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ARTICLE

## Fecundity Assessment of Stone Crabs in the Eastern Gulf of Mexico

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### Abstract

Accurate estimates of reproductive potential are a key component of any stock assessment. Multiple factors influencing the variability in batch fecundity of stone crabs *Menippe* spp. across the Florida fishery were quantified with a negative binomial regression model. Stone crabs were collected bimonthly from Cedar Key, Tampa Bay, Pavilion Key, and Sawyer Key from April 2013 through April 2015 for fecundity analysis. Batch fecundity (number of eggs per clutch) was estimated by using dry weights. Modeling results revealed that fecundity was strongly and positively related to carapace width and highly variable among locations, months, and years. Batch fecundity was lowest in spring and winter and highest in July and August, which agreed with the general understanding of seasonal patterns in crustacean reproductive cycles. Additionally, batch fecundity was 39% lower for crabs with no claws, indicating that claw removal by the fishery negatively affects reproductive output. Comparisons of estimates from a 1993–1995 fecundity study in Tampa Bay indicated that there was little difference in stone crab fecundity between individuals collected in 1993 and those collected in 2013. But this observed temporal pattern represents observations from only a small portion of the fished population and so may not fully reflect the temporal changes in fecundity occurring throughout the fishery. The present study quantified the spatial and temporal factors influencing variability in stone crab fecundity throughout the fished population of Florida. We hypothesize that spatial differences in food quality, food quantity, and fishing effort may be important drivers of variability in stone crab fecundity. Given the intense harvest and variability in reproductive output, further work should be dedicated to identifying critical spawning and recruitment areas, as well as assessments of their connectivity.

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The fishery for stone crabs *Menippe* spp. in Florida has existed since 1902 and reached its full exploitation by 1996 (Muller et al. 2011). Two species of stone crabs and their hybrids exist in the Gulf of Mexico and the Atlantic Ocean, Gulf stone crab *M. adina* (A. B. Williams and Felder) and Florida stone crab *M. mercenaria* (Say 1818). The stone crab is managed as a single taxonomic group in

Florida (Gerhart and Bert 2008; Bert et al. 2016b), and the two species share many of the same population characteristics and relationships between carapace size and legal-sized claws (Perry et al. 1995; Gerhart and Bert 2008). Previous research has suggested that there are no expected differences in reproduction that is related to hybridization (Bert et al. 2016a), such as timing and

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frequency of spawning (Perry et al. 1995), molting and mating (Wilber 1989), and batch fecundity (Bert et al. 2016a). Bert et al. (2016a) found no significant difference in egg diameter or batch fecundity between crabs genotyped as *M. mercenaria* and their hybrids.

Assessment of the heavily exploited stone crab in Florida requires accurate descriptions of the reproductive biology and population dynamics of the stock. In particular, understanding the spatial and temporal variability of the stock's reproductive potential is essential. Fecundity is commonly used as a measure of stock reproductive potential, so biological and fisheries-related reference points with respect to fecundity should be developed for effective management of marine fisheries (Campbell and Robinson 1983; Goni et al. 2003; Tallack 2007; Cooper et al. 2013). However, obtaining an accurate assessment of fecundity in individuals of an exploited stock is challenging, requiring large sample sizes that cover the geographic distribution of the species (Tully et al. 2001).

A positive correlation between body size and fecundity has been well documented in stone crabs and other decapods (Jones et al. 1990; Sainte-Marie 1993; Mantelatto and Fransozo 1997; Pereira et al. 2009; Bert et al. 2016a). Precise estimates of crustacean fecundity, however, are often difficult to obtain because of the variability among females of a similar size (Goni et al. 2003). This variability can be attributed to multiple factors including diet (Griffen 2014), environmental and physical habitat conditions (e.g., food quantity and quality, habitat structure (DeMartini et al. 2003; Zairion et al. 2015), local demographics (population density, competition), and temperature (Lardies and Castilla 2001; Lardies and Wehrtmann 2001; Antonio et al. 2003; Cardoso and Defeo 2003; Bert et al. 2016a). Thus, the factors influencing the spatial and temporal variability of fecundity estimates must be considered when assessing the usefulness of indices for fisheries assessment.

Fecundity studies on *M. mercenaria* have used small sample sizes of fewer than five individuals (Binford 1912; McRae 1950; Noe 1967). The most robust study (Bert et al. 2016a) assessed fecundity of ovigerous females from 1993 through 1995 collected from Tampa Bay, Florida ( $n = 329$ ). That study explored the influence of multiple intrinsic and extrinsic factors on fecundity and revealed the association between carapace width, temperature, and clutch size. The Tampa Bay study was, however, limited to a small region within the extensive latitudinal distribution of the stock along Florida's west coast and likely did not capture the variability inherent to the species throughout its range. This could preclude accurate estimates of stock productivity.

Stone crab mating generally occurs during fall months in shallow waters (McRae 1950; Bender 1971; Sullivan 1979) when females are newly molted (Cheung 1968). The

female subsequently stores spermatophores within the seminal receptacles until mature eggs are present and ready for fertilization (Cheung 1968; Hartnoll 1985). Spawning occurs from June through October throughout Florida (McRae 1950; Bender 1971; González y de la Rosa et al. 2004; Gerhart and Bert 2008), but due to regional variation in water temperature, the spawning season in southern Florida is protracted and occurs from May through November (Noe 1967; Cheung 1968; Sullivan 1979; Bert et al. 1986). Females produce an average of four fertilized egg masses per mating event (Cheung 1969). Upon extrusion, the fertilized eggs are bright orange and progress to dark gray as the embryos develop. During the 11- to 14-d period of embryonic development (Binford 1912; Porter 1960), the eggs grow in diameter, and the egg mass is vulnerable to losses stemming from nonviable eggs, predation, and disease (Darnell et al. 2009; Graham et al. 2012). The stone crab fishing season (October 15–May 15) was implemented in 1985 under the Florida Administrative Code (Chapter 46-13) to protect spawning females from harvest and eliminate fishing mortality during the peak of the spawning season (Savage and Sullivan 1978). During this season fishers remove the claws and release the crab back into the water. It has long been presumed that a legal crab can regenerate a lost limb and contribute to the fishery again in 2–3 years. However, a growing body of evidence suggests that mortality is higher than previously estimated, and few crabs contribute to the fishery a second time (Savage et al. 1975; Wilber 1995; Gandy et al. 2016; Duermit et al. 2017).

Data obtained from the Florida Fish and Wildlife Research Institute (FWRI) Marine Resources Information System's Marine Fisheries Trip Ticket Program indicates that 60% of the stone crabs are harvested in south Florida (Collier–Monroe counties), 20% in southwest to west-central Florida (Lee–Pasco counties), and 20% in northwest Florida (Hernando–Taylor counties). The fishery is closed throughout Florida from May 16 through October 14, so in south Florida spawning overlaps each fall with the beginning of the fishing season. The high percentage of fishery landings in south Florida combined with high predicted mortality (23–85%, depending on the severity of the break and number of claws removed) (Duermit et al. 2015; Gandy et al. 2016) and reduced reproductive output from declawing (Hogan and Griffen 2014; Duermit et al. 2017) may negatively and disproportionately affect females in southern regions compared with those in northern regions.

This study determined the batch fecundity (number of eggs per clutch) of stone crabs collected throughout the Florida fishery and quantified some of the most important factors influencing variability in stone crab fecundity. Crabs were collected monthly and over a wide range of size-classes for 2 years. Our objective was to quantify the

relationship between batch fecundity and carapace width while accounting for spatial differences in batch fecundity among survey locations, temporal differences in batch fecundity over approximately 2 years of sampling, and differences among individuals with missing claws. By encompassing a large latitudinal range and the majority of the Florida fishery, these data will provide an accurate baseline for future assessments of fecundity, which may be used to test for fishery-induced effects on the stock's reproductive output.

