



Abstract—The red deepsea crab (*Chaceon quinque-dens*) supports a small fishery of <2000 metric tons annually along the U.S. East Coast, but little is known about the life history of this crab. We sampled red deepsea crab from 4 sites and 3 depth strata (250–450 m, 450–700 m, and 700–850 m) in the Mid-Atlantic Bight in January 2011 and 2012 and in July 2013. Crab size decreased with depth, whereas shell age indices increased with depth. Crab occurred at temperatures from 4.6°C to 10.6°C (mean: 6.37°C) and there was little difference between sexes. Size at 50% maturity (SM_{50}) could not be determined with chela or abdomen allometry, but SM_{50} was estimated at 61.6 mm in carapace length for females on the basis of gonopore condition. Sex ratios (M:F) involving female crab above the SM_{50} were <0.5, indicating that large males are depleted in comparison with female abundance. The proportion of ovigerous females was 33% in January 2012 and <6% in July 2013, proportions that support the hypothesis of a biennial (or longer) reproductive cycle. Red deepsea crab probably recruit to deep water (>1000 m), move upslope during adolescence, and become mature in the shallowest strata, before undergoing an ontogenetic migration back to intermediate depths.

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Depth and temperature distribution, morphometrics, and sex ratios of red deepsea crab (*Chaceon quinque-dens*) at 4 sampling sites in the Mid-Atlantic Bight

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The red deepsea crab (*Chaceon quinque-dens*) ranges from the Gulf of Maine to the Gulf of Mexico, at depths from 200 to 1800 m, and temperatures of 5–8°C (Haefner and Musick, 1974; Wigley et al., 1975; Serchuk¹; Steimle et al., 2001; Wahle et al., 2008; NEFSC²). Stocks along the Atlantic coast are considered a single population and distinct from the stock in the Gulf of Mexico. Red deepsea crab support a small but valuable fishery in federally managed waters along the continental slope of southern New England and the Mid-Atlantic, a fishery that has

been managed since 2002 by the New England Fishery Management Council (Wigley et al., 1975; Wahle et al., 2008). In recent years, 4 vessels have fished for red deepsea crab and have averaged annual landings of 1360 metric tons (t) over the time period 2002–2013, but landings have declined from 1600 to 930 t during that period (Chute³). Red deepsea crab are a data-poor fishery stock. Very little is known about their biology, abundance, growth, age, or reproduction, and, as a result, management consists primarily of controls on total allowable catch, currently set at 2688 t. Because of inadequate information on biomass, the New England Fishery Management Council Scientific and Statistical Committee has not set a fishing-induced mortality rate or determined whether the stock is in a status of overfished or overfishing (Chute et al.⁴).

¹ Serchuk, F. M. 1977. Assessment of red crab (*Geryon quinque-dens*) populations in the northwest Atlantic. Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Lab. Ref. 77-23, 15 p. [Available at [website](#).]

² NEFSC (Northeast Fisheries Science Center). 2009. The Northeast Data Poor Stocks Working Group report, December 8–12, 2008 meeting. Part A. Skate species complex, deep sea red crab, Atlantic wolffish, scup, and black sea bass. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 09-02, 496 p. [Available at [website](#).]

³ Chute, A. 2014. Personal commun. Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543.

⁴ Chute, A., L. Jacobson, P. Rago, and A.

Because of their extended depth range, few red deepsea crab are captured during semiannual assessment surveys conducted by the National Marine Fisheries Service. Red deepsea crab have been studied during several previous surveys. McRae (1961) found significant concentrations of crab southeast of Ocean City, Maryland, but concluded that they were too sparse to support a commercial fishery. In two surveys, abundance of populations of red deepsea crab was estimated by using towed camera systems. The first survey (Wigley et al., 1975) was conducted in 1974 before the onset of commercial fishing. The second, conducted during 2003–2005 (Wahle et al., 2008), showed a 250% increase in overall biomass (mostly due to juveniles), after a decade of targeted harvesting of males, but a 42% decline in the biomass of large males at depths of 350–500 m where fishing occurs, as well as a decline in body condition indices (carapace length [CL]: weight ratios) (Weinberg and Keith, 2003). In addition, the size of landed crabs has declined from 114 mm in carapace width (CW) in 1974 to <90 mm CW by 2008 (Chute et al.⁴).

There is scant information on biological parameters of red deepsea crab, such as size at maturity, fecundity, or timing of reproduction. Fecundity increases with body size (Hines, 1988). Size at maturity for female red deepsea crab has been estimated by Haefner (1977, 1978) to be between 65–75 mm CL, but a large portion of his samples were barren, indicative of biennial spawning. Size at 50% maturity has been estimated with ratios of chela width (ChW) to CW for the congener *C. affinis* from the Canary Islands (males: 129 mm CW; females: 99 mm CW) (Fernández-Vergaz et al., 2000), by gonad condition for *C. affinis* in the northeast Atlantic (males: 94 mm CW; females: 109 mm CW) (Robinson, 2008), and for male *C. maritae* in South Africa (93 mm CW) by using growth increment analysis (Melville-Smith, 1989). Spawning of *C. affinis* in the Canary Islands occurs from October to May, but ovigerous females were found only in March and April (López Abellán et al., 2002) and from October to March in the Azores (Pinho et al., 2001). In the Gulf of Mexico, male golden deepsea crab (*C. fenneri*) produce sperm in late winter and mate with females during March–April, but females do not extrude eggs until the following fall (Hinsch, 1988a, 1988b). Life history characteristics of other geryonid crab species were reviewed and compared by Hastie (Hastie, 1995).

Maturity of female crabs can be inferred from the presence of eggs, gonopore condition, or ovary development, but maturity of male crabs is difficult to determine. Male crabs may carry spermatophores, indicative of physiological maturity, at sizes well below that at

which they can mate. Many genera (e.g., *Chionoecetes*, *Lithodes*, *Cancer*) exhibit allometric growth of the chela at the pubertal molt, after which they are classified as morphometrically mature and are distinguishable by an increase in the slope and intercept of the ratio of chela height (ChH) to CW (ChH: CW) (Somerton, 1980; Somerton and MacIntosh, 1983; Comeau and Conan, 1992; Stevens, et al., 1993; Corgos and Freire, 2006).

Lack of biological, survey, and fishery information for the red deepsea crab causes major uncertainties about the status of its stock and possible management approaches. Up to 85% of the catch of this species consists of females and undersize crab that are discarded and that result in a possible mortality of about 5% (Tallack, 2007). At present, it is not possible to calculate biological reference points (e.g., biomass or fishing-induced mortality at maximum sustainable yield [B_{MSY} , F_{MSY} , respectively]) because of a lack of information on growth, longevity, and mortality (NEFSC⁵). For the same reasons, it is not possible to predict future stock status, biomass, or response to changes in climate or fishing mortality. Although landings of red deepsea crab have stabilized at intermediate levels in recent years, the landed size has declined from 114 mm CW in 1974 to 105 mm CW in 2005, and there is concern about sperm limitation because of reductions in biomass of large males.

At a minimum, effective management requires information on growth, mortality, and size at maturity. In particular, it is necessary to know the frequency of molt and reproduction in females, the presence or absence of terminal molt and multiple fertilizations, and the status of sperm storage and fecundity. The NOAA Red Crab Working Group has made a variety of high-priority research recommendations for understanding the life history of red deepsea crab, including a better understanding of the reproductive cycle, maturity schedule, and fecundity of female red deepsea crab; of the potential reproductive consequences of removing large males from the population; and of the growth rate and molt cycle of red deepsea crab (Miller et al.⁶).

We began studies of the red deepsea crab in 2011 to provide data on reproduction and life history for this species. Data were collected aboard NOAA research vessels during 3 cruises jointly sponsored by the NOAA Northeast Fishery Science Center and the Living Marine Resources Cooperative Science Center at the University of Maryland Eastern Shore. The objectives for these cruises were to sample the continental shelf fauna during winter (in 2011 and 2012) and

MacCall. 2009. Deep sea red crab. In Northeast Data Poor Stocks Working Group report, December 8–12, 2008 meeting. Part A. Skate species complex, deep sea red crab, Atlantic wolffish, scup, and black sea bass. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 09-02, p. 181–214. [Available at [website](#).]

⁵ NEFSC (Northeast Fisheries Science Center). 2006. 43rd Northeast Regional Stock Assessment Workshop (43rd SAW): 43rd SAW assessment summary report. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 06-14, 54 p. [Available at [website](#).]

⁶ Miller, T., R. Muller, B. O'Boyle, and A. Rosenberg. 2009. Report by the Peer Review Panel for the Northeast Data Poor Stocks Working Group, 38 p. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole, MA. [Available at [website](#).]

