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Abstract—Effective assessment and management of migratory species require an understanding of stock boundaries and habitat use during critical life history periods. The blue crab (*Callinectes sapidus*) is considered a primarily estuarine species and has traditionally been assessed and managed on a state basis, relying on abundance estimates derived from estuarine sampling. Females undertake a seaward spawning migration, and recent evidence indicates that coastal and offshore waters may provide important spawning habitat. We investigated occurrence and reproductive output of spawning blue crab in offshore waters of the northwestern Gulf of Mexico, and results indicate that these waters may be an important spawning area for this species. Densities of blue crab were low offshore compared with those in estuaries, but given the large extent of available offshore habitat, the total abundance of adult females is likely similar in offshore and estuarine waters. Analyses of the reproductive output of females collected offshore indicate that they continue to spawn after leaving the estuaries. Fecundity and measures of egg quality were assessed and were similar to previous estimates for estuarine regions. Future management and assessment efforts should account for this previously understudied portion of the blue crab spawning stock.

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Distribution, relative abundance, and reproductive output of spawning female blue crab (*Callinectes sapidus*) in offshore waters of the Gulf of Mexico

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Fisheries management is most effective when the scale of management matches the scale of the stock (Begg et al., 1999; Al-Humaidhi et al., 2013). The modern stock concept describes units of a population that can be considered homogeneous (in terms of life history, responses to environmental fluctuations, genetic diversity, etc.) and can inform the scale of assessments and management decisions (Begg and Waldman, 1999). The failure to correctly identify spatial complexity within a stock has been identified as one of the main factors contributing to the collapse of some high-profile fisheries in the recent past (Hutchinson, 2008), and studies examining genetic stock structure have identified cases with clear mismatches between the genetic stock structure and the management of the stock as a singular unit (Bonanomi et al., 2015; Kerr et al., 2017).

Migratory stages are common in marine and estuarine species (e.g., Forward and Tankersley, 2001; Potter et al., 2015; Secor, 2015). Large-scale seasonal or annual movements can complicate fisheries management because different life stages may occupy different habitats. For these species, understanding habitat use during critical life history stages (e.g., spawning) is particularly important in the context of temporal or spatial management actions (e.g., season and area closures, spawning sanctuaries, migratory corridors, and ecosystem-based management).

Blue crab (*Callinectes sapidus*) support highly valuable fisheries along the Atlantic and Gulf coasts of the United States, with landings in 2018 totaling over 62,000 metric tons and having a wholesale value of over $193 million (NMFS[1]). Following their terminal molt, female blue crab mate and store the sperm necessary for their life-long reproductive output (Millikin and Williams, 1984). After mating, female blue crab forage for several weeks (Turner et al., 2003) before beginning a seaward spawning migration (Aguilar et al., 2005). This migration ensures that females reach spawning grounds of sufficiently high salinity (>20.1; Costlow and Bookhout, 1959)

[1] NMFS (National Marine Fisheries Service). 2020. Fisheries of the United States, 2018. NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 2018, 140 p. [Available from website.]

for larval survival. Spawning female blue crab are often found in large numbers at or near the mouths of estuaries (e.g., Rittschof et al., 2010; Anderson et al., 2017); these areas are typically assumed to be the primary spawning grounds. The blue crab is a highly fecund species, with females producing multiple clutches of several million larvae at a time (Hines et al., 2003). Each brood of larvae is released into the water column as zoeae that disperse through currents for 30–50 d (Costlow and Bookhout, 1959) before their return and recruitment to coastal habitat as megalopae soon after (Rabalais et al., 1995; Ogburn et al., 2009).

Mature females can travel great distances (>200 km; Aguilar et al., 2005) during their spawning migration, and migration rates can exceed 8 km/d (Carr et al., 2004). Female blue crab continue migrating throughout their reproductive period (Hench et al., 2004) and are, therefore, likely moving out of estuaries and continuing their migration in offshore waters. Adults of this species typically are considered estuarine, but large numbers of spawning female blue crab have been found in waters off both the Atlantic coast (Rittschof et al., 2010; Ogburn and Habegger, 2015) and Gulf coast (Gelpi et al., 2009, 2013) of the United States. Although observed densities of blue crab are typically lower offshore than in estuaries, evidence from the Atlantic coast of the southeastern United States indicates that this often-overlooked offshore population may represent a substantial fraction of the regional spawning stock (Ogburn and Habegger, 2015). In the Gulf of Mexico, Gelpi et al. (2009, 2013) found large numbers of spawning females residing on Ship, Trinity, and Tiger Shoals and surrounding waters, 20–40 km off the coast of Louisiana. All developmental stages of eggs were observed, and 81% of females had full ovaries at the time of capture, indicating that they would continue to spawn at least one additional clutch of eggs during the season (Gelpi et al., 2009). Furthermore, spawning female blue crab are regularly captured in trawl surveys conducted by the Southeast Area Monitoring and Assessment Program (SEAMAP) in the Gulf of Mexico, as far as 200 km offshore.

Given the large extent of relatively shallow offshore habitat in the Gulf of Mexico and with offshore habitat proving to be of larger importance to the spawning stock of blue crab in the Atlantic Ocean than previously thought (Ogburn and Habegger, 2015), we sought to identify the contribution of this offshore habitat to the spawning stock of blue crab in the northwestern Gulf of Mexico. The goal of this study was to conduct an investigation of spawning female blue crab in offshore waters of the northwestern Gulf of Mexico. We examined temporal and spatial variation in catch of blue crab in fishery-independent SEAMAP groundfish trawl surveys over a 20-year period (2000–2019) and examined the reproductive output and overall condition of females collected in offshore waters during the SEAMAP groundfish trawl surveys in 2017. We also compared results for spawning females found offshore in our study with previous findings for blue crab found spawning in inshore areas.

Materials and methods

Survey design and methods

The SEAMAP involves the cooperation of state, federal, and university partners for the collection of fishery-independent data. The SEAMAP-Gulf of Mexico groundfish trawl survey is conducted twice each year during summer and fall at distances from shore up to 370 km (200 nautical miles) and at depths up to 109.7 m (60 fathoms). The summer survey typically occurs in June and July but can start as early as May and end as late as August. The fall survey typically occurs during October and November but can start as early as September and end as late as December. Sampling is done by using a stratified random design and a 12.2-m (40-ft) trawl net with stretched mesh of 40.3–41.9 mm. Environmental conditions, including salinity and temperature, were measured either at 3 positions in the water column, the surface, mid-water, and bottom, or through a profile of the full water column at each sampling location.