## METHODS

*Sample collection.*—Egg-bearing female stone crabs having a recently extruded (bright orange) egg mass were collected in commercial style crab traps, twice a month from April 2013 through April 2015 from four FWRI Stone Crab Fishery Independent Monitoring (SCFIM) locations. Such females were sampled for fecundity analysis to minimize the effect of egg loss that may have occurred before the collection of the crabs, egg growth during embryonic development, and response to predation and disease. The sites were located at Sawyer Key (SK), Pavilion Key (PK), Tampa Bay (TB), and Cedar Key (CK) (Figure 1). These sites were chosen to encompass the latitudinal range of the Florida stone crab fishery, to span multiple habitat types, and to coincide with collection of male and nonovigerous female crabs for related studies (SCFIM, unpublished data). From each location, 1–3 crabs were randomly collected from each of 10 carapace-width size-classes (25–29, 30–39, 40–49, 50–59, 60–69, 70–79, 80–89, 90–99, 100–109, and 110+ mm). Live crabs were taken to the laboratory where they were anesthetized on ice and dissected.

Immediately before dissection, carapace width, claw length, total body weight, and body weight without claws were recorded. The newly extruded eggs and all eight pleopods were removed, placed in a 125- $\mu$ m-mesh sieve, and rinsed under running tap water to remove sediment and hemolymph. The eggs, which were still attached to pleopods, were then transferred to a vial containing 5% formaldehyde solution (diluted from 37% commercial formalin), where they were stored until further processing.

Before eggs were processed for fecundity determinations, a random sample of 25 eggs was used to obtain diameter measurements from each of 410 crabs. Eggs were placed in a petri dish, manually separated, and arranged to lie in a single plane. Images were taken using a Leica stereoscope equipped with a Leica S6D camera, and egg diameters were measured using Leica image analysis software (Leica Microsystems, Buffalo Grove, Illinois). The diameters of the 25 eggs were averaged for each batch. Batch fecundity determinations for 606 crabs were based on a modification to the protocol described by Graham

et al. (2012): the formaldehyde solution was drained from the preserved egg mass through a 125- $\mu$ m-mesh sieve, and the egg mass was then rinsed under tap water for 1 min. To separate the eggs from the pleopods, the sieve was then immersed in a 1:1 bleach (sodium hypochlorite) : seawater solution until the eggs completely separated (Choy 1985). While still in the sieve, the eggs were rinsed under tap water for 15 s and immersed in 4% sodium thiosulfate to neutralize any remaining bleach. Three subsamples of approximately 600 eggs each were removed and counted using a Leica stereoscope and camera, as above. The entire egg mass and subsamples were then placed in separate aluminum dishes of known weight, dried at 80°C to a constant weight (1 week), then placed in a desiccator and cooled to room temperature. All samples were weighed on a Mettler Toledo MS603S balance (Mettler Toledo, Columbus, Ohio). The individual egg dry weight was calculated for each subsample (dry weight of subsample/number of eggs) and averaged across the three samples. To calculate the number of eggs in the clutch, the dry weight of the entire egg mass was divided by the average individual egg dry weight.

*Environmental data.*—Seawater temperature and chlorophyll *a* concentration were used to assess possible environmental influences on batch fecundity. At the time of each collection, bottom temperature was measured with a YSI 650 MDS multiparameter display system (YSI, Yellow Springs, Ohio). Mean monthly temperature was determined by averaging the monthly temperature readings from each location. Ocean color, indicative of the mean monthly chlorophyll *a* concentration, was obtained from satellite virtual-buoy systems (VBS) (Hu et al. 2013) as a representation of productivity at all locations except for Pavilion Key, for which data were not available. These VBS sites were located within 35 km of the collection sites. Logistical constraints precluded the identification of habitat types at each sampling location; therefore, this specific factor was not included in analyses.

*Statistical analyses: historical versus recent fecundity.*—Crabs were binned into 10 carapace-width classes (30–40, 40–50, 50–60, 60–70, 70–80, 80–90, 90–100, and 110+ mm) for frequency analysis and to allow for the comparison of batch fecundity observed during the present study with that in the historical literature (Bert et al. 2016a). The present fecundity data, however, did not meet the assumptions of normality, and only descriptive statistics were available for historical data; therefore, the data from the two studies could not be compared statistically. The present and historical data are presented, but only qualitatively compared.

*Statistical analyses: batch fecundity modeling.*—Our primary modeling objective was to assess the influence on stone crab batch fecundity of crab-specific covariates (Carapace Width [CW]; Crusher Status: Original Crusher

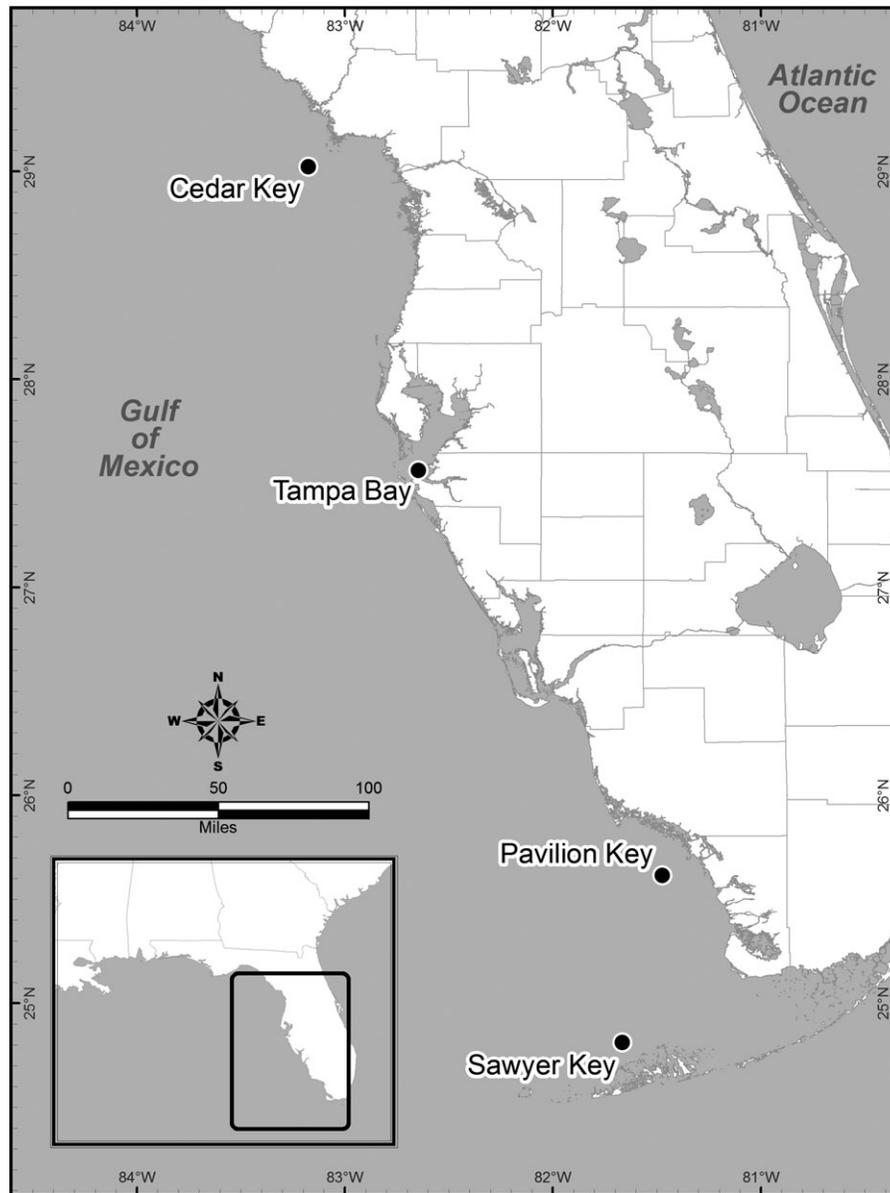


FIGURE 1. Selection of sampling locations for the Florida Fish and Wildlife Stone Crab Independent Monitoring Program.

