By contrast, trawl fisheries encountered ~60% females in canyons along the shelf break during the 1960s (based on reconstructed data from Figures 6 and 7 in Skud 1969), and the most recent American lobster stock assessment (ASMFC 2020) reported a female-skewed sex ratio on Georges Bank, which slopes into the Monument and East areas of our study.

Sex ratio varies widely across the American lobster species' range (ASMFC 2020; Koepper et al. 2021). It is influenced by harvesting pressure since males generally incur higher fishing mortality than females, which can ultimately lead to sperm limitation if populations become heavily female biased (MacDiarmid and Butler 1999; Pardo et al. 2015). Sex ratio can also be affected by localized environmental factors, such as temperature, since mature females tend to favor cooler, deeper waters than males at certain times of the year (Crossin et al. 1998; Cowan et al. 2007). Koepper et al. (2021) found that a combination of fishing pressure and environmental factors affect sex ratios in Nova Scotia waters, with female-skewed sex ratios occurring in areas of high fishing effort and cooler, deeper waters. It is possible, therefore, that future reductions of fishing effort in the Monument will modify sex ratios, presumably towards a lower proportion of females if male-biased fishing mortality is reduced.

## American lobster ovigerous females

Ovigerous female American lobsters have been reported to carry eggs attached to their pleopods for 9–12 months, with peak hatching occurring during summer months (Waddy and Aiken 1995). The female lobsters in our study matched this general seasonal pattern, with the proportion of ovigerous females peaking in spring, then declining in summer. The seasonal changes were probably related to eggs hatching but may also have been affected by ovigerous females migrating towards shallower areas during warmer months (Cooper and Uzmann 1971). Ovigerous females were also more common in depths shallower than 250 m compared with deeper areas, possibly in response to depth-related temperature changes (Campbell 1986; Netburn et al. 2018).

The proportion of ovigerous females did not differ significantly among areas, although within the West area, notable differences occurred at the canyon level. In particular, Veatch and Hydrographer canyons had lower proportions of ovigerous females, which coincided with a lower proportion of females and smaller female sizes.

## American lobster soft shells

There was no significant difference in the frequency of soft-shelled lobsters between areas, seasons, or depth zones, but there was a lower proportion of soft-shelled ovigerous female lobsters compared with nonovigerous females and males. The effect of sex and reproductive condition is not surprising because most mature females switch from an annual molt cycle to a biennial one, and they do not molt while they are carrying eggs (Waddy and Aiken 1986). The lack of a relationship between the frequency of soft-shelled lobsters and depth contrasts with observations from submersible dives in Hydrographer, Oceanographer, and Lydonia canyons, which only recorded American lobsters molting in depths less than 200 m (Uzmann et al. 1977).

## American lobster shell disease

Shell disease was rare among American lobsters in our study (1.8% overall). However, it was significantly more common in ovigerous females (~4%) and less common among males (<1%), as found by others (Castro and Somers 2012; Reardon et al. 2018). Higher prevalence in ovigerous females has been related to their longer intermolt times (Waddy and Aiken 1986; Glenn and Pugh 2006; Chang et al. 2012), since shell disease accumulates unless lost by ecdysis (Stevens 2009; Feinman et al. 2017; Barris et al. 2018).

Shell disease in American lobsters has been of increasing concern since the mid-1990s (Shields 2013) and is associated with stressful habitat conditions, especially warm water temperatures (Glenn and Pugh 2006). We did not detect a significant difference between our three study areas, although shell disease is more prevalent in the Southern New England stock, which lies adjacent to our West area (Barris et al. 2018).

Shell disease was less prevalent in fall compared with other seasons. Other studies have found a similar decrease in fall and, although we did not detect a seasonal cycle in our soft-shell lobsters, others have linked the fall decrease with a summer peak in molting (Glenn and Pugh 2006).

## Jonah crab

Male Jonah crabs were significantly larger than females, which is consistent with other reports throughout the species' range (Haefner 1977; Wenner et al. 1992; Truesdale et al. 2019; Olsen and Stevens 2020). Unlike American lobster, mean Jonah crab sizes did not vary between areas, canyons, depth zones, or seasons, possibly due to their extensive (>400 km) movement patterns (Perry et al. 2019).