Prior to fall 2008, sampling was stratified by depth (with 23 depth strata, including 1-fathom strata for 5–20 fathoms, a 2-fathom stratum of 20–22 fathoms, a 3-fathom stratum of 22–25 fathoms, 5-fathom strata for 25–50 fathoms, and a single stratum of 25–50 fathoms), by geographic area (based on groupings of 2–3 shrimp statistical zones [SSZ], which are defined by the National Marine Fisheries Service), and by time of day (day or night) (Nichols[2]). Trawl tows were conducted perpendicular to the depth contours and covered the entire depth stratum at each sampling location. Tow time ranged from 10 to 55 min; if sufficient depth coverage was not possible in a single 55-min tow, multiple consecutive tows were conducted. Sampling was limited to SSZ 11–21. A survey design change occurred between summer and fall 2008. Under the new survey design, selection of sampling locations was stratified by individual SSZ (Fig. 1), and sampling extended into the eastern Gulf of Mexico. The stratifications for time of day and for depth were dropped. In 2014, depth stratification resumed with 2 depth strata: 5–20 fathoms and 20–60 fathoms (Pollack et al.[3]). The number of randomly selected sampling locations (stations) within each stratum that combined geographic area and depth was proportional to the geographic area of that stratum. The trawl was towed for 30 min at each sampling location.

For all tows, abundance of each species in the catch was recorded. In the case of an extremely large catch (typically >22.7 kg), the catch was subsampled and total abundance of each species was extrapolated. For blue crab, carapace widths (CWs), measured as the distance between the tips of the lateral spines, of up to 20 individuals

[2] Nichols, S. 2004. Derivation of red snapper time series from SEAMAP and groundfish trawl surveys. Southeast Data Assess. Rev. SEDAR7-DW-01, 26 p. [Available from website.]

[3] Pollack, A. G., D. S. Hanisko, and G. W. Ingram Jr. 2016. Wenchman abundance indices from SEAMAP groundfish surveys in the northern Gulf of Mexico. Southeast Data Assess. Rev. SEDAR49-DW-19, 27 p. [Available from website.]

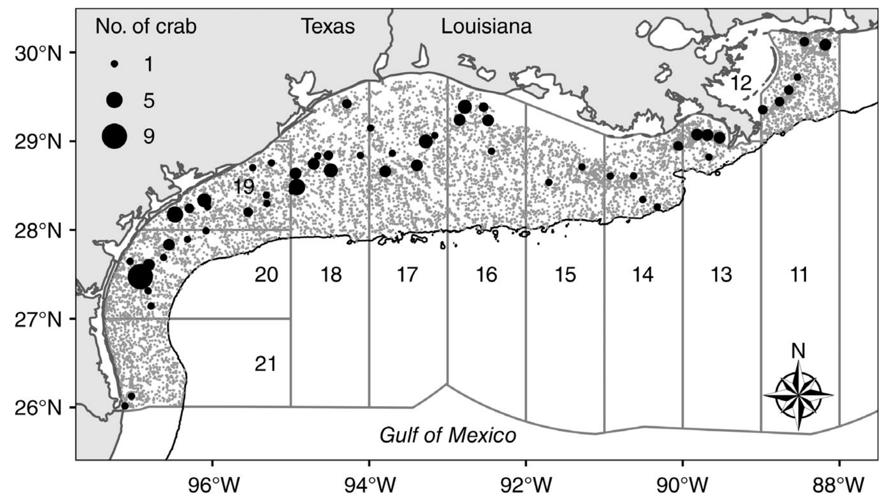

Figure 1

A map of the study area in the northwestern Gulf of Mexico showing the locations where blue crab (*Callinectes sapidus*) were collected in groundfish trawl surveys as part of the Southeast Area Monitoring and Assessment Program (SEAMAP). Small gray dots indicate locations of trawl tows for the study period 2000–2019. Black circles indicate locations where adult female blue crab were caught, for reproductive analyses, during the SEAMAP groundfish surveys conducted in 2017, with circle size proportional to the number of blue crab collected from that location. The boxes outlined in gray and the numerals inside them indicate shrimp statistical zones (defined by the National Marine Fisheries Service), which were used in the stratified random sampling design. The black line indicates the 109.7-m (60-fathom) depth contour, which is used as the outer limit for SEAMAP groundfish surveys.

(chosen haphazardly from the total catch) and the sex of every fifth measured crab were recorded for each station (GSMFC[4]).

Long-term patterns of distribution and relative abundance

Our analyses focused on the period 2000–2019 and included only offshore areas that were sampled before and after the change in survey design in 2008 (SSZ 11 and SSZ 13–21). Chandeleur Sound in Louisiana (SSZ 12) was excluded because this inshore area was not consistently sampled. Over this 20-year period, 7–119 trawl tows were conducted in each SSZ per year (Suppl. Tables 1 and 2). Data collected prior to 2000 were not included because of uncertainty surrounding species identification. Data were filtered to include only tows of 12.2-m trawl nets with stretched mesh sizes ranging from 40.3 to 41.9 mm and conducted at depths >9.1 m (>5 fathoms). Any sampling events with incomplete data for geographic location or vessel speed or with operation codes indicating a bad tow (e.g., if the doors came up crossed, if the codend came untied, or if the net was fouled or torn) were excluded from analysis.

Maturity stage is not recorded for blue crab; therefore, it was necessary to classify crab as adult or juvenile on the basis of CW. We classified blue crab ≥125 mm CW as adults, following the cutoff used in recent Gulf-wide (VanderKooy, 2013) and state-level (West et al.[5]) blue crab stock assessments. Because not all blue crab are measured and only a small proportion are assigned a sex, it was necessary to estimate the catch of adult female blue crab from each trawl tow by using the total catch multiplied by the proportion of measured blue crab from the tow that were ≥125 mm CW and by the proportion of blue crab from the tow that had their sex determined and that were classified as female:

$$\textit{adult female catch} = \textit{total catch} \times \textit{proportion adult} \times \textit{proportion female}.$$

For a small number of trawl tows (n=385 tows, 4.3% of the tows in the data set used in analysis), sex was not recorded, even though adult blue crab were caught during the tow. For these tows, the mean proportion of

[4] GSMFC (Gulf States Marine Fisheries Commission). 2016. SEAMAP operations manual for trawl and plankton surveys, 61 p. GSMFC, Ocean Springs, MS. [Available from website.]

[5] West, J., H. Blanchet, and P. Cagle. 2019. Update assessment of blue crab in Louisiana waters: 2019 report, 32 p. Louisiana Dep. Wildl. Fish., Baton Rouge, LA. [Available from website.]

crab that were female for that year was used. Sex was not determined for blue crab in 2004; therefore, the overall mean proportion that was female (0.930) was used. Catch per unit of effort (CPUE) of adult female blue crab was calculated by dividing the adult female catch (measured as number of individuals) by the area swept by the trawl (calculated by using the recorded speed and duration of a tow and by assuming a 12.2-m net spread). Values of CPUE are given as number of individuals per hectare.