[OC], Missing Crusher [MC], and Regenerating Crusher [RC]; Pincer Status: Original Pincer [OP], Missing Pincer [MP], and Regenerating Pincer [RP]); a spatial covariate (Location: Cedar Key, Sawyer Key, Pavilion Key, and Tampa Bay); and several categorical covariates associated with time (Year: 2013, 2014, and 2015; Month: all months except November; and Month-Year: 20 unique month-year combinations). Initial model assessments indicated substantial overdispersion in the batch fecundity data, which precluded the use of a conventional Poisson regression for modeling egg counts. Hence, a negative binomial model was used, which enabled us to

determine an estimation of an overdispersion parameter (hereafter,  $\theta$ ) that accounted for excessive variability in the count data. Similar to a Poisson regression, the negative binomial model used a log-link function to model batch fecundity as a linear combination of covariates, here: Carapace Width, Crusher Status, Pincer Status, Location, and Time. Carapace Width was included in models as a continuous covariate, Location was included as a categorical predictor representing the four study locations, and Crusher Status and Pincer Status were included by using binary indicator variables that identified the status of each claw (original, missing, or

regenerating crusher and pincer). To account for temporal differences in stone crab fecundity, the Year, Month, and Month–Year effects were always included in the model as categorical covariates that identified the Year (three groups), Month (11 groups), or Month–Year (20 groups) in which stone crabs were collected. When a categorical predictor variable is used to identify group membership, one of the groups must serve as a statistical baseline for comparison (i.e., to serve as the model intercept). During model fitting, Cedar Key served as the statistical baseline when location was included as a predictor in a model, original claws (crusher and pincer) served as the baseline when Crusher Status and Pincer Status were included as predictors, and 2013, January, and April 2013, respectively, served as the baseline when Year, Month, and Month–Year were included in the model.

Due to the large number of possible combinations of covariates, the model-fitting procedure was conducted in a stepwise fashion. The first step (step A) involved identifying the best combination of temporal effects using the global (all predictors) model. Specifically, the relative support for two different models was assessed using Akaike's information criterion (Akaike 1973) with a small-sample bias adjustment ( $AIC_c$ ; Hurvich and Tsai 1989), and each model represented a different covariate associated with Time (Table 1A). For the next step (step B), the best-approximating (i.e., lowest  $AIC_c$ ) model in step A was used to assess the relative support for 31 additional models, each representing a different combination of Carapace Width, Crusher Status, Pincer Status, Location, and Month–Year (Table 1B). To assess differences in mean batch fecundity among locations, we conducted post hoc pairwise Tukey contrasts using the R package “mult-comp” and *P*-values adjusted via the Holm method to account for conducting multiple comparisons. The precision of parameter estimates was assessed by examining 95% CIs, and all parameters with a 95% CI that overlapped zero were considered imprecise. All inferences were based on parameter estimates from the best-approximating model from step B.

We also sought to assess the influence of egg diameter on batch fecundity, but egg diameter measurements were available for only 410 of the 606 total egg batches, which meant that mean egg diameter (calculated by averaging the diameter of 25 eggs per batch) could not be included in models fit to the full data set of 606 batches. To determine support for including egg diameter, we refit the best-approximating model from step B to the reduced data set with and without mean egg diameter as a predictor variable (Table 1C). The relative support for the models was determined by  $AIC_c$ . All negative binomial regression models were implemented in R version 3.2.4 using the

glmmADMB package (Fournier et al. 2012; Skaug et al. 2016).

## RESULTS

During the 2-year sampling period, 606 ovigerous crabs with recently extruded egg masses were collected from four locations and represented a range of carapace widths (Table 2). The number of eggs per batch increased with increasing size-class among all locations and was highly variable within each size-class (Table 3). Egg diameter varied slightly across carapace width and month (Figure 2) and did not appear to influence batch fecundity. Median monthly egg diameter was largest (0.39  $\mu\text{m}$ ) in March and smallest (0.33  $\mu\text{m}$ ) in July (Figure 2). In July, several individuals from multiple locations carried eggs larger than 0.5  $\mu\text{m}$  (Figure 2). Interestingly, the median egg diameter for each site, averaged over all months, was the same (0.35  $\mu\text{m}$ ), and maximum egg diameter (0.42–0.56  $\mu\text{m}$ ) varied only slightly between locations (Table 4). For each size-class category, there appeared to be minimal difference between contemporary and historical estimates of batch fecundity in Tampa Bay stone crabs (Table 5). The absence of crabs in the 30-mm and 110-mm size-classes in the present study precluded comparisons with historical data for those size-classes.

### Batch Fecundity Model Selection

Evaluation of temporal effects for the global model indicated substantial support for the inclusion of Month–Year as a temporal effect in the negative binomial regression model (Table 1A). Thus, subsequent models fit in step B included a Month–Year temporal covariate. Evaluation of the best-approximating model indicated substantial overdispersion (negative binomial overdispersion parameter,  $\theta = 5.47$ ), but model fit was deemed adequate with no evidence of remaining overdispersion (Pearson  $\chi^2$  test statistic: residual degrees of freedom = 0.96). The best-approximating model from step B included Carapace Width, Crusher Status, Pincer Status, Location, and Month–Year as fixed effects; thus, these were all deemed important predictors of stone crab batch fecundity (Table 1B). Evaluation of the model that included egg diameter indicated little support for the inclusion of this parameter (Table 1C). The ratio of  $AIC_c$  weights indicated that the model that excluded egg diameter was 3.09 (0.76/0.24) times more plausible than the model that included egg diameter (Table 1C). Given the lack of support for the influence of egg diameter on batch fecundity in the reduced data set, we based all inferences on modeling results from the full (i.e., 606 egg batches) data set in which the influence of egg diameter was not considered.

TABLE 1. Fixed effects, number of parameters ( $K$ ), log likelihood (logLik),  $AIC_c$ ,  $\Delta AIC_c$ , and model weights ( $w$ ) for the candidate set of negative binomial regression models relating Carapace Width (CW), Location (CK, SK, TB, and PK), Month-Year, Crusher Status (RC and MC), and Pincer Status (RP and MP) to stone crab batch fecundity (see Methods for definition of abbreviations). Modeling proceeded in a step-wise fashion: (A) involved identifying the best approximating model of temporal effects; (B) used the best-approximating model from (A) to assess relative support for the inclusion of Carapace Width, Location, Claw Status, and Month-Year; and (C) used the best approximating model from (B) to assess support for the inclusion of egg diameter (EggD) using a reduced data set with 410 crabs. CK, April 2013, and original claws (OC and OP) served as the baseline (i.e., intercept) in all models.

