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Discovery, Evaluation, and Implications of Blue Crab, *Callinectes Sapidus*, Spawning, Hatching, and Foraging Grounds in Federal (US) Waters Offshore of Louisiana

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Abstract:

Although blue crabs, *Callinectes sapidus* Rathbun, 1896, are ecologically important predators and support the world's most valuable crab fishery, little is known about their spawning and hatching migrations beyond the estuary. We discovered unexpectedly high concentrations of female blue crabs actively spawning, hatching their eggs, and foraging in federal waters within our study area, the Ship, Trinity, Tiger Shoal Complex (STTSC) ≥ 20 km off the Louisiana coast. During a three-year investigation, blue crab abundances were significantly higher on Ship and Trinity Shoals than the surrounding, muddy and deeper seafloor. Crabs from the STTSC compared favorably with those from nationally recognized spawning grounds in terms of condition factor (an index of health), fecundity, and abundance. Ninety percent of females possessed a sponge, large ovary, or both. Eighty-seven percent of non-ovigerous females showed evidence of a previous hatching. An analysis of ovarian development suggests that STTSC crabs produce new sponges approximately every 21 d, and at least seven broods per spawning season (April-October). Monthly declines in sponge weight and a companion study of benthic macrofauna suggest fecundity may be limited by food supply in areas of high crab abundance. Symbionts did not negatively impact condition factor. Carapace width including the lateral spines was a much poorer estimator of crab weight than carapace width excluding the lateral spines, height, length, or estimated volume. Given the increasing national importance of the Louisiana blue crab fishery and declines elsewhere, we recommend that management safeguard these previously unknown spawning, hatching, and foraging grounds.

INTRODUCTION

Blue crabs, *Callinectes sapidus* (Rathbun, 1896), are an ecologically and economically important crustacean, historically common along the US Atlantic and Gulf of Mexico coasts. Blue crabs support the most valuable crab fishery in the world (Eggleston et al., 2008). The US fishery accounted for 87% of the world blue crab catch in 1999 (UN, 2008). Louisiana leads all other US states in recent (1997-2006) hard-shelled landings (26% of the US total), followed by North Carolina (22%), the Chesapeake Bay states of Maryland (16%) and Virginia (15%), and each of the remaining thirteen blue-crab producing states (Rhode Island to Texas, 21%, combined) (NOAA, 2007).

Louisiana's leading position in US blue crab landings is largely attributable to recent 1) increases in Louisiana's yield and 2) declines in the blue crab fisheries of Chesapeake Bay (Maryland and Virginia), and North Carolina (NOAA, 2007). Chesapeake Bay and North Carolina declines are attributed to overfishing and/or habitat degradation (e.g. Zohar et al., 2008). As a result, managers in these areas are implementing methods of increasing spawning stock biomass through regulations, i.e., migration corridors and spawning sanctuaries (Lipcius et al., 2003), augmented by an experimental release of hatchery-raised juveniles (Aguilar et al., 2008; Eggleston et al., 2008).

During a pre-impact sand-mining study, we discovered unexpected abundances of female blue crabs in federal waters off the Louisiana coast (~ 20 and 40 km), first on Ship Shoal in 2005 and 2006, and then on the Ship, Trinity, Tiger Shoal Complex when our study area was expanded in 2007 (hereafter STTSC, Fig. 1). While suggestions that the offshore plays a role in the adult blue crab life cycle may be found in the literature (e.g., Van Engel, 1958; Dudley and Judy, 1971; Adkins, 1972; and

Perry, 1975), no study has demonstrated or quantitatively explored the offshore environment as an important adult blue crab habitat.

This paper provides information about underexplored offshore areas of importance to blue crabs that are vulnerable to fishery exploitation and sand-mining disturbance. Currently, the accepted paradigm of the female blue crab life cycle includes 1) a single, lifetime mating event; 2) a salinity-associated separation of the sexes following mating; 3) spawning in estuarine waters; 4) post-fertilization brooding of attached eggs (a.k.a. sponge); 5) hatching in lower estuarine and coastal waters; 6) offshore larval development; and 7) estuarine development of juveniles (e.g. Churchill, 1919; Van Engel, 1958).

In this paper, we use analyses of condition factor, reproductive condition, and abundance to examine the following four null hypotheses relating to the use of the STTSC as an important spawning, hatching, and foraging ground for mature female blue crabs:

(1) Condition factor, fecundity, and abundance of STTSC crabs do not differ from those of nationally recognized spawning grounds;

(2) STTSC crabs do not undergo a continuous spawning/hatching cycle from April to October;

(3) Morphometric indicators of individual weight are equivalent and not affected by symbionts or reproductive state;

(4) Crab abundance is uniform over space and time across the STTSC.

In addition, we examine the ecological, sand mining, and fishery management implications of our findings.

MATERIALS AND METHODS

STUDY SITE AND FIELD COLLECTION.—The STTSC (Fig. 1) is located in the northern Gulf of Mexico south of Louisiana, within a region where annual bottom-water hypoxia occurs (Rabalais et al., 2002). Ship, Trinity, and Tiger Shoals are relic barrier islands (Roberts, 1997) composed mostly of fine grain sand; the surrounding off-shoal areas are typically much muddier. The depths of these shoals ranged between ~3 and 4 m in our most shallow sampling areas. The stations immediately north of Ship Shoal (but several kilometers seaward of land), designated in Fig. 1 as inshore, ranged in depth from ~4 to 6.5 m. All other non-shoal stations, designated in Fig. 1 as offshore, ranged in depth from ~4.5 to 19 m.

We attempted three collection trips per year: spring, summer, and fall. The spring cruise occurred in June, May, and April for 2005-2007 respectively; the summer and fall, in August and October each year. In 2005 and 2006 we concentrated on Ship Shoal, completing nine nighttime trawls per trip, except in June 2005 (exploratory efforts not reported) and October 2005 (one trawl lost). During each cruise in 2005-06 three replicate trawls were pulled on the western, middle, and eastern portions of the shoal, respectively, using a 7.3 m balloon net with 5.08 cm mesh from the R/V *Acadiana*. In 2007 we sampled the five STTSC areas completing 13-21nighttime trawls per trip using a 12.8 m balloon net with 5.08 cm mesh from the R/V *Pelican*. Sampling effort in all years was 30 minutes per trawl. After enumerating the catch by sex per trawl, all crabs were immediately frozen until laboratory analysis.

Bottom-water salinity, temperature, dissolved oxygen (DO), and depth were measured for each station. Water samples were collected ~1 m from the bottom using a 5-L Niskin bottle. Temperature, salinity, and DO were measured with aYSI 85 handheld multimeter and Winkler titrations during 2005-

06 and using a CTD probe in 2007. Environmental data were taken during daytime benthic sampling prior to nighttime trawl sampling.

MEASUREMENTS.—Blue crabs were thawed in the laboratory before examination. During initial exploratory analysis we recorded basic morphometric measurements and made exploratory measurements of the reproductive states and symbionts of the female blue crabs taken during the August 2005 cruise. Based on these insights we developed a procedure (outlined in Table 1) for making detailed measurements of the 2006 and 2007 blue crabs.

Linear measurements of the carapace were based on Williams (1974). They were carapace width from tip to tip of the lateral spines (TT), carapace width from base to base of the lateral spines (BB), length (L), and height (H). We estimated crab volume (V) as L * H * BB. We used a dial caliper for all linear measurements with the exception of TT where a measuring board was used. All linear measurements were made to the precision of ± 1 mm.

We recorded sex, stage of sexual maturity, and (for mature females) weighed the entire crab with (W_b), and without (W), acorn barnacles *Chelonibia patula* (Ranzani, 1818) and *Balanus* spp. Missing legs were noted and the opposing leg, if present, was removed, weighed, and its weight added to the total. We removed and weighed the abdomen (AW) of all mature females. All wet weights were recorded to the precision of ± 0.01 g.

We took three measurements of acorn barnacles: percent barnacle coverage (BC) in 10% intervals; diameter (D) of the largest; and weight ($BW = W_b - W$). We took two measurements of nemerteans *Carcinonemertes carcinophila* (Kölliker, 1845): nemertean presence/absence on the gills (GN) as 0 or 1 and sponge nemertean intensity (SN) within a 1.6 cm diameter subsection of the sponge

as 0, 1-3, 4-6, or > 7 individuals. Gooseneck barnacle (G) *Octolasmis muelleri* (Coker, 1902) abundance was ranked on a six point scale approximating 0, 10, 25, 50, 100, or more than 200 barnacles on the gills.