To examine overall temporal and spatial patterns in CPUE of blue crab in the SEAMAP survey area, adult female catch was modeled by using a 2D generalized additive model (Potts and Rose, 2018) with a negative binomial error distribution and log link function. Multiple candidate models were fit and compared by using Akaike information criteria (AIC) to determine the most appropriate model. Adult female catch was the response variable. Year was included in all models as a categorical variable. Geographic location was included as a 2D smooth function with thin-plate spline bases. Season (summer or fall) was included as an additional temporal covariate. All models also included an offset term for the area swept by the trawl to account for differences in sampling effort among trawl tows. Following model selection, a Wald chi-square test was used to test for significance of predictor variables.

An index of abundance for the spawning stock in the northwestern Gulf of Mexico was estimated to allow examination of population trends, accounting for spatial and temporal variation in sampling effort. Estimated marginal means for each year were extracted from the model output, reflecting the main effect of year averaged over the full study area and across both seasons. Estimated marginal means were then standardized relative to the average annual estimated marginal mean across the study period by using a Z-transformation, providing an index of abundance in units of standard deviations above or below the mean for the 20-year period for which we analyzed survey data.

Relative importance of offshore and estuarine waters

To assess the importance of offshore spawning areas relative to estuarine spawning areas for the spawning stock of blue crab in the Gulf of Mexico, total abundance of adult female blue crab was estimated and compared between offshore and estuarine waters of the study area. Abundance estimates were limited to the areas west of the Mississippi River (SSZ 13–21), because of the lack of consistent and spatially widespread fishery-independent trawl sampling for blue crab in estuarine waters of the state of Mississippi. Temporal coverage of abundance estimates was limited to the period 2006–2018 because of limitations on availability of data for sampling in estuarine areas in other years. Observed CPUE was used as a proxy for density of blue crab. Because gear efficiencies are unknown for the trawl surveys examined in our study, we were unable to correct for gear efficiency; actual densities of blue crab, and therefore abundances, are likely substantially higher than estimates calculated in our study.

Offshore abundance of blue crab was estimated by using the annual mean observed CPUE of adult female blue crab from the summer SEAMAP groundfish trawl survey and the total area of potential offshore spawning habitat, defined as all waters in the Gulf of Mexico west of the Mississippi River (SSZ 13–21) from the estuarine mouth or barrier islands to the 109.7-m (60-fathom) depth contour (depth contours were derived from gridded bathymetry data from the General Bathymetric Chart of the Oceans (GEBCO_2020 Grid, available from website). Annual mean CPUE values, meaning numbers of individuals per hectare, were multiplied by the total area of potential offshore spawning habitat to estimate total abundance of blue crab in offshore waters for each year. These estimates of offshore abundance were compared with similar estimates of abundance in estuarine waters of Texas and Louisiana, by using CPUE from fishery-independent trawl surveys conducted in estuarine areas by the Texas Parks and Wildlife Department (TPWD) and Louisiana Department of Wildlife and Fisheries (LDWF). Only data collected during June and July were included in these analyses because these summer months represent the time of peak adult female abundance in estuarine waters of Louisiana and Texas and also correspond with the timing of the summer SEAMAP trawl survey.

The TPWD conducts fishery-independent sampling by using 6.1-m trawl nets with 38.1-mm stretched mesh, towed for 10 min at a speed of 4.8 km/h. Sampling is based on a stratified random design, with each of the 8 major bay systems in Texas (Sabine, Galveston, Matagorda, San Antonio, Aransas, Corpus Christi, Upper Laguna Madre, and Lower Laguna Madre) divided into grid cells that were 1.85 by 1.85 km. Each month, 10–20 grid cells in each major bay system are randomly selected for trawl sampling, with the number of cells depending on the bay system. Statewide annual mean CPUE of adult (≥125 mm CW) females was calculated for the period June–July and then was multiplied by the total available habitat area to estimate the total abundance of mature females in estuarine waters of Texas for each year. Habitat area was defined as the total area of the Texas coastal bay systems extracted from geographic information systems data obtained from TPWD (available from website).

The LDWF conducts fishery-independent sampling by using 4.9-m flat trawl nets with a 38.1-mm stretched mesh body and a 12.7-mm stretched mesh bag, towed for 10 min. Sampling occurs at fixed stations, semimonthly during November–February and weekly during March–October. Vessel speed is not recorded but typically ranges from 2.6 to 4.8 km/h (Cagle[6]). For CPUE calculations, an average vessel speed of 3.7 km/h was assumed because it is the midpoint of the typical range. Because stations were added and deleted during the period of interest, we used only data from stations that were sampled in 2018 and had

[6] Cagle, P. 2020. Personal commun. Louisiana Dep. Wildl. Fish., P.O. Box 98000, Baton Rouge, LA 70898.

been sampled for at least 8 years during the period 2006–2018. Additionally, only stations west of the Mississippi River were included, to correspond with the spatial extent of the SEAMAP data used for offshore abundance estimates. Annual mean CPUE of adult (≥125 mm CW) female blue crab was then multiplied by the total available habitat area to estimate the total abundance of mature females in estuarine waters of Louisiana west of the Mississippi River for each year. Total available estuarine habitat area in Louisiana was calculated by using the NOS80K shoreline data set from the NOAA Office of Ocean Resources Conservation and Assessment (NOAA[7]). This shoreline layer was created in 1994, however, and substantial land loss has occurred in Louisiana since that time (Couvillion et al.[8]). The total available estuarine habitat in the Louisiana portion of their study area was, therefore, corrected on the basis of observed rates of coastal land loss in our study area (Couvillion et al.[8]).

Condition and reproductive output of spawning females

Mature female blue crab were collected offshore during the summer and fall SEAMAP groundfish trawl surveys in 2017 for analyses of overall condition and reproductive output. Mature females were haphazardly selected from the haul of each trawl tow, individually bagged and frozen, and sent to the Gulf Coast Research Laboratory in Ocean Springs, Mississippi, for analysis. During the summer survey (30 May–2 July 2017), 109 blue crab were collected from 48 stations, and during the fall survey (13 October–8 November 2017), 11 females were collected from 10 stations (Fig. 1).

Following thawing, CW and total mass were recorded for each crab. Gills were inspected for the presence of the parasitic gooseneck barnacle *Octolasmis muelleri* and for the parasitic nemertean worm *Carcinonemertes carcinophila*. Spermathecae, the paired sperm storage organs, were located to determine if the female had recently mated. A female was determined to have recently mated (within the past 3–5 weeks; Wolcott et al., 2005) if her spermathecae had a large size, firm texture, and pink color (Wolcott et al., 2005; Ogburn and Habegger, 2015). Because females mate only once in their lifetime, following their terminal molt, large, firm, pink spermathecae serve as an indication that a female moved offshore soon after her mating or that a female mated while offshore. Each female was determined to be spawning capable if she had developed, full ovaries or carried an egg mass.