Model	$K$	logLik	$AIC_c$	$\Delta AIC_c$	$w$
<b>(A) Temporal effects assessment</b>					
Intercept + Location + Month – Year + Crusher Status + Pincer Status	29	-7,801.36	15,663.74	0.000	1.000
Intercept + Location + Month + Year + CW + Crusher Status + Pincer Status	22	-7,836.43	15,718.60	54.86	0.000
<b>(B) Main effects assessment given best-approximating model in (A)</b>					
Intercept + Location + Month – Year + CW + Crusher Status + Pincer Status	29	-7,801.36	15,663.74	0.00	0.63
Intercept + Location + Month – Year + CW + Crusher Status	27	-7,804.16	15,664.94	1.20	0.35
Intercept + Location + Month – Year + CW + Pincer Status	27	-7,807.03	15,670.68	6.94	0.02
Intercept + Location + Month – Year + CW	25	-7,810.69	15,673.62	9.88	0.00
Intercept + Month – Year + CW + Crusher Status	24	-7,832.28	15,714.63	50.89	0.00
Intercept + Month – Year + CW + Crusher Status + Pincer Status	26	-7,830.410	15,715.25	51.504	0.00
Intercept + Month – Year + CW + Pincer Status	24	-7,835.560	15,721.19	57.445	0.00
Intercept + Month-Year + CW	22	-7,838.140	15,722.02	58.275	0.00
Intercept + Location + CW + Crusher Status + Pincer Status	10	-7,943.890	15,908.15	244.41	0.00
Intercept + Location + CW + Pincer Status	8	-7,947.890	15,912.02	248.28	0.00
Intercept + Location + CW + Crusher Status	8	-7,949.570	15,915.38	251.64	0.00
Intercept + Location + CW	6	-7,954.270	15,920.68	256.94	0.00
Intercept + CW + Crusher Status + Pincer Status	7	-7,963.830	15,941.85	278.11	0.00
Intercept + CW + Crusher Status	5	-7,968.080	15,946.26	282.52	0.00
Intercept + CW + Pincer Status	5	-7,968.490	15,947.08	283.34	0.00
Intercept + CW	3	-7,973.370	15,952.78	289.04	0.00
Intercept + Location + Month – Year + Crusher Status	26	-7,973.280	16,000.99	337.24	0.00
Intercept + Location + Month – Year + Crusher Status + Pincer Status	28	-7,971.93	16,002.68	338.93	0.00
Intercept + Location + Month – Year	24	-7,976.46	16,002.99	339.25	0.00
Intercept + Location + Month – Year + Pincer Status	26	-7,974.68	16,003.79	340.04	0.00
Intercept + Month – Year + Crusher Status	23	-7,991.49	16,030.88	367.14	0.00
Intercept + Month – Year + Crusher Status + Pincer Status	25	-7,990.25	16,032.74	369.00	0.00
Intercept + Month – Year	21	-7,994.90	16,033.38	369.64	0.00
Intercept + Month – Year + Pincer Status	23	-7,993.29	16,034.48	370.74	0.00
Intercept + Location + Crusher Status + Pincer Status	9	-8,062.53	16,143.36	479.62	0.00
Intercept + Location + Pincer Status	7	-8,064.91	16,144.01	480.27	0.00
Intercept + Location + Crusher Status	7	-8,065.46	16,145.11	481.37	0.00
Intercept + Location	5	-8,068.04	16,146.18	482.44	0.00
Intercept + Crusher Status + Pincer Status	6	-8,081.23	16,174.60	510.86	0.00
Intercept + Crusher Status	4	-8,083.59	16,175.25	511.51	0.00
Intercept + Pincer Status	4	-8,083.89	16,175.85	512.11	0.00
Intercept	2	-8,086.37	16,176.76	513.02	0.00
<b>(C) Egg diameter assessment given best-approximating model in (B)</b>					
Intercept + Location + Month – Year + CW + Crusher Status + Pincer Status	28	-5,264.60	10,589.46	0.00	0.76
Intercept + Location + Month – Year + CW + Crusher Status + Pincer Status + EggD	29	-5,264.57	10,591.72	2.26	0.24

### Parameter Estimates from Best-Approximating Model

Parameter estimates from the best-approximating model revealed that fecundity was strongly and positively related to carapace width (Table 6). The incidence rate ratio (IRR) for Carapace Width, or the expected rate of increase in stone crab batch fecundity for every 1-mm increase in carapace width, was 1.035 (Table 6; Figure 3). Parameter estimates are expressed on the log scale and have been back-transformed (i.e., the inverse log has been taken) to estimate batch fecundity ( $e^{8.996 + 0.035 \times CW + \text{Location} + \text{Month} - \text{Year} + \text{Crusher Status} + \text{Pincer Status}}$ ). For example, the

predicted batch fecundity for a 79-mm stone crab with original claws from the baseline location (Cedar Key) during August 2013 was 266,048 eggs, whereas the batch fecundity for an 80-mm stone crab at this location and time was 275,483 eggs ( $\text{IRR} = 275,483/266,048 = 1.035$ ). Parameter estimates and IRRs also indicated that batch fecundity was, on average, higher at Pavilion Key ( $\text{IRR} = 1.35$ ) and Tampa Bay ( $\text{IRR} = 1.39$ ) than at Sawyer Key and Cedar Key. Tukey post hoc contrasts indicated that mean batch fecundity was similar between Tampa Bay and Pavilion Key ( $P = 0.75$ ), similar between Cedar Key and Sawyer Key ( $P = 0.75$ ), and higher for Tampa Bay and Pavilion Key compared with Cedar Key and Sawyer Key ( $P < 0.001$ ). Parameter estimates also indicated that batch fecundity varied substantially among years and months (Table 6; Figure 4). Peak batch fecundity occurred in July and August 2013, when mean monthly temperatures were highest (Figure 5). In general, batch fecundity was lowest in spring and winter months, when mean monthly temperatures were lower (Figures 4, 5). Finally, modeling results indicated that stone crab batch fecundity was strongly and negatively related to Crusher Status and Pincer Status, for

TABLE 2. Number of stone crabs sampled (*n*), median carapace width, and range of carapace widths across all locations and years.

Location	<i>n</i>	Median (mm)	Minimum (mm)	Maximum (mm)
Cedar Key	140	75.8	42.10	98.30
Pavilion Key	136	79.9	40.90	108.00
Sawyer Key	134	85.5	69.00	111.50
Tampa bay	196	78.0	49.10	103.90

TABLE 3. Number of stone crabs sampled (*n*), measured mean, range, and SD of batch fecundity (number of eggs) estimates across all size-classes and locations. Size-classes are: 40 (40–49), 50 (50–59), 60 (60–69), 70 (70–79), 80 (80–89), 90 (90–99), 100 (100–109), and 110+ mm carapace width.

Location	Size-class	<i>n</i>	Mean	Minimum	Maximum	SD
Cedar Key	40	1	40,438	40,438	40,438	
	50	7	74,233	25,189	148,348	53,117
	60	29	126,174	29,500	264,760	81,761
	70	46	173,827	36,035	491,664	114,538
	80	43	253,908	37,171	606,585	155,415
	90	14	329,968	116,037	710,985	192,672
Tampa Bay	40	4	83,830	73,180	91,427	8,479
	50	9	103,625	30,108	169,639	53,337
	60	39	183,076	23,727	397,490	81,956
	70	54	240,682	11,554	492,123	114,675
	80	65	341,639	71,165	667,407	141,555
	90	23	427,686	119,873	659,542	147,069
Pavilion Key	100	2	663,757	589,696	737,818	104,738
	40	3	63,782	44,679	74,292	16,571
	50	14	122,925	12,922	171,974	45,312
	60	15	192,400	51,376	315,598	78,521
	70	36	279,516	42,111	528,851	96,471
	80	42	350,762	86,000	632,593	150,009
Sawyer Key	90	23	438,076	169,621	658,461	148,401
	100	3	603,070	506,456	699,683	136,632
	60	4	117,301	27,231	221,674	79,833
	70	36	225,286	33,966	649,687	124,646
	80	49	271,909	16,757	859,450	149,191
	90	36	348,307	79,185	643,348	155,203
	100	8	441,830	107,671	71,372	224,390
	110+	1	836,644	836,644	836,644	