We recorded presence/absence of a sponge (P) and of hatched egg casings on the abdominal hairs of non-ovigerous crabs. We classified sponge color (SC) of ovigerous females as bright orange = 1, dark orange = 2, brown = 3, dark brown = 4, and black = 5 and used Jivoff et al. (2007) to estimate development time. We assigned non-ovigerous females with hatched egg casings a value of 6.

We determined egg abundance (E) per sponge from a subsample of twenty crabs stratified by length and month (ten from May and ten from August 2006) using a modification of Prager et al.'s (1990) dry weight technique. Here we generated an error term to test for outliers by using the average dry weight of three replicates of 200 eggs/sponge and did not extrapolate from our subsample to the entire sample of ovigerous crabs.

We established three readily apparent categories of ovarian development (O) after Hard (1945, p.8-9): inconspicuous, intermediate, and large. Inconspicuous was consistent with both Hard's stage 1 (ovary "small, inconspicuous, white in color") and his stage 5 (ovary "collapsed, grey or brownish in color"). Large was consistent with both Hard's stage 3 (ovary "preceding first ovulation…bright orange and of large size") and stage 4 (ovary "between ovulations…orange in color and of large size"). Intermediate was consistent with Hard's stage 2 ovary (ovaries yellow or light orange, and of intermediate size). For statistical analysis, inconspicuous, intermediate, and large were designated as one, two, and three respectively.

STATISTICAL FRAMEWORK.—Statistical tests involved the use of simple regression analysis, ANCOVA, ANOVA, and stepwise multiple regression techniques (Freund and Wilson, 2003). SAS® version 9.1.3 (SAS Institute Inc., 2004) was used for all statistical analyses. PROC GLM was used for all tests with the exception of PROC GLMSELECT (factors affecting condition) and PROC MIXED (analysis of STTSC spaciotemporal patterns of abundance). PROC GLMSELECT allows the user to treat each level of a class variable as an independent effect using the 'split' statement. PROC MIXED adjusts for an unbalanced design, accounts for heterogeneous variance, and is relatively robust to small departures from normality. Analysis results were examined for significant interactions when necessary and appropriate *post-hoc* tests applied.

All size and weight data were $\log_{10}$-transformed with the exception of the national comparison of fecundity where E and TT (cm) were ln-transformed to conform to Prager et al. (1990). All statistical effects were considered significant at $\alpha = 0.05$. As the aggregate catch data we used from previously published literature were untransformed before the published means were computed, with the possible partial exception of Eggleston et al. (North Carolina State University, unpubl. data), we did not transform our catch data. Specific details for individual tests are provided in the descriptions of analyses that follow.

NATIONAL COMPARISON OF CONDITION FACTOR.—The condition factor is the ratio of a fish's weight W to a linear estimate (X) of its volume V. It is normally used to compare differing populations under the assumption that the heavier fish (per unit of volume) are healthier (e.g. Ricker, 1975). When W and X are measured over a range of sizes in at least two different populations, differences in the condition factor are normally tested using a linear form of the general size/weight relationship:

$$\log W = \log a + b * \log X. \qquad \text{(Eq 1)}$$

When raw data are available, an ANCOVA may be used to test differences between populations. When, as with blue crabs, only population-specific equations are available from the literature one can examine plots of the intercepts (log a) against the respective slopes (b) for apparent conformity to, or deviation from, a single relationship which would apply for a homogenous population,

$$\log a = a' + b' * b \qquad \text{(Eq 2)}$$

where log a and b are as in Eq 1, and *a'* and *b'* are constants.

With blue crabs, it is the convention when fitting Eq 1 to eliminate ovigerous females and use TT as a measure of X (e.g. Olmi and Bishop, 1983). Therefore, to compare the condition factor of STTSC crabs with those from nationally recognized spawning grounds we used our measures of W and TT for non-ovigerous STTSC blue crabs in Eq 1 and then employed the intercept and slope of the resulting 'STTSC' equation in Eq 2 to compare these parameters with those reported in the literature for other spawning areas where wet weights were used (i.e., Newcombe et al., 1949; Pullen and Trent, 1970; Olmi and Bishop, 1983; Rothschild et al., 1992; modified from Perry in Guillory et al., 2001; and Lipcius and Stockhausen, 2002).

NATIONAL COMPARISON OF FECUNDITY.—To compare egg abundance E from our area and Chesapeake Bay we manually extracted the 1986 data from Prager et al.'s Fig. 3. These data represent the time period before recent declines in blue crab fecundity (Lipcius and Stockhausen, 2002). In an ANCOVA we regressed E versus TT, with area as a class variable.

NATIONAL COMPARISON OF SPAWNING GROUNDS.—Fishery independent catch rates of mature female blue crabs in areas recognized as blue crab spawning grounds were reported by More (1969) for Galveston Bay, TX; Adkins (1972) for Terrebonne Bay, LA; Archambault et al. (1990) for Charleston Harbor, SC; Lipcius and Stockhausen (2002) for Chesapeake Bay, VA; and Eggleston et al. (North Carolina State University, unpubl. data) for Pamlico Sound, NC. Size and duration of the trawling efforts varied across these studies, as did number of areas sampled, duration and timing of study, and temporal aggregation of the published data. Most of the published studies represent at least two years of sampling and report data in monthly averages by area. Lipcius and Stockhausen (2002) divided their catches into two time periods (t) based on abundance: high, pre-1992 (t_1) and low, post-1991 (t_2). No study statistically compared catch rates among years with different times and trawl dimensions with another study.

To compare catch rates we calculated the area and trawl width specific average untransformed peak monthly catch rates (PC) of mature female blue crabs and adjusted it for 30 min trawls for each of the above studies and for our study. Using ANCOVA we regressed PC versus trawl width (TW) and included Lipcius and Stockhausen's division of time as a class variable.

CONTINUOUS SPAWNING / HATCHING CYCLE.—To estimate the recovery time for an ovary between successive sponge productions, we regressed the average ovarian condition of ovigerous females per sponge color against the respective embryo age in days (d, where d = 0 at spawning) assuming that each successive sponge color represented three days of embryo development time (based on Jivoff et al., 2007). Then using the resulting regression equation, an average ovarian condition value for inter-brood females was predicted.

BEST MORPHOMETRIC INDICATOR OF WEIGHT.—To find the best morphometric model, we first examined the relationship between crab weight W and four measurements of size: carapace width including TT, and excluding BB, the lateral spines; length L; and height H. Then we used the best indicator of carapace width along with the measurements of L and H to calculate an estimated volume V for each crab. Five ANCOVAs were run testing the relationship of these morphological variables and W with sponge present/absent as a class variable.

EFFECTS OF SYMBIONTS, OVARIAN/EMBRYONIC DEVELOPMENT, MONTH, AND AREA ON WEIGHT.—The variables included in the GLMSELECT procedure were estimated volume V, sponge presence/absence P, sponge color SC, ovarian development O, gill nemertean intensity GN, sponge nemertean intensity SN, gill barnacle intensity G, acorn barnacle weight BW, percent coverage of acorn barnacles BC, acorn barnacle diameter D, month (M), and area (A). A split statement was used to treat each level of month and area as an independent effect.

To test for an effect of M on weight of the abdomen AW with eggs, we ran an ANCOVA in which we regressed AW on V with M as a class variable. The data limited us to a consideration of ovigerous crabs with well developed embryos (sponge color > 3).

To test for an effect of embryonic development on the abdominal weight of the ovigerous crabs, we ran an ANCOVA in which we regressed AW on V with SC as a class variable.

STTSC SPACIO-TEMPORAL PATTERNS OF ABUNDANCE.—We used PROC MIXED in an ANOVA to test for the effects of month (April, August, and October) and area (Ship, Trinity, Tiger, inshore, and offshore in Fig. 1) on blue crab abundance (crabs / 30 min. trawl) for 2007. Interactions were examined and *post-hoc* pairwise comparisons were made using a Tukey-Kramer adjustment.

RESULTS

GENERAL DESCRIPTION.—During three years of seasonal sampling, 505 blue crabs were caught within the STTSC (Table 2). Overall, 99% were mature females of which 49% were ovigerous. Sponge colors of ovigerous crabs indicated an approximately equal distribution of embryonic developmental stages from spawning to hatching with a slightly higher percentage possessing late stage eggs (Fig. 2A). Most of the non-ovigerous crabs possessed a large ovary (Fig. 2B) and showed evidence of a previous spawn in the form of hatched egg casings on their abdominal hairs (Fig. 2C). In addition, more than 25% of ovigerous females with late stage eggs also had a large ovary. One soft-shelled female was newly mated as evidenced by an enlarged and hardened spermathecae, and two hard-shelled females had recently mated as evidenced by an enlarged but softening spermathecae corresponding to Wolcott et al. (2005) scale's 1 and 2 respectively. The most common symbionts and their relative frequencies of occurrence were acorn barnacles *C. patula* and *Balanus* spp., 63%; gooseneck barnacles *O. muelleri*, 63%; nemerteans *C.carcinophila* on the gills, 24%, and nemerteans in sponges, 34%.