For ovigerous females, the egg mass was carefully separated from the pleopods and weighed. A subsample <1 g (typically 500–1000 eggs) was then removed and weighed, and the total number of eggs in the subsample was counted by using a stereoscopic microscope. Total fecundity was estimated for each ovigerous female by dividing the number of eggs in the subsample by the mass of the subsample and multiplying by the mass of the entire egg mass. Relationships between fecundity and body size were examined by using generalized linear models (GLMs) with a Gaussian distribution and log link function and with fecundity as the response variable. Separate GLMs were fit to model fecundity as a function of CW and body mass (excluding the mass of the egg mass). Because of missing data for body mass of 16 of the 73 ovigerous blue crab, it was not possible to directly compare the model fits by using AIC or the AIC corrected for bias of small sample sizes (AICc) because the 2 models used slightly different data sets. For comparisons, the GLM with CW as the predictor was refit by using only individuals with data for both CW and body mass, and then the models were compared by using AICc.

The embryonic developmental stage for each egg sample was determined by visual examination under a compound microscope and classified as early (stages 1–3 of DeVries et al., 1983), middle (stages 4–6 of DeVries et al., 1983), and late (stages 7–9 of DeVries et al., 1983). The percentage of embryos that were developing normally (Darnell et al., 2009) was visually assessed for each egg mass on the basis of 20 eggs chosen at random from the subsample. Egg size for 20 normally developing embryos was determined by measuring along the long axis and the perpendicular axis with a compound microscope. Egg volume was calculated for each measured egg as the volume of a prolate spheroid by using the short and long axis measurements. Egg volume measurements were averaged for each egg mass, and this mean volume for each egg mass was then used in subsequent analyses. Egg volume was analyzed by using a GLM with a gaussian distribution and a log link function and with egg volume as the response variable. Egg volume was modeled as a function of CW and embyronic developmental stage (early, middle, and late).

Results

Long-term patterns of distribution and relative abundance

A total of 8996 trawl tows were conducted in offshore waters across the study area in 2000–2019. During that time, 97.7% of summer sampling occurred in June and July, with 1.3% occurring in May and 1.0% occurring in August. Fall sampling was primarily (97.7%) conducted during October and November, with 2.2% occurring in September and 0.1% occurring in December. Depths sampled were 9.2–109.5 m. Salinities measured at the bottom of the water column at sampling locations were 10.9–39.5, with 97.3% of trawl tows conducted in waters with salinities ≥30.0. Bottom temperatures were 16.0–30.5°C.

Blue crab were caught in 19.4% of all trawl tows, with 11,021 caught during 2000–2019 across the full study

[7] NOAA. 1994. NOS80K: medium resolution digital vector U.S. shoreline shapefile. Strategic Environ. Assess. Div., Off. Ocean Resour. Conserv., Natl. Ocean Serv., NOAA, Silver Spring, MD. [Available from website, accessed May 2020.]

[8] Couvillion, B. R., H. Beck, D. Schoolmaster, and M. Fischer. 2017. Land area change in coastal Louisiana 1932 to 2016: U.S. Geological Survey scientific investigations map 3381, 16 p. [Pamphlet.] [Available from website, accessed May 2020.]

area. Recorded CWs were 3–281 mm (median: 136 mm), with 99.5% of blue crab having CWs of 20–200 mm. Although sex was not recorded for all blue crab, 93.0% of the 1597 blue crab for which sex was determined were female. Adult female blue crab were caught in 17.1% of all trawl tows, with a total of 6355 caught. The overall mean CPUE of adult females was 0.25 individuals/ha (standard error of the mean [SE] 0.01) over the full study period, with annual mean CPUE ranging from 0.06 individuals/ha (SE 0.02) in 2013 to 0.53 individuals/ha (SE 0.09) in 2010. Annual frequencies of occurrence for adult female blue crab ranged from 8.5% in 2000 to 25.7% in 2011 (Table 1). The maximum annual mean CPUE of adult females observed during the summer surveys was 0.87 individuals/ha (SE 0.31) in 2006, and the maximum annual mean CPUE of adult females observed during the fall surveys was 0.29 individuals/ha (SE 0.09) in 2011.

Following comparisons of candidate models, the selected model included year, season, an interaction of year and season, and separate smooth terms for geographic location in each season (Table 2), with the selected model explaining 47.9% of the deviance in catch. Results of the Wald chi-square test indicate that all predictors had a significant effect on catch (Table 3). Averaged over the full study period, CPUE of adult female blue crab was higher during the summer surveys (0.39 individuals/ha [SE 0.03]) than during the fall surveys (0.11 individuals/ha [SE 0.01]), although this pattern was not consistent across all years (Fig. 2). The spatial distribution of adult female blue crab also differed between the 2 seasons (Table 3). In summer surveys, CPUE was generally highest in nearshore regions off Louisiana and along the central and upper coasts of Texas, primarily at depths <36.6 m (<20 fathoms). The CPUE from fall surveys was generally highest off southeastern Louisiana and at intermediate distances from shore (Fig. 3).

Estimated marginal mean CPUE for each year, standardized relative to the 20-year average, provides a standardized index of abundance for the offshore spawning stock of blue crab in the northwestern Gulf of Mexico (Fig. 4). With the exception of 2010 and 2011, the index of abundance for each year was within 1.5 standard deviations of the mean value. The index indicates a trend of slight increases in abundance from 2000 to 2009, followed by a large increase in 2010, a sustained high level of abundance in 2011, and a marked decrease after 2011. After a low in 2012, the index has steadily increased back to average levels of abundance.

Table 1

Summary information by year for adult female blue crab (*Callinectes sapidus*) collected in the northwestern Gulf of Mexico during groundfish trawl surveys conducted in 2000–2019 as part of the Southeast Area Monitoring and Assessment Program. The number of trawl tows; total catch (number of individuals); mean catch per unit of effort (CPUE), calculated by dividing catch by the area swept by the trawl (number of individuals per hectare) and given with standard error of the mean (SE) in parentheses; and percent occurrence of female adult blue crab are provided.

