NEGATIVE CONSEQUENCES OF ALLEE EFFECT ARE COMPOUNDED BY FISHING PRESSURE: COMPARISON OF QUEEN CONCH REPRODUCTION IN FISHING GROUNDS AND A MARINE PROTECTED AREA

Allan W Stoner, Martha H Davis, and Catherine J Booker

ABSTRACT

Relationships between density of mature adults and mating frequency in queen conch (*Strombus gigas* Linnaeus, 1758) were observed at three sites in the central Bahamas including one no-take marine reserve (Exuma Cays Land and Sea Park) and two historically important fishing grounds (Berry Islands and Andros Island). No mating was observed in any one count with density < 47 adults ha^{-1}, consistent with an earlier study suggesting a mate-finding Allee effect in queen conch. The unfished site had larger and older conch, and mating at that site increased rapidly with adult density, reaching an asymptote at 12%–14% of the population mating at highest density levels. Logistic modeling showed that a 90% probability of mating occurred at 100 adults ha^{-1}. Mating frequencies increased more slowly with density on the fishing grounds; asymptotic mating frequencies were 6.3% in the Berry Islands and just 2.3% at Andros Island. In contrast to the marine reserve, 90% probability of mating required 350 and 570 adults ha^{-1} at Andros Island and the Berry Islands, respectively. Higher densities required for successful mating in the fished areas were associated with numerical dominance by small, thick-shelled adults. The small phenotype in adults appears to result from selectivity imposed by fishing pressure, and those adults had low mating frequencies, compounding the density effect on reproduction. Because releases of hatchery-reared queen conch have not been successful, preserving the integrity of spawner density and population structure will be critical for conch conservation.

Benefits associated with marine protected areas include the preservation of natural population structures such as density, size, and age distributions (Roberts and Polunin 1991, Halpern 2003, Sobel and Dahlgren 2004). Positive effects of population density or size on various indicators of fitness are referred to as Allee effects, and negative rates of population growth that often occur below a critical population density are termed depensation (Stephens and Sutherland 1999, Courchamp et al. 2008, Gascoigne et al. 2009). Allee effects can be divided into directly-observed components of individual fitness such as mate finding or predator avoidance (component Allee effects) and demographic Allee effects, where there is positive density dependence in the per capita population growth rate (Stephens et al. 1999).

Biomass of mature adults is recognized as a critical parameter in marine population dynamics, and a sufficiently high number or density of spawners is required to ensure a stable fishery. With the demise of important fishery resource species around the world, it is increasingly clear that depensatory mechanisms, including reproductive failure, can occur even in highly fecund marine species (Shelton and Healey 1999, Frank and Brickman 2000, Gascoigne and Lipcius 2004a, Lundquist and Botsford 2011). Animals that mate or require close proximity for fertilization

of eggs (e.g., some gastropods and urchins) are particularly vulnerable to depensatory problems, although the demographic consequences are difficult to determine (Gascoigne et al. 2009).

The obvious effects of fishing on density and biomass can be exacerbated by effects on animal size. Fishing typically removes large individuals, leaving smaller, less fecund individuals in the spawning stock (Berkeley et al. 2004, Carr and Kaufman 2009). There is also increasing evidence that fishing pressure can affect important phenotypic changes such as decreasing size-at-age and age-at-maturation (Law 2000, Conover et al. 2005, Hutchings 2005, Walsh et al. 2006). Most of the observations on fisheries-induced evolution have been reported for fishes, but shifts in size-at-maturity have also been reported recently for commercially exploited crustaceans (Melville-Smith and de Lestang 2006, Zheng 2008) and gastropods (Torroglosa and Giménez 2010). Therefore, both the direct and indirect effects of fishing on population dynamics need to be understood for conservation of heavily exploited species.

Appeldoorn (1988a) pointed out the possibility of depensatory mechanisms in reproduction of the economically important gastropod *Strombus gigas* Linnaeus, 1758 (queen conch), suggesting that there might be a critical density for egg production. In fact, the queen conch is an ideal subject for study of density-dependent reproduction because the sex ratio is typically 1:1, fertilization is internal, and the adults are large, relatively sedentary, and easy to count in mostly open habitat. Stoner and Ray-Culp (2000) reported an apparent component Allee effect for the species, observing that mating behavior and egg-laying in natural field populations in The Bahamas never occurred below 56 and 48 adults ha^{-1}, respectively. Since that time, others have attempted to test density dependence in queen conch reproduction in field experiments (Gascoigne and Lipcius 2004b). Meanwhile, the species remains listed in Appendix II of the Convention on International Trade in Endangered Species (CITES, Daves and Fields 2004), and populations of queen conch around the Caribbean region continue to decline under intense fishing pressure (Bell et al. 2005).

In 2009 and 2010, broad-scale surveys in the central Bahamas yielded new data on spawner density and reproductive frequency for historically important queen conch fishing grounds (Stoner et al. 2009, Stoner and Davis 2010). These new studies provided the opportunity to compare direct observations from heavily fished sites with an earlier study focused in a large no-take marine protected area (Stoner and Ray-Culp 2000). Surveys repeated at the protected site in 2011 provided a test of temporal stability in the reproductive function.