ENVIRONMENTAL MEASUREMENTS.—No seasonal trend was observed for salinity variation within the STTSC for 2007 (Table 3). Salinity ranged from 25.4 to 34.8 and was generally lower for the stations closer to shore (e.g. inshore and Tiger Shoal) during all sampling cruises. There was a seasonal trend observed for temperature: the lowest recorded April temperature was 20.4°C followed by a peak of 31.4°C in August, and a decrease to a low of 27.6°C in October. There was also a seasonal trend for dissolved oxygen. Highest dissolved oxygen values were recorded in April and October with lowest

values for all areas recorded in August. Bottom water oxygen values below 2 mg/L (i.e., hypoxia) occurred only at deeper offshore trawling locations in August 2007. No hypoxic bottom water was found at stations shallower than 8 m. We observed one hypoxic reading at our deepest Ship Shoal station (no trawl), though shallower Ship Shoal stations remained free of hypoxia consistent with other shoal stations.

NATIONAL COMPARISON OF CONDITION FACTOR.—The transformed STTSC data for non-ovigerous females provided the following significant fit to the linear form of the general size/weight relationship (Eq 1):

$$\log W = -3.0743 + 2.3966 * \log TT \qquad \text{(Eq 3)}$$

($P < 0.0001$, $R^2 = 0.80$). Use of all the available and comparable estimates of the constants log a and b in Eq 2 generated a single significant regression of the form:

$$\log a = 1.9066 - 2.0603 * b \qquad \text{(Eq 4)}$$

($P < 0.0001$, $R^2 = 0.99$, Fig. 3). The condition factor comparison (Eq 4 and Fig. 3) suggests a single width-weight relationship applies to all female blue crab populations reported in the literature despite wide geographical and temporal differences (Chesapeake Bay to Texas coasts, 1966-2007).

NATIONAL COMPARISON OF FECUNDITY.—The ANCOVA comparing the fecundity of Chesapeake Bay and STTSC crabs found no significant interaction or class effect and generated the following single significant equation:

$$\ln E = -4.8453 + 2.1151 * \ln TT \qquad \text{(Eq 5)}$$

($P < 0.0001$, $R^2 = 0.31$, Fig. 4). Eq 5 predicts a linear increase in E with increasing TT and finds no significant difference in the E versus TT relationship of ovigerous blue crabs from the two areas/time periods.

NATIONAL COMPARISON OF SPAWNING GROUNDS.—In the ANCOVA run to compare abundance across known spawning grounds, the class variable t was significant ($P = 0.0073$), but not TW ($P = 0.8058$). The mean observed PCs for t_1 and t_2 were 35.5 and 8.3 crabs/30 min trawl respectively, representing a 76% decline in the mean peak monthly catch rates between these two time periods. As such, peak monthly catch rates for all areas within the STTSC are comparable to other known spawning grounds within the current time period (t_2, Table 4).

CONTINUOUS SPAWNING / HATCHING CYCLE.—The regression of O versus d was significant,

$$O = 0.9908 + 0.0971 * d \qquad \text{(Eq 5)}$$

($P = 0.0023$, $R^2 = 0.97$), and predicts that the ovary of non-ovigerous crabs will fully recover (O = 3) 21 days after hatching. At the midpoint of the predicted inter-brood period (18 d) the predicted ovarian condition, O = 2.74, is remarkably similar to the observed average ovarian condition of non-ovigerous STTSC crabs where O = 2.73 (Fig 5). This suggests a linear increase in ovarian development between successive spawns of STTSC crabs and that the STTSC crabs were in a continuous cycle of spawning, hatching, and ovarian replenishment from April through October.

BEST MORPHOMETRIC INDICATOR OF WEIGHT.—In the comparison of estimators of weight derived from linear measurements, the volumetric estimator, V = L * H * BB, provided a slightly better predictor of W ($R^2 = 0.966$) than all single linear measurements (Table 5). Of the single linear estimators, L was the

best estimator of W ($R^2 = 0.961$), though it was followed closely by BB and H. The traditionally used TT was the poorest estimator ($R^2 = 0.806$).

EFFECTS OF SYMBIONTS, OVARIAN/EMBRYONIC DEVELOPMENT, MONTH, AND AREA ON WEIGHT.—The stepwise procedure chose V, P, O, $M_{(August)}$, and GN as the most predictive combination of variables:

$$\log W = -3.0894 + 0.9743 * \log V + 0.0960 * P + 0.0104 * O + 0.0081 * GN - 0.0105 * M_{(August)} \quad \text{(Eq 6)}$$

($P < 0.0001$, $R^2 = 0.9715$). However, a more parsimonious model included only V and P,

$$\log W = -3.2462 + 1.0085 * \log V + 0.0838 * P \quad \text{(Eq 7)}$$

($P < 0.0001$, $R^2 = 0.9654$) with a slight 0.006 decrease in R^2.

Eq 6 predicted the weight of a crab where P and GN = 0, M = 8, O = 3, and V = 229.6 cm^3 was 142.8 g. For this case, when O = 1, predicted weight declined by 4.7%; when GN = 1, predicted weight increased by 1.9%; and when M = April, May, and October, predicted weight increased by 2.4%.

The ANCOVA run using abdominal weights with black/brown sponges found a significant main effect of month on the relationship between V and AW, but no significant interaction of M and AW. The resulting equation,

$$\log AW = a + 0.7151 * \log V,$$

where a = -0.0159 for April,
= -0.0522 for May,
= -0.0815 for August, and

= -0.0907 for October (Eq 8)

($P < 0.0001$, $R^2 = 0.61$) suggests that the observed weight of black/brown sponges for a given length interval of STTSC crabs declined from April to October (Fig. 6).

The analysis of an effect of embryo development as evidenced by sponge color SC on the relationship between V and AW found a significant relationship,

$$\log AW = a + 0.7802 * \log V,$$

where a = -0.2748 when SC = 1,

= -0.2678 when SC = 2,

= -0.2479 when SC = 3,

= -0.2158 when SC = 4, and

= -0.2301 when SC = 5 (Eq 9)

($P < 0.0001$, $R^2 = 0.60$), which indicates an approximate 10% increase in wet weight from stage 1 to stage 5, and suggests a fairly sudden increase in the wet weight of the sponge as SC increases above 2 (Fig. 7).

STTSC SPACIO-TEMPORAL PATTERNS OF ABUNDANCE.—The ANOVA found a significant area effect ($F_{4,36} = 5.57$, $P < 0.01$) and month effect ($F_{2,36} = 10.71$, $P < 0.01$) as well as a significant area by month interaction ($F_{8,36} = 2.62$, $P = 0.02$) on female blue crab abundance in the STTSC for 2007. Pairwise comparisons found that mean area catch rates for Ship and Trinity Shoals in August were significantly greater than those from the STTSC offshore area and Tiger Shoal for all months (Fig. 8; Tukey-Kramer; $P < 0.05$). In addition, Ship Shoal had significantly greater mean area catch rates across all months than the STTSC offshore area and Tiger Shoal, while Trinity Shoal had significantly greater mean area catch

rates across all months than Tiger Shoal (Tukey-Kramer; $P < 0.05$). Mean monthly catch rates across all areas were significantly higher in August than April and October (Tukey-Kramer; $P < 0.01$).

DISCUSSION

All of our statistical tests support the argument that STTSC female blue crabs compare favorably to those from other recognized spawning grounds in terms of condition factor (Fig.3), fecundity (Fig. 4) and abundance (Table 4). Actively spawning, hatching, and foraging blue crabs were present from at least April through October within the STTSC with highest abundances occurring in August on Ship and Trinity Shoals (Fig. 8). These results strongly suggest that Ship Shoal and Trinity Shoal, within the STTSC, are locally important, though unprotected, offshore blue crab spawning, hatching, and foraging grounds which may have national significance for the blue crab fishery.

Blue crab catch rates for STTSC inshore areas were highest during April and August but declined in October toward the end of the spawning season. STTSC offshore areas had their highest catch rates in August and October suggesting an increased utilization of the offshore later in the spawning season while high concentrations were sampled on Ship and Trinity Shoals throughout the spawning season. These patterns may reflect a continued seaward migration to the offshore region including Ship and Trinity Shoals. A continued seaward migration of our ovigerous female blue crabs is consistent with behavioral experiments and field observations in Bogue Sound, North Carolina (Hench et al., 2004), where the authors found that females with late-stage eggs and post-release females used ebb-tide-transport and suggested that crabs may continue a seaward migration to release subsequent clutches.