Year	No. of trawl tows	Total catch	Mean CPUE (SE)	Percent occurrence
2000	585	159	0.14 (0.06)	8.55
2001	525	179	0.14 (0.03)	10.86
2002	575	292	0.19 (0.03)	17.39
2003	528	454	0.26 (0.05)	16.48
2004	533	319	0.26 (0.05)	14.63
2005	517	457	0.31 (0.04)	22.63
2006	529	673	0.48 (0.16)	18.34
2007	510	327	0.26 (0.05)	16.86
2008	642	557	0.23 (0.05)	13.86
2009	689	575	0.33 (0.05)	20.90
2010	431	692	0.53 (0.09)	23.43
2011	381	520	0.49 (0.08)	25.72
2012	336	161	0.16 (0.04)	15.18
2013	261	55	0.06 (0.02)	9.58
2014	342	111	0.11 (0.02)	15.79
2015	346	126	0.12 (0.02)	18.21
2016	309	147	0.16 (0.03)	20.71
2017	333	259	0.26 (0.05)	19.82
2018	308	122	0.13 (0.02)	17.86
2019	316	170	0.17 (0.03)	18.35

Table 2

Candidate models used to estimate catch of adult female blue crab (*Callinectes sapidus*) collected from the northwest Gulf of Mexico between 2000 and 2019. Model selection criteria also are given for each model: the difference in Akaike information criterion (AIC) between each model and the model with the lowest AIC (ΔAIC), AIC weight (w_{AIC}), and the proportion of deviance explained. The characters "s()" indicate that a continuous variable was included as a smooth term. All models included an offset term for the area swept by the trawl to account for differences in sampling effort among trawl tows.

Model formulation	AIC	ΔAIC	w_{AIC}	D^2
Year + season + (year × season) + s(geographic location) × season	12,947.7	0.00	1	0.479
Year + season + s(geographic location) × season	13,072.6	124.93	0	0.454
Year + season + (year × season) + s(geographic location)	13,302.3	354.60	0	0.402
Year + season + s(geographic location)	13,410.7	462.99	0	0.376
Year + s(geographic location)	13,636.8	689.07	0	0.334
Year + season	14,560.2	1612.55	0	0.104
Year	14,797.0	1849.35	0	0.043

Table 3

Results from the Wald chi-square (χ^2) test for significance of predictor variables in the 2D generalized additive model used to examine overall temporal and spatial patterns in catch of adult female blue crab (*Callinectes sapidus*) collected during trawl surveys in the northwestern Gulf of Mexico between 2000 and 2019. The characters "s()" indicate that a continuous variable was included as a smooth term. Degrees of freedom (df) and estimated degrees of freedom (edf) are shown for parametric factor terms and smooth terms, respectively.

Source	df or edf	χ^2	*P*
Year	19	240.40	<0.0001
Season	1	21.54	<0.0001
Year × season	19	174.71	<0.0001
s(geographic location): summer	66.16	745.00	<0.0001
s(geographic location): fall	69.20	530.10	<0.0001

Relative importance of offshore and estuarine waters

During 2006–2018, considering only SSZ 13–21, CPUE of adult females from summer surveys in offshore waters of the Gulf of Mexico averaged 0.38 individuals/ha (SE 0.03), compared with the CPUE values of 0.46 individuals/ha (SE 0.03) in estuaries of Texas and of 3.92 individuals/ha (SE 0.17) in estuaries of Louisiana. Total available habitat area was estimated to be 11,473,937.0 ha for the offshore SSZ 13–21 in the SEAMAP study area, 578,310.7 ha for estuaries of Texas, and 853,436.2 ha for estuaries of Louisiana west of the Mississippi River. Rough calculations made by using CPUE of adult females (as a proxy for density) and total habitat area indicate that estuarine areas during June–July supported a minimum abundance of 1,248,675 adult female blue crab in 2017 and a maximum abundance of 8,631,449 adult female blue crab in 2006 and that the offshore SEAMAP survey area during June–July supported a minimum abundance of 664,203 adult female blue crab in 2013 and a maximum abundance of 9,509,020 adult female blue crab in 2010 (Fig. 5). On average, across the 13-year period of 2006–2018, the offshore SEAMAP survey area supported 48.8% of the total spawning stock in the northwestern Gulf of Mexico, although this percentage ranged from 26.5% in 2014 to 79.7% in 2017.

Condition and reproductive output of spawning females

Collection of blue crab for reproductive analyses occurred on each state and federal leg of the SEAMAP groundfish trawl surveys during summer and fall 2017. In total, 120 mature female blue crab were collected, with CWs ranging from 110 to 209 mm. The vast majority of blue crab (109 of 120) were collected during the summer survey (30 May–2 July 2017), and the rest of the individuals (11 of 120) were caught during the fall survey (13 October–8 November 2017).

Of the 109 mature females collected during summer, 95 individuals (87.2%) were spawning capable, as evidenced by an external egg mass (65 individuals) or mature ovaries (30 individuals). All embryonic developmental stages were observed in ovigerous blue crab collected during the summer survey, with 56.9% (37 individuals) in the early developmental stage, 10.8% (7 individuals) in the middle developmental stage, and 32.3% (21 individuals) in the late developmental stage. Additionally, 26.2% (17 individuals) of the ovigerous females collected during the summer survey also possessed developed, full ovaries, indicating the capacity to produce at least one additional clutch of eggs following the clutch carried at the time of collection. Only 1 female (0.9%) collected during the summer survey had mated recently.

Of the 11 mature females collected during the fall survey, 6 individuals (54.4%) were spawning capable, as evidenced by an external egg mass (5 individuals) or developed, full ovaries (1 individual). Of these 5 ovigerous individuals, 4 crab carried eggs in the early

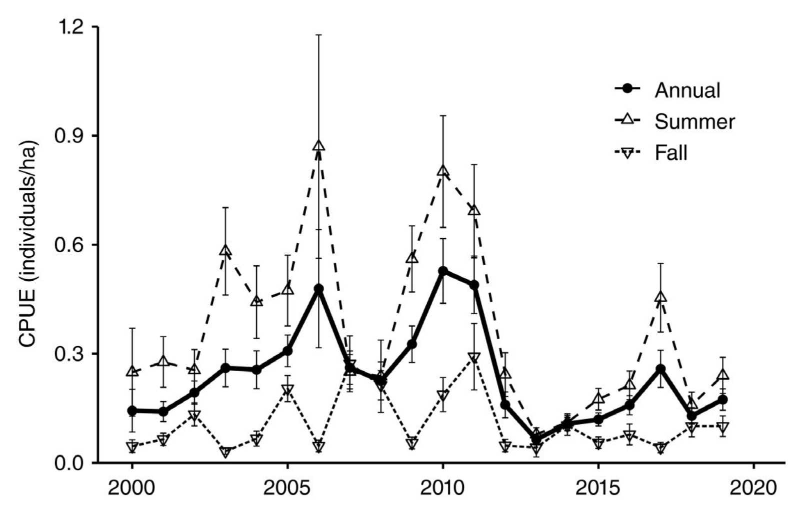

Figure 2

Observed mean annual (solid line) and seasonal (broken lines) catch per unit of effort (CPUE) for adult female blue crab (*Callinectes sapidus*) collected during groundfish surveys conducted in the northwestern Gulf of Mexico from 2000 through 2019 as part of the Southeast Area Monitoring and Assessment Program. Values of CPUE were calculated by dividing catch by the area swept by the trawl. Error bars indicate standard errors of the mean.