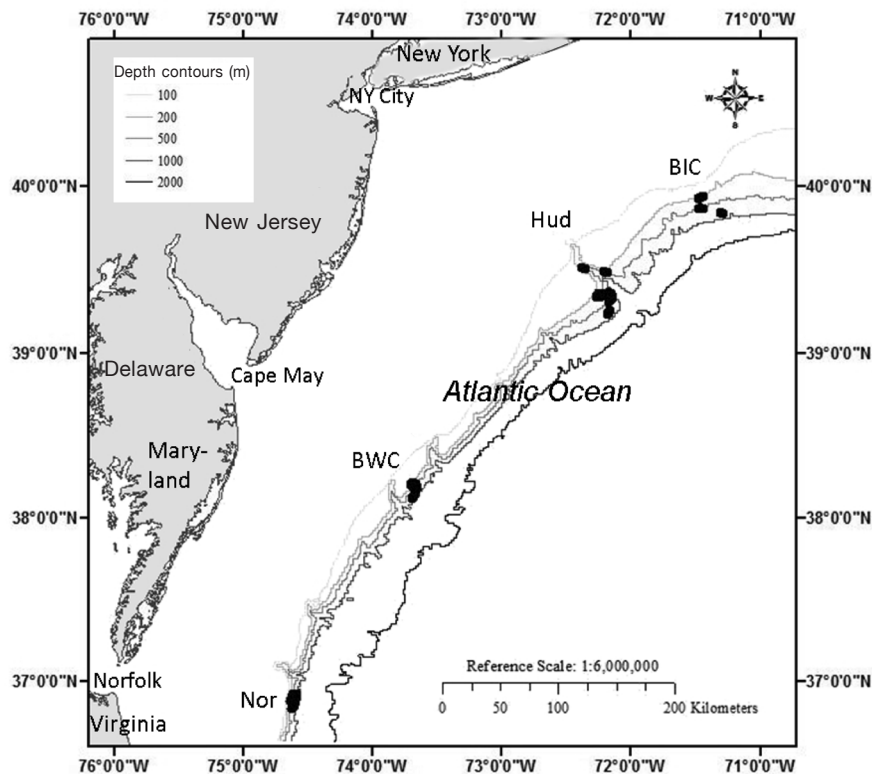


Figure. 1

Locations of sampling sites for red deepsea crab (*Chaceon quinque-dens*) during cruises aboard the NOAA Ship *Delaware II* in the Mid-Atlantic Bight in 2011 and 2012 and aboard the NOAA Ship *Gordon Gunter* in 2013. The sites were Block Island Canyon (BIC), Hudson Canyon (Hud), Baltimore and Washington Canyons (BWC), and Norfolk Canyon (Nor).

to collect samples of red deepsea crab. Specific goals for research of red deepsea crab were to determine 1) the distribution of crab by sex, size, shell condition, depth, and temperature, 2) to obtain morphometric data for determination of sexual maturity, and 3) to collect specimens for studies of reproductive biology. This article presents information on distribution and morphometry of red deepsea crab collected during the 3 NOAA cruises.

Materials and methods

Sampling locations

Two research cruises were conducted aboard the NOAA Ship *Delaware II* (10–21 January 2011 and 21–30 January 2012) and one cruise was completed aboard the NOAA Ship *Gordon Gunter* (5–8 July 2013). Red deepsea crab were sampled in 4 general areas within the Mid-Atlantic Bight (defined as coastal waters along the U.S. Atlantic coast from Cape Cod to Cape Hatteras), and stations were selected to cover a range of latitudes and depths: near Block Island Canyon (BIC), at

the mouth of Hudson Canyon (Hud), on the continental slope between Baltimore and Washington Canyons (BWC), and on the slope near Norfolk Canyon (Nor; Fig. 1). Actual locations within each site where trawl nets were hauled were chosen for their relatively flat contours within specified depth ranges (see below) after reconnaissance with multibeam sonar. Goals of the cruise in 2011 were primarily focused on sampling fish; red deepsea crab were caught incidentally in the deeper (>300 m) tows, and sampling of crab was mostly opportunistic. In 2012 and 2013, stations were specifically defined to capture red deepsea crab, and tows were made in 3 depth strata defined as shallow (250–450 m), middle slope (450–700 m), and deep (700–850 m) (Table 1). One attempt to tow a trawl net at a depth of 1000 m failed when the net was snagged and both trawl warps were broken, resulting in loss of a trawl net. Because of inclement weather and technical delays, site BIC was sampled only in 2012, and site BWC was not sampled in 2011.

Water temperature and depth profiles were recorded with a conductivity, temperature, and depth profiler before each trawl tow at each site and depth stratum. In 2011, a Yankee 36 otter trawl with an 18.3-m headrope,

Table 1

Data collected from trawl tows and expanded catch data from surveys of red deepsea crab (*Chaecon quinque-dens*) conducted in the mid-Atlantic Bight during 3 cruises (2011–2013): depth stratum of trawl (Strat; 1=shallow [250–450 m], 2=middle slope [450–700 m], and 3=deep [700–850 m]); bottom temperature (Btemp, °C); swept area (Area, m²); number of male crab caught (Males), number of female crab caught (Females); total number of crab caught (Total); density of male crab (Mdens, individuals/ha); density of female crab (Fdens, individuals/ha), total density of crab (Tdens, individuals/ha); expansion factor for subsampled tows (ExpFac); mean weight of male crab (Mwt, kg); and mean weight of female crab (Fwt, kg). Stations were located at 4 sites: Block Island Canyon (BIC), Hudson Canyon (Hud), Baltimore and Washington Canyons (BWC), and Norfolk Canyon (Nor).

Station	Year	Date	Strat	Depth		Area	Males	Females	Total	Mdens	Fdens	Tdens	ExpFac	Mwt	Fwt
				(m)	Btemp										
Hud-1	2011	1/15/2011	1	403.7	7.8	30,512	170	307	477	55.7	100.7	156.3	3.613	0.236	0.265
Hud-2	2011	1/15/2011	2	499.4	6.4	33,057	480	655	1134	145.1	198.0	343.1	5.643	0.357	0.206
Hud-2	2011	1/15/2011	2	558.5	7.3	31,866	1017	1645	2662	319.2	516.1	835.3	10.820	0.213	0.156
Hud-3	2011	1/14/2011	2	631.7	5.5	31,413	725	1755	2480	230.7	558.8	789.5	10.206	0.289	0.130
Nor-1	2011	1/18/2011	1	363.4	9.0	29,312	20	177	197	6.8	60.2	67.0	2.487	0.360	0.350
Nor-3	2011	1/17/2011	2	580.8	5.1	26,645	388	509	897	145.7	190.9	336.6	6.693	0.263	0.284
BIC-1	2012	1/19/2012	1	246.9	10.2	47,921	0	0	0	0.0	0.0	0.0	0		
BIC-2	2012	1/19/2012	2	483.6	6.1	41,463	103	211	315	25.0	51.0	75.9	4.312		
BIC-3	2012	1/19/2012	3	731.5	4.6	30,482	214	62	276	70.1	20.3	90.4	3.444		
Hud-1	2012	1/21/2012	1	294.0	11.5	42,011	0	0	0	0.0	0.0	0.0	0		
Hud-2	2012	1/26/2012	1	298.3	8.8	32,071	277	92	369	86.3	28.8	115.1	5.127		
Hud-3	2012	1/26/2012	2	644.2	6.9	34,345	125	200	326	36.5	58.3	94.8	2.022	0.278	0.20
BWC-1	2012	1/25/2012	1	134.8	14.2	30,847	0	5	5	0.0	1.6	1.6	1		
BWC-2	2012	1/25/2012	2	571.4	5.6	25,973	520	2092	2612	200.2	805.3	1005.5	11.556	0.386	0.190
BWC-3	2012	1/25/2012	3	760.5	5.1	27,007	100	51	151	37.0	18.9	55.9	1		
Nor-1	2012	1/23/2012	1	321.4	9.2	37,555	0	0	0	0.0	0.0	0.0	0		
Nor-2	2012	1/23/2012	2	521.9	6.8	42,703	377	882	1259	88.3	206.5	294.7	6.389		
Nor-3	2012	1/22/2012	3	773.7	4.8	25,800	90	64	154	34.8	24.8	59.6	1.830		
Hud-1	2013	7/7/2013	1	263.6	8.1	34,124	0	0	0	0.0	0.0	0.0	0		
Hud-2	2013	7/7/2013	2	569.2	5.7	42,385	0	0	0	0.0	0.0	0.0	0		
Hud-3	2013	7/7/2013	3	792.5	4.8	32,560	113	26	139	34.7	8.0	42.7	1	0.27	0.326
BWC-1	2013	7/8/2013	1	288.7	11.2	34,070	1	10	11	0.3	2.9	3.2	1	0.306	0.221
BWC-2	2013	7/8/2013	2	500.8	6.5	33,171	387	1391	1778	116.7	419.4	536.1	5.610	0.306	0.221
Nor-1	2013	7/5/2013	1	236.5	12.2	37,488	0	0	0	0.0	0.0	0.0	0		
Nor-2	2013	7/5/2013	1	414.4	8.1	31,094	151	416	567	40.4	110.8	151.2	3.883	0.401	0.332
Nor-3	2013	7/5/2013	3	750.0 ^a	7.1	33,694	336	78	414	99.8	23.1	122.9	2.101	0.211	0.185

^a Conductivity, temperature, and depth sensor failed; depth estimated from chart.

a codend that had a 1-cm mesh liner, and deepwater headrope floats (“rock hoppers”) was deployed from the stern trawl A-frame by using both trawl winches and 2.5-cm trawl wires. In 2012 and 2013, a similarly size 4-seam otter trawl net (with 6.0-cm body mesh and 2.5-cm codend liner) was used. In all years, a 30-min tow was made at ~1.5 m/s (3 kt) along a specified depth contour at each site and stratum. Distance towed was determined from GPS coordinates, and area towed was estimated as the distance multiplied by average net width (13.0 m). Tows were made during all hours of day or night. Time constraints prevented measuring all crab in tows with larger catches (catch for 6 of the tows exceeded 1000 crab); as a result, a goal of 150–200 crab per catch was set. All catches that consisted of up to 3 baskets or a total of 60 kg of red deepsea crab (approximately 150 crabs) were sampled completely,

whereas, for larger catches, a subsample of 2–3 baskets that composed from 10% to 50% of the catch was taken. The subsample was sorted by sex, after which males and females were weighed separately to determine the proportion of their biomass in the whole catch. A sampling factor for each tow was recorded along with each crab for later data expansion.