Methods

Study Sites.—Surveys for adult conch and their mating behavior were conducted at three different sites in the central Bahamas including the Exuma Cays, the Berry Islands, and Andros Island (Fig. 1). The Exuma Cays site was located in the middle of the Exuma Cays Land and Sea Park (ECLSP), a no-take marine reserve at the eastern edge of the Great Bahama Bank. This site was well protected from fishing for at least 20 yrs prior to the first survey in 1995. Stoner and Ray (1996) described the habitat and queen conch distributions, and considered the conch population near the Park center to be undisturbed. Observations were made on the island shelf east of Cistern Cay and Waderick Wells Cay in depths 11–19 m (mean = 12 m) on bare sand habitat where queen conch are abundant and where reproductive behavior is commonly observed. Juvenile queen conch in the Exuma Cays are located primarily on the shallow nursery grounds west of the Cays (Stoner 2003) and not in the spawning
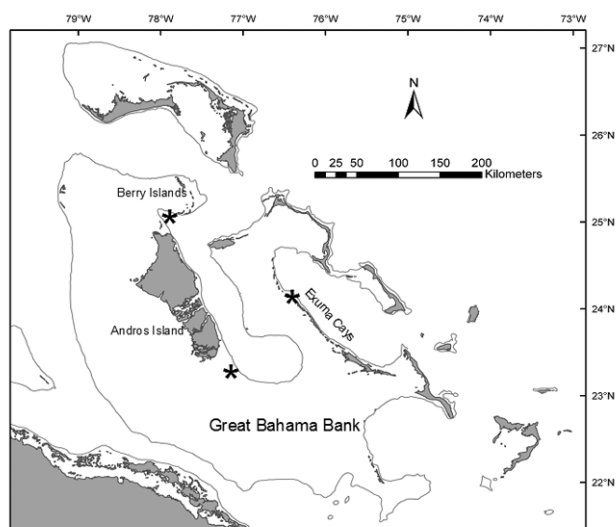
Figure 1. Map of the northern and central Bahamas showing the general locations of three study sites in the Exuma Cays, Berry Islands, and Andros Island. The first site is located in Exuma Cays Land and Sea Park, a no-take marine fishery reserve. The other two sites are historically important fishing grounds. 200-m isobaths surrounding the shallow banks are shown.

grounds. Data for the Exuma Park were collected from 12 to 29 July, 1995, and bottom water temperature ranged from 27.5 to 28.2 °C. The Exuma Cays site was surveyed again from 7 to 14 July, 2011, exploring a broader range of depth (4–29 m; mean = 14 m) on bare sand and hard-bottom. Temperature ranged from 27.8 to 29.9 °C. This Exuma Cays site, near the headquarters of the ECLSP, continues to be well protected from fishing by resident park staff and the Royal Bahamian Defense Force.

Two historically important fishing grounds were surveyed for comparison with the unfished marine reserve. The first, surveyed from 6 June to 10 July, 2009, is on the south edge of the Great Bahama Bank near the Berry Islands. Adults at this site were abundant on the shallow bank in both sand and hard-bottom habitat in depths of 2–13 m (mean = 5 m). During the survey, bottom water temperature ranged from 26.6 to 31.9 °C. The second fishing ground is located at the south end of Andros Island near the Grassy Creek Cays and Pigeon Cays. Adult conch were surveyed over a depth range of 2–9 m (mean = 5 m) in sand, seagrass (primarily *Thalassia testudinum* Banks & Sol. ex K. D. König), and hard-bottom habitats. Andros surveys were conducted from 23 May to 5 June, 2010, and bottom water temperatures ranged from 26.1 to 28.3 °C. These represent two of the most important commercial fishing grounds for queen conch in The Bahamas, supplying meat and shells for the large tourist trade and for export-related processors located in the city of Nassau. Conch are captured primarily by freediving from small boats and with increasing use of hookah systems (i.e., surface-supply air) in deeper locations. As in the Exuma Cays, juveniles at the two fishing grounds were located in generally shallower habitats than the adults and they were not quantified for our study.

While adult conch were abundant on the broad 11–19 m deep shelf east of the Exuma Cays, equivalent habitat at Andros Island and the Berry Islands was limited to a very narrow band, sometimes just a few meters wide on the steep shelf edge. Consequently, the surveys were focused on the reproductive grounds at each location to yield the best possible assessment of the relationships between spawner density and mating behavior. This range of habitat was determined by our experience at each site, and restricted to locations where mating was observed first hand.

Starting dates for the surveys varied by almost 7 wks (end of May to mid-July); however, we do not believe that this impacted the results. Stoner et al. (1992) have shown that queen conch in The Bahamas mate and lay eggs over a long reproductive season, with a relatively flat peak between April and August. In other areas, the reproductive season appears to be even more protracted (Aldana-Aranda 2004). Seasonal cycles are associated with periods of increasing or long natural photoperiod and high temperature (Stoner et al. 1992). Day length and temperatures were sufficiently elevated during each of the survey periods to elicit maximum mating behaviors.

Survey Methods.—Densities of adult conch (see below for definitions) and frequencies of mating behavior were estimated in highly replicated counts made at each of the study sites. Methods for the Exuma Cays site in 1995 were described by Stoner and Ray-Culp (2000). Briefly, this entailed counting the number of adult conch in sets of three closely spaced circles with 20-m radii. Fifty-four diver surveys were dispersed evenly over an area of ~40 km² in the habitat described above. At the Berry Islands and Andros Island fishing grounds, surveys were dispersed systematically over a grid of 1-min blocks of latitude and longitude (~3.10 km² at the study locations). One 1-km long belt transect 6 m wide was surveyed in each of 68 locations in the Berry Islands and 58 locations at Andros Island. Thus, samples were evenly dispersed over ~210 and 180 km² at the Berry Islands and Andros Island, respectively. The 2011 surveys in the Exuma Cays site were conducted with a series of belt transects (as above) dispersed evenly over five depth strata in five lines running directly offshore from Waderick Wells Cay.

The number of adults in each pre-determined area were counted by divers and the corresponding numbers of conch engaged in mating behavior were recorded. Any two adults with shells touching in stereotypic copulating alignment were recorded as mating.