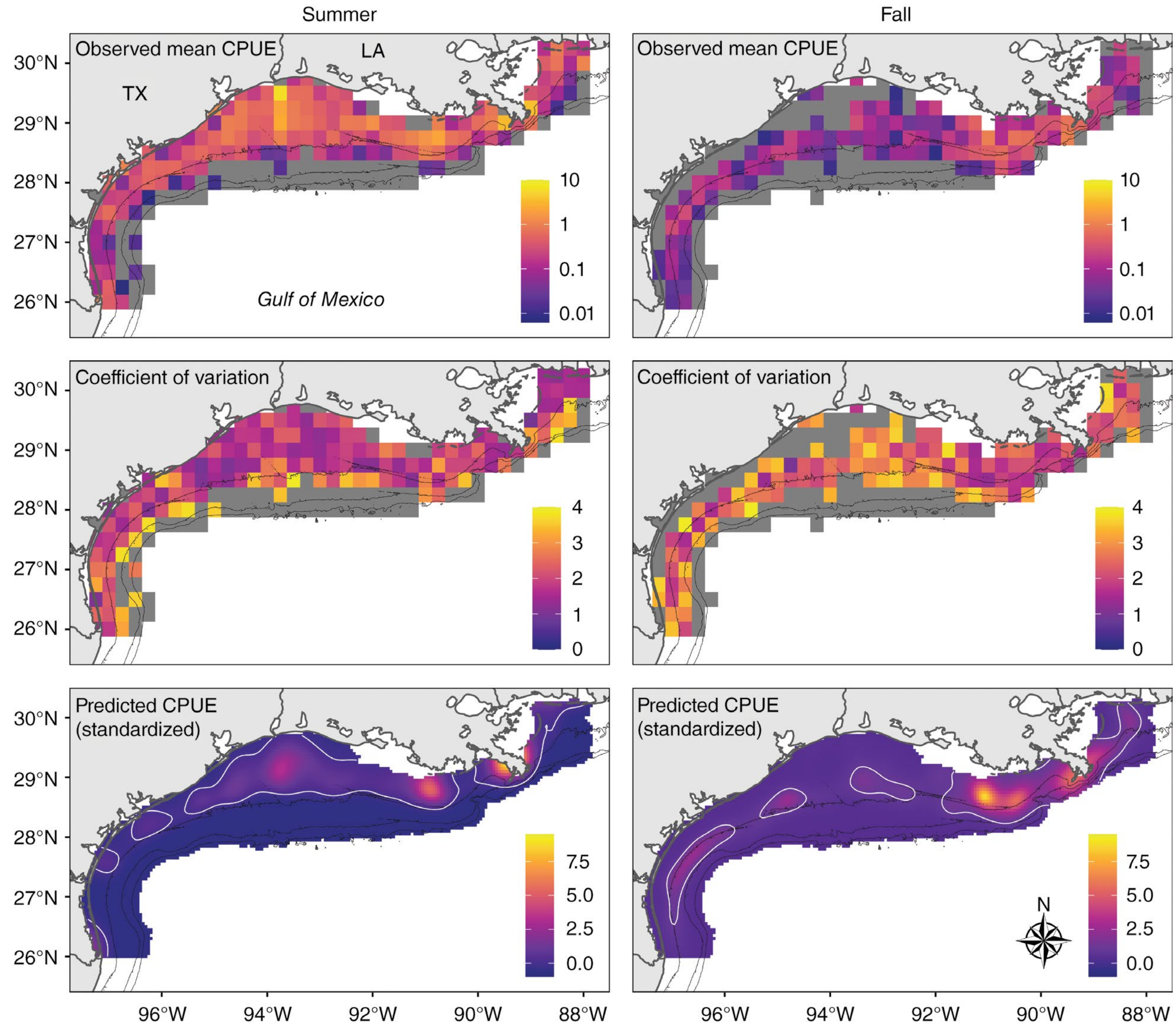

Figure 3

Spatial patterns of catch per unit of effort (CPUE) for adult female blue crab (*Callinectes sapidus*) collected during groundfish trawl surveys conducted in the northwestern Gulf of Mexico in summer (left panels) and fall (right panels) across the study period 2000–2019. The top panels show observed CPUE (number of individuals per hectare), binned into 0.25° grid cells and averaged across all years on a log scale. White areas represent areas that were not sampled, and gray grid cells represent areas with no catch of adult female blue crab over the full study period. The middle panels show interannual variability in catch rates, calculated as the coefficient of variation of observed annual mean CPUE. The bottom panels show predicted CPUE of adult female blue crab for each season from the generalized additive model, averaged across all years and standardized by using a Z-transformation based on the mean and standard deviation for that particular season. Values are depicted in units of standard deviations above (positive values) or below (negative values) the mean. White contours delineate a standardized value of zero, representing the mean for that season. Black lines represent the 36.6-, 73.2-, and 109.7-m (20-, 40-, and 60-fathom) depth contours.

developmental stage and 1 crab carried eggs in the late stage. None of the females collected during the fall survey had mated recently.

Fecundity was 1.07–8.93 million eggs (mean: 3.27 million eggs [SE 0.15 million]) and was strongly related to size of female crab, with larger females having higher fecundity. This relationship was evident when both CW ($P<0.0001$, deviance explained [D^2]=0.539) and body mass ($P<0.0001$, D^2=0.712) were considered (Fig. 6). Results of the comparison of model fits based on AICc indicate that body mass was a better predictor of fecundity than CW, with an AICc weight >0.98.

Figure 4

Standardized index of abundance for adult female blue crab (*Callinectes sapidus*) in the northwestern Gulf of Mexico during the study period 2000–2019. The gray shaded area indicates the 95% confidence interval. The horizontal dotted line indicates a value of zero, representing the average annual predicted catch per unit of effort across the full study period.

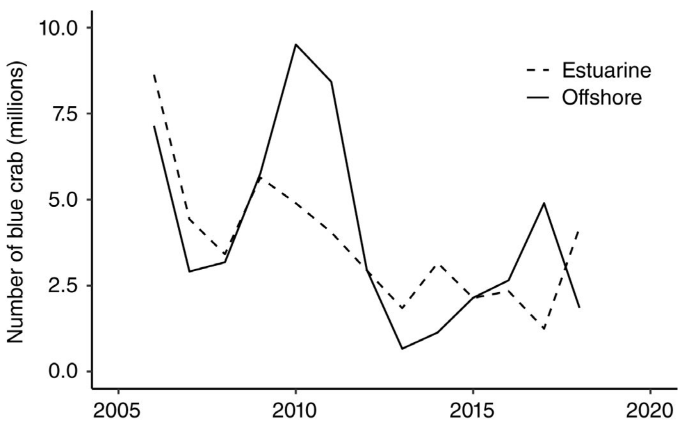

Figure 5

Estimated total abundance (in millions) of adult female blue crab (*Callinectes sapidus*) in offshore (solid line) and estuarine (dashed line) areas of the northwestern Gulf of Mexico west of the Mississippi River during June and July in 2006–2018.

