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Authors: Bert, Theresa M., Geiger, Stephen P., Gerhart, Susan D., and McCarthy, Kevin J.

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FACTORS INFLUENCING REPRODUCTIVE ATTRIBUTES OF STONE CRABS (*MENIPPE*) IN TAMPA BAY, FLORIDA

THERESA M. BERT,[1]* STEPHEN P. GEIGER,[1] SUSAN D. GERHART[2] AND KEVIN J. MCCARTHY[3]

[1]Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 Eighth Ave. SE, St. Petersburg, FL 33701; [2]National Marine Fisheries Service, Southeast Regional Office, 263 13th Avenue South, St. Petersburg, FL 33701; [3]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr., Key Biscayne, FL 33149

ABSTRACT Understanding aspects of reproduction is important for studies of life history strategy and for resource management. The influences of nine factors (five intrinsic, four extrinsic) on the reproductive attributes egg diameter, egg dry weight, and clutch size (i.e., number of eggs in egg mass) of female stone crabs (genus *Menippe* (Say)) from Tampa Bay, FL, waters were investigated. Two intrinsic factors influenced reproductive attributes: carapace width was positively correlated with clutch size, and egg stage was positively related to egg size. Three intrinsic factors—genotype class, damaged or missing pleopods, and missing claws or legs—had no influence on any reproductive attribute. The four extrinsic factors each influenced at least two reproductive attributes. Egg diameter and weight were significantly larger and clutch size was significantly smaller (1) in females uninfested by *Octolasmis mülleri*; (2) during the early part of the spawning season, when water temperature was 27°C or less; and (3) during the first year of the 3-y study. In addition, egg diameter varied significantly among season/year combinations. In all cases, when egg diameter and weight decreased, clutch size increased; suggesting that, in female stone crabs, selection for filling the available abdominal space with eggs is strong. Large eggs are known to produce larvae of high fitness in crabs. Because the largest eggs are produced during the early part of the spawning season, females should be protected from harvest during that time. Shortening the harvest season in spring would eliminate those females from vulnerability to the fishery.

KEY WORDS: clutch size, egg size, egg weight, fishery, Florida, Gulf of Mexico, *Menippe*, missing appendage, *Octolasmis mülleri*, reproduction, stone crab, temperature

INTRODUCTION

Reproduction is an important life-history component for iteroparous marine organisms that produce multiple large egg clutches each year because the production of eggs is energetically expensive and competes with energy needed for growth and maintenance (Llodra 2002). Two important components of female reproduction—the quality and the quantity of eggs—are also related to offspring survival (Olive 1985, Bell & Fish 1996). Thus, these attributes reflect the apportionment of energy needed for reproduction and growth and maintenance, balanced so as to maximize the probability of reproductive success in an evolutionary sense, by contributing to the species continuation. Their evolutionary importance makes these components of reproduction susceptible to selective pressures (Llodra 2002).

Egg quality, that is, egg size and weight, can be particularly important for organisms that do not extend parental care beyond egg hatching, such as most decapod crustaceans (Galeotti et al. 2006, but see Moran & McAlister 2009). In crustaceans, egg size and weight are broadly correlated with nutrient levels and energy reserves available for the developing offspring (Shakuntala & Reddy 1982, Clarke 1993, Jaeckle 1995). Variation among females in these egg quality estimators reflects real differences in investment per larva (Clarke 1993). Egg size is directly correlated with the amount of yolk present (Steele & Steele 1975) and egg weight is reflective of egg energy content, which can be indicative of the selection acting on the eggs (Moran & McAlister 2009). Thus, both estimates are needed to evaluate egg quality.

An understanding of clutch size (i.e., the number of eggs per spawn) in females through the reproductive season, together with demographic information on the reproductively active component of the female population, is needed to estimate population-level reproductive potential. Estimates of clutch size are also important for understanding ecological relationships such as influences of environmental factors on fecundity (Mashiko 1990). In harvested species, knowledge of clutch size is needed for reproductive potential estimates (Restrepo & Watson 1991), spawning stock assessments, and population modeling (Darnell et al. 2009).

The quality and quantity of eggs produced by a female decapod crustacean at any given time are the result of interactions between factors inherent to the female and ambient environmental factors that can influence reproduction (intrinsic and extrinsic factors, respectively). Intrinsic factors include genetic background (Harrison 1993), female size and age (Llodra 2002), egg developmental stage (Reid & Corey 1991, Kobayashi & Matsuura 1995), and appendage loss [pleopods and abdominal segments, which carry the eggs, and major appendages (legs and claws), which impose high energy demands for regeneration] (Norman & Jones 1993, Devi & Adiyodi 2000, Maginnis 2006, Lindsay 2010). Extrinsic factors include parasite and epibiont infestation (Jeffries et al. 1982, Dickinson et al. 2006), season, temperature (Sastry 1983), and broader temporal periods (e.g., year; Kobayashi & Matsuura 1995).

The influences of these factors on egg diameter, egg dry weight, and egg-mass clutch size of stone crabs (genus *Menippe* (Say, 1819)) from the Tampa Bay, FL area (Fig. 1), was investigated. The analyses reveal the relationships of the three reproduction attributes to each other; the few effects of the intrinsic factors and multiple effects of the extrinsic factors on

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*Corresponding author. E-mail: theresa.bert@myfwc.com

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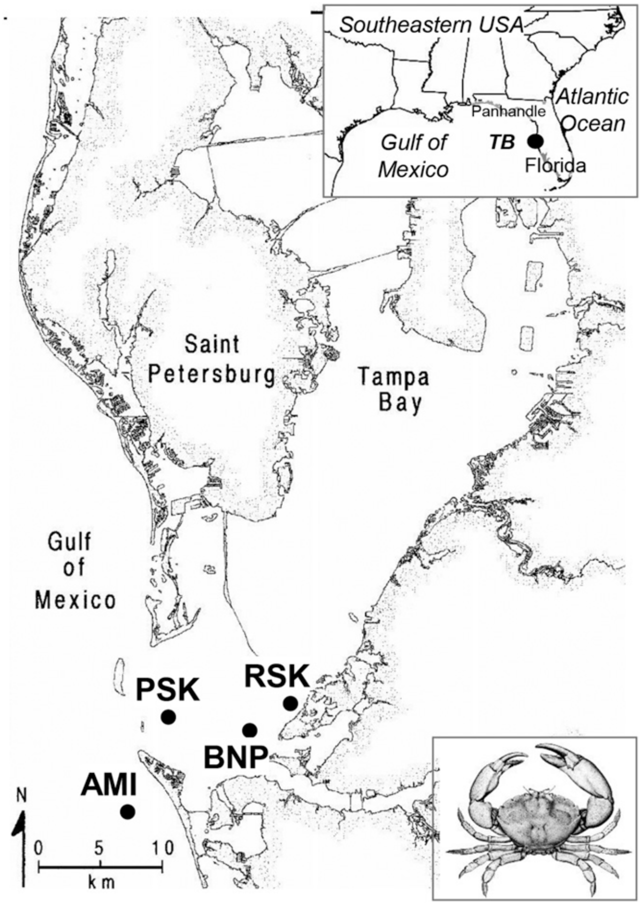

Figure 1. Region and station locations for study of factors influencing reproductive attributes in female stone crabs (genus *Menippe*). RSK, Rattlesnake Key; BNP, Bean Point; PSK, Passage Key; AMI, Anna Maria Island. Top inset: location of Tampa Bay, FL (TB) in the southeastern United States. Bottom inset: illustration of a stone crab, genus *Menippe*.

the three reproductive attributes; and the nature of the reproductive strategy inherent in stone crabs to maximize offspring production. These findings are relevant to both addressing stone crab life history strategy and developing management options for the stone crab fishery.

Background on Menippe

Two of the three species of western Atlantic *Menippe* inhabit the Gulf of Mexico (Bert 1986, Williams & Felder 1986): *Menippe mercenaria* (Say, 1819) and *Menippe adina* (Williams & Felder, 1986). These species are long-lived, high-level carnivores with large, strong claws that can account for >50% of total body weight (Davis et al. 1978). Females of greater than or equal to 90 mm carapace width (CW) and males of greater than or equal to 110 mm CW are considered to be large adults. The two species hybridize at the junction of their ranges in waters off northwest Florida (Bert 1986). Introgression of *M. adina* genes into *M. mercenaria* occurs at progressively lower frequencies from that area southward to waters off southwest Florida (Bert 1986, T. M. Bert, unpublished data). The Tampa Bay area is inhabited principally by *M. mercenaria* and *M. mercenaria* backcross hybrids (Gerhart & Bert 2008).

Female stone crabs mate immediately after they molt. They retain sperm internally in spermathecae, sometimes even after molting again (Cheung 1968). As long as females retain sperm, they can spawn and fertilize multiple clutches of eggs (Cheung 1968, 1969). Low percentages of females from 20 to 60 mm CW spawn, but nearly all females attain sexual maturity between 55 and 65 mm CW (Gerhart & Bert 2008).