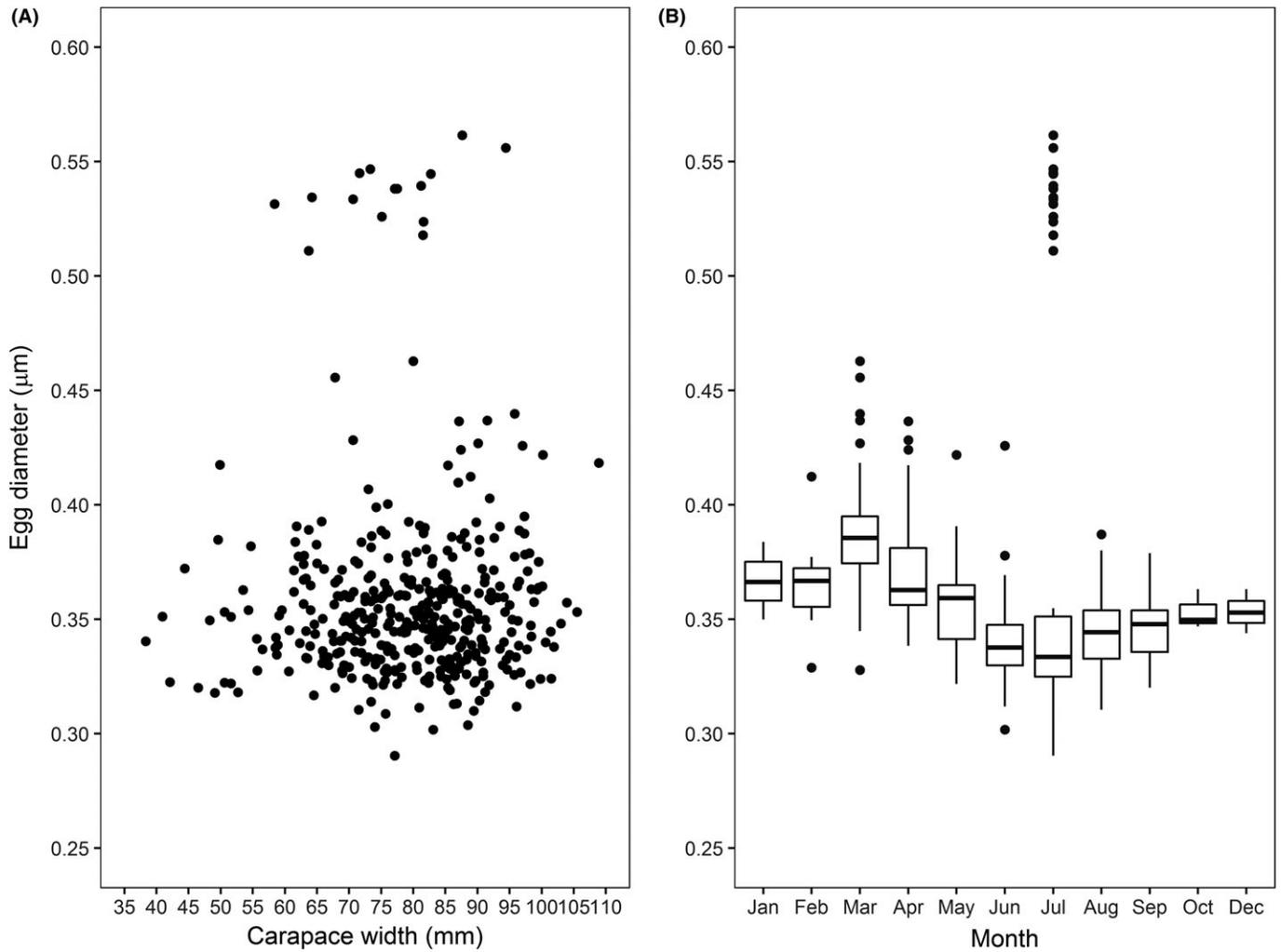


FIGURE 2. (A) Measured egg diameters across all carapace widths ( $n = 417$ ) and (B) median monthly egg diameters across all months, combined for all years. Ovigerous crabs were not present in field sampling in November, so no egg diameter measurements were possible. Solid horizontal line in box plot (B) represents the median egg diameter.

TABLE 4. Number of stone crab egg diameters measured ( $n$ ), median diameter ( $\mu\text{m}$ ), and range of diameters across all locations and years.

Location	$n$	Median diameter	Minimum diameter	Maximum diameter
Cedar Key	66	0.35	0.31	0.56
Pavilion Key	101	0.35	0.31	0.42
Sawyer Key	96	0.35	0.31	0.56
Tampa Bay	147	0.35	0.29	0.55

which lower batch fecundity was associated with missing crushers, regenerating crushers, and missing pincers, relative to crabs with original crushers and pincers. The presence of regenerating pincers appeared to have no effect on batch fecundity (Table 6). Parameter estimates were used to estimate the reduced fecundity of a crab that had their claws been harvested by the fishery (Table 2). For

example, the batch fecundity of an average-size crab in our study (79 mm) from Cedar Key in August 2013, with an original crusher and original pincer, can be described by  $(e^{8.996 + 0.035 \times 79 + 0.742})$ , and a crab with a missing crusher and pincer can be described by  $(e^{8.996 + 0.035 \times 79 + 0.742 - 0.277 - 0.216})$ . The result is 104,753 fewer eggs, and thus a 39% reduction. The magnitude of this difference would be slightly less, for example, if a crab had a regenerating crusher or pincer.

The inclusion of Location–Month–Year as a categorical covariate was considered during model development to account for the possibility that temporal variability in fecundity was unique to each location. As a fixed effect, however, this covariate was represented by 65 groups, which meant that its inclusion in the model would result in the estimation of 64 additional parameters (one group would serve as the statistical baseline). Given the large

TABLE 5. Tampa Bay stone crab batch fecundity (mean number of eggs per clutch  $\pm$  SD) and number of individuals sampled ( $n$  [ $n$  represents the number of individuals sampled for each size class]) from present study and from Bert et al. (2016a). See Table 3 for size-class ranges.

Size-class (mm)	Bert et al. (2016a)			Present study		
	Mean	SD	$n$	Mean	SD	$n$
40	64,051	17,936	2	83,830	8,479	4
50	99,577	38,159	16	103,624	53,336	9
60	178,542	80,384	30	183,075	81,955	39
70	278,816	100,634	58	240,681	114,675	54
80	376,071	116,800	94	341,638	141,555	65
90	438,205	132,978	88	427,686	147,069	23
100	522,031	168,089	35	663,757	104,738	2

number of estimated parameters and the relatively small sample size associated with each Location–Month–Year group (mean = 9.30 observations per group, range = 1–20), we excluded this covariate from consideration to avoid any biased parameter estimates resulting from small sample sizes. Moreover, including the Location–Month–Year covariate would have complicated our ability to address more fundamental questions related to spatial and temporal variability in stone crab fecundity, which was our primary interest. Our decision to limit the complexity of the temporal covariate to a Month–Year categorical predictor variable, which itself resulted in the estimation of 19 additional parameters, meant that temporal patterns in fecundity were assumed to be identical among locations (Figure 4).

## DISCUSSION

Determining accurate potential fecundity of the population is important not only for proper development of management indices, but also in monitoring how fishing, anthropogenic changes to the environment, and changes in other natural extrinsic factors influence it. The present study determined that the batch fecundity of stone crabs was strongly influenced by carapace width and the status of claw regeneration and varied spatially and temporally. The predictive capacity of the model developed in this study, combined with information on population size composition, improves our ability to assess the impact of changes in fecundity on the stone crab's reproductive potential.

The crabs sampled in this study spanned a range of carapace widths. Fecundity increased with increasing carapace width but varied substantially within each 10-mm size-class. Variability in batch fecundity between crabs of a similar size is common in crustaceans and can be attributed to seasonal variation (Verísimo et al. 2011;

TABLE 6. Parameter estimates and SEs, 95% CIs (lower and upper limits), and rate ratios (RR) from the best-approximating negative binomial regression model relating Location (CK, SK, PK, and TB), Month–Year, Carapace Width (CW), and claw status (MC, RC, MP, RP) to stone crab fecundity. Cedar Key (CK), April 2013, and original claws (OC and OP) served as the baseline (i.e., intercept) in all models. See Methods for definition of abbreviations.

Parameter	Estimate	SE	Lower CI limit	Upper CI limit	RR
Intercept	8.996	0.161	8.681	9.311	
PK	0.301	0.055	0.194	0.409	1.352
SK	0.050	0.057	−0.061	0.161	1.052
TB	0.328	0.051	0.228	0.428	1.389
May 2013	−0.389	0.118	−0.621	−0.158	0.678
Jun 2013	−0.176	0.104	−0.380	0.029	0.839
Jul 2013	0.635	0.105	0.428	0.842	1.887
Aug 2013	0.742	0.110	0.527	0.957	2.101
Sep 2013	0.597	0.113	0.376	0.817	1.816
Oct 2013	0.678	0.161	0.363	0.994	1.970
Dec 2013	0.612	0.267	0.089	1.135	1.844
Feb 2014	0.508	0.148	0.218	0.798	1.662
Mar 2014	0.438	0.130	0.183	0.694	1.550
Apr 2014	0.464	0.108	0.253	0.676	1.591
May 2014	0.365	0.113	0.143	0.586	1.440
Jun 2014	0.706	0.118	0.474	0.937	2.025
Jul 2014	0.828	0.111	0.610	1.045	2.288
Aug 2014	0.752	0.115	0.526	0.979	2.122
Sep 2014	0.710	0.109	0.498	0.923	2.035
Oct 2014	0.671	0.213	0.253	1.089	1.956
Jan 2015	−0.048	0.265	−0.567	0.471	0.953
Feb 2015	0.440	0.157	0.133	0.747	1.553
Mar 2015	0.713	0.125	0.468	0.957	2.039
CW	0.035	0.002	0.032	0.038	1.035
MC	−0.277	0.103	−0.478	−0.076	0.758
RC	−0.114	0.047	−0.207	−0.021	0.892
MP	−0.216	0.093	−0.399	−0.034	0.806
RP	0.022	0.048	−0.072	0.116	1.022
$\theta$	5.470	0.310			

González-Pisani et al. 2012; Hjelset et al. 2012), the number of previously extruded clutches (Mantelatto and Fransozo 1997; Verísimo et al. 2011), food availability (Annala and Bycroft 1987; France 1992; Lardies and Wehrtmann 2001; Bas et al. 2007; Verísimo et al. 2011; Hjelset et al. 2012), latitude and temperature (Lardies and Castilla 2001; Lardies and Wehrtmann 2001; Antonio et al. 2003; Cardoso and Defeo 2003), geographic region (Hjelset et al. 2012), and the density of animals in an area (DeMartini et al. 2003).