On average across both seasons, 91.7% (SE 0.01) of eggs were fertilized and embryos were developing normally, with 91.6% (SE 0.01) of embryos developing normally in the summer and 93.0% (SE 0.05) of embryos developing normally in the fall. Eggs that were not developing normally were either unfertilized or fertilized but had ceased development in an earlier developmental stage than the majority of the egg mass. Average egg size was 243.6 µm (SE 0.5) along the long axis and 236.1 µm (SE 0.5) along the perpendicular axis. Average egg volume was 0.0073 mm^3 (SE 0.0001). There was a significant relationship between egg volume and embryonic developmental stage (F=29.76, P<0.0001), with a general increasing trend as the embryos develop further (Fig. 7). There was no significant relationship between egg volume and maternal CW (F=2.371, P=0.1286) and no significant interaction between maternal CW and embryonic developmental stage (F=2.363, P=0.1023).

The parasitic barnacle *O. muelleri* was commonly found on the gills of blue crab, with prevalence of 66.1% in summer and prevalence of 100.0% in fall. The nemertean worm *C. carcinophila* that is a predator of crab eggs was less common, with prevalence of 6.4% in summer and prevalence of 0.0% in fall.

Discussion

Results of this study indicate that the offshore waters of the northwestern Gulf of Mexico are an important spawning habitat for blue crab. Mature female blue crab are routinely caught in offshore waters of the northwestern Gulf of Mexico each year in the SEAMAP groundfish trawl survey, as far as 200 km from shore (Fig. 3). Our results support the substantial numbers of spawning blue crab in offshore areas of the Gulf of Mexico documented in previous studies (Gelpi et al., 2009, 2013).

The CPUE of adult female blue crab in offshore waters was greater in the summer than in the fall during most years (Fig. 3). This difference in CPUE between summer and fall may be indicative of a postspawning return to inshore habitats, as proposed by Tankersley et al. (1998). Given that findings from more recent studies indicate that migration back to estuaries is unlikely (Hench et al., 2004; Darnell et al., 2012), this pattern more likely is indicative of an offshore population decline from natural mortality due to predation and the high energy expenditures of migration and reproduction. It is important to note that the SEAMAP-Gulf of Mexico groundfish surveys are limited to summer (primarily June–July) and fall (primarily October–November). Blue crab recruitment in the northwestern Gulf of Mexico generally peaks from August to October (Rabalais et al., 1995; Perry et al. 2003), which corresponds with the observed peak in adult female densities during the summer SEAMAP trawl survey. Given that earlier recruitment peaks are observed in some areas (Rabalais et al., 1995; Sullivan and Neigel, 2017), late spring may also be an important time for offshore spawning in this region (data are not available to test this hypothesis).

Throughout the study period, the highest densities of adult female blue crab were present in the waters off

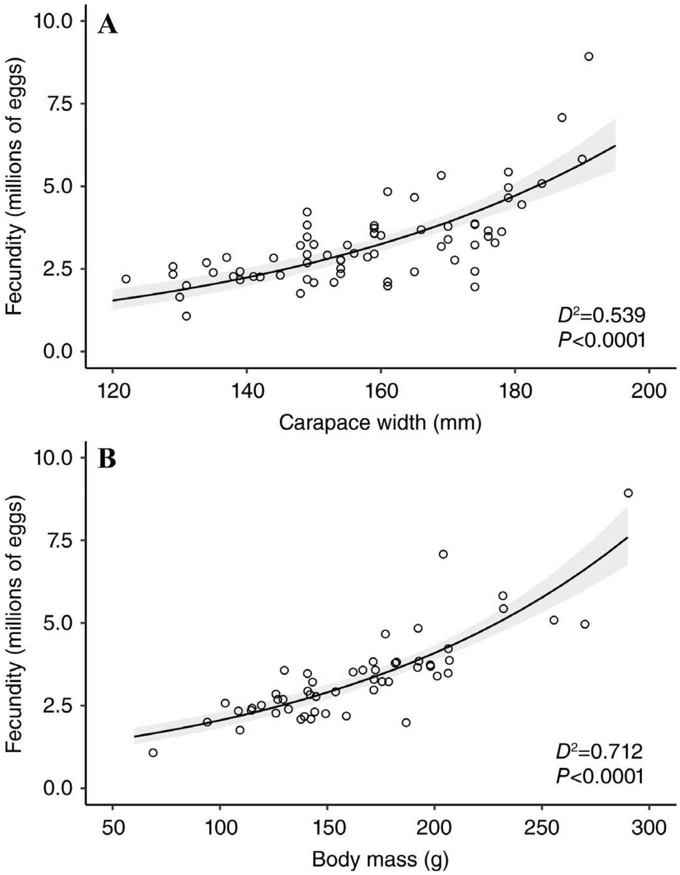

Figure 6

Relationships between fecundity and (**A**) carapace width and (**B**) body mass for ovigerous female blue crab (*Callinectes sapidus*) collected during the groundfish trawl survey conducted in 2017 in the northwestern Gulf of Mexico as part of the Southeast Area Monitoring and Assessment Program. Lines indicate relationships from generalized linear models. Shaded regions represent the 95% confidence interval. D^2=deviance explained.

Louisiana, and this pattern was consistent for both summer and fall surveys (Fig. 4). This spatial pattern reflects reported inshore fishery landings, with areas off Louisiana accounting for 88% of the blue crab landings in the Gulf of Mexico in 2018 (NMFS[9]). The large numbers of blue crab caught offshore of Louisiana relative to catch in other regions likely reflect the low salinities present in estuaries of Louisiana. Egg hatching and larval survivorship is negatively affected by salinities <20.1 (Costlow and Bookhout, 1959); during the spawning migration, therefore, females move to spawning grounds suitable for offspring survival. It is possible that the low salinities in estuaries of Louisiana result in greater numbers of females migrating out of the estuaries and continuing to migrate into the offshore environment, compared with the numbers of females that migrate out of estuaries in other regions. Although CPUE was highest off Louisiana in both seasons, the spatial distribution of the CPUE differed between summer and fall (Fig. 4). During summer, adult females were primarily caught in nearshore regions, at depths <36.6 m (<20 fathoms). During fall, adult females were primarily caught at depths of 36.6–73.2 m (20–40 fathoms) off both Texas and Louisiana.