Of the three western Atlantic *Menippe* species, egg diameter has been estimated only for *Menippe nodifrons* (Stimpson, 1859) (Hines 1992, Oshiro 1999). Egg weight has not been measured for any western Atlantic *Menippe*. Records for clutch size in female *Menippe* are also incomplete. McRae (1950) estimated clutch size for a 71-mm-CW female from northwest Florida waters and Noe (1967, Figure 10) estimated clutch size for five females of various sizes, from southeast Florida waters. Ros et al. (1981) estimated clutch size for three size classes (mm CW) of females from Cuban waters. Bender (1971) found the highest numbers of eggs on northwest Florida females 90–105 mm CW and Ros et al. (1981) found the highest numbers on Cuban females 95–100 mm CW. Ros et al. (1981) also noted that egg numbers generally declined in the largest females. Other estimates have been given for clutch size in *Menippe* females from southeastern U.S. waters, but without including the corresponding female size (Binford 1913, Bender 1971, Schlieder 1980, Beck 1995). Ros et al. (1981) found that numbers of eggs varied greatly among females in the same size class but Beck (1995) suggested that most variation among females of similar size arose from the number of clutches produced and not the number of eggs in individual clutches. The relationship between clutch size and female size has been calculated as a power function for *M. nodifrons* (Oliveira et al. 2005) and as a logarithmic function for *Menippe* from northwest Florida waters (Noe 1967). Reports on the number of clutches produced during a spawning season have similarly varied. Bender (1971) observed that one female produced 10 egg masses during one spawning season. Wilber (1989) observed that one northwest Florida female produced at least 5 egg masses in 93 days. Other estimates of number of viable spawns per season are 6 (Binford 1913, Noe 1967), 4 (Porter 1960), 10 (Cheung 1968, Yang 1971), and an average of 4.5 (Cheung 1969). Based on six spawnings per year, Noe (1967) estimated annual egg production of a single female (of unknown size) as 2.0–2.5 million eggs.

Stone crabs lose appendages naturally through combats and accidents, and unnaturally through fishery handling and declawing (Bert et al. 1978). Fishers harvest the claws only (with restrictions on size, season, and reproductive state of females) by breaking the legal-sized claws off (in Florida, both claws can be taken if legal-sized) at or near the basi-ischial fracture plane (Simonson & Hochberg 1986). They then return the crabs to the sea (Bert et al. 1978). The trauma of forced removal of even one claw can stimulate the crabs to autotomize the second claw, or one or more legs, and declawed ovigerous females can cast off their eggs. Abdominal pleopods, to which the eggs are attached during incubation, can also be accidentally torn off or damaged through fishery practices. Harvesting pressure is heavy (Muller et al. 2011); thus many more adult stone crabs without claws and other appendages are in a population than that would be if appendage loss was only through natural pathways. If crabs survive appendage losses, they can regenerate the appendages (Morgan 1898), but injury and regeneration can decrease fecundity (Norman & Jones 1993). In stone crabs, claw loss because of fishery practices significantly decreases growth (Savage & Sullivan 1978), survival (Davis et al. 1978, Simonson & Hochberg 1986, Gandy et al. 2016), and quality of food consumption (Duermit et al. 2015). Both claw regeneration and reproduction are energetically demanding (Llodra 2002), and female stone crabs may derive the energy for both processes from the same energy stores (Hogan 2013). Thus, regenerating appendages may also reduce egg quality or clutch size in stone crabs.

Stone crabs can be infested with the gill epibiont *Octolasmis mülleri* (Coker, 1902). This gooseneck barnacle can attain high infestation rates and high numbers of individuals per crab (50 or more, T. M. Bert, unpublished data). In blue crabs *Callinectes sapidus* (Rathbun), *O. mülleri* infestation causes increased heartbeat and scaphognathite fluttering rates, and severely weakens individuals with heavy infestations (Gannon & Wheatly 1994, Wu & Liu 1995). The effects of these stresses on female reproductive attributes are unknown. Together with the metabolic demands of egg production, these combined stresses may result in reduced egg quality or clutch size.

Seasonal water temperature (henceforth, ‘‘temperature’’) variability is highly important in reproduction because, in ectotherms, the rates of most physiological processes, including reproduction, slow down at low temperatures (Darnell et al. 2009). Temperature is negatively correlated with egg size in many marine taxa, including decapods (Hamasaki et al. 2006), and thus indirectly affects larval survival (Moran & McAlister 2009). Conversely, high temperatures increase metabolic rate and growth rate, which can result in less energy available for egg production, and consequently, fewer (Diaz 1980) or smaller (Kobayashi & Matsuura 1995, Hamasaki et al. 2006) eggs than that would be produced at lower temperatures. No detailed analysis of the relationship between egg quality or quantity and seasonal temperature has yet been done for western Atlantic *Menippe*.

MATERIALS AND METHODS

Sample Collection

From 1993 to 1995, 329 ovigerous female stone crabs (henceforth, ‘‘females’’ or singularly, ‘‘female’’) were collected during February, March, April (collectively, early season: $n = 2$, 27, 74, respectively), June (mid-season: $n = 85$), August, September, and October (collectively, peak season: $n = 95$, 41, 5, respectively), by trapping with standard plastic commercial stone crab traps (40.6 cm wide × 40.0 cm long × 30.5 cm high, with slat width and throat specifications according to Florida Statutes (Chapter 68B, Section 13) at established stations near the mouth of Tampa Bay, FL (Fig. 1). Each collected female was placed individually in a sealable plastic storage bag to protect the egg mass and was held for one to several hours in an insulated cooler. In the field, data recorded for each female were CW to the nearest 0.1 mm, egg-mass color, number of missing or injured pleopods, number of missing claws and legs; number of *Octolasmis mülleri* in the gill chambers, and scores for the five coloration characteristics identified by Bert et al. (1996) as being diagnostic for characterizing genetic background.

Egg color typically changes with egg maturation in decapods (Moriyasu & Lanteigne 1998), and it is an estimator of egg maturity in stone crabs (Table 1). Females with orange egg masses were targeted because females may lose or shed eggs during development (Graham et al. 2012); because the contents of early-stage eggs are homogeneous, facilitating accurate measurement of egg diameter; and because later-stage eggs broke more frequently. Nevertheless, egg masses with eggs in various stages of development were collected, so the egg masses were staged following a condensed form of a classical categorization (Meridith 1952) (Table 1).

For storage of the eggs, the abdomen with associated pleopods and attached eggs was cut away from the body of the female, labeled, rinsed in deionized water, placed in a sealable plastic storage bag, frozen at –20°C for one to several days, and then moved to a –40°C freezer. Samples of heart and hepatopancreas were taken from each female for allozyme electrophoresis of the three diagnostic loci used by Bert and colleagues (Bert & Harrison 1988, Bert et al. 1996) for taxonomic identification (*Menippe mercenaria*, *Menippe adina*, or a hybrid form). These samples were frozen immediately in liquid nitrogen and stored at –80°C.

Near-bottom temperature and salinity were recorded. Bottom water was collected in a Niskin bottle and measured at the surface using a standard mercury thermometer and temperature-corrected refractometer.

Laboratory Procedures

The females included in this study were among those included in a recent study of maturity, growth, and age in stone crabs (Gerhart and Bert 2008). For both studies, standard, single-pass starch gel electrophoresis, as described in Bert (1986) and Bert and Harrison (1988), was conducted to identify the genotype of each female at the *ALP*-2, *IDH*-2, and *SOD* loci.

To determine egg quality and clutch size, each egg mass was first thawed in deionized water for 30–60 min. Preliminary trials revealed that thawing the eggs in seawater caused the egg yolk to coagulate in the center of the eggs and prevented us from

TABLE 1.

Qualitative characterization of stone crab (genus *Menippe*) egg stages.

Stage	Egg color	Developmental stage	Corresponding stages of Meridith (1952)	*n*
A	Orange	No detectable cell differentiation	A, A+	165
B	Red-brown	Clearly visible gastrula or early embryo	B–, B, B+	115
C	Brown-red, mottled	Eye spot visible	C–, C, C+	44
D	Brown eggs with black spot	Eye spot well developed, abdomen visible and free from head	D	5

taking accurate size measures. Thawing in deionized water maintained the dispersion of the egg yolk and allowed us to unambiguously view each egg and measure it accurately. For measuring, the pleopods with their attached eggs were removed from the abdomen and rinsed at least three times in deionized water to remove particles trapped among the eggs. The eggs were then gently separated from the pleopods with fine forceps. Nearly all of the eggs remained attached to their tendrils (fibers that connected the eggs to pleopods).

Egg diameter and dry mass per egg (DME) were determined for each female using approximately 500–2,000 eggs that had been separated from their tendrils by hand-rolling them gently across a 63-μm brass screen sieve. These eggs were divided into five subsamples; each subsample was placed on a depression slide. The maximum diameters of five eggs per subsample were measured to the nearest 1.0 μm using a Zeiss stereo-dissecting scope at 100× magnification coupled to a digital imaging camera; the images were contrast-enhanced and corrected for aberrations with Optimas digital imaging software, version 3.1. The mean of the 25 egg diameters was calculated. To determine mean DME, all eggs in each subsample were first counted with the assistance of the Optimus software. The subsamples were then placed individually in preweighed aluminum weighing pans, dried in a drying oven for 3 days at 60°C, and weighed to the nearest 0.01 mg. Preliminary tests indicated that the DME decreased during the first 3 days of drying, but changes thereafter were insignificant. Mean DME for each crab was calculated by dividing the dry mass of each subsample by the number of eggs in the subsample to obtain an average DME for the subsample and then calculating the overall mean of the five averages.