Based on our analysis of ovarian replenishment (Fig. 5), STTSC blue crabs are capable of producing at least seven sponges in a spawning season. This is consistent with the *in situ* findings of Hines et al. (2003) and Dickenson et al. (2006) that documented the production of up to seven broods by mature female crabs in Indian River Lagoon, Florida, and Beaufort, North Carolina, respectively. In these studies female blue crabs were fed daily, which suggests that a consistent food source such as that found on Ship and Trinity Shoals (Dubois et al., in press) is beneficial to sustain successive brood production. There was no significant difference in egg abundance between STTSC crabs and those from Chesapeake Bay (Fig. 4) using data from that area before recent declines in abundance of spawning females. There was also a 20% decrease in the sponge wet weight (for at least females with broods close to hatching) from April to October for STTSC crabs (Fig. 6). This may be due to the seasonal decrease in macrofaunal prey as was noted by Dubois et al. in press for Ship Shoal in 2006 and a subsequent reduction in available energy for egg production or to some effect of age of the female (i.e., Dickenson et al., 2006), a decline in the number of viable sperm in subsequent fertilization events (i.e., Hines et al., 2003), or changes in environmental gradients (i.e., Jivoff et al., 2007).

We speculate that abundant prey resources for crabs contribute to high crab abundance on Ship and Trinity Shoals as we have found 2007 STTSC macroinfaunal biomass higher on the shoals than off the shoals (C. Gelpi, Louisiana State University, unpubl. data). In turn, macroinfaunal biomass on Ship Shoal may be more dependent upon benthic microalgae than phytoplankton, while the inverse may be true for Trinity and Tiger Shoal's macroinfauna (M. Grippo, Louisiana State University, unpubl. data). Seitz et al. (2003) found blue crab and bivalve *Macoma balthica* (Linnaeus, 1758) densities were positively correlated on sandy substrate within the York River of Lower Chesapeake Bay. In 2006, macrofaunal biomass declined on Ship Shoal (Dubois et al., in press) concurrent to the influx of

spawning blue crabs, which is consistent with blue crab predator/prey responses in the Chesapeake Bay (Hines et al., 1990; Eggleston et al., 1992). Tiger Shoal catch rates were lower than those on Ship or Trinity Shoals and possibly an artifact of lower sampling frequency or suggestive of differences in environmental quality, fishing pressure, predation pressure, or recruitment rates that may exist among shoals. More study is needed to determine if such differences among shoals exist.

STTSC's high-relief shoals may provide other ecological services that enhance blue crab fitness. Principally, shoals may also be acting as hypoxia refuges. They are located within an area of seasonal bottom-water hypoxia (Rabalais et al., 2002). Bottom water on the Shoals was not hypoxic (i.e. DO < 2 mg/L) during our cruises with the exception of the deepest shoal station during the August 2007 sampling when many of the deeper off-shoal stations were also hypoxic. It is possible that blue crabs avoid local low oxygen conditions by seeking refuge on the shoals. This observation would be consistent with Pihl et al. (1991) who concluded that blue crabs were "shown to migrate from deeper hypoxic to shallower normoxic areas in Chesapeake Bay."

In higher latitude estuaries around Chesapeake Bay female blue crabs are known to concentrate in polyhaline areas before brood production, while "at lower latitudes, mature and ovigerous females also aggregate in high salinity zones" (Hines, 2007). Salinity ranged from 23.8 to 36.3 for our trawl areas within the STTSC, though the salinity in areas further from shore (e.g. Ship, Trinity, offshore) was generally higher (Table 3). The offshore location of the shoals may benefit blue crab larvae compared with larval release locations in lower estuarine areas or those offshore areas close to the shore. High salinities, like those on the shoals, are necessary to prevent osmotic stress (Sandoz and Rogers, 1944). Larval mortality may be reduced in offshore waters through avoidance of estuarine predators (Morgan,

1990). The offshore location of the shoals may provide a broader dispersal range thus reducing density-dependent mortality (Eggleston et al. 1992), decreasing the likelihood of passive transport into the estuary before the zoeal larval stages are completed, and benefiting the genetic diversity of a northern Gulf metapopulation. Cochrane and Kelly (1986) and Walker et al. (2005) describe a westward coastal current off central/western Louisiana and eastward return flow along this portion of the Louisiana shelf. This should move larvae west along the coast yet retain them on the Louisiana-Texas shelf (Cowan et al., 2008). Perry et al. (2003) found wind patterns in the northern Gulf of Mexico aid in recruitment by returning megalope to the nearshore within the Mississippi Bight. Thus, previous studies suggest that blue crab larvae hatched in STTSC also have access to coastal marshes and that juveniles will enter the marsh populations.

With the possible exception of Perry (1975), blue crab mating is reported to occur in the lower salinity waters of upper estuaries. Although rare in our sampling, we found evidence of blue crabs mating on Trinity and Ship Shoals suggesting that mating pairs are not strictly confined to the upper estuary. This finding suggests blue crab populations have the potential to successfully mate in the open ocean; a potential which could conceivably prove advantageous given the current threat of estuarine habitat loss exacerbated by sea-level increases associated with global climate change.

MANAGEMENT IMPLICATIONS.—Accurately predicting blue crab weight from a linear measure of crab size is an important tool in assessing blue crab stocks and health. Most previous blue crab studies incorporating size measured carapace width including the lateral spines TT. However the lateral spines introduce variability due to broken tips and differences in spine morphology (Olmi and Bishop, 1983). The finding that estimated volume (V = L * H * BB) is the best predictor of crab weight (Table 5) has

implications for future research in the blue crab fishery and the fisheries of other heavily exploited swimming crab species such as *Portunus trituberculatus* (Miers, 1876) and *P. pelagicus* (Linnaeus, 1758). Measurement of V, although slightly more time consuming, is a much better predictor than TT and may be more forgiving of small measurement errors than any one of the single linear estimators of which it is composed. We suggest future studies phase out the use of TT and replace it with V. In addition, we encourage the measurement of crab weight and volume for ovigerous as well as non-ovigerous crabs.

Ship and Trinity Shoals potentially support an important component of the Gulf of Mexico spawning stock. Ship and Trinity Shoals' blue crab spawning grounds have a combined area of ~1000 km^2, none of which is protected. By comparison, the historical blue crab spawning sanctuary in lower Chesapeake Bay apparently encompassed ~775 km^2 (Fig. 1 in Lipcius et al., 2003). Amid decreasing spawning stocks, this protected area has since been expanded to include a migration corridor of post-mated females (Lipcius et al., 2003). North Carolina has established five Pamlico Sound spawning sanctuaries which total ~120 km^2. Eggleston et al. (North Carolina State University, unpubl. data) present evidence that these "spawning sanctuaries are too small to protect the spawning stock in North Carolina".

Presently, there does not appear to be a directed fishery currently operating on female blue crabs within the STTSC. The current social norm in Louisiana, Gulf of Mexico, and the nation seems to favor a protection of ovigerous females. In contrast, there is a national/international market for non-ovigerous female blue crabs with 'full ovaries', a condition characteristic of at least our 'sponge color = 6' females, (Fig. 5). The current lack of a directed fishery on the reproductively active STTSC crabs,

particularly on Ship and Trinity Shoals, likely enhances the stability of Louisiana and the Gulf's traditional inshore blue crab fishery. A conservative management would help maintain the stability of the current inshore blue crab fishery by protecting Ship and Trinity Shoals, as well as all other STTSC blue crabs, from a directed harvest of STTSC blue crabs until their contribution to the health of the current inshore fishery can be assessed.

There is an increasing need to understand the potential impact of sand and gravel mining in coastal-ocean systems to aid in policy decisions. Few ecological studies have examined the functional value of high-relief sandy shoals in their ecosystems, especially in terms of biodiversity and associated ecological services. Within our study area, sand mining may have negative impacts on spawning blue crabs given the possibility that fecundity of blue crabs on Ship Shoal becomes seasonally limited by prey abundance (Dubois et al., in press) under prevailing natural conditions. Palmer et al. (2008) reported significant sand-mining related declines in macrofaunal abundance, biomass, and diversity within coastal Louisiana. It is likely that sand-mining disturbance and subsequent reduction in available macrofauna prey would result in negative effects on spawning blue crab health and fecundity. Sand mining may also alter the sediment composition from that preferred by STTSC females. Schaffner and Diaz (1988) found that over-wintering females in the Lower Chesapeake spawning grounds preferred certain sediment types with high concentrations of sand. Other studies (Ryan, 1967b; Kuris, 1991) have suggested that sediment is necessary for the successful spawning and egg adherence to the hairs of the pleopods. In addition, the threat of hypoxia would increase if the depth on the shoals were increased to a point where wave action could no longer keep the bottom water well oxygenated (Kobashi et al., 2007).