For each crab in a subsampled tow, the sex and shell condition were recorded. Shell condition includes coloration and abrasions of the carapace, sternum, and dactyls, and therefore provides a crude but integrated index of time since molt. Shells were classified into 4 standard categories, defined by the National Marine Fisheries Service for brachyuran crabs (see Jadamec et al., 1999), that represented relative time since molting, determined by radiometric aging (Nevissi et al., 1996). We have adapted the following cat-

egories for red deepsea crab: 1) new-shell crab were relatively soft, clean, and brightly colored, had sharp dactyls, and indicated that the crab had molted (probably) within the last 1–2 months; 2) hard-shell crab had harder shells with some discoloration and scratches but were still glossy and may have molted within the last 6–12 months; 3) old-shell crab had lost their glossy, reflective sheen, had numerous dark patches, scratches, and dull dactyls, and probably had not molted for 2 or more years; 4) very-old-shell crab were much darker and discolored, indicating these crab had not molted for 4–6 years.

Electronic calipers were used to measure different dimensions of the crab. We used CL instead of CW as our standard dimension of size, measured from the rear margin of the right eyesocket to the rear midline of the carapace. Carapace length is a more accurate measurement because spines are usually included in CW, and spines can wear down over time. In addition, we redefined the width measurement between spine tips as spine width (SW), as opposed to CW, which is often measured across the carapace in front of the spines. For comparative purposes, we also recorded SW for 48% and CW for 12% of the measured crab to allow for conversions between them. Time constraints prevented taking all measurements on all crabs, but additional measurements were taken for a subset of the sampled crabs that were systematically selected to fill out size categories for reproductive studies. Additional measurements included chela propodus length (ChL), ChH (males only), abdomen width (AW) at the widest point (females only), and presence and condition of eggs (females).

Haefner (1977) reported that abrasion and discoloration (blackening) around the gonopores (which he termed “vulvae”) of female red deepsea crab were indications of previous mating, and he demonstrated that 87% of 67 female red deepsea crab with open, discolored gonopores contained sperm, whereas none of the 38 crabs with immature (closed) gonopores contained sperm. Therefore, in 2012 and 2013, in our surveys maturity of females was estimated on the basis of gonopore condition; females with closed and unabraded gonopores were classified as immature, whereas those with open or discolored gonopores (or external eggs) were considered mature.

Data analysis

For subsampled tows, the average weight of crab was calculated separately for males and females, and the proportion of each sex by weight was determined. Total catch for each sex (C_{sex}) was calculated by multiplying the total catch weight (W_t) by the weight proportion (P_{sex}) and dividing the result by mean weight (MW_{sex}) of each sex in the subsample:

$$C_{\text{sex}} = W_t \cdot P_{\text{sex}} \cdot MW_{\text{sex}}^{-1}.$$

Density of crab was calculated as the catch (total number) of each sex divided by the area towed and

expressed as the mean number of crab-per hectare, for comparison with results reported by Wahle et al. (2008).

Because replicate tows were not made at each station, density of each sex was compared separately between years, sites, and depth strata by using single-factor analysis of variance (ANOVA), and P -values <0.05 were considered significant. If factor effects were significant, pairwise comparisons were made with the Bonferroni correction. Likewise, differences in mean size (CL) were compared between sexes, sites, and depth strata with a weighted ANOVA, where the sampling factors were used as weights to account for unequal subsampling. Weighting had little impact on post-hoc pairwise comparisons; therefore, post-hoc comparisons were unweighted. Proportions of male and female crab within 0.5°C categories were also compared by using ANOVA and a Kruskal-Wallis test.

Sex ratios were calculated after summing the catch of crab in bins of 5 mm CL. Comparisons were made between sites (with depths as replicates) because sites were geographically separated. Red deepsea crab may make seasonal vertical migrations for reproduction, and crab at different depths would comeingle; therefore, they were considered to represent a single local mating pool. In most brachyuran species, males are larger than females, and assortative mating is common: females pair with males up to 40% larger, as reported for snow crab (*Chionoecetes opilio*; Sainte-Marie et al., 1999) and southern Tanner crab (*C. bairdi*; Stevens et al., 1993). Male red deepsea crabs in 10 mating pairs observed by Wahle et al. (2008) were 50% larger than their female partners, and males in 3 mating pairs observed in another study were 28% larger than their female counterparts (Elner et al., 1987). Therefore, in our study, sex ratios were calculated between numbers of crab in offset size categories. Given that the mean size of females was about 75 mm CL, the number of females in each 5-mm bin was compared with the number of males in bins that were 20 mm larger (e.g., number of females in the bin of 50–55 mm CL was compared with that of males in the bin of 70–75 mm CL).

Relationships between morphometric characters, such as CL, ChL, ChH, and AW were determined for selected crabs by using analysis of covariance, with sex as a categorical factor. Data were linear and therefore were not transformed, but the slopes of the log-transformed relationships were calculated to determine the allometry coefficient. The size at 50% maturity (SM_{50}) for females was calculated by using logistic regression with maturity (0, 1; determined on the basis of gonopore condition) as the dependent variable, and CL as the independent variable. Standard error (SE) of SM_{50} was calculated with a bootstrap analysis with 1000 repetitions. Shell conditions and proportion of mature crab with eggs were determined and plotted. All data analysis was conducted with R, vers. 3.0.2 (R Core Team, 2013). Most mean values are presented with standard deviations (SDs), and a few are noted with SEs.

Table 2

Mean temperatures ($^{\circ}\text{C}$), with standard deviations (SD) and results of analysis of variance between years, from surveys of red deepsea crab (*Chaecon quinque-dens*) conducted in the Mid-Atlantic Bight in 2011, 2012, and 2013. Results are averaged across all trawl tows made at each site (Temp_s), weighted by numbers of crabs caught (Temp_c), and for females with eggs (Temp_e). Also shown are results of analysis of variance between years, including F -value (F), probability (P), and degrees of freedom (df).

Year and results of variance	Tows	Temp_s	Temp_c	Temp_e
Jan 2011	6	6.9 (SD 1.5)	6.41 (SD 0.96)	6.05 (SD 0.76)
Jan 2012	12	7.8 (SD 3.0)	6.07 (SD 1.10)	6.27 (SD 0.62)
Jul 2013	8	8.0 (SD 2.6)	6.71 (SD 1.11)	7.68 (SD 0.72)
Total	26	7.8 (SD 2.5)	6.37 (SD 1.09)	6.25 (SD 0.82)
F		0.361	44.48	26.08
P		0.701	<0.001	<0.001
df		2, 23	2, 2813	2, 330

Results

Catch and density

During cruises of NOAA research vessels in 2011, 2012, and 2013, 26 deepwater tows were completed for research of red deepsea crab (Table 1). One site (BIC) was sampled only in 2012, whereas others were omitted in some years (e.g., BWC in 2011), and not all depths were sampled each year because of time constraints. Mean bottom temperatures at all sampled stations did not differ significantly between years despite sampling in January of 2011 and 2012 and in July of 2013 (Table 2). Temperatures weighted by number of crab captured differed significantly among

years, but the greatest difference was $<0.7^{\circ}\text{C}$. Temperatures at which ovigerous females occurred also differed significantly among years and temperatures were warmer in July 2013 than in January of either 2011 or 2012. Although differences between stations were minimal, crab concentrated at specific depths in each season, and, as a result, crab-weighted temperatures showed greater differences because of changes in crab distribution.

During the 3 cruises combined, 5594 male and 10,627 female crab were captured for a total of 16,221 crab, of which 2815 crab (17.4%) were measured, including 1191 males (21.3% of males) and 1624 females (15.3% of females). Highest mean densities occurred in the middle slope depth stratum

(450–700 m; Table 3) for both males (131 individuals/ha) and females (300 individuals/ha), but differences between sites were not significant (Table 3). However, mean densities of male crab were significantly greater in 2011 than in 2012 or 2013; a similar but nonsignificant decline occurred for females. This difference remained even after removal of site BIC (only sampled in 2012) and was mostly due to samples at sites Hud and Nor. Estimates of biomass density were calculated with mean weights from 13 subsampled tows and ranged from 0 to 241 kg/ha, with a mean of 49.7 kg/ha (SD 69.6). Biomass averaged across years was lowest at site BIC (14.7 kg/ha [SD 13.1]) and highest at site BWC (77.4 kg/ha [SD 106.4]) (Table 4).

Table 3

Mean density (individuals/ha), with standard deviations (SDs), of red deepsea crab (*Chaecon quinque-dens*) averaged across depth strata, years, and sites sampled in the Mid-Atlantic Bight during 2011–2013. Analysis of variance results include F -value (F), probability (P), and degrees of freedom (df). Superscript letters indicate similar groups (within columns) where $P < 0.05$. Sampling occurred at 3 depth strata, shallow (250–450 m), middle slope (450–700 m), and deep (700–850 m), at 4 sites, Block Island Canyon (BIC), Hudson Canyon (Hud), Baltimore and Washington Canyons (BWC), and Norfolk Canyon (Nor).