To determine clutch size of each egg mass, five additional subsamples, each of approximately 75–500 eggs still attached to their tendrils, were counted using the Optimas software. The eggs in each subsample and the entire egg mass were placed individually in preweighed aluminum weighing pans and their dry masses determined as described above. The mean DME of an egg with tendrils was determined by dividing the dry mass of each subsample by the number of eggs it contained and then calculating the mean of the five subsample averages. Clutch size was then estimated by dividing the dry weight of the egg mass by the mean DME of an egg with tendrils. The range of the number of eggs in a clutch was estimated by dividing the dry weight of the egg mass by the smallest and the largest DME values obtained from the subsamples. Because the relatively small numbers of eggs used for those measurements encompassed a range far less than the ranges of the clutch size estimates, those egg measurements were not included in measures of egg size or DME estimates.

Statistical Analyses

Both clutch size and fecundity have been variously defined (Graham et al. 2012) and need to be specified for each study (Llodra 2002). Here, "clutch size" is the number of eggs in a single egg mass spawned by a single female stone crab and "fecundity" is the estimate of number of eggs produced from multiple clutches during a single spawning season.

Unless otherwise denoted, all statistical methods followed Sokal and Rohlf (1995).

To first understand the basic relationships between the reproductive attributes of interest and to facilitate interpretation of the effects of the influential factors on those attributes, correlations for each pairwise combination of attributes were calculated and the *r* values tested for significance. To facilitate some analyses, the females were grouped into to 10-mm-CW size classes (Table 2). Average annual fecundity for females in each size class was estimated as follows: mean number of eggs per clutch × average number of clutches per spawning season, based on estimates given by previous researchers (number of spawns per year: 10, 5, 6, 6, 4, 10, 10, 4.5; references given in the section "Background on Menippe").

Genotype Determination

Each individual was assigned to a genotypic class (*Menippe mercenaria*, *M. mercenaria* backcross, intermediate hybrid, *Menippe adina* backcross, *M. adina*) by applying principal components analysis followed by discriminate function analysis to the allozyme genotype data (which were transformed into numerical genetic index scores) combined with the coloration data, as described in Bert et al. (1996). To serve as a standardized data set, the genetic index scores and color index scores of 2216 individuals collected from 25 nearshore locations ranging from Brownsville, TX, to Beaufort, NC, in the United States and from Caulker Cay, Belize, and Yucatan, Mexico, were also entered into the principal components analysis (807 of those individuals from nine locations were included in Bert et al. 1996). This geographic coverage extends well into the ranges of both species and includes pure-species samples as well as samples containing the full spectrum of hybrid forms (Bert 1986, Bert & Harrison 1988, Bert & Hochberg 1992).

TABLE 2.

Temporal distribution of sample sizes of female stone crabs (genus *Menippe*) from Tampa Bay, FL, grouped into size classes.

		Temp. (°C)	Size class*									
Year	Season†	Mean (range)	30‡	40‡	50‡	60	70	80	90	100	110‡	Total
1993	Early	21 (20–22)	0	0	0	2	3	9	11	1	0	26
	Mid	28 (26–34)	0	0	0	3	7	13	6	2	0	31
	Peak	30 (26–30)	0	0	3	2	6	11	10	5	1	38
1994	Early	23 (18–27)	0	0	1	4	7	10	10	5	1	38
	Mid	29 (28–30)	0	0	1	1	7	10	10	8	0	37
	Peak	30 (28–32)	1	1	3	9	10	12	11	3	1	50
1995	Early	23 (17–26)	0	0	4	3	7	11	8	5	1	39
	Mid	31§	0	0	1	0	1	6	7	2	0	17
	Peak	30 (26–31)	1	1	3	6	10	12	15	4	0	53
Total			2	2	16	30	58	94	88	35	4	329

Temp., water temperature.

* Size classes (mm carapace width, CW): 30, 30.0–39.9; 40, 40.0–49.9; 50, 50.0–59.9; 60, 60.0–69.9; 70, 70.0–79.9; 80, 80.0–89.9; 90, 90.0–99.9; 100, 100–109.9; 110, ≥110.

† Early, March–April (includes 3 females from late February); Mid, June; Peak, August–September (includes five females from early October).

‡ For many analyses, females in size classes 30, 40, and less frequently, 50 were combined; and females in size classes 100 and 110 were combined.

§ All temperatures measured were 31°C.

Effects of Influential Factors

Calculation of a comprehensive, multiway analysis of variance (ANOVA) or general linear model analysis was not possible because the degrees of freedom were insufficient in some cases; some data conformed to parametric expectations, whereas other data did not; and some data sets were composed of continuous variables but other data sets were composed of categorical variables. Therefore, the effects of each factor on each of the three reproductive attributes were first analyzed separately. Then, tests for interactive effects between the categorical factors that, individually, significantly influenced each reproductive attribute were conducted.

The variables for all factors except *Octolasmis müllerì* infestation (number infesting each female), CW, and temperature were categorical. For some analyses, *O. müllerì* infestation was categorized into ''infested'' or ''not infested.'' When any categorical data set conformed to parametric assumptions of homogeneity of variances and normality or could be transformed such that the data met the requirements, the effects of the target factor on each reproductive attribute were analyzed by ANOVA if the number of variables designated for a factor was >2 and by *t*-test when the number of variables was 2 (SigmaStat, version 2). When an ANOVA was significant, the significantly homogeneous groupings of variables for each factor were identified using the Tukey–Kramer method. When a factor with categorical data could not be transformed such that it met the parametric assumptions, the effects of the factor on each reproductive attribute were analyzed using the Kruskal–Wallis test, first applied to all data and then, if significant, applied to all pairwise combinations of the categorical data to identify statistically homogeneous groupings of target-factor variables.

The effects of *Octolasmis müllerì* as a continuously varying factor on egg diameter and DME and the effects of CW and temperature on each reproductive attribute were evaluated using regressions. The effects of *O. müllerì* as a continuously varying factor on clutch size were analyzed using multiple regression analysis. For these analyses, a check for a size bias (CW) in the distribution of females among temperatures was performed using regression. In all analyses, if a regression was nonlinear, either the CW data were transformed (usually square-root transformed) to linearize the data or the lowest-order polynomial equation with a regression coefficient of determination (r^2) that was similarly high compared with higher-order polynomial equations was fitted to the data using the Trendline option in Microsoft Excel. All linear regression r^2 values were tested for significance.

To test for interactive effects between the individual factors that influenced the reproductive attributes, multivariate analyses of variance (MANOVAs; SigmaStat, version 2) were performed on combinations of those factors. If the MANOVA detected interactive effects, *t*-tests on all pairwise combinations of influential factors were performed to further elucidate the nature of the interactions between the factors.

RESULTS

The data for egg diameter and clutch size met the criteria for parametric assumptions, but the data for DME did not. Inverse-transformed DME data met parametric assumptions and were used in all analyses of the effects of individual factors on DME.

All reproductive attributes were significantly correlated with each other ($P < 0.001$ for all). Egg diameter and DME were positively correlated (*r*, 0.44) (Fig. 2A); but both egg diameter and DME were negatively correlated with clutch size (*r*, –0.30 for both) (Fig. 2B, C). The proportions of the variation attributable to the relationships were small (19%, 9%, and 9%, respectively) due to high levels of variation in all measures.

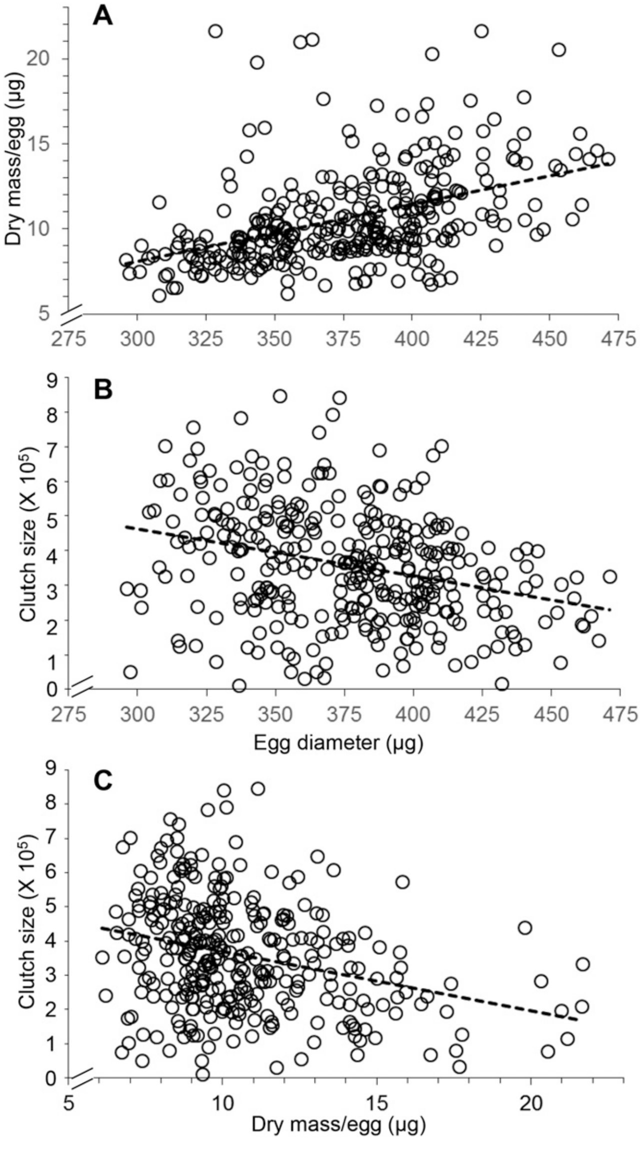

Figure 2. Correlations between pairs of reproductive attributes for Tampa Bay female stone crabs (genus *Menippe*). Least-squares lines illustrate trajectories of principal trends in relationships. (A) Egg diameter and dry egg mass. (B) Egg diameter and number of eggs in egg mass. (C) Dry mass/egg and number of eggs in egg mass. Four large outlier values (30, 31, 33, and 44 µg) were omitted from the calculations involving dry mass/egg. Their inclusion essentially masked the fundamental relationships between dry mass/egg and the other reproductive attributes.