Management should act now to create a blue crab spawning sanctuary in the STTSC. National efforts to restore the Chesapeake Bay and North Carolina populations have found no inexpensive "quick fixes". For example, Chesapeake Bay stock enhancement scientists "expect the production cost of blue crab juveniles will be in the range of US $0.15 – 0.30/juvenile" and that there will be a "10% survival of cultured females until spawning in the sanctuary" (Zohar et al., 2008). Under this scenario, the production costs associated with the arrival of mature female blue crabs from a hatchery to the STTSC spawning grounds would be $18 to $36/dozen, or approximately the current retail price of blue crabs in the Louisiana market. In light of the blue crab crisis on the east coast and the extensive efforts under way to restore the east coast spawning stock, it makes financial and ecological sense to protect these natural, though previously unknown, blue crab spawning, hatching, and foraging areas in the offshore federal waters of the STTSC.

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Figure legends

Figure 1. Ship, Trinity, Tiger Shoal Complex (STTSC) and trawl station locations for 2005-07. Areas within the STTSC are divided into five groups (see legend). Ship, Trinity, and Tiger Shoals are partly outlined by the 8 m contour associated with each shoal (based on Braud, 1999).

Figure 2. Percentages of: (A) different sponge colors (stage 1 to stage 5) for ovigerous STTSC blue crabs 2006-2007, (B) non-ovigerous females with and without a full ovary, (C) non-ovigerous females with and without evidence of a previous spawn (hatched egg casings on abdominal hairs).

Figure 3. Results of an ANCOVA demonstrating the conformity of all published carapace width (TT, mm) – weight (W, g wet wt) relationships of non-ovigerous female blue crabs, logW = log a + b * logTT, where TT = carapace width including the lateral spines.

Figure 4. Results of ANCOVA comparing egg abundance in millions (E) vs. carapace width (TT, cm) including the lateral spines for mature female blue crabs from the Chesapeake Bay, VA (Prager et al., 1990) and Ship Shoal, LA, 2006.

Figure 5. Average ovarian development (O) for mature female blue crabs vs. estimated embryo development time in days, based on respective sequential egg color as follows: orange, dark orange, light brown, dark brown, and black. The regression was fit to our data for ovigerous crabs and then used to predict a time for the recovery implicit in the average ovarian condition of non-ovigerous crabs.

Figure 6. Results of ANCOVA testing the effect of month (M) on the logarithmic relationship between abdomen-sponge weight (AW) of ovigerous crabs with well developed embryos and estimated volume (V). Lines fit to the data are the solution to: logAW = a + 0.7151 * logV; where a = -0.0159 for April, -0.0522 for May 5, -0.0815 for August, and -0.0907 for October ($P < 0.0001$, $R^2 = 0.61$). V is estimated as L * H * BB; where L = length, H = height, and BB = carapace width excluding lateral spines.

Figure 7. Results of ANCOVA testing the effect of the embryo development stage on the relationship between abdomen-sponge weight (AW) of ovigerous crabs and estimated volume (V). Lines fit to the

data are the solution to logT = a + 0.7802 * logV, where a = -0.2748 when SC = 1, -0.2678 when SC = 2, -0.2479 when SC = 3, -0.2158 when SC = 4, and -0.2301 when SC = 5 ($P < 0.0001$, $R^2=0.60$). V is estimated as L * H * BB; where L = length, H = height, and BB = carapace width excluding lateral spines.

Figure 8. Comparison of mean monthly catch rates of mature female blue crabs in the Ship, Trinity, Tiger Shoal Complex, April-October 2007.

Table. 1 Definitions of variable abbreviations. All weights are in gm; all linear measurements, in cm.

WHOLE CRAB MEASUREMENTS	
BB	carapace width between the bases of the lateral spines
H	carapace height
L	carapace length
TT	carapace width between the tips of the lateral spines
V	crab volume (L * BB * H)
W	crab weight without acorn barnacles, (*Chelonibia patula*, *Balanus* spp.)
REPRODUCTION	
AW	weight of the abdomen
d	average age (days) of the embryos in a sponge
E	number of eggs (in millions) in a crab sponge
O	fullness of the ovary (ranked from 1 to 3 as inconspicuous, intermediate, or large)
P	presence/absence of a sponge
SC	sponge color (bright orange = 1, dark orange = 2, brown = 3, dark brown = 4, black = 5, and no sponge = 6)
SYMBIONTS	
BC	acorn barnacle (*Chelonibia patula*, *Balanus* spp.) coverage of the exoskeleton (10% intervals)
BW	weight of acorn barnacles (*Chelonibia patula*, *Balanus* spp.) removed from the exoskeleton
D	diameter of the largest acorn barnacle (*Chelonibia patula*, *Balanus* spp.) on the exoskeleton
G	gooseneck barnacle (*Octolasmis muelleri*) intensity on the gills (based on a six point scale approximating 0, 10, 25, 50, 100, or more than 200)
GN	nemertean (*Carcinonemertes carcinophila*, presence/absence) on the gills; gill nemerteans
SN	nemertean abundance(*Carcinonemertes carcinophila*) on a sponge (measured within a 1.6 cm diameter subsection and ranked from 0 to 3 as 0, 1-3, 4-6, or > 7 individuals)
OTHER VARIABLES	
A	area (Ship, Trinity, Tiger, inshore, offshore)
M	month (April, May, August, October)
PC	average peak monthly catch rate of mature female blue crabs (n/mo-30 min)
t	time (t_1 = 1988-91 and t_2 = 1992-2000)
TW	trawl width (m)

Table. 2 Total number of female blue crabs sampled on Ship Shoal during 2005-06 and within the Ship, Trinity, Tiger Shoal Complex during 2007 as well as the percentage of the total that were ovigerous for 2006-2007.

	2005	2006		2007	
	number	number	% ovigerous	number	% ovigerous
Ship	98	178	53	101	35
Trinity	-	-	-	72	46
inshore	-	-	-	31	68
offshore	-	-	-	15	67
Tiger	-	-	-	8	75

Table 3. Salinity (sal), temperature (temp), and dissolved oxygen (DO) readings [mean (range)] for 2007 trawl stations by area and month.