Stratum	Male	Female	Year	Male	Female	Site	Male	Female
Shallow	18 ^b (SD 30.7)	30 ^b (SD 47.7)	2011	151 ^a (SD 114)	271 (SD 214)	BIC	32 (SD 35.6)	24 (SD 25.6)
Middle	131 ^a (SD 100)	300 ^a (SD 263)	2012	48 ^b (SD 57.9)	101 (SD 229)	BWC	71 (SD 86.6)	250 (SD 358)
Deep	55 ^b (SD 29.0)	19 ^b (SD 6.6)	2013	37 ^b (SD 47.6)	73 (SD 147)	Hud	81 (SD 98.2)	125 (SD 193)
						Nor	55 (SD 61.4)	96 (SD 95.9)
Analysis of variance								
F	2.559	0.47		7.263	2.97		0.319	0.817
P	0.123	0.5		0.013	0.09		0.811	0.498
df	2, 23	2, 23		1, 24	1, 24		3, 22	3, 22

Table 4

Total biomass density (kg/ha) of red deepsea crab (*Chaceon quinque-dens*) at each site and depth stratum sampled in the Mid-Atlantic Bight during 2011–2013, and summaries across sites and depth strata are provided. Sampling occurred at 3 depth strata, shallow (250–450 m), middle slope (450–700 m), and deep (700–850 m), at 4 sites, Block Island Canyon (BIC), Hudson Canyon (Hud), Baltimore and Washington Canyons (BWC), and Norfolk Canyon (Nor).

Year	Site	Depth stratum			Mean
		Shallow	Middle	Deep	
2011	Hud	39.8	126.8		105.1
2011	Nor	0	92.5		92.5
2012	BIC	0	18.9	25.2	14.7
2012	Hud	16.0	21.6		17.9
2012	BWC	0.0	241.4	17.9	86.4
2012	Nor	0.0	72.8	15.9	29.5
2013	Hud	0.0	0.0	9.7	3.2
2013	BWC	1.0	128.4		64.2
2013	Nor	32.0		25.3	29.8
Mean		13.6	95.6	18.8	47.4

Size of crab

Carapace length was measured on all sampled crabs except for 133 crab from site BIC in 2012; for those crab, CL was calculated from the regression of CL on SW and used in all further analyses. The mean size of male crab captured (79.4 mm CL [SD 14.7], range: 31.6–126.5 mm CL) was significantly greater ($t=11.62$, $df=1974$, $P<0.0001$) than that of female crab (73.7 mm CL [SD 10.1], range: 26.5–103.6 mm CL). Mean size of males differed between years (weighted F , Table 5) and was lower in July 2013 (73.9 mm CL [SD 17.5]) than in January 2011 (80.5 mm CL [SD 10.6]) or 2012 (83.2 mm CL [SD 13.6]). Mean size of females also differed between years (weighted F , Table 5), but pairwise comparisons among years were not significant. Lack of sampling at some sites and depths prevented making annual comparisons among all samples; therefore, further comparisons were made by combining data across years. Mean weights determined from 13 subsampled tows (for which sexes were weighed in aggregate) were 294 g (SD 68) for males and 227 g (SD 71) for females.

Length-frequency distribution of males showed a mode in the range of 80–90 mm CL, and a distinct drop in abundance at sizes >90 mm CL (Fig. 2). Hard-shell crab predominated below 70 mm CL, old-shell crabs were more abundant from 75 to 100 mm CL, and most crabs >100 mm CL were classified as very-old-shell. Female crab exhibited a mode at 70–75 mm CL. Hard-shell females predominated below 60 mm CL, and old-shell females were more abundant in all size groups above 60 mm CL.

Morphometrics

Sex did not affect the relationship between CL and SW; therefore, a combined regression equation was derived for both sexes (Tables 5 and 6; Fig. 3A). The inverse relationship was also determined and used to predict CL for 133 crab that were missing CL measurements. The relationship between ChL and CL differed between sexes with a significant interaction (Table 5); males had longer chelae at sizes >50 mm CL, but females had longer chelae below 50 mm CL (Fig. 3B). Males had an allometry coefficient (the log-transformed slope) of 1.09, indicating isometric growth, whereas females had an allometry coefficient of 0.862, implying slight negative allometry. Among male crab, the relationship between ChH and CL had an allometry coefficient of 1.16, indicating slightly positive allometry (Table 6, Fig. 3C), and the relationship between ChH and ChL had an allometry coefficient of 1.06 (Fig. 3D). Neither the relationship between ChL and CL nor the relationship between ChH and ChL revealed any apparent inflections in the growth pattern that could be used to determine maturity. The relationship between female AW and CL was significant but did not differ with maturity status (Table 5). Nonetheless, there was a significant interaction effect; therefore, combined and separate equations for immature and mature females are presented in Table 6.

Distribution by depth, temperature, crab size, and shell condition

Females were more abundant than males at depths from 400 to 650 m, but males predominated at greater depths (Fig. 4). Weighted ANOVA showed that size varied with both depth and sex, and a significant interaction occurred (Table 5). Mean CL of male crab decreased with depth: 83.1 mm CL (SD 13.7), 79.7 mm CL (SD 11.6), and 78.2 mm CL (SD 17.9) in the shallow, middle slope, and deep strata, respectively (Fig. 5A). Mean CL for males differed significantly between the shallow and deep strata (pairwise t -test, $P<0.05$ with Bonferroni correction), but the values for neither strata differed from the middle slope stratum. Mean CL of females also decreased with depth to a greater degree than it did for males (Table 5, Fig. 5B): 80.6 mm CL (SD 10.1), 73.8 mm CL (SD 9.1), and 67.0 mm CL (SD 12.8) in the shallow, middle slope, and deep strata, respectively, and all differed significantly ($P<0.05$). Mean CL of male crab did not differ between sites (Table 5, Fig. 6C), whereas mean CL of female crab was significantly greater at site Nor than at all other sites ($P<0.05$; Fig. 6D).

Mean shell condition for males was significantly less in stratum 1 (2.2) than in stratum 2 (2.6) or stratum 3 (2.5), but the latter 2 strata did not differ significantly (Fig. 6A). Mean shell condition for females was significantly greater in stratum 2 (2.8) than in either stratum 1 or 3 (both 2.4), but strata 1 and 3 did not differ significantly (Fig. 6B). New-shell male crab were most

Table 5

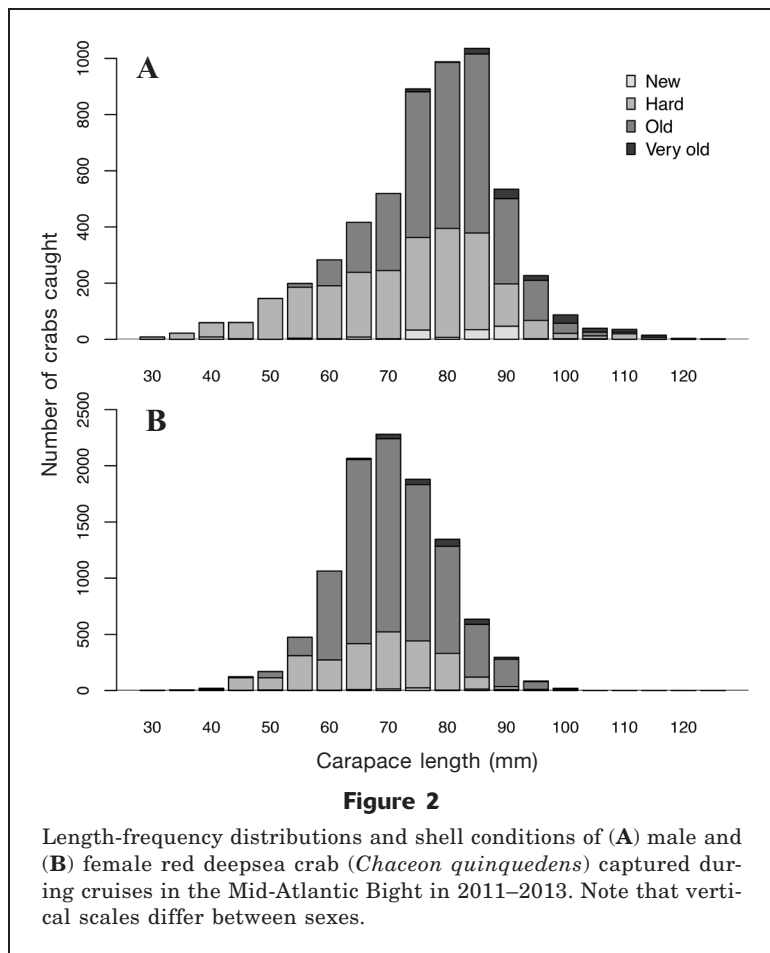
Analysis of variance results for comparisons among carapace length (CL), year, sex, shell width (SW), chela propodus length (ChL), site, depth or stratum, shell condition, bottom temperature (Btemp), abdomen width (AW), and maturity (females only) of red deepsea crab (*Chaecon quinquedens*) captured from the Mid-Atlantic Bight during 2011–2013. Other abbreviations: df=degrees of freedom, SS=Sum of squares, MS=Mean square, F =F-value, P =P-value.