Shell morphology provides important insight into the age and sexual maturity of queen conch. Approximately 3.5 yrs after larval settlement, individuals reach terminal shell length (ranging ~140–300 mm, Appeldoorn 1988b). At about this time, the edge of the shell lip turns outward to form the characteristic flared lip of the "adult" form. Subsequent growth of the shell occurs only in thickness (i.e., not length) and tagging studies show that lip thickness provides a relative index for conch age (Appeldoorn 1988b, Stoner and Sandt 1992). The flared lip is an obvious field characteristic and is required for legal harvest of conch in The Bahamas and in several other Caribbean nations. However, maturity of the gonads does not occur until the shell lip reaches a thickness of 8–10 mm (Egan 1985, Aldana-Aranda and Frenkiel 2005), as long as 6–10 mo following initial formation of the shell flare. To ensure that density estimates were limited to sexually mature individuals, only conch with shell lips ≥ 10 mm were classified as adults in our study. Those with a lip flare < 10 mm thick were considered subadults. This approach eliminated inclusion of immature individuals in density estimates that might inflate the density requirements for mating frequency.

Measurements of shell length and lip thickness, following the methods of Appeldoorn (1988b), were made by scuba divers after the distributions of large conch were characterized for each study site. Thirty to 133 conch with flared shell lips (adults and subadults) were measured from nine to 12 locations dispersed throughout each site. The proportions of conch with shell lip thickness ≥ 10 mm were then used to calculate the densities (number per hectare) of mature conch in each site. This method was appropriate because it provided the best age-stratified data for the populations observed mating. Mating frequency was calculated as the percent of mature adults engaged in mating behavior.

Analysis.—Logistic regression was used to evaluate the possible relationships between conch mating and environmental variables, including mature conch density, water depth, and bottom water temperature. Models were fitted by the method of maximum likelihood for binary data (i.e., presence or absence of mating behavior) with the regression module of Systat 13 (SYSTAT Software, Inc., San Jose, CA; Peduzzi et al. 1980). A backward stepwise approach was used to determine the most parsimonious model for mating occurrence, with

an alpha value of 0.15 to remove a variable from the full model (i.e., that including all of the available independent variables). The model for mating behavior was described by the following equation:

$$\log_e (p/(1 - p)) = \alpha + \beta x,$$

where p = proportion of $y = 1$, $y = 1$ if mating occurred, and 0 if no mating occurred, α = intercept, β = model coefficients (slope), and x = the model matrix of independent variables.

The maximum likelihood estimates for mating behavior (ρ) were calculated as:

$$\rho = e^{(\alpha + \beta x)}/1 + e^{(\alpha + \beta x)}.$$

Initially, the data for each site were split randomly into equal halves, one representing a learning set and the other a test set. The most parsimonious logistic model was developed with the learning set and validated with the test set. After cross-validation, a final model was fitted to the entire data set for each study site. Finally, the logistic model for each study site was used to develop a curve showing the probability of mating based upon fixed values for the key predictor of mating behavior (e.g., conch density), and a prediction success matrix was calculated from the model with a cutoff point of 0.5 to evaluate quality of the logistic model.

Site differences in shell length and lip thickness, including all adult and subadult conch, were tested with standard ANOVA followed by Fishers LSD test for differences among means. This analysis was also conducted with Systat 13.

Results

Observations on > 13,000 queen conch with flared shell lips over the three study sites yielded data on size and age structure, conch density, and the occurrence of mating behavior (Table 1). Shell lengths varied significantly across the three study sites (ANOVA: $F_{3,244} = 70.383$, $P < 0.001$) despite a wide range of size at each (Fig. 2). Conch in the Exuma Cays, averaging 206 and 202 mm in the two surveys, were larger than those at the other sites, 156 mm and 177 mm in the Berry Islands and at Andros Island, respectively. Lengths at the three sites all differed significantly (Fisher's LSD

Table 1. Summary of survey results for queen conch with flared shell lips (i.e., adult and subadult conch, see text) at three spawning grounds in The Bahamas. In the present study, the term "adult" is applied only to those individuals with lip thickness values ≥ 10 mm to ensure reproductive maturity. All but one individual observed at the Exuma Cays site were adults. Shell length and shell lip thickness are mean ± SD and represent all adults and subadults with flared shell lips. Distributions for shell measures are shown in Figure 2. Values for adult density are mean ± SD.

| Study site	Exuma Cays	Exuma Cays	Berry Islands	Andros Island
Year	1995	2011	2009	2010
Total surveys	54	33	68	58
Surveys with adult or subadult conch	54	25	48	47
Total area surveyed (ha)	20.4	13.1	40.8	34.8
Total number observed	4262	732	4787	4075
Shell length (mm)	206 ± 18	203 ± 20	156 ± 19	177 ± 27
Shell lip thickness (mm)	26 ± 7	28 ± 5	15 ± 6	15 ± 7
Mean density of adult conch (no. ha^{-1})	209 ± 394	60 ± 83	131 ± 272	118 ± 139
Range of adult density observed (no. ha^{-1})	2.0–2793.0	2.3–275.0	1.4–1411.0	1.4–529.0
Number of mating conch	444	72	232	78
% of adults mating	10.4	9.8	5.9	2.4
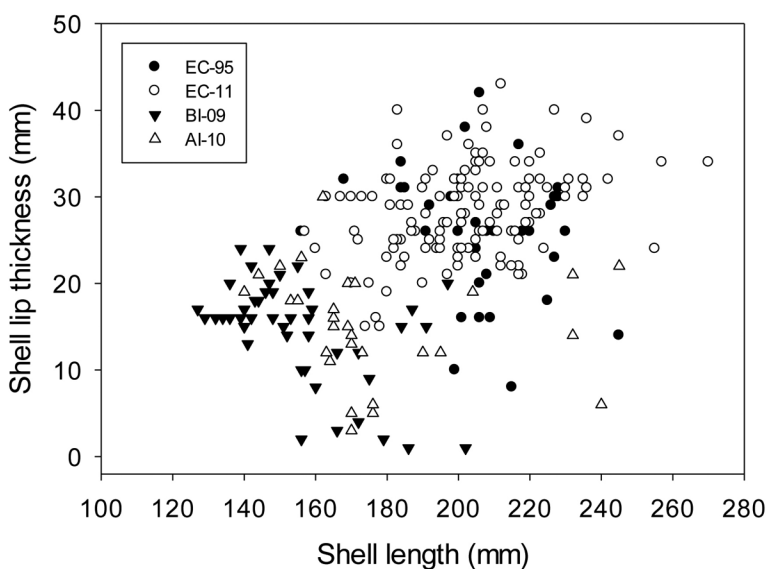
Figure 2. Length and lip thickness plots for the shells of adult queen conch at three study sites in The Bahamas. Shells were measured during two surveys in the Exuma Cays Land and Sea Park, in 1995 and 2011 (EC-95, EC-11), and in important fishing grounds in the Berry Islands in 2009 (BI-09) and near Andros Island in 2010 (AI-10).