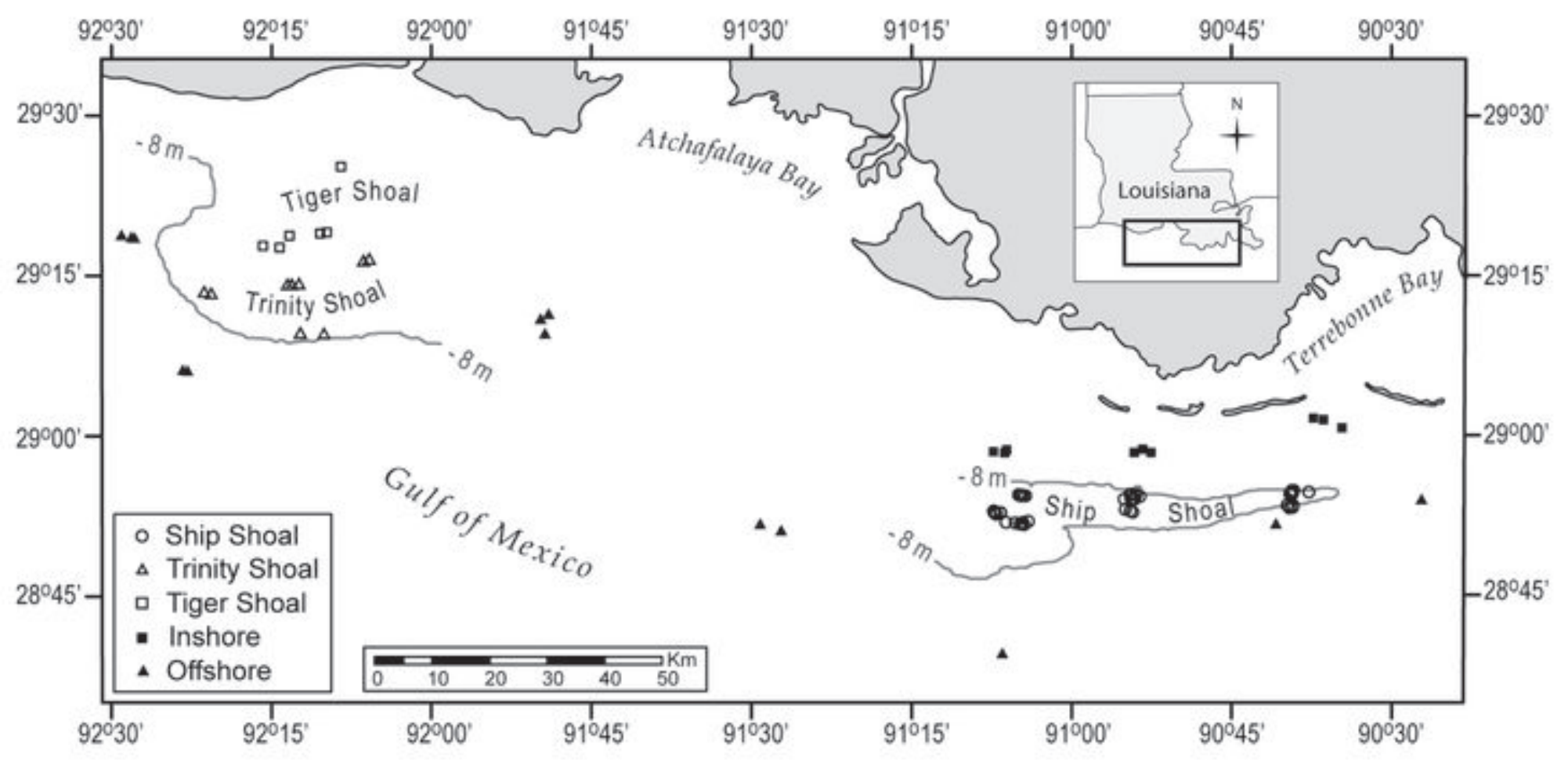
		Ship	Trinity	Tiger	inshore	offshore
Sal (ppt)	April	32.6 (27.2 - 35.4)	29.8 (27.8 - 32.5)	26.5 (24.1 - 28.3)	27.4 (25.4 - 29.5)	34.8 (33.3 - 36.3)
	Aug	27 (25.3 - 29.1)	29.5 (28.9 - 29.9)	28.1 (27.7 - 28.6)	25.4 (23.8 - 26.8)	33.3 (30.1 - 36.1)
	Oct	31.4 (30.1 - 33.3)	31.1 (31 - 31.1)	30.4 (30.4)	29.6 (29 - 30.1)	30.2 (30.1 - 30.2)
Temp (°C)	April	22.2 (21.6 - 22.8)	22.9 (22.1 - 23.4)	23.3 (23.1 - 23.5)	22.2 (22.1 - 22.3)	21.4 (20.4 - 22.1)
	Aug	30.8 (30.6 - 31.1)	31 (30.7 - 31.3)	30.9 (30.8 - 30.9)	31.1 (30.9 - 31.4)	29.3 (27.5 - 31.2)
	Oct	28.1 (28.1 - 28.2)	27.8 (27.8)	27.6 (27.6)	27.9 (27.8 - 27.9)	27.9 (27.7 – 28)
DO (mg/L)	April	6.8 (5.5 - 7.7)	7.1 (6.7 - 7.7)	7.1 (7.0 - 7.4)	4.3 (3.6 – 5)	5.5 (2.5 - 6.9)
	Aug	4.1 (2.9 - 5.2)	4.7 (4.4 - 5.2)	4.5 (4.4 - 4.5)	4.4 (2.3 - 5.6)	3.7 (0.5 - 5.5)
	Oct	5.9 (5.6 – 6)	6.4 (6.3 - 6.4	6.2 (6.2)	5.8 (5.6 – 6)	6.1 (5.9 - 6.3)

Table 4. Listing of the trawl width (TW) and peak catch rates (PC) of mature female blue crabs (adjusted for 30 minutes of trawl time) for studies of blue crab spawning grounds.

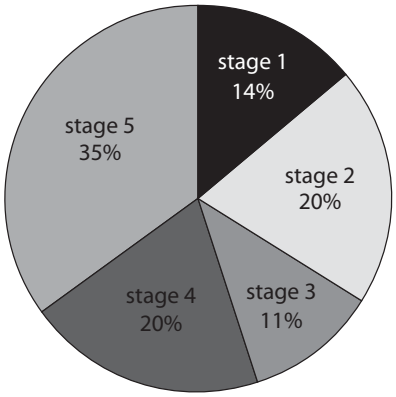
Author	TW (m)	Years of study	Area of study	PC
More (1969)	3	1966-1977	Galveston Bay, TX	44
			surf zone off Galveston Bay, TX	46
Adkins (1972)	4.9	1969-1972	lower Terrebonne Bay, LA	31.5
			mid Terrebonne Bay, LA	30.0
Archambault et al., (1990)	6	1979-1987	Charleston Harbor, SC	15.7
Lipcius and Stockhausen (2002)	9.1	1988-1991	Chesapeake Bay, VA	45.8
		1992-2000		8.8
Eggleston et al., (unpublished data)	6.7	2002	Pamlico Sound, NC	4.8
Present study	7.3	2005-2006	Ship Shoal	13
	12.8	2007		15.3
			Trinity Shoal	15
			Inshore STTSC	6
			Offshore STTSC	2
			Tiger Shoal	1.7

Table 5. Comparison of size (X) vs. weight (W) relationships, logW = loga + b(logX), for mature female blue crabs from the Ship, Trinity, Tiger Shoal Complex. Length equals L; height, H; carapace width including lateral spines, TT; carapace width excluding lateral spines, BB. Solutions are results of ANCOVAs testing the effect of ovigery, where X is varied as in column one. Base equation are for ovigerous females. Weights of the non-ovigerous females are obtained by adding c to log(a) and d to b (where a and b are the intercept and slope for ovigerous crabs and c and d are the adjustments for non-ovigerous crabs). When d = 0, the ANCOVA's interaction term was not significant and the equations reflect parallel slopes.

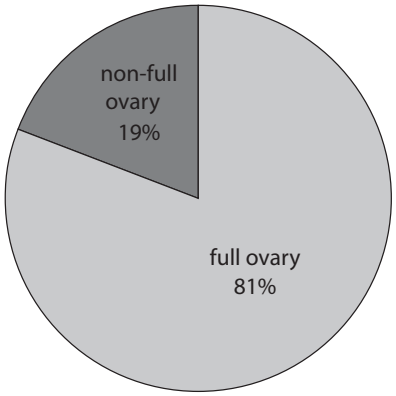
X estimator	R^2	log(a)	b	c	d
L	0.961	-2.8452	2.8651	-0.5165	0.2424
H	0.925	-1.977	2.7446	-0.4573	0.2445
BB	0.942	-3.7103	2.9111	-0.0887	0
TT	0.806	-2.3349	2.1025	-0.7394	0.2942
L*H*BB	0.966	-2.9455	0.9682	-0.4627	0.0706


92°30'
92°15'
92°00'
91°45'
91°30'
91°15'
91°00'
90°45'
90°30'
29°30'
29°15'
29°00'
28°45'
-8 m
Tiger Shoal
Trinity Shoal
-8 m
Atchafalaya Bay
Louisiana
N
Terrebonne Bay
-8 m
Ship Shoal
-8 m
Gulf of Mexico
Ship Shoal
Trinity Shoal
Tiger Shoal
Inshore
Offshore
0 10 20 30 40 50 Km