Response	Predictor	df	SS	MS	F	P
CL (males)	Year	1	5233	5233	6.67	0.01
	Residual	1189	932,745	784		
CL (females)	Year	1	19,286	19,286	33.88	<0.001
	Residual	1622	923,249	569		
SW	CL	1	427,647	427,647	52,382	<0.001
	Sex	1	0	0	0.020	0.887
	Residual	1313	10,719			
ChL	CL	1	76,716	76,716	13,008	<0.001
	Sex	1	3505	3505	594	<0.001
	CL × sex	1	1555	1555	263	<0.001
	Residual	321	1893	6		
AW (females)	CL	1	19,761	19,761	5310	<0.001
	Maturity	1	8.1	8.1	2.17	0.143
	CL × maturity	1	20.2	20.2	5.43	0.021
	Residual	179	666.2	3.7		
CL	Depth	1	90,540	90,540	144	<0.0001
	Sex	1	140,428	140,428	224	<0.0001
	Sex × depth	1	24,764	24,764	39.4	<0.0001
	Residual	2811	1,765,210	628		
CL (male)	Depth	1	7915	7915	10.1	0.002
	Residual	1189	930,063	782		
CL (female)	Depth	2	35,721	17,861	31.9	<0.001
	Residual	1621	906,814	559		
CL (male)	Site	3	3644	1215	1.54	0.202
	Residual	1187	934,334	787		
CL (female)	Site	3	57,588	19,196	35.14	<0.001
	Residual	1620	884,947	546		
Shell (male)	Stratum	2	82.2	41.1	25.5	<0.001
	Residual	1188	1911	1.61		
Shell (female)	Stratum	2	103	51.6	33.2	<0.001
	Residual	1621	2518	1.55		
Btemp	Sex	1	31.4	31.4	6.02	0.014
	Residual	2813	14,683	5.22		
Btemp (female)	Eggs	1	362	362	75.4	<0.001
	Residual	1406	6759	4.81		

abundant in the shallow stratum (<450 m), whereas new-shell females were most abundant in the deep stratum (>700 m). Hard-shell male crab predominated in the shallow and deep strata, whereas old-shell crab predominated in the middle slope stratum. Hard-shell female crab predominated in the shallow strata, whereas old-shell females predominated in the middle slope and deep strata.

Bottom temperatures at which crabs were captured ranged from 4.6°C to 10.6°C, but mean temperatures differed by sex (Table 5). The mean temperatures at which

crab were captured were 6.27°C (SD 1.18) for males ($n=1191$) and 6.45°C (SD 1.01) for females ($n=1624$). Because these data were not normally distributed, a Kruskal-Wallis analysis was conducted and also indicated significant differences ($\chi^2=20.12$, $P<0.0001$). Oviparous females occurred at slightly colder temperatures (6.25°C [SD 0.82]) than those temperatures at which females without eggs were found (6.59°C [SD 1.05]; Kruskal-Wallis test ($\chi^2=26.69$, $P<0.0001$). Only 11 crabs were caught at temperatures above 9.0°C; these crabs were captured in one sample at a temperature of 11.2°C and



depth of 288 m. There was no relationship between temperature and size (CL) of male crab ($F=0.833$, coefficient of determination [r^2]= -0.0001 , $P=0.362$, $df=1189$), but size of female crab increased with temperature ($F=31.3$, $r^2=0.018$, $P<0.001$, $df=1622$).

Sex ratios (M:F) varied greatly both among sizes and between sampling sites. For pairs in the smallest size group for their sex (females: 55–60 mm CL; males: 75–80 mm CL) and in which females carried eggs, sex ratios ranged from 2.1 to 3.6; however, for the interval in which female sexual maturity occurs (60–65 mm CL), ratios exceeded 1.0 only at sites BIC and Nor (Fig. 7). For females between 70 and 80 mm CL, only site BIC had a sex ratio >0.5 , and ratios at all other sites were <0.4 . For females >80 mm CL, there were no sites or size categories where sex ratios exceeded 0.1. At female sizes above 60 mm CL, crab at sites BIC and Nor generally had higher sex ratios than crab at sites Hud or BWC.

Female maturity and ovigerity

The smallest female with external eggs was 58.5 mm CL. Logistic regression of maturity, based on gonopore condition, showed that the SM_{50} was 61.6 mm CL (SE 0.1), equivalent to 78.2 mm SW (Fig. 8). In

January 2012, 33.3% of mature female crab were ovigerous, and the maximum proportion exceeded 50% only in the size group of 95–100 mm CL (Fig. 9). In contrast, in July 2013, only 5.9% of mature female crab were ovigerous, and the maximum proportion was 17.9% in the size group of 80–85 mm CL. Analysis of egg samples taken in July 2013 indicated that 80% of eggs were at stage 6 (prehatching or hatching stage), whereas 20% of eggs were at stage 1 (early cell division).

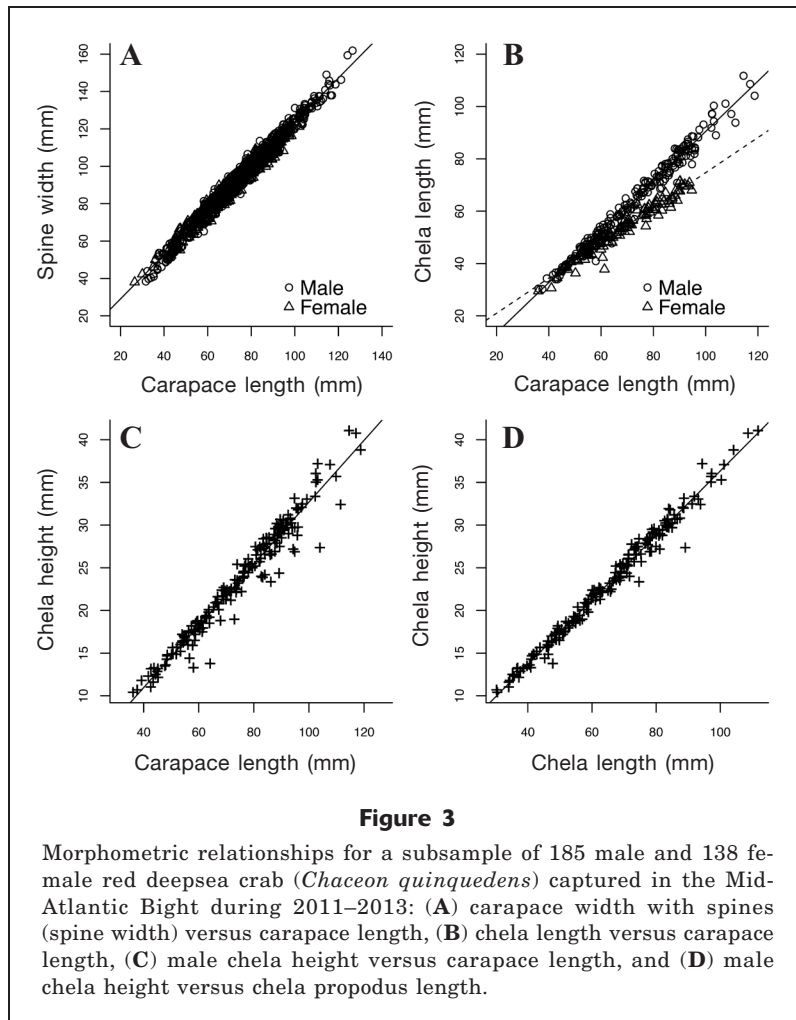
Discussion

Our results add significantly to previous studies of red deepsea crab. Wigley et al. (1975) sampled extensively off the southern New England shelf but included only 2 stations off the Maryland coast, and all sites sampled by Wahle et al. (2008) were north of Delaware Bay (at approximately $38^{\circ}40'N$). We sampled 2 sites (BWC and Nor) that were farther south and that represent locations that are targeted heavily by the current commercial fishery. In addition, we captured about 10 times more crabs than Wigley et al. (1975) and twice as many as Wahle et al. (2008), and we sampled twice as many females as Haefner (1977). Our report is the first to conduct detailed analysis of morphometrics of the red deepsea crab and the first to provide detailed information on distribution by temperature and shell condition.

Catch and density

Tows made during our cruises were not optimized for estimating abundance of red deepsea crab because the net was not outfitted with mensuration gear to measure the net width or bottom contact. As a result, area towed was estimated on the basis of the operator's (subjective) estimate of contact time, distance towed, and average net width. Furthermore, differences in vessel characteristics, operational protocols, and net efficiency make any direct comparisons with previous surveys questionable. The trawl nets we used had a belly mesh of 6 cm and smaller mesh codend liners than those in nets with 3.8-cm mesh used by Wigley et al (1975) and Wahle et al (2008), but all trawl nets caught a similar size range of crab and few crab <50 mm SW. Nonetheless, because there are no other estimates of density of red deepsea crab, our data can be compared with previous estimates in a relative context.