test: P < 0.001), while those at the Exuma Cays site did not change with time (Fisher's LSD test: P = 0.370). Shell lip thickness also varied significantly across the study sites (ANOVA: $F_{3,244}$ = 87.727, P < 0.001; Table 1, Fig. 2). Mean values in the Berry Islands and at Andros Island (15 mm at both) were not different (Fisher's LSD test: P = 0.836), but significantly lower than the two mean values observed in the Exuma Cays (26–28 mm; Fisher's LSD test: P < 0.001). Only one individual measured in the Exuma Cays had lip thickness < 10 mm (in 1995), while the proportions of subadult conch in the Berry Islands and Andros Island were 18% and 20%, respectively. Small adult conch that are thick-shelled and highly eroded (i.e., smooth and missing shell spines, etc.) are often called "sambas" by Bahamian fishers. This small phenotype adult was the dominant form at the two fishing grounds and was rare at the unfished Exuma Cays study site. These are represented in the cloud of triangles (open and closed) lying on the left side of Figure 2, with shell lengths of 130–170 mm and lip thickness of 9–25 mm.

The mean density of mature adults was nearly twice as high at the Exuma Cays site in 1995 as at the two fishing grounds, but the range of values within each site was very large, from just 1.4 to 2793 adults ha^{-1} (Table 1). The overall site difference was not significant (ANOVA: $F_{3,172}$ = 1.659, P = 0.178) because of the large variation. The mean density at the Exuma Cays site in 2011 was lower than that in 1995 (Fisher's test: P = 0.055), but a broader range of habitat was surveyed in the second survey (see above).

Mating behavior was observed at all three survey sites and ranged from 0% to 34.5% of the mature queen conch at any one count. Overall, ~10% of the adults observed in the Exuma Cays were engaged in mating behavior during both survey years while mating frequencies at the Berry Islands and Andros Island sites were 5.9% and
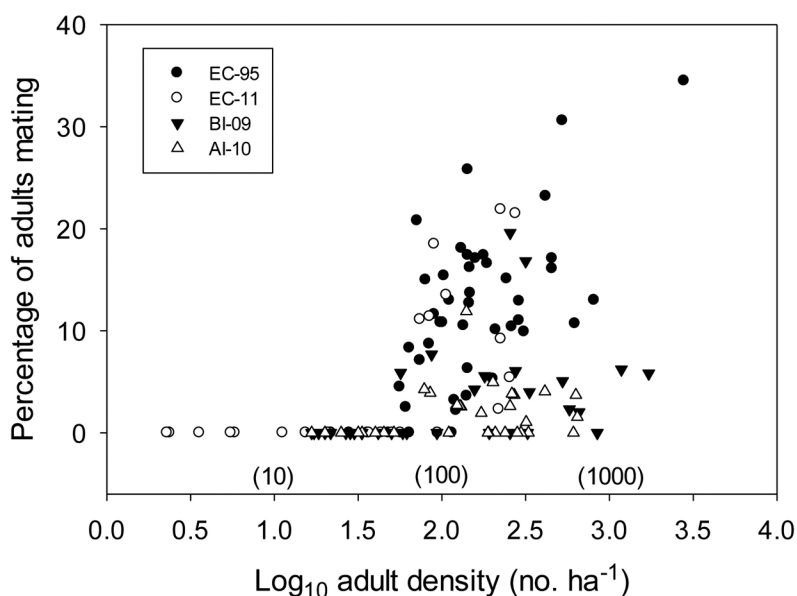
Figure 3. Association between mating frequency in queen conch and density of mature adults (shell lip thickness ≥ 10 mm) in surveys conducted at three sites in the Bahamas. Density is shown on a log_{10}-transformed axis (untransformed values in parentheses). Mating frequency is shown as the percentage of the adult population engaged in mating behavior.

2.4%, respectively (Table 1). The occurrence of mating behavior was clearly density dependent (Fig. 3). In fact, no mating whatsoever was observed in 88 counts where adult density fell below 47 mature adults ha^{-1} (Table 2). This was the lowest density where mating was observed at the Berry Islands fishing ground, and that count included just one mating pair. Lowest densities for mating ranged from 56 to 74 adults ha^{-1} in the Exuma Cays and at Andros Island. The occurrence of mating increased rapidly at levels > ~100 adults ha^{-1}, particularly in the Exuma Cays, but mating frequency was highly variable both within and among the study sites (Fig. 3). Little to no mating was observed in many belt transects with high densities, particularly at the Berry Islands and Andros sites. When compared across sites considering only those locations with densities > 100 mature adults ha^{-1}, the Exuma Cays had mean mating frequencies (1995 and 2011) significantly higher than frequencies observed at the Berry Islands and at Andros Island (Table 2; ANOVA: $F_{3,69}$ = 15.951, P < 0.001). There was no difference between the two fishing grounds (Fisher's LSD test: P = 0.067) or between the two survey dates in the Exuma Cays (P = 0.609).