A


stage 1
14%
stage 2
20%
stage 3
11%
stage 4
20%
stage 5
35%

B


non-full
ovary
19%
full ovary
81%

C

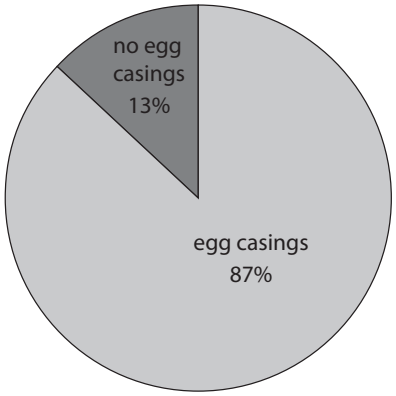

no egg
casings
13%
egg casings
87%

Fig. 3

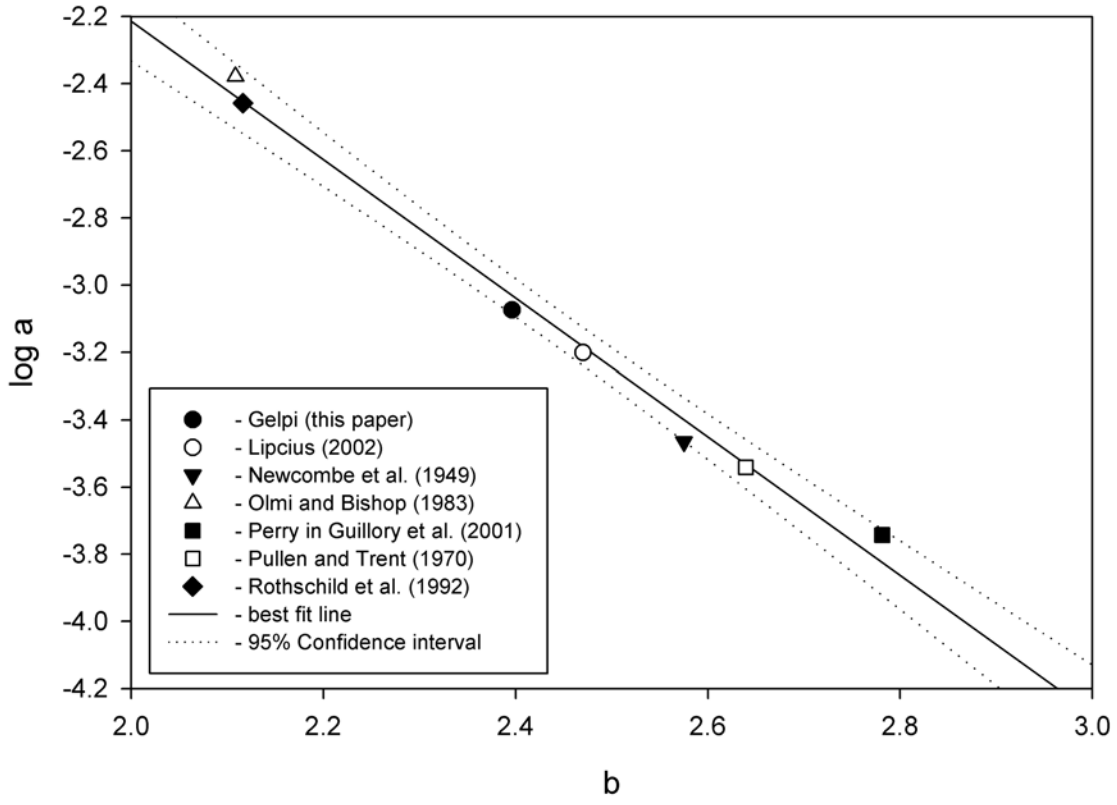

log a
b
-2.2
-2.4
-2.6
-2.8
-3.0
-3.2
-3.4
-3.6
-3.8
-4.0
-4.2
2.0
2.2
2.4
2.6
2.8
3.0
- Gelpi (this paper)
- Lipcius (2002)
- Newcombe et al. (1949)
- Olmi and Bishop (1983)
- Perry in Guillory et al. (2001)
- Pullen and Trent (1970)
- Rothschild et al. (1992)
- best fit line
- 95% Confidence interval

Fig. 4

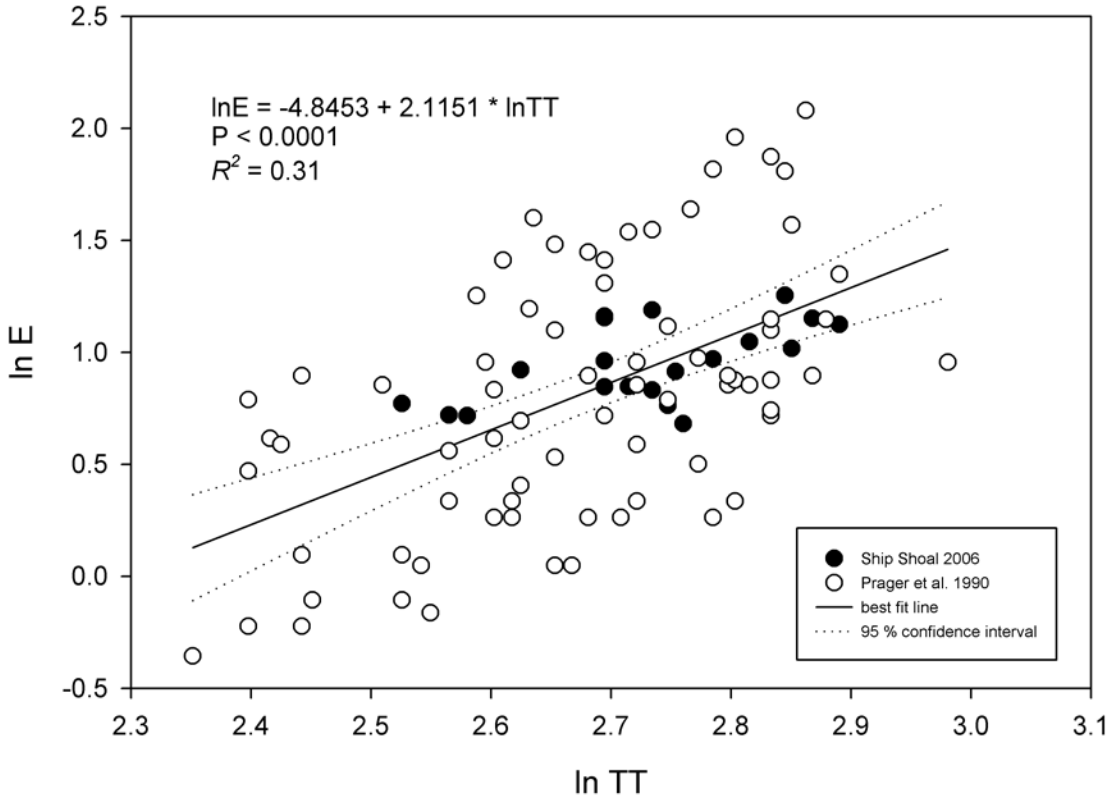

lnE = -4.8453 + 2.1151 * lnTT
P < 0.0001
R^2 = 0.31
Ship Shoal 2006
Prager et al. 1990
best fit line
95 % confidence interval
ln E
ln TT
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
2.3
2.4
2.5
2.6
2.7
2.8
2.9
3.0
3.1

Fig. 5

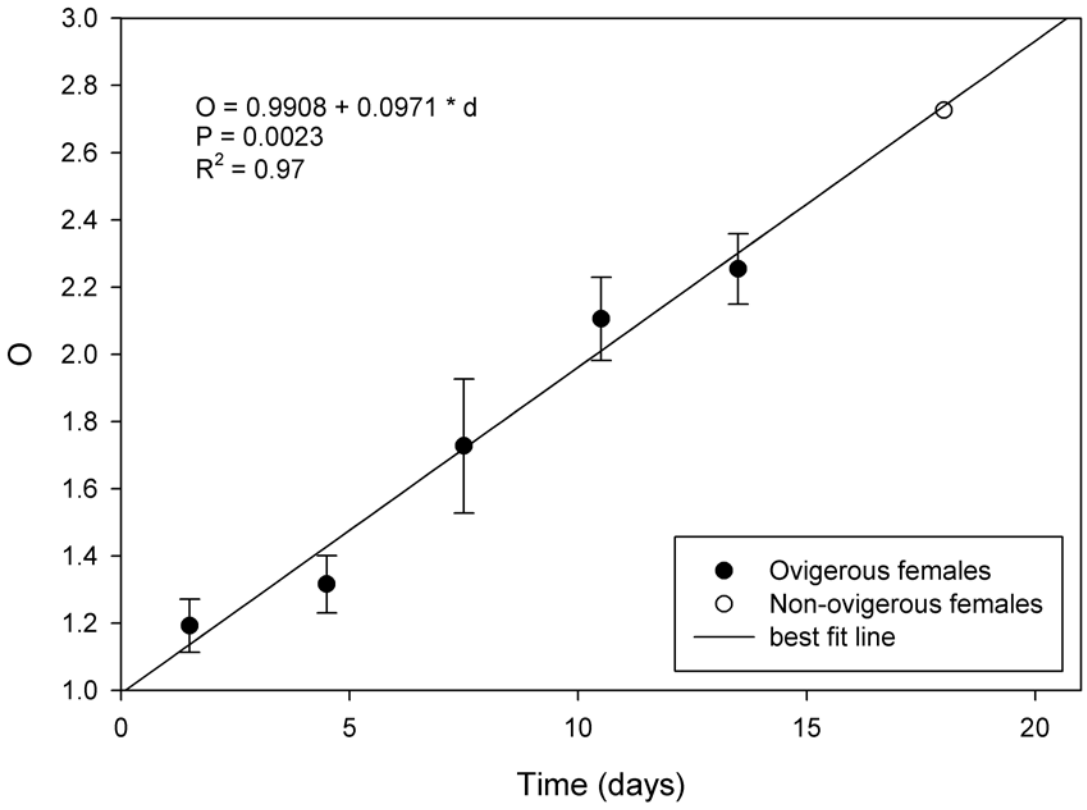

O = 0.9908 + 0.0971 * d
P = 0.0023
R2 = 0.97
O
Time (days)
Ovigerous females
Non-ovigerous females
best fit line
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0
5
10
15
20