Two of our sites (Hud and BWC) overlap with the area defined as "geographic zone A" by Wigley et al. (1975) (referred to as "sectors" by Wahle et al [2008]). Therefore, we estimated biomass density of red deepsea crab separately within each depth stratum over those 2



sites (12.6, 107.5, and 13.8 kg/ha, respectively), and we multiplied those values by area estimates for similar depth strata within the same geographic sector from Wahle et al. (2008) to provide a depth-stratified estimated biomass of 9143 t for sector A. This value was lower than the approximately 30,000 t estimated by Wahle (2008) during 2003–2005, but it is almost identical to the 9000 t estimated by Wigley et al. (1975) 20 years earlier. We could not separate biomass by sex or size because crab were usually weighed in aggregate. During the survey by Wahle et al. (2008), the highest biomass densities occurred in sectors C and D along the edge of the southern New England shelf, whereas most of our tows were made in sectors A and B, which had the lowest biomass in both the 1974 and 2003–2005 surveys. Mean biomass density over all our stations (42.8 kg/ha) was in the same range (7–80 kg/ha) as levels observed for *C. maritae* off Namibia (Hastie, 1995), but it was much greater than the 1.9 kg/ha calculated for the golden deepsea crab off the coast of South Carolina (Wenner and Barans, 1990) that were surveyed with an occupied submersible.

Size of crabs

Selectivity of commercial crab traps ranges from 0% at 80 mm CW to 100% at 120 mm CW (Wahle et al., 2008),

Table 6

Morphometric relationships for male and female red deepsea crab (*Chaceon quinque-dens*) captured from the mid-Atlantic Bight during 2011–2013. Response and predictor variables are, abdomen width (AW), chela propodus length (ChL), carapace length (CL), spine width (SW). Fem(i or m) refers to immature or mature females. Other abbreviations: intercept (Int), coefficient of determination (r^2), degrees of freedom (df), and allometry coefficient (AC; slope of log-transformed relationship).

Sex	Response	Predictor	Int	Slope	r^2	df	AC
Both	SW	CL	5.45	1.180	0.976	1313	0.94
Both	CL	SW	-2.65	0.826	0.976	1313	1.03
Male	ChL	CL	-5.78	0.962	0.977	184	1.09
Fem	ChL	CL	7.55	0.671	0.952	137	0.86
Fem(i)	AW	CL	-13.0	0.735	0.967	105	1.40
Fem(m)	AW	CL	-8.38	0.677	0.937	74	1.19
Fem(all)	AW	CL	-12.26	0.725	0.966	182	
Male	ChH	CL	-3.52	0.362	0.954	184	1.16
Male	ChH	ChL	-1.44	0.378	0.983	184	1.06

equivalent to a range of 63.4–96.5 mm CL, and the median size of crab captured by traps was 92.5 mm CW, or 73.8 mm CL. Therefore, abundance of males declines abruptly above 90 mm CL, which approximately corresponds with the minimum size captured by the fishing industry. Width frequencies of crab captured by Wahle et al. (2008) during 2003–2005 showed a mode in the range of 65–75 mm CW (equivalent to 51–59 mm CL) for males and in the range of 95–105 mm CW (76–84 mm CL) for females. In contrast, male red deepsea crab captured during our study were larger, with a mode in the range of 80–90 mm CL, whereas females were slightly smaller, with a mode at 70–75 mm CL.

Differences in mean size of male and female red deepsea crab (79.4 and 73.7 mm CL, respectively, equivalent to 99.1 and 92.4

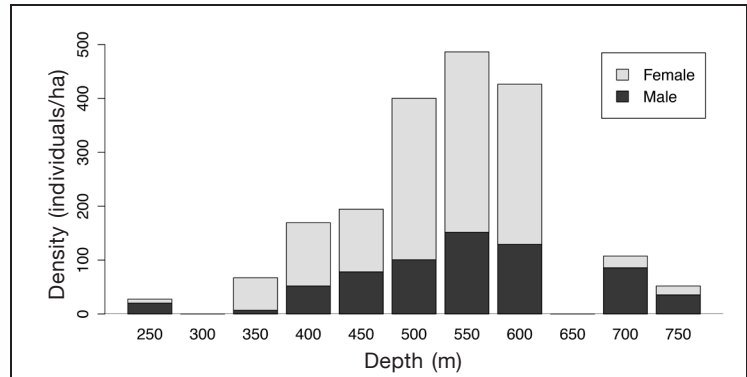


Figure 4

Depth distribution of male and female red deepsea crab (*Chaceon quinque-dens*) captured during 2011–2013 in the Mid-Atlantic Bight, expressed as density or number of crab per hectare (ha). Minimum depths are shown for each 50-m depth bin.

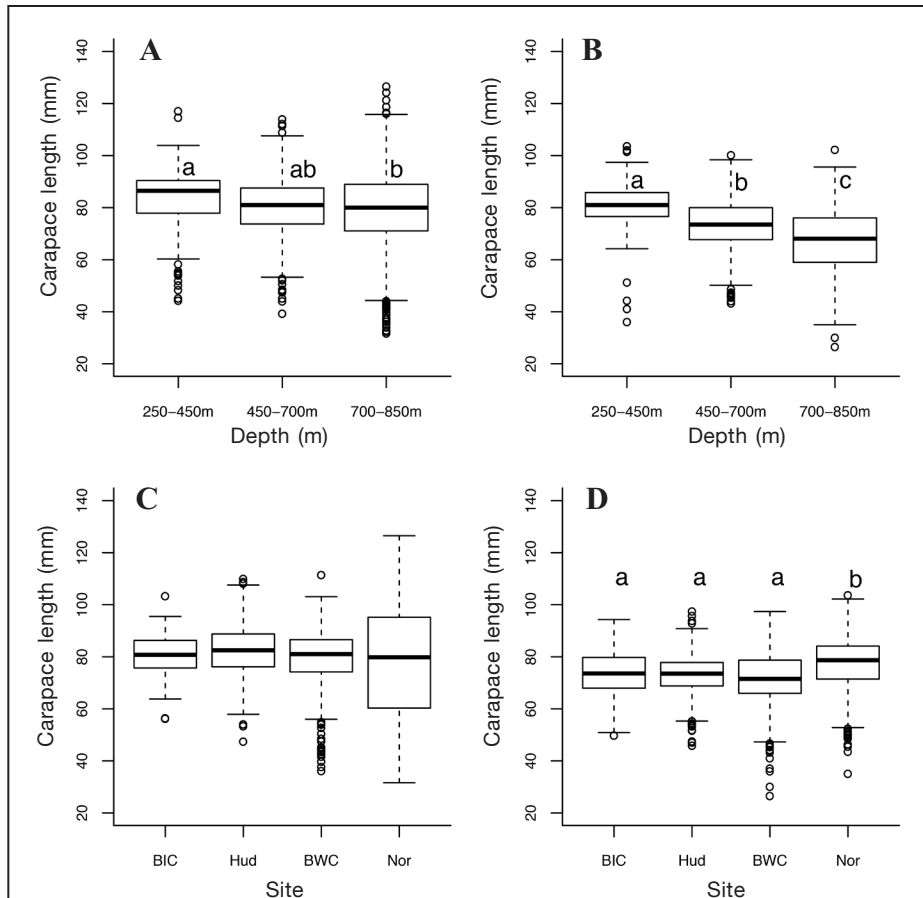
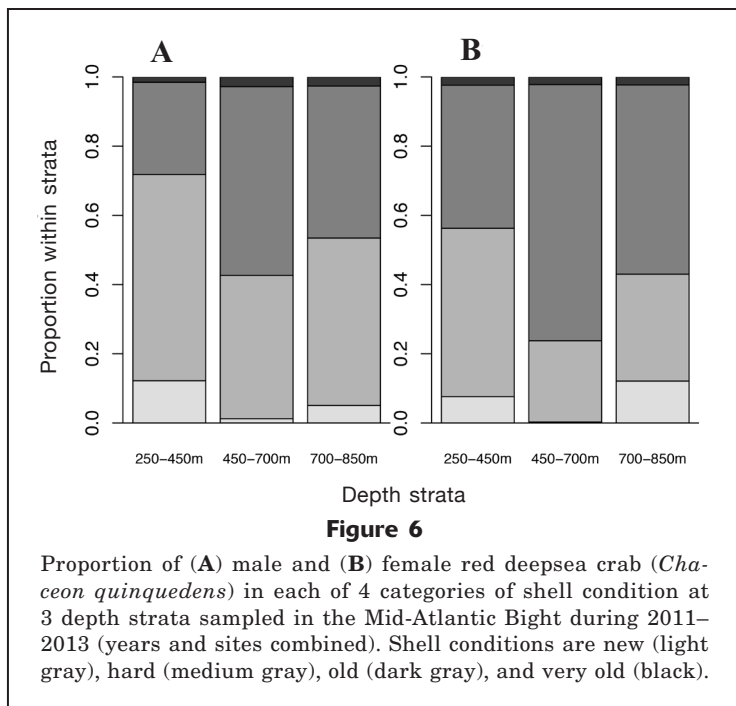


Figure 5

Mean size of red deepsea crab (*Chaceon quinque-dens*) sampled during 2011–2013 at 3 depth strata (years and sites combined) for (A) males and (B) females and at 4 sites (years and depth strata combined) for (C) males and (D) females. Letters indicate similar groups within frames. The 4 sites in the Mid-Atlantic Bight were Block Island Canyon (BIC), Hudson Canyon (Hud), Baltimore and Washington Canyons (BWC), and Norfolk Canyon (Nor)