In Canadian waters, to the northeast of our study area, the size distribution of commercially caught Jonah crab males is similar to male sizes in our study (Pezzack et al. 2010). By contrast, in statistical area 537, to the west of our study area (Figure 1A), Truesdale et al. (2019) reported that commercially caught Jonah crab males had a mean carapace width of 126 mm ($n = 8535$), which is smaller than the 136-mm mean male size in our study. This may be associated with higher fishing pressure and a smaller allowable size (121 mm) in statistical area 537, since fishing selectively removes large males from the population due to market preference (ASMFC 2021).

We did not detect a relationship between Jonah crab size and depth, which seems to disagree with the findings of Haefner (1977) and Wenner et al. (1992). However, their studies covered a much broader range of depths

(274–898 m and 15–2000 m, respectively), which likely explains the discrepancy between their studies and ours.

The overall proportion of females was low (~10%) in our Jonah crab samples, which is not surprising because commercial traps select larger individuals from the populations (i.e., the males; Mercer et al. 2018). Nevertheless, female proportion varied between depth zones, with a greater proportion of female crabs caught in the shallow zone (≤250 m; 17.0%) versus the deep zone (>250 m; 9.0%). The higher female proportion in shallower depths agrees with previous studies (Carpenter 1978; Stehlik et al. 1991), possibly because females select warmer waters to enhance reproductive success (Krouse 1980; Wenner et al. 1992).

The proportion of female Jonah crabs also varied seasonally, with a maximum occurring in fall (18.2%) and a minimum in spring (10.1%), which matches the seasonal cycle described on the continental shelf by Haefner (1977) and Stehlik et al. (1991). The proportion of female Jonah crabs that were ovigerous also varied seasonally, with a peak in spring and a significant decline in summer, coinciding with the reported time of molt (Haefner 1977; Truesdale et al. 2019).

## Annual variability

While our analyses examined numerous life history variables of American lobster and Jonah crab across multiyear timeframes, we did not explicitly test for annual patterns of variation. This was partly because our focus was to identify broad spatial effects, while controlling for seasonal and sex effects, but also because model limitations occurred when year was added as an additional factor. Visual inspection of the American lobster data plotted annually implied that carapace length, proportion of females, and proportion of ovigerous females (Figures S2–S4) were relatively stable over the sampling period, whereas soft-shelled American lobsters appeared to become less common during the later years (Figure S5) as shell disease appeared to become more common (Figure S6). With Jonah crab, carapace width was relatively stable across sampling years (Figure S7) as was the proportion of female crabs (Figure S8). The proportion of ovigerous female crabs (Figure S9) and the proportion of soft-shell crabs (Figure S10) appeared more variable, but their noisy signals were likely due to smaller observation numbers, since female crabs and soft-shell crabs were comparatively rare in the Jonah crab catches.

## Monitoring future responses to the MPA

Our study quantified demographic parameters of American lobster and Jonah crab populations inside a recently established MPA (the Northeast Canyons and Seamounts Marine National Monument) and in two areas outside the MPA, to the west and east of its boundaries. American lobsters in the West area were smaller and had a lower proportion of females than those from the Monument and East areas. These differences were mainly attributable to the westernmost canyons within the West area, where females were also less likely to be ovigerous. By contrast, none of the Jonah crab parameters varied significantly between areas or canyons.

Our results describe long-term biological baselines for size, sex ratio, female egg status, molt status, and shell disease status prior to a proposed fixed-gear fishing ban inside the MPA (currently scheduled for September 2023). They provide essential reference points needed for evaluating potential effects of a fishing closure, and they also provide important data that are used in stock assessments (ASMFC 2020, 2021).

Continuing surveys will be needed to evaluate the effectiveness of conservation policies implemented within the MPA once the proposed ban on fixed-gear fishing occurs. To do this, future monitoring programs will need to collect American lobster and Jonah crab data that are comparable with the baseline data described in this study and at a sufficient spatial and temporal resolution. This will require samples to be collected using comparable gear to control for selectivity, and for samples to be collected across a range of depths and seasons, since these factors had additional effects on most of the demographic parameters that were examined.

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## CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

## DATA AVAILABILITY STATEMENT

Data are available through the Atlantic Coastal Cooperative Statistics Program Public Data Warehouse (www.accsp.org).

## ETHICS STATEMENT

This study leveraged commercial fishing effort for all data collection. All fishermen followed specific federal Exempted Fishing Permit guidelines to collect data.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.