Genotype Determination

Of the Tampa Bay *Menippe* females sampled, 251 were classified as *Menippe mercenaria*, 66 as *M. mercenaria*-backcross hybrids, 11 as intermediate hybrids, one as a *Menippe adina*–backcross hybrid, and none as *M. adina*. Egg diameter, DME, and clutch size, did not differ significantly among the three principal genotype groups (*F* range: 0.610–1.17; *P* range: 0.31–0.54). Nor did values for the single *M. adina*–like backcross individual differ significantly from the mean values of the three principal groups for any of these attributes (*t*-test for a single individual versus mean for all other genotype classes combined; *t* range: 0.04–0.90, *P* range: 0.28–0.88). As a second approach, all hybrid forms were consolidated into a single genotype class (hybrid). The three reproductive attributes were compared between that class and the *M. mercenaria* genotype class, both including CW as a covariate and combining females of all sizes. No significant difference was detected between the consolidated hybrid genotype class and the *M. mercenaria* genotype class in any measure of reproduction, including analyses where CW was added as a covariate. Therefore, the data were analyzed as a single data set, disregarding genotype-class composition.

Individual Influential Factors

The females collected ranged in size from 36.6 to 114.2 mm CW (mean, 84.2), but most were in size classes 70 – 90 (Table 2).

The effects of CW on egg diameter, DME, and clutch size were investigated first, to determine whether CW should be included as a covariate in other analyses. The factor CW was normally distributed within any year and the size distribution of females sampled did not vary significantly among season/year combinations. Although the mean egg diameter of females 30.0–39.9 mm CW was much smaller than the mean for females in all larger size classes (328.7 versus 376.9 μm) and mean weight of eggs generally increased with increasing size class (from 8.8 μg, size class 30+40 to 12.2 μg, size class 110), no coefficients for regressions of either egg diameter or DME on CW using untransformed or transformed data were significant, and no *r* value explained more than 1% of the data, principally because each data subset was highly variable. Thus, egg diameter and egg weight were not well related to female size; their overall values averaged, respectively, 375.5 μm and 10.9 μg.

Clutch size was influenced by CW (Table 3). The best-fit equation for the dependence of clutch size on female size was a power function when all females were analyzed (Table 4), but was a third-order polynomial function when the females were grouped into size classes (clutch size = $-2{,}329\ \mathrm{CW}^3 + 35{,}257\ \mathrm{CW}^2 - 81{,}446\ \mathrm{CW} + 93{,}715$; $r^2 = 1.00$) (Fig. 3A). An analysis using square-root-transformed CW explained almost as much of the variation as did the power relationship ($r^2 = 0.56$) and linearized the data. Therefore, analysis of covariance was used in further analyses involving clutch size and included square-root-transformed CW as the covariate.

The inverse relationship between egg diameter or DME and clutch size suggests that egg-mass volume (EV) is limited by female size. If so, then the product of egg volume and clutch size, adjusted for female size, should vary around a constant value over all sizes of females. This idea was tested by estimating, for each female, the ratio EV:CW as $[(\mathrm{CS} \times (4/3 \times \pi \times (D/2)^3))/\mathrm{CW}]$ where CS is the clutch size and D is the egg diameter. Stone crab eggs are almost spherical. Using the volume of a sphere as an estimator may slightly overestimate egg volume, but the bias was in the same direction for all sizes of females because maximum diameter was always recorded. Rather than varying around a constant value, as expected, the ratio increased with size of female in a power-function relationship ($\mathrm{EV} = 0.0001\mathrm{CW}^{1.68}$; $r^2 = 0.41$; $P < 0.01$; Fig. 3B). Both clutch size and EV (even when it is adjusted for female size) generally increased disproportionately with increasing female size.

Egg masses in the various stages were well distributed among females of different sizes. Mean clutch size decreased somewhat, but not significantly, as developmental stage advanced (stage, clutch size/10^5: A, 3.84; B, 3.33; C + D, 3.27). Only egg diameter differed significantly among egg developmental stages. Although variation in egg diameter was highly dependent on egg stage ($r^2 = 0.97$; Table 4), only the mean diameter of stage-A eggs differed significantly from the mean diameters of eggs in other stages (Table 5). Broad variation in egg diameters at each stage and low sample sizes for stages C and D probably limited statistical resolution.

No significant differences were observed in egg diameter, DME, or clutch size in the five crabs with damaged or missing pleopods compared with all other females within ±5 mm CW

TABLE 3.

Average clutch size and fecundity of Tampa Bay female stone crabs (genus *Menippe*) grouped into size classes.

Size class*	Sample size	Mean no. eggs per clutch	SD	No. eggs, smallest clutch	No. eggs, largest clutch	Estimated annual fecundity†
30	2	40,511	13,842	30,723	50,299	279,526
40	2	64,051	17,936	51,368	76,734	441,952
50	16	99,577	38,159	33,119	163,427	687,081
60	30	178,542	80,384	11,772	352,534	1,231,940
70	58	278,816	100,634	104,762	625,422	1,923,830
80	94	376,071	116,800	166,544	689,835	2,594,890
90	88	438,205	132,978	110,075	842,168	3,023,615
100	35	522,031	168,089	143,393	1,204,773	3,602,014
110	4	513,328	123,304	133,962	855,485	3,541,963

no., number; SD, standard deviation.

* Defined in Table 2.

† Mean no. eggs per clutch × 6.9 (the average number of spawns per season, see Statistical Analyses section).

TABLE 4.

Summary of results for tests of effects of factors on Tampa Bay, FL, female stone crab (genus *Menippe*) reproductive attributes.

Influential factor	Reproductive attribute		
	Egg diameter (ED)	**Dry mass/egg (DM)**	**Clutch size (CS)**
Intrinsic			
Genotype class	NS*	NS*	NS*
CW	NS, $r^2 = 0.16$	NS, $r^2 = 0.12$	$P < 0.001$, $r^2 = 0.59$ $\text{CS} = 2.36 \times \text{CW}^{2.67}$
Egg stage (ES)	$P < 0.001$, $F = 22.55$; $\text{ED} = (17.1 \times \text{ES}) + 348.2$, $r^2 = 0.97$	NS, $F = 0.53$	NS, $F = 3.26$
Damaged or missing pleopods	NS, $t = 0.38$	NS, $t = 1.9$	NS, $F = 2.21$
Damaged or missing claws or legs	NS*	NS*	NS*
Extrinsic			
Octolasmis mülleri infestation	$P < 0.01$, $t = 3.04$; regression NS, $r^2 = 0.03$	$P < 0.001$, $t = 3.40$; regression NS, $r^2 = 0.02$	$P < 0.001$, $t = 3.59$; regression NS, $r^2 = 0.00$
Season	$P < 0.001$, $F = 57.2$	$P < 0.001$, $H = 124.1$	$P < 0.001$,† $F = 30.4$
Water temperature (WT)	$P < 0.001$, $r^2 = 0.24$ $\text{ED} = (-4.79 \times \text{WT}) + 507.12$	$P < 0.001$, $r^2 = 0.14$ $\text{DM} = (-0.39 \times \text{WT}) + 21.49$	$P < 0.01$, $r^2 = 0.08$ $\text{CS} = (12{,}147 \times \text{WT}) + 26{,}322$
Year	$P < 0.001$, $H = 31.2$	NS, $F = 0.40$	$P = 0.015$†, $F = 4.2$

NS, nonsignificant.

* Statistics and P values are given in text.

† Seasonal and annual variations in clutch size were also dependent on female CW; see Results section and Figure 4.

(egg diameter or DME: *t*-test for comparing a single observation with the mean of a sample, *n* range: 12–66; clutch size: analysis of covariance) (Table 4). Nor was any reproductive attribute related to missing major appendages (divided into categories of 0, 1, 2, or 3 or more missing appendages; each injured female had at least one missing claw, $n = 127$), either when the four injury categories were maintained (*F* range: 0.69–0.87, *P* range: 0.46–0.55) or when the females were divided into two groups: injured and not injured (*t* range: 0.55–1.89, *P* range: 0.20–0.50).

Of the 147 females infested with *Octolasmis mülleri*, 97 were infested with 1–10 barnacles, 42 with 11–49 barnacles, and 8 with 50 or more barnacles. The average number of barnacles on infested females was 12. The mean size of females infested with *O. mülleri* (87.2 mm CW, $\text{SD} = 11.6$) did not differ significantly from the mean size of uninfested females (82.2 mm CW, $\text{SD} = 14.6$; *t*-test), so CW was not included as a cofactor in the analyses comparing infested and uninfested females. In those analyses, egg diameter and DME were significantly smaller and clutch size was significantly larger in infested females than in uninfested females (Tables 4 and 5; *O. mülleri* infestation as a categorical factor). Due to high variation in all reproductive attributes irrespective of infestation level, variation in reproductive attributes was not related to level of *O. mülleri* infestation (r^2 range: 0.00–0.03; Table 4; *O. mülleri* infestation as a continuous factor).