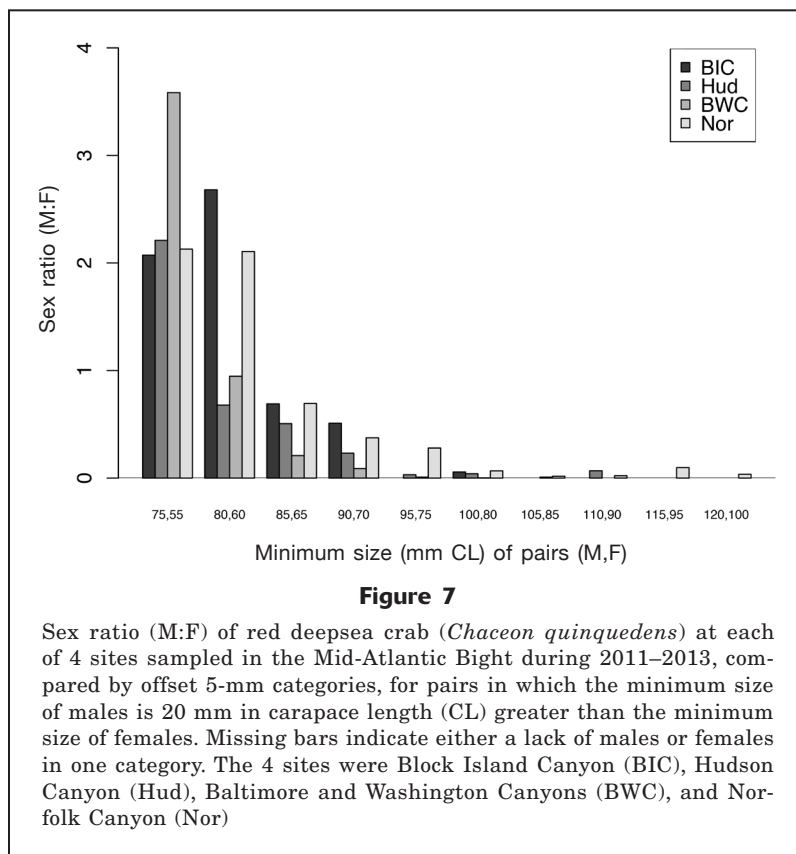


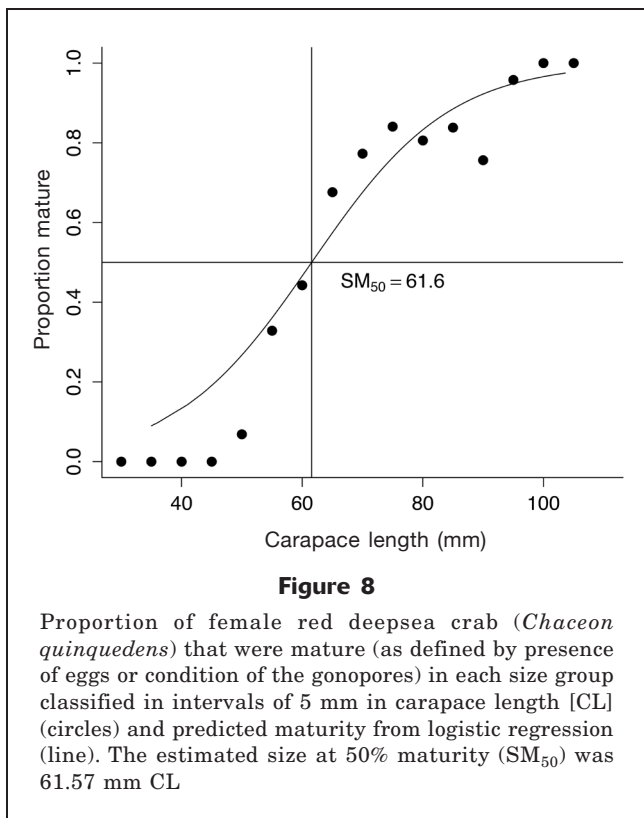
mm SW) have been previously noted (McRae, 1961; Haefner, 1978; Weinberg and Keith, 2003). According to McRae (1961), mean weights for a “random sample” of crabs were 794 g for males, and 312 g for non-ovigerous females, equivalent to sizes of 116.4 mm CL and 88.4 mm CL, respectively, or 144.2 and 110.2 mm SW (converted with the equation for CW from Weinberg and Keith, 2003). The source of this sample was not described, but presumably it was near our sampling area. Therefore, either mean size of red deepsea crab has declined significantly since McRae’s study in 1960, or his random sample was biased toward large crab. The mean size of male crab reported by McRae (1961) was 31% larger than the mean size of females. This difference is similar to the mean size differential of 27.9% reported by Elner et al. (1987) for 3 pairs of crab (involving 2 males and 2 females) observed mating in captivity, but it is smaller than the differential of 50% between 10 mating pairs observed by Wahle et al. (2008) during tows with video cameras. Although sample sizes for the latter 2 studies were small, they indicate that the relative size of male and female crabs observed by McRae (1961) offered adequate opportunities for mating.

Sex ratios are commonly used to determine whether fishing has affected a crab

population, but they are usually calculated over large geographic areas. However, functional maturity (i.e., the ability of male crabs to mate in competitive, natural environments) is dependent on both size (Paul, 1984) and shell condition (Stevens, et al., 1993) because harder shells are necessary to grasp females and defend them from other males. As a result, the effective sex ratio of mating-capable partners may vary greatly over small geographic areas. For this reason we calculated effective sex ratio only within sampling sites, where the samples were geographically close, and these ratios were calculated between abundance of females in 5-mm-CL bins and abundance of males that were 20 mm CL larger. We also ignored shell condition and depth because both could change between the time sampled and mating season, and we did not include year effects in order to preserve adequate sample sizes.

Sex ratios were generally biased toward males in the smaller size intervals, but for intervals larger than the SM_{50} for female red deepsea crab, all ratios were <0.7 , and many ratios were much lower. These data indicate that male mating partners for females become exceedingly scarce as females grow. Mating of male crab with multiple females has been observed for red deepsea crab (Elner, et al., 1987), southern





Tanner crab (Paul, 1984), and snow crab (Rondeau and Sainte-Marie, 2001). Male southern Tanner crab may mate with as many as 10 partners, but usually with less than 5 (Paul, 1984). Guarding time and the amount of sperm transferred by male snow crabs declines with sex ratio because males try to conserve sperm and, therefore, may leave females with inadequate supplies to fertilize a clutch of eggs (Rondeau and Sainte-Marie, 2001). Blue crab (*Callinectes sapidus*) show a marked decline in the rate of courtship initiation at sex ratios below 2 (Jivoff and Hines, 1998). The minimum sex ratio for successful fertilization of all females in a crab population is unknown, but may lie between 0.1 and 0.5; a conservative estimate would be 0.25, indicating that most females above the mean size in our study do not have access to an adequate number of males.

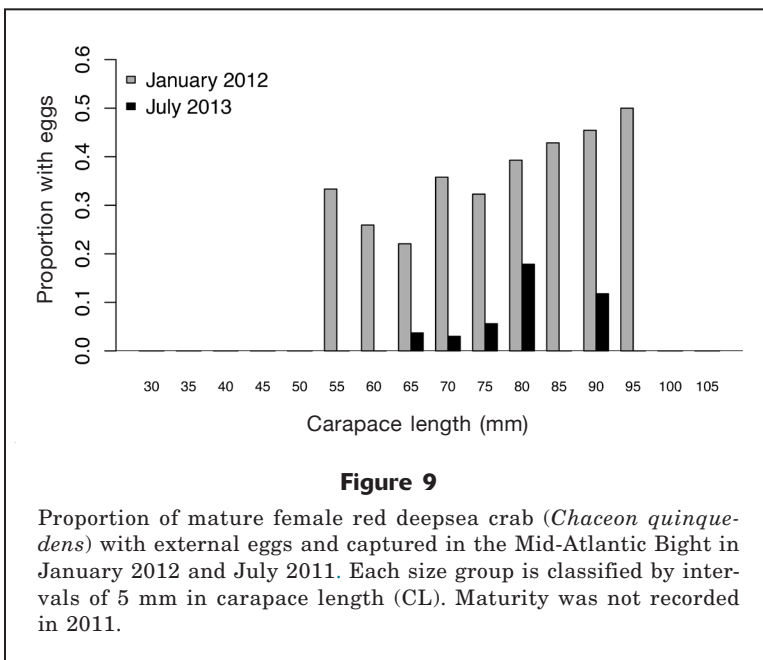
The crab in our study were considerably smaller than *C. affinis* from the Canary Islands (mean sizes of males and females were 130 and 120 mm CW) (Fernández-Vergaz et al., 2000) or the Azores (107 and 91 mm CL) (Pinho et al., 2001); however, crab in the Canaries and Azores were captured by traps, which are highly size selective; only 3 crab <80 mm CW were caught by Fernández-Vergaz et al. (2000).

Morphometrics

Sexual maturity in our sample of red deepsea crab cannot be inferred from morphometric characteristics. A variety of methods have been proposed for determining the maturity of crabs. Somerton (1980) described a computer technique that determined SM_{50} for male crabs by fitting morphometric data with a logistic regression. He defined 4 patterns of allometric growth, based on the relationship between chela and carapace measurements, and applied those relationships to determine size at sexual maturity for male snow crab in the Bering Sea (Somerton, 1981) and later for blue king crab (*Paralithodes platypus*; Somerton and MacIntosh, 1983). Allometric patterns in species of *Chionoecetes* are curvilinear, and variation increases with size, but patterns become linear when log-transformed. The slope of the log-transformed relationship is defined as the allometry coefficient.