Fig. 6

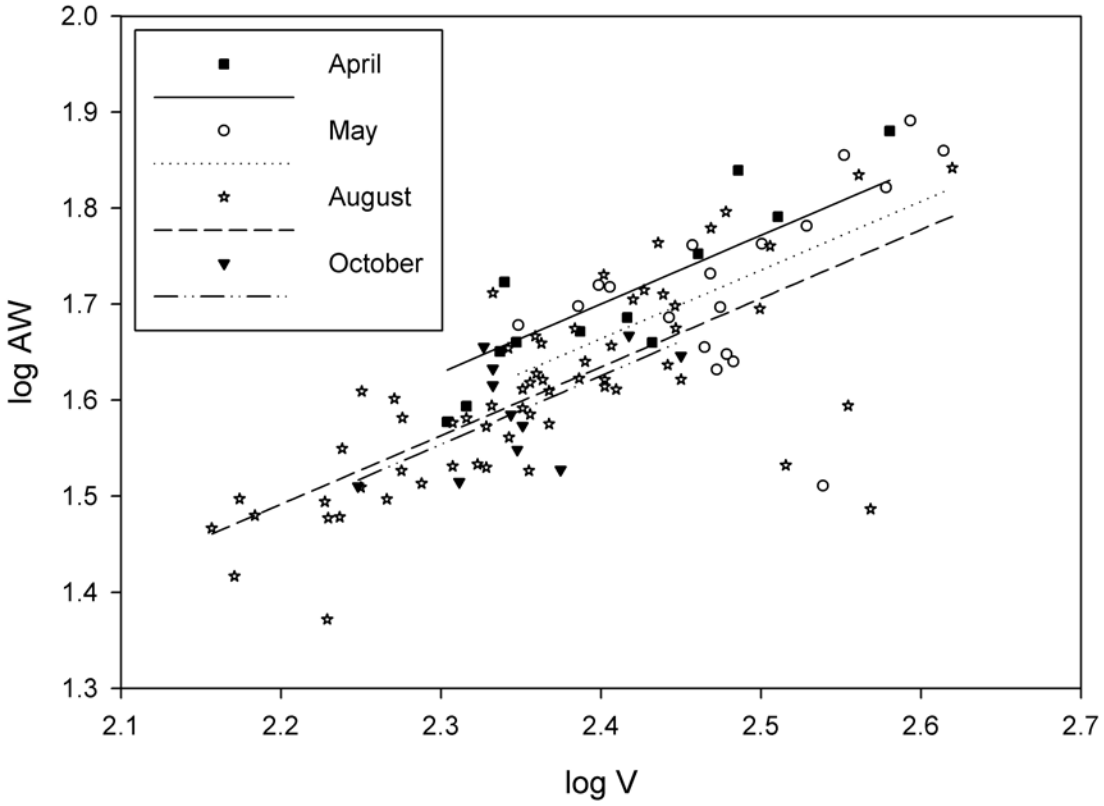

April
May
August
October
log AW
log V
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
2.1
2.2
2.3
2.4
2.5
2.6
2.7

Fig. 7

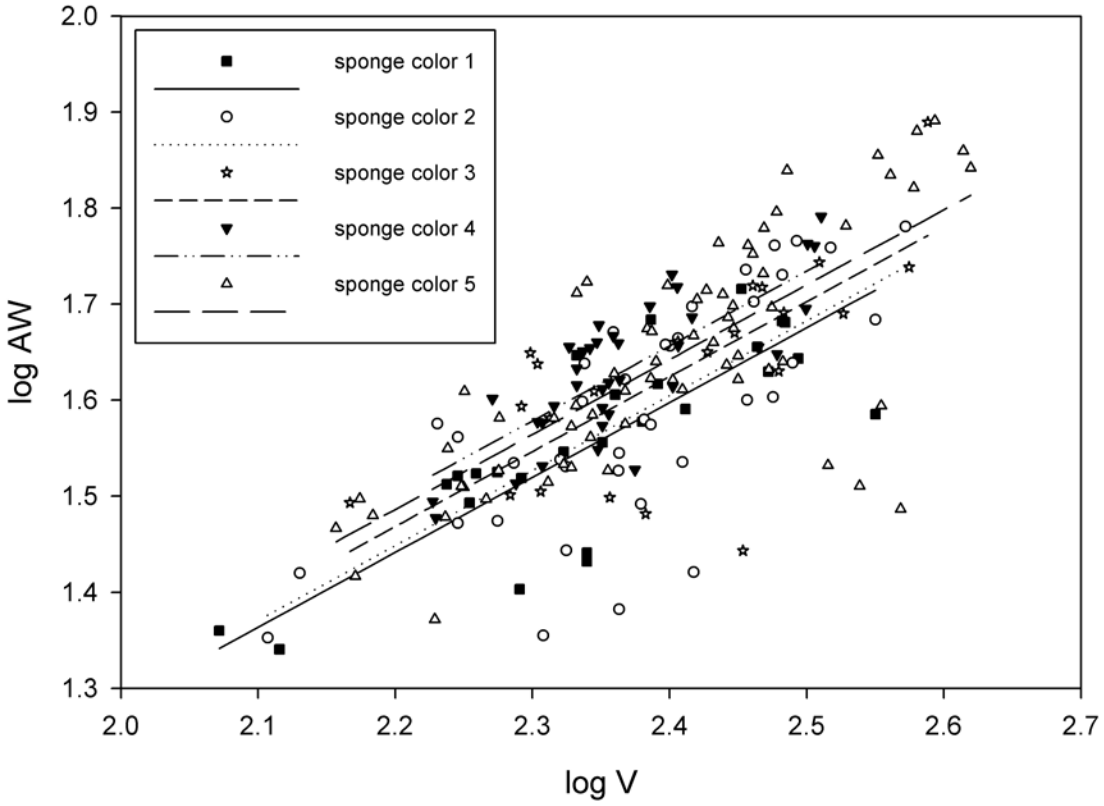
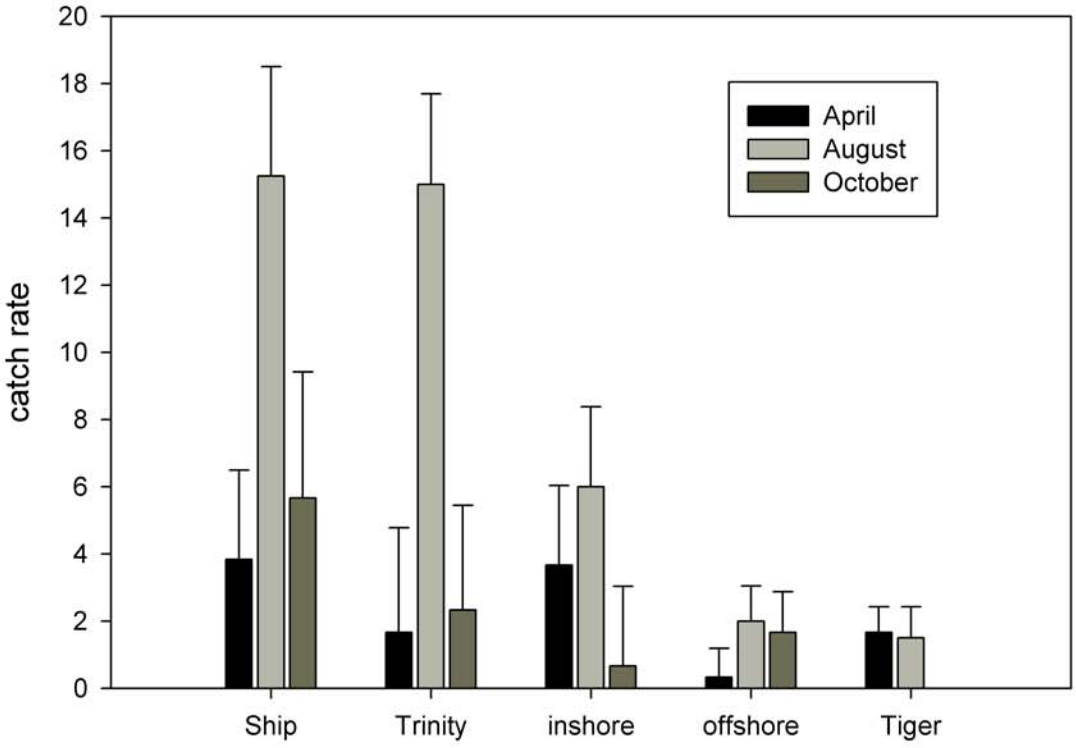

sponge color 1
sponge color 2
sponge color 3
sponge color 4
sponge color 5
log AW
log V
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7

Fig. 8


20
18
16
14
12
10
8
6
4
2
0
catch rate
April
August
October
Ship
Trinity
inshore
offshore
Tiger