Egg diameter, DME, and clutch size varied seasonally (Table 4). Mean egg diameter declined significantly through the spawning season and mean DME was significantly higher during early season than during mid or peak season (Table 5). In contrast, mean clutch size was significantly smaller during early season and was similarly large during mid-season and peak season (Table 5). Clutch size was also differentially dependent on female size during each part of the spawning season (Fig. 4A); large females produced higher numbers of eggs per clutch during peak season than earlier in the season, but those eggs were significantly smaller than the eggs produced early in the season. Power functions best explained the changes in clutch size through seasons (early: $\text{CS} = 0.43 \times \text{CW}^{3.00}$, $r^2 = 0.67$; mid: $\text{CS} = 26.0 \times \text{CW}^{2.14}$, $r^2 = 0.44$; late: $\text{CS} = 2.00 \times \text{CW}^{2.73}$, $r^2 = 0.66$). Female size accounted for considerably higher proportions of the variation in clutch size during the early and peak parts of the season than during mid-season, when clutch size was more variable among females of similar size and did not increase as much with increasing female size. (Note lower exponent, 2.14, in equation for mid-season compared with exponents in equations for early and peak seasons—3.00 and 2.73, respectively.)

Variation in female CW was not dependent on variation in temperature ($r^2 = 0.000$). Thus, all females could be combined into a single data set for the temperature analyses. Variations in egg diameter and DME were significantly and negatively related to variation in temperature (Table 4; Fig. 5A, B). Linear regression yielded highly significant r^2 values; but low proportions of the variation in either attribute were explained by variation in temperature (24% and 14%, respectively; Table 4). A small but significant portion of the variation in clutch size (8%) was also explained by variation in temperature (Table 4), but the relationship was positive (Fig. 5C). To determine if polynomial regressions better fit the data, polynomial regressions were calculated for each data set from second order to sixth order. None of those regressions accounted for significantly more variation in the data than did the linear regressions, but all had inflections at approximately 27°C. At temperatures ≤27°C, the distribution of data for each reproductive attribute seemed to be centered on a mean different from the mean of the analogous data at temperatures >27°C (Fig. 5).

The possibility that the data for each attribute were better described when divided into two subsets at 27°C was examined by calculating the regression of each data subset on each

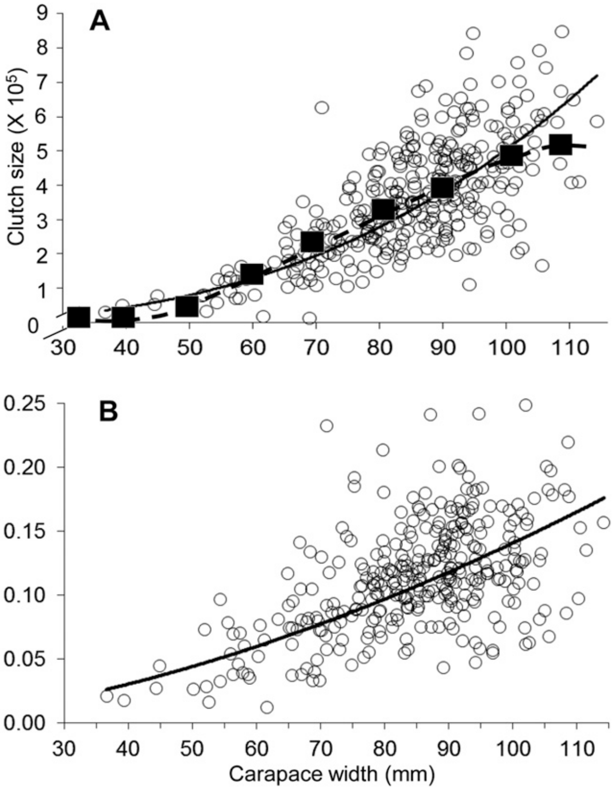

Figure 3. Relationship between clutch size and female size in Tampa Bay female stone crabs (genus *Menippe*). Equations and significance levels are provided in Table 4 and Results section. (A) Dependency of variation in clutch size on variation in maternal female size (carapace width, CW). Curved solid line: regression for individual data points (open circles); dashed line: regression for data grouped into size classes (defined in Table 2; black-filled squares). (B) Dependency of variation in egg mass volume (vol.), adjusted for maternal female size (fem. CW), on variation in maternal female size.

attribute (Fig. 5). Except for the regression coefficient for egg diameter versus temperature >27°C, the regression coefficients did not differ significantly from zero, indicating that the data were centered around means specific to the data subsets (Table 6). All r^2 values were very small, indicating that within the temperature range analyzed, variation in the reproductive attribute was not dependent on variation in temperature. Moreover, the two means for the pair of data subsets in each attribute differed significantly from each other (Wilcoxon two-sample test; $P < 0.001$ for each). Thus, the regressions for the partial data sets indicated that in temperatures of 27°C or less the reproductive attributes functioned significantly differently than they did in temperatures greater than 27°C.

Egg diameter and clutch size varied annually, but DME did not (Table 4). Overall, egg diameter was significantly larger and clutch size was significantly smaller in 1993 than in 1994 and 1995 (Table 5). Power equations best described CW - clutch size relationships for each year (1993, $\mathrm{CS} = 4.26 \times \mathrm{CW}^{2.52}$; 1994, $\mathrm{CS} = 4.34 \times \mathrm{CW}^{2.53}$; 1995, $\mathrm{CS} = 0.98 \times \mathrm{CW}^{2.88}$) (Fig. 4B) and female size accounted for 53%, 48%, and 75% of clutch size variation in the respective years. During 1995, the largest females had larger clutches than in other years, and variation in female size accounted for a higher proportion of the variation in clutch size than in other years.

Combined Factors

The categorical factors *Octolasmis müfleri* infestation, season, and year significantly influenced multiple reproductive attributes and were included in multivariate analyses of each reproductive attribute; CW was included as a covariate in the analysis of clutch size. Egg stage influenced egg diameter and was included in a multivariate analysis of factors that affected egg diameter (stages B–D grouped into "advanced stage").

The degrees of freedom were insufficient to include all four factors in a single MANOVA when assessing the interactions of factors that influenced egg diameter. Therefore, the analysis was performed in phases, first eliminating egg stage, then eliminating *Octolasmis müfleri* infestation. In both analyses involving egg diameter, season and year varied interactively (Table 7A, B). The pairwise analyses of season/year combinations revealed that the principal difference between season/year combinations was a difference between 1993 and later years in the seasons during which mean egg diameter was significantly larger than the means for other season/year combinations (Fig. 6). In contrast to the overall pattern of significantly larger eggs only during early season, mid-season mean egg diameter did not differ significantly from early-season mean egg diameter in 1993. Consequently, for both stage-A and advanced-stage eggs, mean diameters for both early season and mid-season 1993 were significantly larger than mean diameters for mid-season and peak season 1994 and 1995 (P range: 0.05–0.001). In addition, few other pairwise significant differences between season/year combinations were principally between early season means and mid or peak season means. They followed no broad pattern but also contributed to the interaction between season and year.

As in the analysis of individual factors, egg diameter differed significantly among egg stages, but without interaction with season or year. Contrary to the individual analysis of *Octolasmis müfleri* infestation, this factor did not significantly affect egg diameter in the multivariate analysis (Table 7B). The influence of *O. müfleri* infestation on egg diameter was subtle. Comparing infested and noninfested females, mean egg diameter differed by a small amount, standard deviations overlapped, and ranges were essentially the same (Table 5).

Of the factors included in the multivariate analysis of DME (*Octolasmis müfleri* infestation, season), only season was significant ($F = 29.4$, $P < 0.001$); and no interaction terms were significant. Each of the factors included in the multivariate analysis of clutch size (*O. müfleri* infestation, season, year) was significant (F range: 8.6–31.0; P range: 0.05 to <0.001); but, again, no interaction terms were significant.

Overall, the analyses revealed that season and associated temperature, as well as egg stage, were the most important factors affecting egg diameter. Year less influenced egg diameter, and seasonal effects varied among years. The only factors highly influential on DME were season and temperature. Both mean egg diameter and mean DME were significantly larger during early season, when temperature was cool but rising. Mean egg diameter could remain relatively large during midseason or be exceptionally large in a particular year. Female size, together with reproductive attributes egg diameter and DME most influenced clutch size. Clutch size increased

TABLE 5.

Summary of statistically significant groupings for effects of categorical influential factors on Tampa Bay, FL, female stone crab (genus *Menippe*) reproductive attributes.