Previous estimates of stone crab fecundity were reported by Bert et al. (2016a) for crabs collected in Tampa Bay from 1993 through 1995. The present study confirmed the positive relationship between batch

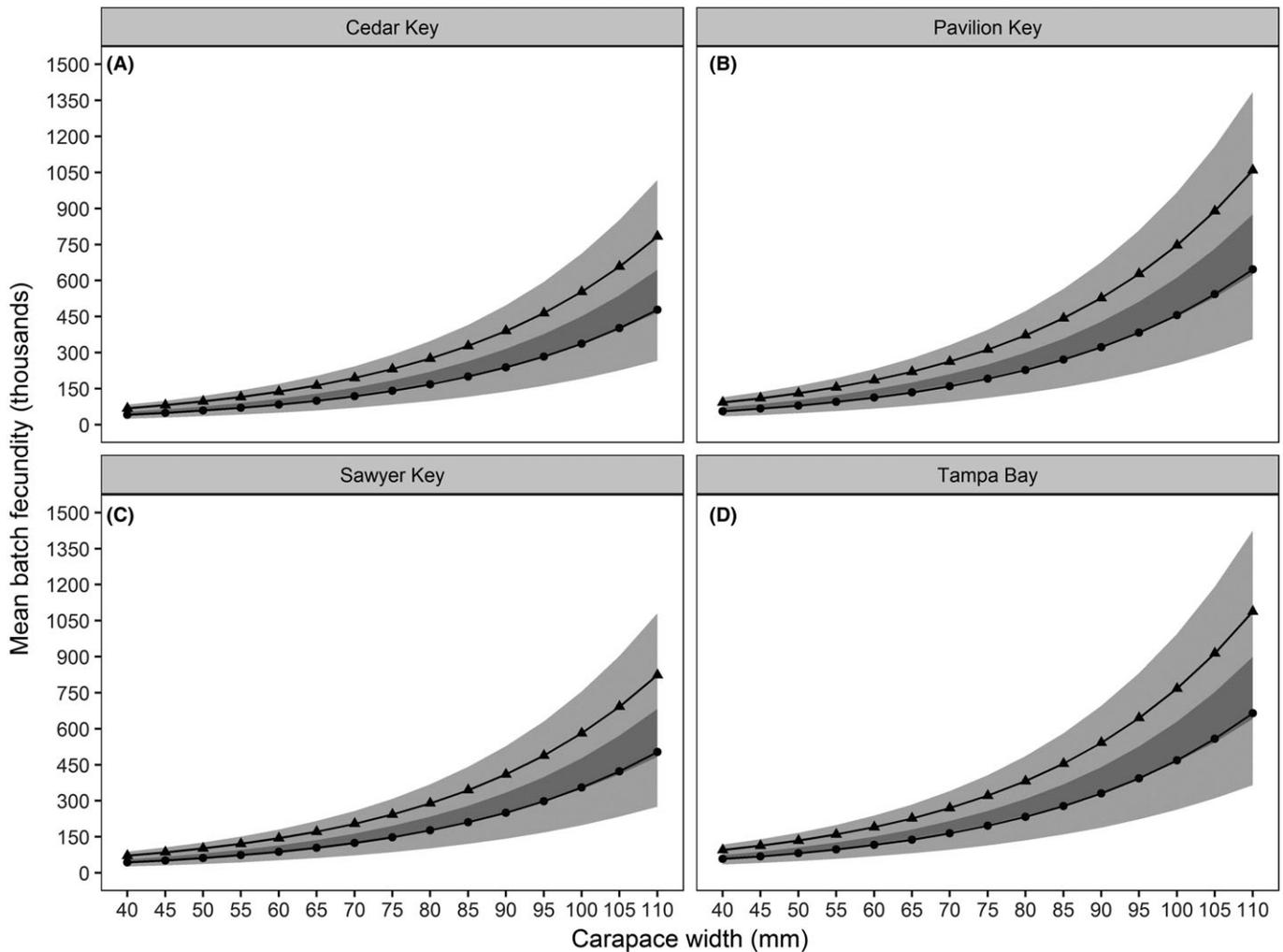


FIGURE 3. Modeled expected batch fecundity (number of eggs) as a function of carapace width for crabs with two original claws (triangles) or two missing claws (circles), from (A) Cedar Key, (B) Pavilion Key, (C) Sawyer Key, and (D) Tampa Bay in August 2013, corresponding to peak spawning season.

fecundity and carapace width, common in crustaceans, that Bert et al. (2016a) found in stone crabs, and found that egg diameter did not contribute to the variability in batch fecundity. The lack of a relationship between egg diameter and fecundity could be attributed to the methodological differences in sample selection between the two studies. Bert et al. (2016a) assessed fecundity for crab egg masses in all developmental stages, whereas the present study used only newly extruded, orange egg masses. Crustaceans often have considerable egg loss and egg diameter changes during brooding between the first egg extrusion and larval release due to embryonic growth, loss of unviable eggs, disease, and predation (Darnell et al. 2009; Graham et al. 2012). Changes during brooding significantly affect the accuracy of fecundity estimates. Our study followed the methodology of Graham et al. (2012) in determining potential fecundity based on newly

extruded egg masses, which minimized the effect of egg loss or change in diameter during embryonic development and processes following egg extrusion. Interestingly, there was a small number of crabs caught in July 2013 that produced eggs with substantially larger egg diameters than most crabs in this study (Figure 2). Upon investigating the origin of these specific cases, crabs were found to be from all locations except Pavilion Key and ranged in size from 58.4 to 98.4 mm carapace width. The cause of this anomaly may be environmental or physiological but was beyond the scope of this study.

A key identifier of fishery-induced evolution is temporal change in reproductive effort, as indicated, for example, by fecundity (Ricker 1969; Pitt 1975; Leaman 1991). Historical and contemporary fecundity estimates from Tampa Bay provided the only temporal data on fecundity, but they could not be compared statistically due to lack of