Ogburn and Habegger (2015) conducted a similar examination of blue crab spawning in offshore waters of North Carolina, South Carolina, Georgia, and Florida, by using data from the SEAMAP-South Atlantic trawl surveys, with similar results. The highest CPUE of mature female blue crab occurred during the summer, females were actively spawning offshore, and a substantial portion of the spawning stock in Georgia occurred in offshore waters. Using only data from summer surveys, we observed a maximum annual mean CPUE of 0.87 individuals/ha (SE 0.31) (in 2006), a level substantially lower than the maximum of 1.58 individuals/ha observed (in 1991) by Ogburn and Habegger (2015). When interpreting this difference in CPUE, however, it is important to consider the differences in survey design between the SEAMAP trawl surveys conducted along the Atlantic coast of the southeastern United States and in the Gulf of Mexico. The SEAMAP-South Atlantic survey samples at depths of 4.0–10.0 m (2–5 fathoms), and the SEAMAP-Gulf of Mexico survey samples at depths of 9.1–109.7 m (5–60 fathoms). If the SEAMAP-Gulf of Mexico data set examined in this study is limited to depths <15 m, mean adult female CPUE was 1.96 individuals/ha (SE 0.97) in summer 2006, 1.58 individuals/ha (SE 1.13) in summer 2010, and 1.53 individuals/ha (SE 1.09) in summer 2000.

Although densities of adult female blue crab observed in the SEAMAP study area were relatively low, the offshore areas sampled in our study support a substantial portion (up to 79.7%, depending on the year) of the spawning stock in the northwestern Gulf of Mexico. We acknowledge that our estimates of total abundance of the spawning stock are rough, with multiple potential sources of error. A size-based cutoff was used to classify blue crab as adults or juveniles, rather than a visual morphological examination. Although the fishery-independent trawl surveys conducted by the LDWF and TPWD record maturity stage for blue crab, this information is not recorded in the SEAMAP trawl surveys. For consistency, we therefore classified all blue crab ≥125 mm CW as adults for data from all 3 survey programs. Additionally, these estimates do not account for differences in gear or gear efficiencies in the 3 survey programs. Actual abundances, therefore, are likely to be substantially

[9] NMFS (National Marine Fisheries Service). 2018. Commercial landings query, release 3.1.0.2. Off. Sci. Technol., Natl. Mar. Fish. Serv, Silver Spring, MD. [Available from website, accessed March 2020.]

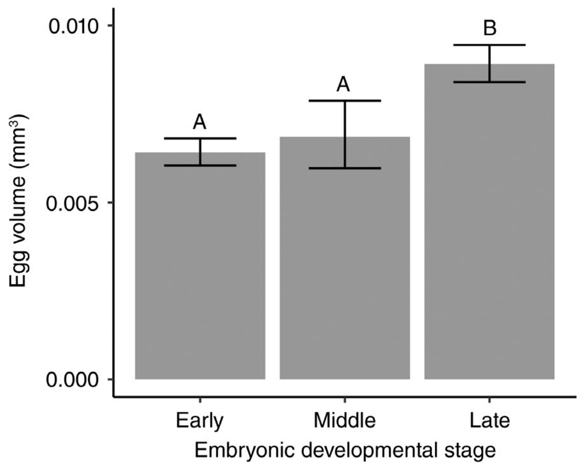

Figure 7

Mean egg volume for each embryonic developmental stage for ovigerous female blue crab (*Callinectes sapidus*) collected during the groundfish trawl survey conducted in 2017 in the northwestern Gulf of Mexico as part of the Southeast Area Monitoring and Assessment Program. Mean egg volumes are estimated marginal means from the generalized linear model. Error bars indicate the back-transformed 95% confidence intervals. The different letters above the bars indicate statistically significant differences between developmental stages.

higher than the estimates presented here. It is also important to consider the fate of larvae spawned offshore. There may be some distance offshore beyond which it is highly unlikely that a blue crab larva could successfully make it back to an estuary. To date, most larval transport modeling efforts for blue crab in the Gulf of Mexico have focused on spawning occurring at or near the estuarine mouth (e.g., Johnson and Perry, 1999; Jones et al., 2015; Criales et al., 2019). Further work is needed to better understand the fate of larval blue crab that have been spawned offshore.

Our analyses of the reproductive health of female blue crab collected in offshore habitats gave no indication that these females are of poor health or that they are of any lesser value to the spawning stock than females spawning in estuarine waters. Estimated fecundity was 1.07–8.93 million eggs, with an average of 3.27 million eggs (SE 0.15 million). In comparison, Graham et al. (2012) reported fecundity estimates of ~0.9–7.0 million eggs for ovigerous blue crab collected from estuarine waters of Mississippi Sound, and Prager et al. (1990) reported fecundity estimates of ~0.5–8.0 million eggs (mean: 3.2 million eggs) for ovigerous blue crab collected from Chesapeake Bay. Egg size in our study was also similar to that found in previous studies of ovigerous females collected in estuarine waters. We observed egg measurements of 243.6 µm (SE 0.5) along the long axis and of 236.1 µm (SE 0.5) along the perpendicular axis. In comparison, Graham et al. (2012) reported egg diameters of ~215–310 µm (~215–275 µm during the summer and fall only) for blue crab from Mississippi Sound, and Darnell et al. (2009) reported an average egg diameter of 267.5 µm (SE 1.9) for blue crab from North Carolina.

Fecundity of blue crab declines with age, with the greatest fecundity in the first clutch of eggs produced by a female (Darnell et al., 2009). That females collected in offshore and estuarine waters produce similar quantities of eggs indicates that offshore females are at a similar stage of their reproductive period as females spawning in estuarine areas. This notion is supported by our observation of a high percentage of eggs that were fertilized with embryos developing normally (91.7% [SE 0.01]). Darnell et al. (2009) observed a decrease in the percentage of embryos developing normally in later clutches, from 96.7% (SE 0.9) in a female's first clutch to 55.0% (SE 20.1) in its fourth clutch. Assuming a similar pattern in blue crab from the Gulf of Mexico, this finding indicates that the females assessed in our study were producing their first or second clutch of eggs. We observed full, developed ovaries in >50% of females collected offshore during the summer, indicating that these blue crab would spawn at least once more in their lifetime. Our results also indicate that oviposition and continued spawning is occurring in offshore waters, and we observed all stages of embryonic development.

The results of this study indicate that the coastal and offshore waters of the northwestern Gulf of Mexico are an important spawning habitat for blue crab. Although densities of blue crab offshore were low, these crab were primarily adult females and were actively spawning. Given the large amount of available shelf habitat, our results indicate that offshore areas support a substantial portion of the spawning stock in the northwestern Gulf of Mexico. Fecundity of females caught offshore was similar to that reported for estuarine spawning crab, and these females are continuing to spawn multiple clutches of eggs in offshore waters. Additional research is needed to understand the causes of temporal and spatial variation in densities of spawning female blue crab in the Gulf of Mexico. Furthermore, it is critical that this previously understudied portion of the spawning stock of blue crab in the Gulf of Mexico be considered and accounted for in future management and assessment efforts in the Gulf of Mexico.

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