Reproductive attribute Influencing factor Statistics	Category			
Egg diameter (µm)*				
Egg stage†	A	B	C	D
Mean (SD)	362 (33)	388 (36)	398 (30)	415 (34)
Range	296–487	297–471	337–465	369–464
n	165	115	43	5
Group	2	1	1	1
Octolasmis mülleri	Infested	Not infested		
Mean (SD)	370 (37)	381 (36)		
Range	296–471	297–462		
n	181	147		
Group	2	1		
Season‡	Early	Mid	Peak	
Mean (SD)	403 (32)	373 (35)	359 (30)	
Range	303–471	304–462	296–414	
n	103	85	140	
Group	1	1/2	2	
Year	1993	1994	1995	
Mean (SD)	394 (30)	368 (40)	371 (33)	
Range	314–462	296–467	297–464	
n	95	124	109	
Group	1	2	2	
Dry mass/egg (µg)				
O. mülleri	Infested	Not infested		
Mean (SD)	10.1 (3.0)	11.6 (4.3)		
Range	6.2–30.0	6.1–43.7		
n	148	181		
Group	2	1		
Season	Early	Mid	Peak	
Mean (SD)	13.3 (4.6)	9.7 (1.6)	9.8 (3.7)	
Range	8.2–43.7	6.9–17.4	6.1–31.8	
Group	1	2	2	
Clutch size				
O. mülleri	Infested	Not infested		
Mean	392,577	328,342		
(SD)	(164,527)	(161,866)		
Range	11,772–847,243	30,723–756,837		
Group	1	2		
Season	Early	Mid	Peak	
Mean	297,589	402,851	374,258	
(SD)	(136,680)	(159,088)	(177,082)	
Range	17,566 –648,888	119,862–793,076	11,772–847,243	
Group	2	1	1	
Year	1993	1994	1995	
Mean	335,993	361,472	372,119	
(SD)	(140,159)	(175,907)	(173,551)	
Range	33,119–784,356	11,772–847,243	17,566–842,168	
Group	2	1	1	

Group: Statistically homogeneous grouping of means that includes category with highest (1) or lowest (2) mean.

* Egg diameter was not recorded for one barnacle-infested female with egg stage C, captured in August 1994. DME and clutch size were recorded for that female, so sample sizes differ among attributes.

† Defined in Table 1.

‡ Defined in Table 2.

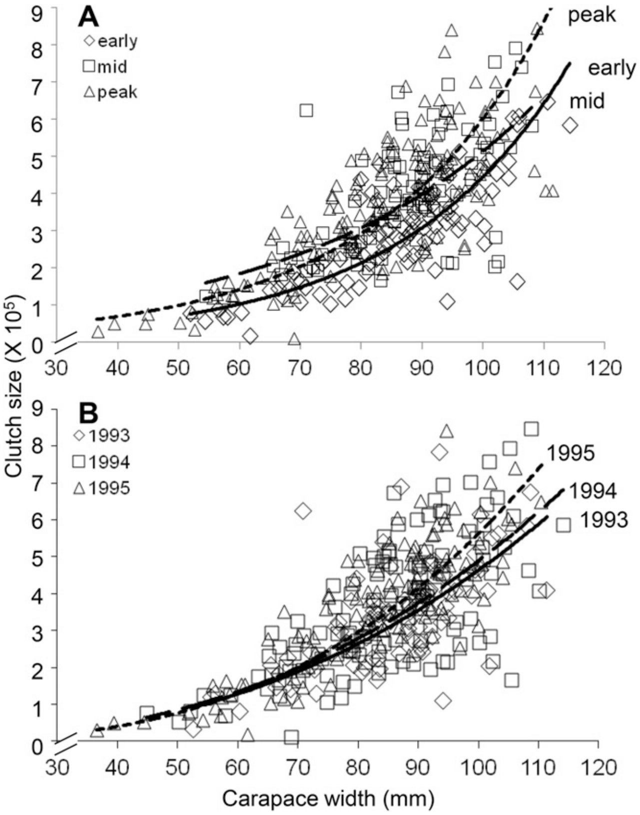

Figure 4. Temporal variation in relationship between clutch size and maternal female size for Tampa Bay stone crabs (genus *Menippe*). Regression equations and their significances given in Results section. (A) Seasonal variation (seasons defined in Table 2). Solid line, early; long-dash line, mid; short-dash line, peak. (B) Annual variation. Solid line, 1993; long-dash line, 1994; short-dash line, 1995.

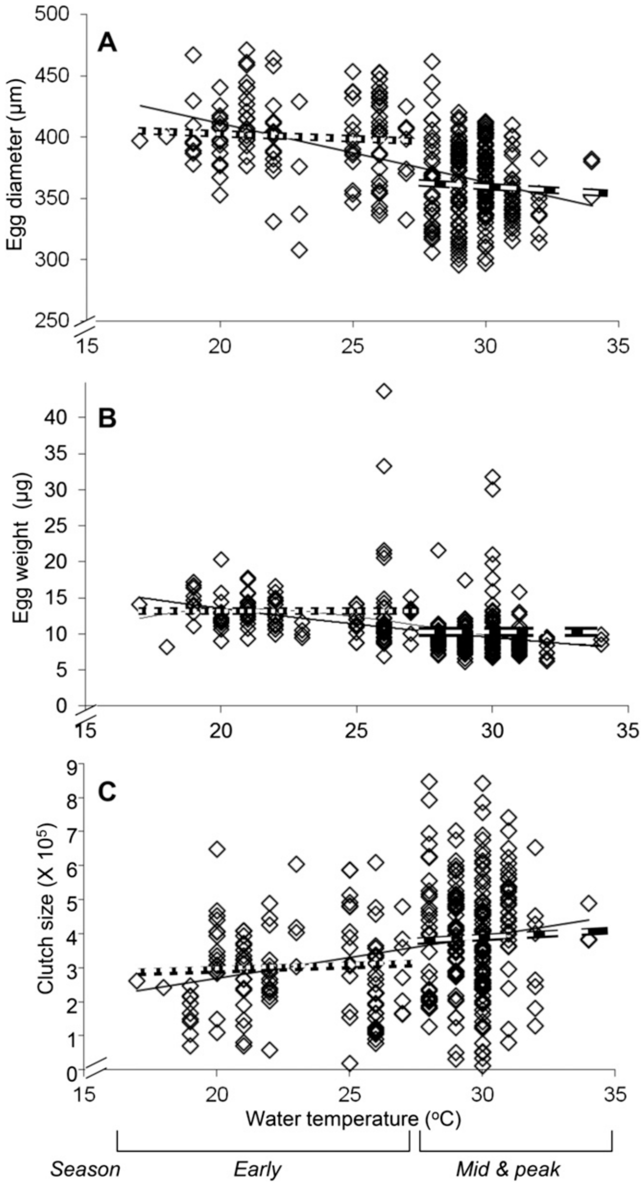

Figure 5. Effects of water temperature on Tampa Bay female stone crab (genus *Menippe*) reproductive attributes. Solid black lines: linear regressions fitted to all data. Regression equations and coefficients of determination and their significance levels are given in Table 4. Dashed black-and-white lines: linear regressions fitted to data for temperatures 27°C or less or more than 27°C. Bars at bottom of graph group temperatures according to part of reproductive season during which they occur (see Table 2). (A) Egg diameter. (B) Dry weight per egg. (C) Number of eggs in egg mass.

exponentially with female size. For females of a specific size, clutch size was small when egg diameter and DME were large, and *vice versa*. Season, temperature, and year also influenced clutch size complexly, but not interactively. Although *Octolasmis mülleri* infestation significantly reduced egg diameter and DME and increased clutch size, the overall effect was small because the values for each reproductive attribute varied widely, even among females of similar size.

DISCUSSION

Reproductive Attributes

Overall average diameter of the eggs produced by Tampa Bay female stone crabs compared favorably with reported diameters of *Menippe nodifrons* eggs (Hines 1992, Miyako & Oshiro 1999, Oshiro 1999) and with diameters of eggs from other brachyuran crabs (Wild 1980, Hines 1991, Zimmerman & Felder 1991, Kobayashi & Matsuura 1995); but was much larger than the values given by Noe (1967) (141–180 µm). Average DME (henceforth, egg weight) was light compared with that reported for the mangrove crab *Sesarma rectum* (Leme 2005). Size-class-specific mean number of eggs per clutch was higher for large Tampa Bay females than the value reported by Noe (1967) for a similarly sized *Menippe* female, but was nearly equal to that reported by McRae (1950) (estimated 280,000 eggs, 71 mm CW; versus approximately 279,000 eggs for size class 70; Table 3). The estimates of mean clutch size for Tampa Bay females grouped into size classes also varied from those of Ros et al. (1981) for the same size classes of *Menippe mercenaria* from Cuba. The estimates of annual fecundity for large Tampa Bay females were somewhat higher than those of Noe (1967), but he did not specify female size. Stone crab egg masses have characteristics typical of crabs that have no parental care of offspring. Clutch size usually ranges from ten thousands to millions within species and varies greatly even

TABLE 6.

Means and regression statistics for regressions of reproductive attributes versus temperature using partial data sets for Tampa Bay, FL, female stone crabs (genus *Menippe*) (see Fig. 5).

	Mean (SD)		Regression coefficient		r^2	
Reproductive attribute	≤27°C	>27°C	≤27°C	>27°C	≤27°C	>27°C
Egg diameter (μm)	402.7 (32.4)	363.2 (31.5)	–1.14	–3.51	0.009	0.019
Egg dry weight (μg)	13.1 (4.5)	9.8 (3.0)	–0.03	–0.26	0.000	0.011
Clutch size*	289,813 (132,390)	395,575 (170,552)	0.14	0.90	0.001	0.004

* Regressions calculated using (clutch size $\times 10^{-5}$).

among similarly sized females (Erdman & Blake 1988, Diesel 1988, Hines 1991, Clarke 1993, Haddon 1994, Mantelatto & Fransozo 1997, Kotb & Hartnoll 2002, Darnell et al. 2009), and even when the eggs are in the same developmental stage and the maternal females are reared in the same environmental conditions (Efford 1969, Giménez & Anger 2001).