Logistic regression showed that the probability of mating was highly dependent upon density of mature conch for all of the survey sites (Tables 3–5), and neither depth nor bottom water temperature significantly improved the logistic models at the two sites (Berry Islands and Andros Islands) where surveys were conducted over a broad range of depth. The most parsimonious models for both of these sites included just adult density (Tables 4, 5). The relationships between adult conch density and the probability of observing mating behavior were described by distinctly sigmoid functions at all of the study sites, but the shape of the curves varied substantially (Fig. 4). During both 1995 and 2011, probability of mating near the Exuma Cays increased

Table 2. Summary of density-related mating behavior in queen conch at three spawning grounds in The Bahamas. Density values reported in the first three lines are numbers of mature adults per hectare required to achieve the specified level of mating. Probability results are based upon logistic regression (see text). Values for percentage of adults mating are mean ± SD.

Study site	Exuma Cays	Exuma Cays	Berry Islands	Andros Island
Survey year	1995	2011	2009	2010
Lowest density observed for mating	56	74	47	64
50% probability	70	76	300	180
90% probability	100	100	570	350
% mating where densities are >100 mature conch ha^{-1}	13.7 ± 7.6	12.3 ± 8.2	6.3 ± 6.0	2.3 ± 2.7

rapidly after about 50 adults ha^{-1} and reached an asymptote near 110 adults ha^{-1}. The rise in mating probability was much slower at the Berry Islands and Andros Island. Fifty percent probability of mating occurred at 70, 180, and 300 adults ha^{-1} for the Exuma Cays, Andros Island, and Berry Islands sites, respectively (Table 2). Ninety percent probability occurred at 100, 350, and 570 adults ha^{-1}, respectively. The logistic models, therefore, were consistent with obvious thresholds of density-dependent mating frequency seen in Figure 3.

Quality of the logistic models can be evaluated with prediction success matrices. The best fit occurred with data from the Exuma Cays in 1995 where 94.4% of the predicted behaviors (presence or absence of mating) were correct (Table 3). Model success was lowest (74.5%) for the Andros Island surveys (Table 5) where incorrect

Table 3. Results of logistic modeling for mating in *Strombus gigas* (queen conch) in the Exuma Cays, The Bahamas, in 1995 and 2011. The parameter for adult density represents sexually mature adults with shell lip thicknesses ≥ 10 mm. The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively, along with the percentage of correct predictions.

1995	Parameter	Estimate	Z	P value
	Constant (α)	−3.978	−2.636	0.008
	Adult density (β)	0.069	3.011	0.003
		Predicted observation		
	Field observation	No mating predicted	Mating predicted	Actual total
	No mating	39	1	40
	Mating	2	12	14
	Total predicted	41	13	54
	Correct (%)	95.7	85.7	
	Total correct (%)			94.4
2011	Parameter	Estimate	Z	P value
	Constant (α)	−7.167	−3.123	0.002
	Adult density (β)	0.094	2.404	0.016
		Predicted observation		
	Field observation	No mating predicted	Mating predicted	Actual total
	No mating	15	1	16
	Mating	1	8	9
	Total predicted	16	9	25
	Correct (%)	93.8	88.9	
	Total correct (%)			92.0

Table 4. Results of logistic modeling for mating in *Strombus gigas* (queen conch) in the Berry Islands, The Bahamas. The parameter for adult density represents sexually mature adults with shell lip thicknesses ≥ 10 mm. A backward stepwise approach was used to determine the most parsimonious model for mating behavior. The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively, along with the percentage of correct predictions.

Parameter	Estimate	Z	P value
Full model			
Constant	−22.861	−1.764	0.078
Adult density	0.008	3.070	0.002
Depth	0.204	1.626	0.104
Temperature	0.661	1.524	0.127
Most parsimonious model			
Constant	−2.382	−4.122	< 0.001
Adult density	0.008	2.939	0.003

Field observation	Predicted observation		Actual total
	No mating predicted	Mating predicted	
No mating	34	2	36
Mating	5	7	12
Total predicted	39	9	48
Correct (%)	94.4	58.3	
Total correct (%)			85.4

predictions for both the presence and absence of mating occurred. At all three sites, predictions of no mating were more accurate (87%–96%) than predictions for mating, and the occurrence of mating behavior was under-predicted by the models to varying degrees.

Discussion

Density-Dependent Reproduction.—Density dependence in mating frequency is not surprising for an animal that needs to locate a partner for internal fertilization of eggs. The topic of mate-finding Allee effect, including evolutionary implications, was well covered in a recent comprehensive review (Gascoigne et al. 2009), and Stoner and Ray-Culp (2000) discussed the relevance to queen conch. They also reported that 56 mature adults ha^{-1} was the lower threshold for mating in conch in the Exuma Cays in 1995, and this value is often cited in discussions of conch management in the Caribbean region. In fact, thresholds in the Berry Islands and Andros Island fishing grounds (47 and 64 adults ha^{-1}) were close to the earlier estimate. The threshold was slightly higher in 2011 at the Exuma Cays site, but the observed lower threshold for mating appears to be robust between about 50 and 75 mature adults ha^{-1}. However, these density values represent the absolute minima for reproduction, and it is more important for management purposes to consider mating behavior at higher levels. In fact, mating frequencies above the threshold were highly variable at each site, and the apparent asymptotes were substantially different. For example, mating frequencies at Andros Island and the Berry Islands fishing grounds were very low, leveling off at just 6.3% and 2.3% of mature adults, compared with 12%–14% at the unfished Exuma Cays site. Also, logistic models showed that mating increased rapidly with density in the Exuma Cays, reaching the maximum level at just over 100

Table 5. Results of logistic modeling for mating in *Strombus gigas* (queen conch) at Andros Island, The Bahamas. The parameter for adult density represents sexually mature adults with shell lip thicknesses ≥ 10 mm. A backward stepwise approach was used to determine the most parsimonious model for mating behavior. The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively, along with the percentage of correct predictions.