The relationship between ChL and CL for our male red deepsea crab was linear, did not show increased variance with size, and did not require transformation. It has an allometry coefficient of 1.09, indicating isometric growth and has no inflection point that could be used to define the onset of sexual maturity. The relationship between ChL and CL for female crabs, however, indicated clear sexual dimorphism and was negatively allometric. The relationship between male ChH and CL was also isometric, with an allometry coefficient of 1.06. Similar to that of males, the relationship between female AW and CL was linear, had no apparent inflexion point corresponding to maturity, and did not differ between maturity types.

Similar results were obtained for *C. affinis* in the Azores; no inflections were found in the relationships between CL and CW, ChW (height), or female AW, and



male:female dimorphism was present in the chelae but not in CW (Pinho et al., 2001). In contrast, allometric relationships for ChL and ChW in *C. affinis* from the Canary Islands were strongly positive (approximately 1.3–1.5) and were used in hierarchical cluster analysis to distinguish immature from mature individuals of both sexes (Fernández-Vergaz et al., 2000). Logistic regression of these crab indicated SM₅₀ values of 129 mm CW for male *C. affinis*—a size that would be equivalent to 103 mm CL for red deepsea crab if converted with the regression of CL on SW for the latter (Fernández-Vergaz et al., 2000).

Determination of sexual maturity on the basis of morphometrics works well for crabs of the families Oregonidae (*Chionoecetes* spp.) and Majidae. The spider crab (*Maja brachydactyla*) shows a typical curvilinear relationship between CL and ChH that becomes linear upon log-transformation, and Corgos and Freire (2006) used discriminant analysis to separate immature and mature male clusters. Their data were fitted even better by a 3-stage growth model, which included an inflection point between juveniles and adolescent males. Therefore, excluding one study on *C. affinis*, morphometric relationships have not proved useful for determining sexual maturity in the genus *Chaceon*.

Distribution by depth and temperature

At our sampling sites, highest abundance of red deepsea crab occurred at depths between 500 and 650 m, and few crab were captured at depths <400 m. Female red deepsea crab dominated catches taken at depths shallower than 600 m, and males were more prevalent at greater depths. Haefner et al. (1974) reported that the highest abundance occurred at depths between 265 and 512 m, and they observed that females dominated trawl catches above 400 m in and near Norfolk Canyon but that males became dominant below 400 m.

Our data show a slight but significant decline in size of crab with increasing depth—a drop that was much more apparent for females. This decline in size is consistent with other reports that indicate that juvenile red deepsea crab are more common at greater depths (Wahle et al., 2008). We also found that the proportion of males increased with depth. Off the Namibian coast, *C. maritae* (misidentified as *C. quinquedens*) show similar depth ranges; females predominate above 400 m at temperatures of ~8°C and males are more abundant down to 900 m and 4°C (Beyers and Wilke, 1980; as cited by Melville-Smith, 1989). In contrast, Kilgour and Shirley (2008) caught red deepsea crab by traps at depths of 533 to 1950 m in the Gulf of Mexico but found no significant relationships between depth and crab size or sex. Pinho et al. (2001) caught *C. affinis* with traps around the Azores Islands and found that the highest abundance occurred at depths between 700 and 900 m. In that study, size of both sexes decreased slightly with increasing depth, but the proportion of males declined with increasing depth, in contrast to our results.

Despite differences in depth distribution observed for red deepsea crab in our surveys, the differences in temperature distribution by sex were minor, and much overlap occurred between males and females. Similarly, differences in bottom temperature between years were minor despite sampling in either January or July, and differences weighted by crab catch were even less. These data indicate that temperatures at the depths sampled do not show great annual variation, and red deepsea crab tend to stay within a narrow range of preferred temperature. This information indicates that red deepsea crab recruit as juveniles to waters deeper than those sampled, move upslope during development, and become mature in the shallowest zones, after which they undergo an ontogenetic migration back to intermediate depths.

Female maturity and ovigerity

Our estimate of SM₅₀ for female red deepsea crab (61.6 mm CL) was calculated by nonlinear logistic regression; therefore, a point estimate was possible. Haefner (1977) estimated female maturity on the basis of the relationship of AW to CL for females classified as mature or immature by gonopore condition, and he determined that maturity occurred over a size range of 65–75 mm CL. Haefner (1977) calculated 2 separate regression equations for females with mature or immature gonopores (total $n=251$) for the relationship between AW and CL that had similar slopes but different intercepts. However, the equation for immature females was influenced by 3 extremely small crab. Likewise, AW of *C. affinis* has been reported to change in intercept at maturity, between 95 and 105 mm CW (equivalent to 76–84 mm CL) (Fernández-Vergaz et al., 2000).

In contrast, covariance analysis of our data did not support the hypothesis that the 2 relationships were different, and there were no extreme outliers (total number of females analyzed=182). Abdomen morphology indicated that *C. affinis* females become functionally mature (i.e., capable of bearing eggs) before reaching physiological maturity (which is assessed on the basis of apparent ovarian stage) (Fernández-Vergaz et al., 2000). Logistic regression indicated SM₅₀ values of 108 mm CW (equivalent to 86.6 mm CL) for abdominal maturity and 113.4 mm CW (91 mm CL) for gonopore maturity of crab in the Canary Islands (Fernández-Vergaz et al., 2000), whereas the SM₅₀ for female red deepsea crab in the Azores determined by gonopore condition was 83.1 mm CL (Pinho et al., 2001).

The presence of eggs on <50% of female crabs is a strong indicator that reproduction occurs at biennial (or longer) intervals. Haefner (1977) examined female red deepsea crab from the Norfolk Canyon, and reported that only 25.5% of females >71 mm CL were ovigerous in January 1976. He also reported that abraded gonopores were present in 93.5% of female red deepsea crab ≥71 mm CL but not in any crab <70 mm CL. In the Azores, ovigerous *C. affinis* were found only in the fourth and first quarters of the year, with a maximum

of 33% ovigerous crab. Lack of annual mating for red deepsea crab was previously hypothesized by other authors (Weinberg and Keith, 2003). Female *C. maritae* in South Africa were also reported to have asynchronous molting and aseasonal reproductive cycles (Melville-Smith, 1989).

Reproductive cycles >1 year may occur among crabs living at extremely low temperatures. Blue king crab in the Bering Sea living at temperatures ranging from -1°C to 4°C reproduce biennially (Somerton and MacIntosh, 1985; Jensen and Armstrong, 1989; Stevens et al., 2008), and approximately 50% of females bear fertilized embryos each spring. Female snow crab reproduce biennially in the Gulf of St. Lawrence at temperatures $<1.0^{\circ}\text{C}$ and have only 2 broods over their reproductive lifespan (Moriyasu and Lanteigne, 1998; Comeau et al., 1999), whereas snow crab living at higher temperatures (and greater depths) reproduce annually, potentially producing 4 lifetime broods (Kuhn and Choi, 2011).

Switching from biennial to annual reproduction can potentially halve or double lifetime reproductive output, depending on direction of change (Webb et al., 2007). A change of only 1°C can advance or delay hatching of red king crab (*Paralithodes camtschaticus*) by about 2 weeks, possibly contributing to year class failure from a mismatch between larval hatching and food sources (Stevens et al., 2008). Other crabs with reproductive cycles longer than 1 year include the golden king crab (*Lithodes aequispinus*) and others that live at depths >500 m and produce lecithotrophic larvae (Shirley and Zhou, 1997; Paul and Paul, 2001). Biennial spawning has been reported only for crab species living at temperatures $<4^{\circ}\text{C}$, and for those with lecithotrophic larvae, but has not been reported for crabs with planktotrophic larvae living at temperatures $>6^{\circ}\text{C}$. Therefore, crabs of the genus *Chaceon* are unusual in this respect.

The extremely low proportion of egg-bearing females and the advance stage of egg development observed in July 2013 indicate that hatching was nearly completed at that time, and some crab bore newly fertilized eggs in very early developmental stages. These observations indicate that hatching and ovulation events are separated by a time interval, possibly up to a year in red deepsea crab (*Brachyura*). This separation of events is in contrast with the reproductive strategy of red king crab (*Anomura*), which molt, mate, and extrude a new clutch of eggs within hours after releasing larvae (Stevens and Swiney, 2007). All species of king crab lack the ability to store sperm, however, and, as a result, comparisons to brachyurans are more appropriate. Snow crab (*Brachyura*) can store sperm, and multiparous crab may use stored sperm to produce additional clutches of eggs; however, those crab that re-mate must do so within 4–7 days after releasing larvae in order to produce viable clutches (Paul and Adams, 1984). Therefore, it appears that red deepsea crab differ from species of *Chionoecetes* in their ability to separate the process of larval release (and presumably mating) from that of ovulation and fertilization.

The current fishery for red deepsea crab is expanding into the southern portion of the Mid-Atlantic Bight, including the Norfolk and Washington Canyon areas. This expansion is a result of changing abundance, as well as of changes in the availability of processing facilities close to fishing grounds (Williams⁷). Therefore, the population targeted by the fishery is different from that fished 20 years or even 10 years previously. The results of this study lay a foundation for other synoptic studies on red deepsea crab in the Mid-Atlantic Bight. As we went to press (May 2016), we were continuing our work with red deepsea crab, analyzing tissue samples from crab collected during the cruises in 2011–2013, as well as from samples collected aboard commercial fishing vessels in 2014 and 2015. The results of this further analysis should reveal more details about the biology of the red deepsea crab, including size at maturity, reproductive cycles, fecundity, and embryonic and larval development.

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