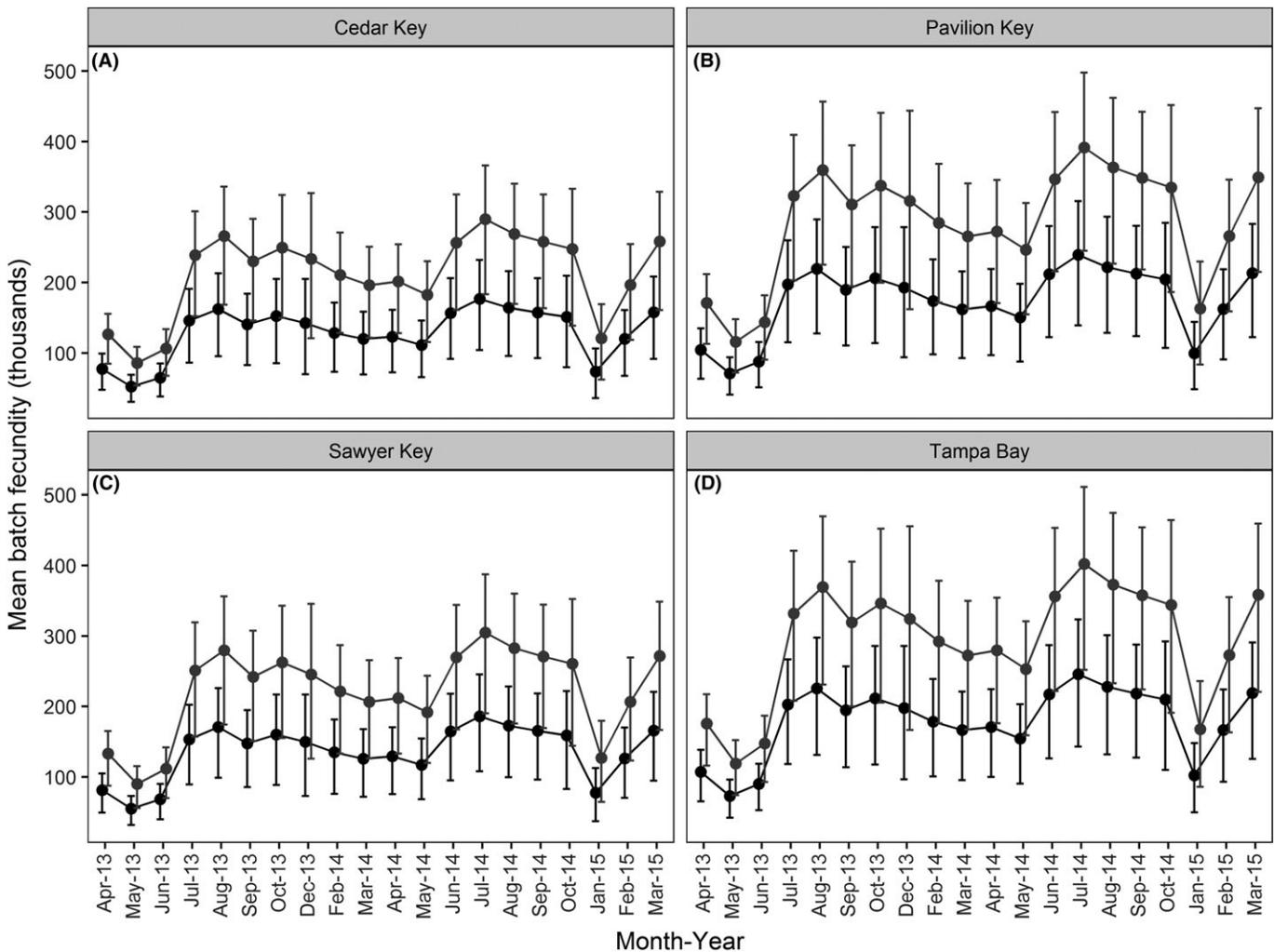


FIGURE 4. Modeled expected batch fecundity (number of eggs) of the average carapace width (79 mm) for all Month-Year combinations, for crabs with two original claws (triangles) or two missing claws (circles), from (A) Cedar Key, (B) Pavilion Key, (C) Sawyer Key, and (D) Tampa Bay.

access to the raw data from Bert et al. (2016a). There did not appear to be a large difference in batch fecundity (number of eggs) of any size class between 1993 and 2013. The largest (110+ mm) and smallest (30 mm) size-classes could not be compared because no crabs of those sizes were collected in 2013. The apparent lack of change between these periods suggests that, despite intense fishing pressure since the 1980s, there was no impact on this life history parameter for stone crabs in Tampa Bay. A conclusion with implications of this magnitude should not be extended to the entire fishery. Tampa Bay contributes only a small percentage to Florida landings and does not reflect the estimates of fecundity found in all regions of the crab's range.

Using data from only one region of the fished stock risks overestimation or underestimation of reproductive output. For example, under the predictive equation of

Bert et al. (2016a), the fecundity of a 70-mm crab during August was estimated at 217,845 eggs. The model of the present study, which incorporated fishery-wide data, indicated that the fecundity of a 70-mm crab during August 2013 was 269,957 eggs in Tampa Bay, 262,816 eggs in Pavilion Key, 204,448 eggs in Sawyer Key, and 194,420 eggs in Cedar Key (August 2014 was similar; Table 6). Fecundity is an important aspect to be considered in fisheries management and stock assessment modeling (Tully et al. 2001) that, in part, determines reproductive potential and output of a fished stock. Differences in fecundity with latitude or region occur in crustaceans (Annala and Bycroft 1987; Lardies and Wehrmann 2001; Hjelset et al. 2012). Thus, it is important to account for latitudinal variability when estimating fecundity.

Parameter estimates of the model developed in this study indicate that batch fecundity varies by region and

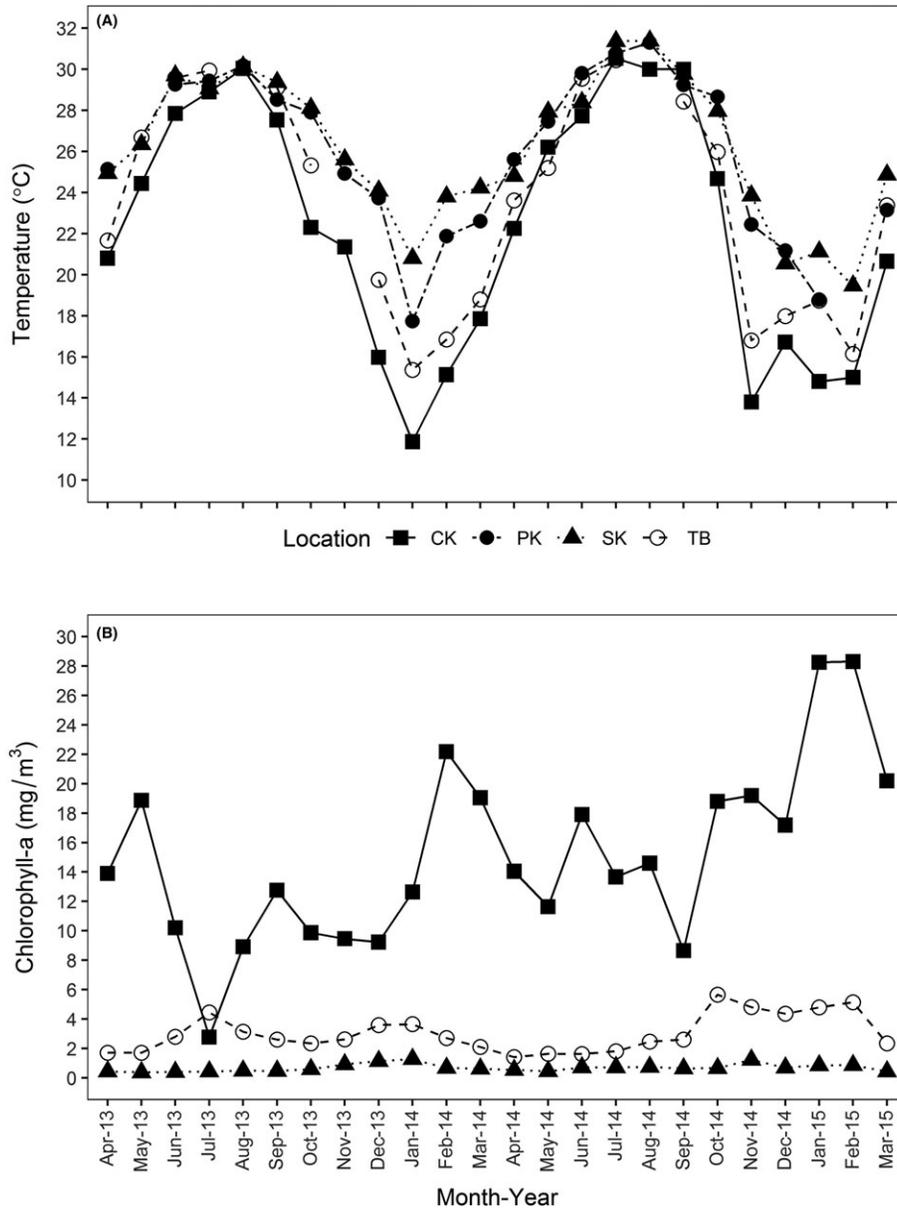


FIGURE 5. Mean monthly in situ (A) bottom seawater temperatures (°C) and (B) chlorophyll-a concentrations (mg/m<sup>3</sup>) from April 2013 to March 2015. Average monthly temperature and chlorophyll-a readings were calculated for each of the four locations represented in this study: Cedar Key (squares), Pavilion Key (closed circles), Tampa Bay (open circles), and Sawyer Key (triangles). Chlorophyll-a concentration data were unavailable for Pavilion Key.