Parameter	Estimate	Z	P value
Full model			
Constant	−38.081	−2.104	0.035
Adult density	0.015	3.058	0.002
Depth	0.230	0.745	0.456
Temperature	0.821	0.954	0.097
Most parsimonious model			
Constant	−2.321	−3.617	< 0.001
Adult density	0.013	3.176	0.001

Field observation	Predicted observation		Actual total
	No mating predicted	Mating predicted	
No mating	27	4	31
Mating	8	8	16
Total predicted	35	12	47
Correct (%)	87.1	50.0	
Total correct (%)			74.5

adults ha^{-1}. The probability of mating rose much more slowly in the fishing grounds, particularly in the Berry Islands where the population was dominated numerically by very small thick-shelled adults. On the fishing grounds, maximum mating probability occurred only at the relatively few locations where densities were > 350 mature adults ha^{-1}.

While density dependence in mating is not surprising, differences in the shapes of the mating probability curves represent a new and challenging observation. Several possible explanations exist, including differences in habitat and differences in the phenotype, age, and maturity structures of the conch populations. The obvious habitat features, depth and water temperature, had no significant effects in the logistic models for mating. All of the study sites offer high abundance of the algal foods typical of queen conch diets, and none of the sites surveyed had bottom types that would inhibit locomotion or mate finding.

Differences in size, age, or phenotype of adult conch provide the most likely explanation for differences in mating frequencies and probabilities among the three study sites, particularly the contrast between the marine protected area and the two fishing grounds. First, the protected Exuma conch were 32%−40% larger in shell length than those in the Berry Islands, which are among the very smallest adults known for the species' geographic range (AWS, MHD, CB, pers obs). Second, the unfished Exuma Cays population had a mean shell lip thickness nearly twice that observed at the fishing grounds. Consequently, the Exuma conchs were older.

While it is possible that gonadal maturity occurs later in the small adults found on the fishing grounds than in the Exuma population, we observed mating in the small phenotype conch which dominated the Berry Islands population and we believe that the 10 mm shell lip thickness used as a threshold for maturity is robust. However, the obvious differences in mating probability function provide strong impetus for
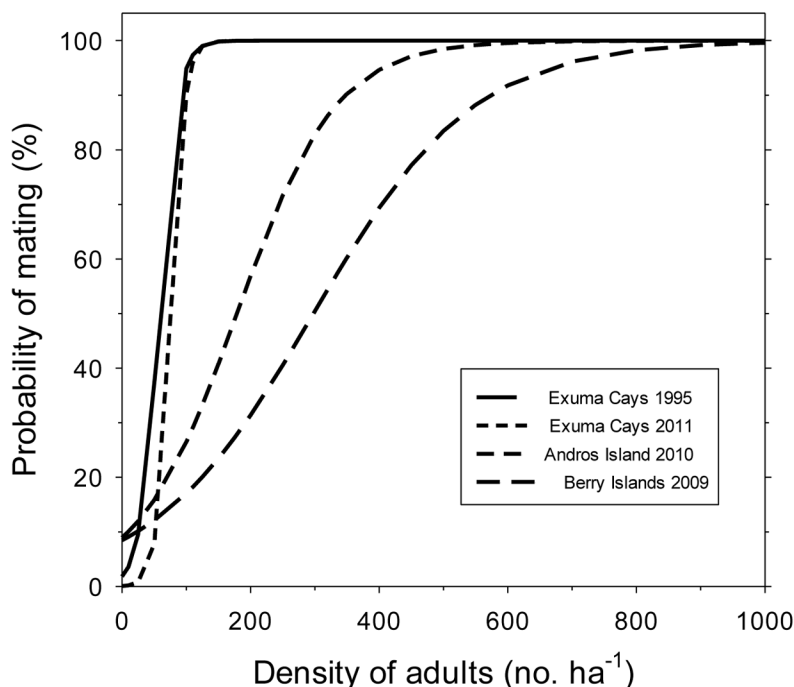
Figure 4. Logistic regression curves showing relationships between the density of mature adult queen conch (shell lip thickness ≥ 10 mm) and the probability of observing mating behavior at the Exuma Cays marine protected area and at two sites where fishing pressure is high.

future expanded analysis of size- and age-related variation in maturity, reproductive behavior, and fecundity in this important fishery species. Individual studies (e.g., Egan 1985, Appledoorn 1988a, Aldana-Aranda and Frenkiel 2005) provide important insights, but the age-thickness and thickness-maturity relationships, for example, appear to vary geographically and are critical to fisheries management decisions. More specifically, in The Bahamas it will be important to evaluate whether the small phenotype "samba" adults that now dominate the fishing grounds of Andros and the Berry Islands have reproductive potential equal to the more typical conch phenotype.

Possible Effects of Fishing on Conch Phenotype.—Declining mean size of individuals is one of the characteristics of heavily exploited fish and invertebrate populations in marine systems (Roberts and Polunin 1991), and this often occurs as a direct result of selective harvesting of large animals. Consequently, marine protected areas usually have larger fishes and lobsters than surrounding fishing grounds, and those larger animals produce larger numbers of eggs (Sobel and Dahlgren 2004). Reflecting that trend, the no-take reserve surveyed in the present study had larger and older queen conch than the two fishing grounds. There are at least three possible explanations for this dichotomy: selective harvest, differential growth, and fishing-related evolution. (1) Fishers receive a higher price for large conch in the market, and they confirm selective fishing for large individuals at both Andros Island and the Berry Islands. The very small sexually mature "samba" conch observed at those