Egg diameter and weight were positively correlated with each other and negatively correlated with clutch size in Tampa Bay *Menippe*. There is a significant trade-off between ovum size and the number of eggs per brood in most decapods (Hines 1982, Sainte-Marie 1993, Harlioğlu & Türkgülü 2000, Lardies & Castilla 2001, Graham et al. 2012). This trade-off is a fundamental consideration in life history models because offspring size is related to offspring survival and offspring survival is a product of egg size. Larger eggs produce larger larvae (Giménez & Anger 2001) that have numerous developmental and survival advantages over larvae produced from smaller eggs (Steele & Steele 1975, Fox & Czesak 2000), including advantages that appear after metamorphosis (Moran & McAlister 2009); however, reduced probability of survival of offspring hatched from small eggs may be compensated for by higher numbers of eggs per clutch (Miranda et al. 2006).

Intrinsic Factors

Many intrinsic factors that influence egg diameter, egg weight, or clutch size in other decapod crustaceans had no significant effect on these attributes in Tampa Bay *Menippe*. Only two factors significantly influenced single attributes. Egg diameter increased linearly and significantly with advancing egg stage; and clutch size increased exponentially with female size.

Average egg size continually increases as eggs develop in most crab species (Efford 1969, Reid & Corey 1991, Kobayashi & Matsuura 1995, Furota 1996, Turra & Pereira Leite 2001). The size increase can be substantial—a doubling of volume (Norman & Jones 1993) and increase of >10% in width (Erdman & Blake 1988). In this study, average egg diameter increased 14% from stage A to stage D. The increase is likely due, at least in part, to water absorption, structural organization, and embryo growth (Nazari et al. 2003).

Although neither egg diameter nor DME are strongly related to female size in Tampa Bay females (unusual in decapods, but lack of a relationship does occur; Haddon 1994), clutch size is; but the relationship may not be mathematically straightforward. Clutch size and EV are frequently related to maternal female size or age in decapods (Fielding & Haley 1976, Hines 1982, Sainte-Marie 1993, Mantelatto & Fransozo 1997, Turra & Pereira Leite 2001, Graham et al. 2012) in linear, exponential, or logarithmic relationships (Haynes et al. 1976, Simons & Jones 1981, Somerton & MacIntosh 1985, Somers 1991, Haddon 1994, Lardies & Castilla 2001, Tully et al. 2001, Kotb & Hartnoll 2002, Litulo 2004, Lawal-Are 2010). Both the regression of clutch size and the regression of size-adjusted EV on female stone crab CW using ungrouped data were exponential functions, indicating that large female stone crabs produce disproportionately high numbers of eggs; however, grouping the females into size classes suggested a slightly different interpretation. On average, females in the largest size class (≥110) may not produce more eggs than females in one size class lower (100–110). Although the sample for size class ≥110 was small, this result is supported by other research. Ros et al. (1981) also found a slight decline in average clutch size of the largest size classes. Ros et al. (1981), Gerhart and Bert (2008), and Bert et al. (in review) noted small, but sometimes significant, decreases in percentage of ovigerous females in the largest size classes they designated. Together, these results indicate a shift in reproduction in very large

TABLE 7.

MANOVA results for test for interactive effects between factors influencing diameter of eggs collected from Tampa Bay, FL, female stone crabs (genus *Menippe*).

Factors	df	MS	F	P	% of tot. var.
(A) Year, season, and egg stage					
Year (Y)	2	13165.5	22.69	**<0.001**	18
Season (S)	2	27141.7	46.78	**<0.001**	38
Egg stage (St)	2	28402.8	48.95	**<0.001**	40
Y X S	4	1861.0	3.21	**0.013**	3
Y X St	4	612.4	1.06	0.378	1
S X St	4	82.7	0.14	0.906	~0
Y X S X St	8	614.3	1.06	0.392	1
Error	301	580.2			
(B) Year, season, and infestation of maternal females with *O. mülleri*					
Year	2	15760.0	19.20	**<0.001**	24
Season	2	43598.0	53.10	**<0.001**	65
Octolasmis mülleri (O)	1	1501.9	1.83	0.177	2
Y X S	4	2496.4	3.04	**0.018**	4
Y X O	2	1402.1	1.71	0.183	2
S X O	2	1403.8	1.71	0.183	2
Y X S X O	4	912.2	1.11	0.351	1
Error	310	821.0			

Significant P values are in bold. df, degrees of freedom; MS, mean square; F, MS_{factor}/MS_{error}; P, significance level; tot. var., total variation.

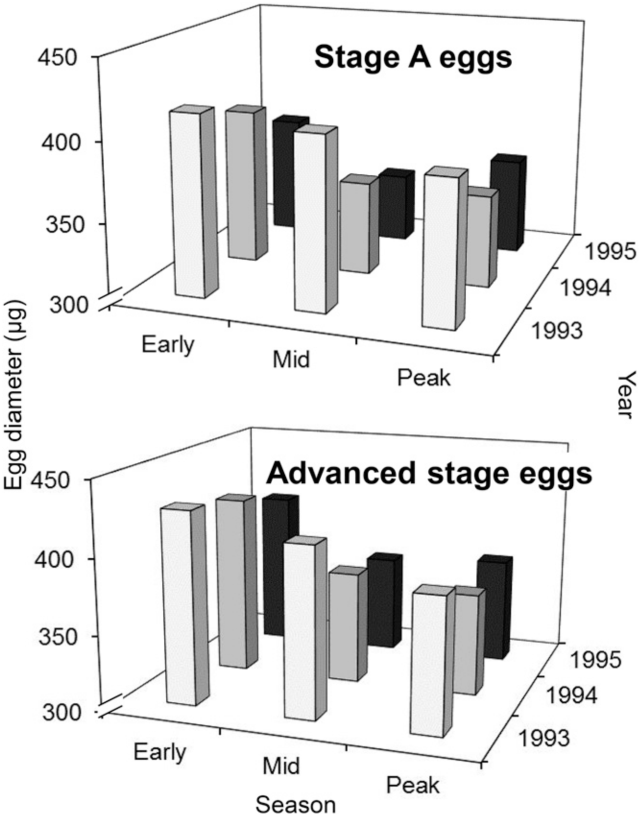

Figure 6. Temporal variation in mean diameter of early- and advanced-stage eggs from Tampa Bay, FL, female stone crabs (genus *Menippe*). Variation differed interactively among seasons and years (see Table 7).

females. Gonadal development time to egg maturation may be longer, reducing the number of spawns and the number of eggs per spawn in these females. The largest females are also the oldest females (Gerhart & Bert 2008); partial senescence might be occurring. The metabolic cost of surviving and growing may be higher in these females, leaving less energy available for reproduction. Theoretically, selection works to optimize lifetime reproductive success (Stearns 1992). It may be more beneficial for old females to allocate less energy per clutch and more energy to staying alive and maintaining fitness so they can continue to reproduce for a longer period of time. Alternatively, or additionally, fishery-related claw removal in relatively high proportions of these females and the attending impacts on growth and reproduction (T. M. Bert, unpublished data) may be reducing their annual fecundity. Lastly, the annual fecundity estimates presented in Table 3 may be inflated for several size classes of larger females. The estimates were based on the assumption that females of all sizes produced, on average, the same number of clutches each year—an assumption that may not be true. Large blue crabs produce larger clutches than do small blue crabs, but they produce fewer clutches per spawning season, resulting in equivalent annual reproductive output among size classes (Dickinson et al. 2006).

Neither genotype class nor missing appendages influenced any female reproductive attribute. The finding of no difference among genotype classes in the reproductive attributes of Tampa Bay females is not surprising. Hybrids between two species are often less reproductively fit than either parental species (Harrison 1993, Palumbi 1994). In contrast, hybrid *Menippe* from the northwest Florida hybrid zone showed no evidence of reduced spawning frequency or egg viability compared with those attributes in the parental species (Wilber 1989), and comparisons of various physiological and reproductive attributes among hybrid and parental-species genotype classes revealed some, but not extensive, evidence for overall decreased performance of hybrids compared with either parental species (Bert & Harrison 1988, Combs et al. 1997). Moreover, several biological and physiological attributes of *Menippe mercenaria*–like hybrids are indistinguishable from those of pure *M. mercenaria* (e.g., size class distribution of frequency of ovigerous females, spawning season, frequency of infestation by *Octolasmis mülleri*; postsettlement juvenile salinity/temperature tolerance; T. M. Bert, unpublished data).

In contrast to similar studies (Norman & Jones 1993, Luppi et al. 1997), missing appendages also had no effect on egg quality or quantity in Tampa Bay females, regardless of the number or type of appendages missing. One might expect a trade-off between limb regeneration and clutch size. If a limb is lost before or during the spawning season, limb regeneration, spawning, or both could be delayed or stunted because the available energy would be needed for both gonad development and limb regeneration (Norman & Jones 1993). In female stone crabs with missing claws, the number of clutches per spawning season may be reduced (T. M. Bert, unpublished data), rather than egg size, egg weight, or clutch size.

Extrinsic Factors

All extrinsic factors influenced at least two reproductive attributes in Tampa Bay *Menippe* females, some interactively.