by years and months. There was discernable difference in fecundity between years and months. This pattern is not surprising given the well-documented association between fecundity and seasonality in many crustaceans (Lardies and Castilla 2001; Lardies and Wehrmann 2001; Antonio et al. 2003; Cardoso and Defeo 2003; Bert et al. 2016a). In this study temperature corresponded with seasonality, and highest temperatures occurred in the summer months of both years and lowest temperatures occurred in the winter months. Notably, the catch of ovigerous crabs was not

limited to May through November as described in previous work (McRae 1950; Noe 1967; Cheung 1968; Bender 1971; Sullivan 1979; Bert et al. 1986; González y de la Rosa et al. 2004; Gerhart and Bert 2008), as spawning females were found in all months except November. Similar to Bert et al. (2016a), crabs were found spawning outside of this season but also in lower proportions. In addition to temporal differences, there was also a discernable difference in fecundity among locations. Batch fecundity was 1.35 times higher at Pavilion Key and 1.39 times higher at Tampa

Bay than it was at the baseline location, Cedar Key. Differences in fecundity between locations are likely a result of complex interactions and not driven solely by latitude, temperature, or productivity. When they exist, latitudinal differences in crustacean fecundity are attributed to thermoclines, resulting in a trade-off between egg size and number of eggs (Lardies and Castilla 2001; Lardies and Wehrmann 2001; Antonio et al. 2003). If this were true for stone crabs in this study, the fecundity at the northernmost site, Cedar Key, would not be statistically similar to that at the most southern site, Sawyer Key. Crabs at both Cedar Key and Sawyer Key had statistically lower fecundity than at the intervening Pavilion Key and Tampa Bay, leading to the conclusion that latitude alone does not ultimately determine fecundity in stone crabs.

There is an apparent latitudinal cline in stone crab fishery harvest (claw removal) throughout the eastern Gulf of Mexico, along Florida's coast. Sixty percent of the state's stone crab landings are reported in south Florida (Collier to Monroe counties) (Muller et al. 2011). Despite a protracted spawning season in south Florida, i.e., May–November, rather than June–October (McRae 1950; Bender 1971; González y de la Rosa et al. 2004; Gerhart and Bert 2008), the large fishery harvest, and mortality associated with declawing in seasonally high temperatures (Gandy et al. 2016), negatively affects spawning females and their reproductive output. We found that females with no claws showed a reduction in batch fecundity, on average, of 39%. Hogan and Griffen (2014), who measured the energetic cost of claw regeneration, and the potential energetic cost of a crab changing diet to compensate for its inability to consume bivalves, also found a reduction in batch fecundity. The regrowth of one claw requires approximately 37.5% of the annual reproductive output (Hogan and Griffen 2014). Additionally, one-clawed crabs showed a 50% decrease in bivalve consumption, a primary prey item of stone crabs (Bender 1971; Brown et al. 1979; Griffen 2014; Hogan and Griffen 2014), which further decreases reproductive output (Hogan and Griffen 2014).

In addition to the inability to consume bivalves and other hard-shelled prey, the availability of food likely varies within and among locations along Florida's coast. Habitat type, which varies throughout the west coast of Florida (Continental Shelf Associates 1991; Hine et al. 2003; Kingon 2013), influences the quality and quantity of benthic food sources, carrying capacity, population density, and stresses from predators, all of which influence the health of spawning females and, in turn, the quality and quantity of the eggs produced (Annala and Bycroft 1987; Dugan et al. 1991; Lardies and Castilla 2001; Lardies and Wehrmann 2001; Bas et al. 2007; Hjelset et al. 2012; Griffen 2014; Belgrad and Griffen 2016). Although sea-floor habitat differences among the sampled sites were not documented in this study, habitat within and among

locations is likely to have varied. Griffen (2014) demonstrated that long-term and short-term variation in diet was responsible, in part, for variation in fecundity. Fecundity was greater when the diet consisted of animal protein and was not influenced by consumption of algae (Griffen 2014). Stone crabs supplement their diet with plant protein when necessary (Bender 1971; Brown et al. 1979; Griffen 2014). Prey variation and availability can be a result of specialization, competition, and natural and anthropogenic environmental changes that can directly affect fecundity (Griffen 2014). We examined chlorophyll *a* concentrations to determine whether higher phytoplankton availability might correlate with increased batch fecundity, but there does not appear to be a direct relationship. If increased productivity indicates increased food availability, it would be expected that the locations with the highest productivity (Cedar Key and Tampa Bay) would yield the highest batch fecundity. In this case the higher mean chlorophyll *a* of Cedar Key corresponded with a batch fecundity lower than that at both Tampa Bay and Pavilion Key (Figure 5). Productivity may play a role in fecundity, but other factors, not examined in this study, may play a larger or a confounding role. Harvest also decreases the density of the harvested species, increasing relative prey density, which could result in a compensatory increase in fecundity (Pollock 1995; DeMartini et al. 2003). DeMartini et al. (2003) suggests that catch per unit effort is a suitable representation of species density. Catch data and continued monitoring of fecundity at these locations would provide a basis for determining how fishing mortality impacts density and, subsequently, reproductive output.

The implications and applications of these findings extend beyond the exploration of the evolutionary and biological processes of stone crabs. Quantifying reproductive output is crucial for understanding population dynamics (Annala and Bycroft 1987) and a necessary component of fisheries assessment and management (Trippel 1999; Tully et al. 2001; Gudrun and Gavin 2002; Fitzhugh et al. 2012; Swiney et al. 2012). Incorrect assumptions regarding reproductive traits may skew productivity estimates and limit stock-assessment capabilities. Fitzhugh et al. (2012) demonstrated that sources of error in batch-fecundity estimates directly affect estimates of spawning stock biomass, recruitment indices, and modeling of spawner–recruit relationships. The observed regional variation in fecundity in this study indicates that the size-specific fecundity of females in the southern and northern regions is lower than that in the central regions. Based on this parameter, the central regions of Tampa Bay to Pavilion Key may be critical spawning areas crucial to the reproductive output and resiliency of the Florida stone crab population overall. Reduced batch fecundity, latitudinal variation in the length of the spawning season, and variable spawning

biomass may result in fewer eggs in the northern and southern regions of Florida. Consequently, this may decrease larval recruitment locally or in locations that rely on external sources of larvae (Green et al. 2014). While the trajectory and ultimate settlement of stone crab larvae from spawning areas is unknown, the complex nature of tidal currents, wind direction, geostrophic flow, diel vertical migration, and selective tidal stream transport dictates recruitment to nurseries (Criales et al. 2015). Therefore, larval recruitment and subsequently population abundance in one region may be facilitated by spawning in another.

Given the intense harvest and variability in stone crab reproductive potential, both natural and fishery induced, we suggest that further work be dedicated to identifying critical spawning and recruitment areas. Management protection of the reproductive stock and critical recruitment areas may increase resiliency of the stone crab population. Resiliency of the population in times of environmental and harvest fluctuations will ensure that the population can persist and contribute to future landings. To advance our understanding of the variability in reproductive potential and how this variability influences the dynamics of the stone crab population, we must continue to explore the influences of regional ecological processes, fishery practices, stock–recruitment relationships, and larval distribution. The elucidation of these dynamics will allow for a comprehensive look into the stone crab’s life history and its response to exploitation and anthropogenic environmental changes, and the development of more effective management of the fishery.

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