two sites are rare in other less heavily fished parts of The Bahamas. (2) Small size of mature conch at Andros and the Berry Islands could result from naturally slow growth. Field experiments have shown that growth in juvenile conch varies strongly with habitat (Ray and Stoner 1994), and growth to maximum size in conch is determinate, whereby growth in length ends about the time that sexual maturity is achieved at 3.5–4 yrs age (see Survey Methods). Therefore, slow growth to maximum size may provide the most parsimonious explanation for small conch in the two fishing grounds. However, transplant experiments show that slow-growing conch tend to be small with long apical spines (Martín-Mora et al. 1995) in contrast with the small "samba" conch which have almost no spines, and a third alternative should be considered. (3) Fishing pressure can cause selection for reduced size-at-age and age-at-maturity in fishes (Law 2000, Conover et al. 2005, Hutchings 2005, Walsh et al. 2006). We know less about invertebrate subjects, but shifts in size-at-maturity have been observed over the long term for exploited crustaceans (e.g., Melville-Smith and de Lestang 2006, Zheng 2008), and histological data exist for at least one gastropod (*Zidona dufresnei* Donovan, 1823) showing that size-at-maturity decreased significantly over a 10-yr period of heavy fishing (Torroglosa and Giménez 2010). Similarly, it is possible that decades of intensive fishing effort on queen conch in the Berry Islands and Andros Island has reduced the size- or age-at-maturity. This, of course, requires that the progeny of the effected populations are retained within those fishing grounds. Although the oceanography of The Bahamas is poorly known, it is reasonable to believe that conch larvae from Andros and Berry Islands spawning populations are retained in the deep-water basin bordered by Andros on the west, the Great Bahama Bank on the south and east, and the Berry Islands to the north.

A logical next step will be to test how conch age and size, and mating frequency in the different spawning populations translate to numbers of viable eggs and larvae produced. Davis et al. (1984) showed that reproductive output can be tracked in queen conch, and Gascoigne and Lipcius (2004b) conducted the first manipulative experiment testing for density effects. We already know that a female conch with the mean shell length and thickness observed in the Berry Islands fishing ground has a gonad weight less than one-quarter that of the mean Exuma Cays female (Stoner et al., unpubl data). In any case, it is clear that the small phenotype individuals underperform more typical large conch.

Fishery Management Implications.—Regardless of the exact mechanisms for density-dependent reproductive behavior and size structure in queen conch, the fishery management implications are large. We agree with Gascoigne and Lipcius (2004a) that including Allee effects in population models will be critical for precautionary management of this over-fished species. The primary imperative must be to increase the density of mature conch over sufficient space to provide progeny for a sustainable fishery. It is clear that a no-take fishery reserve established in the appropriate location can help to preserve a naturally high density of spawning stock with adults old enough and large enough to yield high reproductive output (Stoner and Ray 1996), and recent theoretical models indicate that marine reserves can help to prevent evolutionary effects of fishing on size-at-maturity (Miethe et al. 2009). However, we also know that a single reserve may not be self sustaining (Botsford et al. 2001, Gaines et al. 2003, Kaplan et al. 2009), and new surveys in the Exuma Cays Land and Park show that adult densities declined significantly between 1994

and 2011 (Stoner et al., unpubl data). This speaks for a larger proportion of fishing grounds to be incorporated into a reserve network (see Lubchenco et al. 2003, Jones et al. 2007, Kininmonth et al. 2011), and for reduced total harvest through whatever means possible.

Sustainable fishing for queen conch will depend upon preserving a natural size and age structure in the spawning grounds as well as high density of adults. Large, old queen conch tend to accumulate in deep-water (perhaps unfished) environments, and gear that allows deep-diving (e.g., hookah and scuba) should not be used in conch fishing. A long-term ban of scuba diving for conch in The Bahamas may be one of the reasons that the conch fishery remains viable there. Unfortunately, the use of hookah is increasing in The Bahamas because shallow-water stocks are declining. Also, queen conch are managed by size or shell-lip criteria in most nations of the Caribbean (Aldana-Aranda and Frenkiel 2005, Clerveaux et al. 2005), and there have been repeated reminders that thin-lipped adults are not functionally mature (Egan 1985, Appeldoorn 1988b, Stoner and Sandt 1992, Gascoigne and Lipcius 2004b). Shell length requirements do not protect reproduction adequately, and it is clear that lip-thickness measures will provide the best criterion to ensure that conch are allowed to mature and reproduce before harvest. Finally, fishing quotas that preserve high spawning stock density need to be instituted and enforced. Detailed analysis and simulation modeling (Valle-Esquivel 2003) indicates that the optimal management strategy for queen conch will include limits on shell lip thickness, a fishing closure during reproductive season, and control of total fishing effort.

Neither complete fishing moratoria nor releases of hatchery-reared juveniles have proven successful in restoring queen conch populations once reduced to a low level. For example, since the complete closure of fishing in the Florida Keys in 1986, the conch population has gradually increased over annual surveys; however, the gains are modest, from a mean abundance of ~18,000 adults in the 1990s to ~34,000 in the 2000s (R Glazer, Florida Fish and Wildlife Conservation Commission, pers comm). In comparison, 208,000 adult conch were estimated for an 8-km-long segment of the shelf edge (22 km²) in the center of the Exuma Cays Land and Sea Park in 1994 (Stoner and Ray 1996). Greatest success in improving reproductive output in the Florida Keys was achieved by translocating adults, placing them in the best possible spawning habitats to reduce the negative consequences of an Allee effect (Delgado et al. 2004). Given a general lack of success with releases of hatchery-reared conch (Stoner and Glazer 1998), it is clear that the best practice with this species will be to preserve the integrity of spawner density and population structure.

of the sites who provided help with travel, logistics, and guidance on queen conch distribution. We thank RA Glazer who participated in extensive discussion on the subject of density-dependent reproduction and three anonymous reviewers who provided thoughtful criticism.

Literature Cited

Aldana-Aranda D. 2004. Overview of reproductive patterns of the queen conch *Strombus gigas* from different reef systems in the Caribbean. Proc Gulf Carib Fish Inst. 57:771–790.