Compared with uninfested females of similar size, egg diameter was 3% smaller, egg weight 13% lighter, and clutch size 20% larger in females infested with *Octolasmis mülleri*. But these alterations did not change with the level of infestation, and in multivariate analyses of *O. mülleri* combined with environmental factors, infestation significantly influenced only clutch size. The overall effects of *O. mülleri* infestation on Tampa Bay females seems to be minor, but *O. mülleri* infestation could have substantial effects if it is prolific and heavy. Infestation with *Octolasmis* spp. can change crab behavior (Dickinson et al. 2006). Heavy infestation can elevate metabolism (Gannon & Wheatly 1994) and increase mortality in stressful situations (Gannon & Wheatly 1992). Moreover, infestations can afflict nearly all individuals in a crab population (Dickinson et al. 2006). The species *O. mülleri* seems to preferentially infest stone crab hybrid forms (T. M. Bert, unpublished data), which are common in Tampa Bay and predominate in northwest Florida (Bert & Harrison 1988), where the second-largest stone crab fishery is located. Because egg size and weight are correlated with offspring survival in decapod crustaceans (Llodra 2002), *O. mülleri* infestation could negatively affect reproduction in those areas over the long term by chronically contributing to reductions in egg size and weight.

Season strongly influenced the reproductive attributes of Tampa Bay *Menippe* females. Early-season mean egg diameter and mean egg weight were, respectively, 11% and 26% higher than that they were later in the season, whereas mean number of eggs per clutch was 35% smaller than in mid-season and 26% smaller than in peak season. Thus, egg quality was high but clutch size was small during early season, whereas egg quality was lower but clutch size larger during mid-season and peak season. This inverse relationship between egg quality and clutch size, as well as that related to *Octolasmis müller*i infestation, suggests that regardless of the manner in which external factors change egg quality, clutch size will be maximized (or optimized) to compensate. Producing smaller, lighter eggs allows abdominal space for more eggs, but the trade-off between egg quality and egg quantity may result in reduced larval recruitment (Hines 1982, 1992). Alternatively, the production of more eggs may offset the lesser quality factor and result in equivalent larval recruitment among seasons (Moran & McAlister 2009).

Larger eggs are produced early in the spawning season in the estuarine crab *Chasmagnathus granulatus* (Dana, 1851) (Ituarte 2006) and mud crab *Macrophthalmus hirtipes* (Jacquinot, 1853) (Simons & Jones 1981), possibly because the quality and quantity of food for adults are high and temperature conditions are optimal (Graham et al. 2012). Tampa Bay *Menippe* females may spawn larger eggs during early season because gonadal development has been ongoing for several months, during winter (Bert et al., in review), whereas later in the spawning season, the gonads must develop eggs to maturation every few weeks. The longer overwinter gonad development time may result in more robust eggs for the first clutch of the spawning season. Moreover, the early season contribution to annual fecundity may be the most important of the spawning season. Stone crab larvae and postsettlement juveniles grow rapidly in water of 25–30°C (Brown et al. 1992, Brown & Bert 1993), which are mid- and peak-season temperatures. Larvae and, subsequently, postsettlement juveniles produced from early-season eggs would have a longer period of warm weather in which to grow and develop than would recruits produced from the generally smaller eggs spawned later in the reproductive season. The combination of comparatively large eggs and long growing season for recruits could result in disproportionately high survival of recruits hatched from early-season eggs.

Unsurprisingly, water temperature influenced the three stone crab reproductive attributes in the same direction as did the factor "season." The polynomial regressions and partial-data regressions indicated that a threshold effect—a switch—from the development of fewer, larger, heavier eggs to more, smaller, lighter eggs in similarly sized females occurs at or about 27°C. This temperature is usually reached during May, which was the month between the early-season and mid-season samplings. Important changes in frequencies of gravid females and ovigerous females also seem dependent on threshold temperatures (Bert et al., in review). Similar temperature-related changes in the reproductive attributes investigated here have also been recorded for other crab species, principally as latitudinal differences (Jones & Simons 1983, Lardies & Castilla 2001, Brante et al. 2003, Hamasaki et al. 2006). In a study where temperature was treated as a continuous variable, as in this study, the Japanese mitten crab *Eriocheir japonicas* (de Haan, 1835) produced increasingly smaller eggs as water warmed (Kobayashi & Matsuura 1995). An advantage to this approach is that details of temperature effects on reproductive attributes can be obtained, such as the apparent threshold effect observed at 27°C.

Compared with other years, mean diameter of stone crab eggs was larger during 1993 (approximately 6%, 1993 versus other years). More specifically, mean egg diameter was particularly large in early and mid-season 1993, as well as in early season 1994, compared with means for other season/year combinations—particularly those for mid-season and peak season 1994 and 1995. The large eggs in both early and mid-season 1993 deviated from the overall pattern of significantly larger eggs only during early season compared with other seasons. This deviation may have been related to temperature. Average temperature during January 1993 (21.0°C) was the warmest recorded and average temperature during June 1993 (27.0°C) was the coolest recorded during multiple monthly samplings taken regularly at the four Tampa Bay stations from 1989 through 2010. Both the January and June 1993 means were peripheral to the respective monthly averages for all years combined, and to their standard deviations (January: 17.0°C ± 2.3; June: 28.8°C ± 0.8; T. M. Bert, unpublished data). Moreover, the average temperature in June had not yet exceeded the 27°C threshold that apparently triggers the switch from production of fewer, larger eggs to more, smaller eggs during the spawning season. Also of interest is the production of notably large clutches by large females during 1995. Mean temperatures for May and June, 1995, were the warmest recorded for the period 1989 to 2010 (28.5 and 30.2°C, respectively). These, too, exceeded the long-term averages and their standard deviations (26.3°C ± 1.4 and 28.8°C ± 0.8, respectively) and were well above the 27°C threshold. Perhaps in large females, these warm temperatures accelerated the switch from the production of smaller clutch sizes composed of larger eggs to the production of large clutch sizes composed of smaller eggs.

If larger eggs produced early in the spawning season yield zoeae and postsettlement juveniles with better survivorship, then the number of postsettlement juveniles should have been high in 1993, and possibly 1994, compared with 1995, assuming that overall spawning effort was statistically similar over months and years. Indeed, mean numbers of postsettlement juveniles collected per month during 1993 and 1994 (respectively, 31.0, 30.1; T. M. Bert, unpublished data) were significantly higher than the mean number collected during 1995 (12.4; $P < 0.001$, Kruskal–Wallis test). Interannual variation in stone crab recruitment is high (T. M. Bert, unpublished data). It may be related to interannual variation in egg size, particularly during the early months of the spawning season.

Comparisons of egg quality or clutch size in crabs among years are rare. Jones (1980) and Bas et al. (2007) reported interannual differences in some aspect of egg quality or clutch size. In a third study (Prager et al. 1990), the researchers changed sampling methods between years, calling into question their report of interactive effects between season and year in varying patterns of clutch size in blue crabs.

Fisheries Implications

For at least the past 40 y, the Florida stone crab fishery has been among the top five most economically important commercial fisheries in Florida. Approximately 95% of all claws landed are harvested in the Gulf of Mexico off Florida. Landings increased linearly from 1962 to 1992 ($y = 98.887x + 6.0543$, $r^2 = 0.92$); fluctuated around approximately 3,200,000 pounds (lb) (1451,500 kg) from 1993 to 2002; fluctuated around approximately 2,700,000 lb (1224,700 kg) from 2003 to 2010, and then markedly declined (Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, fisheries database). Landings for the 2013 to 2014 and 2014 to 2015 harvesting seasons were slightly more than 1,900,000 lb (862,000 kg). Since the initiation of data collection for this fishery (1962 to 1985, National Marine Fisheries Service; after 1985, Fish and Wildlife Research Institute), catch per unit effort (number of pounds landed/number of traps registered) has declined exponentially (catch per unit effort $= 18.0e^{-0.052 \times \text{year}}$, $r^2 = 0.90$). The fishery is considered to be overcapitalized and overfished (Muller et al. 2011).

The very large females that produce very large egg masses are very rare in the Tampa Bay population (100–109.9 mm CW, 6.3%; ≥110 mm CW, 0.7%; $n = 30{,}026$ females). Because large crabs of both sexes are preferentially retained in traps (Bert 1985), high percentages of these females are declawed. Declawing mortality is high, and essentially doubles when both claws are removed (Davis et al. 1978, Gandy et al. 2016). In surviving females, size-class–specific frequency-ovigerous is significantly lower for females missing claws than for females with both claws, and the decrease doubles when two claws are missing (T. M. Bert, unpublished data). All females in size class 90 with original claws (not regenerated) have one legal-sized claw, and essentially all females in size classes 100 and 110 with original claws have two legal-sized claws (Gerhart & Bert 2008, T. M. Bert, unpublished data). In Tampa Bay, the proportions of size-class-90 females missing one claw and size-class-100 females missing two claws are relatively high (T. M. Bert, unpublished data). Therefore, the reproductive potential of females in size classes with high egg production is significantly reduced by both declawing and mortality from declawing. Some measures should be taken to protect these females. Gerhart and Bert (2008) suggested setting a maximum harvestable size of 110 mm CW for males. This size would protect 0.6% of the males in the Tampa Bay vicinity ($n = 22{,}975$ males) but would protect only the few very largest females because the claws of males are proportionally larger than those of females (Sullivan 1979, Gerhart & Bert 2008), and claw size (propodus length, which has a tight allometric relationship with CW; Perry et al. 1995) is the defining measurement for legal size (Florida Statutes Chapter 68B, Section 13.007).

Harvesting the claws of ovigerous females is prohibited (Florida Statutes Chapter 68B, Section 13.007); but this regulation is very difficult to enforce and, thus, is dependent upon the individual fisher to honor. Changing the closing date of the harvest season from May 15 to April 1 would be a simple, highly enforceable way to protect all females during the time of final ovarian development (Bert et al., in review) and production of the high-quality, early-season egg masses.

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