Aldana-Aranda D, Frenkiel L. 2005. Lip thickness of *Strombus gigas* (Mollusca: Gastropoda) versus maturity: a management measure. Proc Gulf Carib Fish Inst. 58:431–442.

Appeldoorn RS. 1988a. Fishing pressure and reproductive potential in strombid conchs: is there a critical stock density for reproduction? Mem Soc Natur LaSalle. 48:275–288.

Appeldoorn RS. 1988b. Age determination, growth, mortality, and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. Fish Res. 6:363-378. http://dx.doi.org/10.1016/0165-7836(88)90005-7

Bell JD, Rothisberg P, Munro JL, Lonergan NR, Nash WJ, Ward RD, Andrew NL. 2005. Restocking and stock enhancement of marine invertebrate fisheries. San Diego: Elsevier Academic Press.

Berkeley SA, Hixon MA, Larson RJ, Love MS. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries. 29:23–32. http://dx.doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2

Botsford LW, Hastings A, Gaines SD 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett. 4:144–150. http://dx.doi.org/10.1046/j.1461-0248.2001.00208.x

Carr JP, Kaufman L. 2009. Estimating the importance of maternal age, size, and spawning experience to recruitment of Atlantic cod (*Gadus morhua*). Biol Conserv. 142:477–487. http://dx.doi.org/10.1016/j.biocon.2008.10.004

Courchamp F, Berec L, Gascoigne J. 2008 Allee effects in ecology and conservation. Oxford: Oxford University Press. http://dx.doi.org/10.1093/acprof:oso/9780198570301.001.0001

Clerveaux W, Danylchuk AJ, Clerveaux V. 2005. Variation in queen conch shell morphology: management implications in the Turks and Caicos Islands, WI. Proc Gulf Carib Fish Inst. 56:714–724.

Conover DO, Arnott SA, Walsh MR, Munch SB. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Can J Fish Aquat Sci. 62:730–737. http://dx.doi.org/10.1139/f05-069

Daves N, Fields J. 2004. Recent developments in CITES concerning the international trade in queen conch (*Strombus gigas*). Proc Gulf Carib Fish Inst. 57:763–770.

Davis M, Mitchell BA, Brown JL. 1984. Breeding behavior of the queen conch *Strombus gigas* Linne held in a natural enclosed habitat. J Shellfish Res. 4:17–21.

Delgado GA, Bartels CT, Glazer RA, Brown-Peterson NJ, McCarthy KJ. 2004. Translocation as a strategy to rehabilitate the queen conch (*Strombus gigas*) population in the Florida Keys. Fish Bull. 102:278–288.

Egan BD. 1985. Aspects of the reproductive biology of *Strombus gigas.* MS thesis, University of British Columbia. 147 p.

Frank K, Brickman D. 2000. Allee effects and compensatory population dynamics within a stock complex. Can J Fish Aquat Sci. 57:513–517. http://dx.doi.org/10.1139/f00-024

Gaines SD, Gaylord B, Largier JL. 2003. Avoiding current oversights in marine reserve design. Ecol Appl. 13:S32–S46. http://dx.doi.org/10.1890/1051-0761(2003)013[0032:ACOIMR]2.0.CO;2

Gascoigne J, Berec L, Gregory S, Courchamp F. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. Popul Ecol. 51:355–372. http://dx.doi.org/10.1007/s10144-009-0146-4

Gascoigne J, Lipcius RN. 2004a. Allee effects in marine systems. Mar Ecol Prog Ser. 269:49–59. http://dx.doi.org/10.3354/meps269049

Gascoigne J, Lipcius RN. 2004b. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. Mar Ecol Prog Ser. 284:185–194. http://dx.doi.org/10.3354/meps284185

Halpern BS. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol Appl. 13(1 Suppl):S117–S137. http://dx.doi.org/10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2

Hutchings JA. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci. 62:824–832. http://dx.doi.org/10.1139/f05-081

Jones GP, Srinivasan M, Almany GR. 2007. Population connectivity and conservation of marine biodiversity. Oceanography. 20:100–111.

Kaplan DM, Botsford LW, O'Farrell MR, Gaines SD, Jorgensen S. 2009. Model-based assessment of persistence in proposed marine protected area designs. Ecol Appl. 19:433–448. PMid:19323201. http://dx.doi.org/10.1890/07-1705.1

Kininmonth S, Beger M, Bode M, Peterson E, Adams VM, Dorfman D, Brumbaugh DR, Possingham HP. 2011. Dispersal connectivity and reserve selection for marine conservation. Ecol Model. 222:1272–1282. http://dx.doi.org/10.1016/j.ecolmodel.2011.01.012

Law R. 2000. Fishing, selection, and phenotypic evolution. ICES J Mar Sci. 57:659–668. http://dx.doi.org/10.1006/jmsc.2000.0731

Lubchenco J, Palumbi SR, Gaines SD, Andelman S. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecol Appl. 13:S3–S7. http://dx.doi.org/10.1890/1051-0761(2003)013[0003:PAHITO]2.0.CO;2

Lundquist CJ, Botsford LW. 2011. Estimating larval production of a broadcast spawner: the influence of density, aggregation, and the fertilization Allee effect. Can J Fish Aquat Sci. 68:30–42. http://dx.doi.org/10.1139/F10-125

Martin-Mora E, James F, Stoner A. 1995. Developmental plasticity in the shell of the queen conch, *Strombus gigas*. Ecology. 76:981–994. http://dx.doi.org/10.2307/1939361

Melville-Smith R, de Lestang S. 2006. Spatial and temporal variation in the size at maturity of the western rock lobster *Panulirus cygnus* George. Mar Biol. 151:183–195. http://dx.doi.org/10.1007/s00227-006-0349-6

Miethe T, Dytham C, Dieckmann U, Pitchford JW. 2009. Marine reserves and the evolutionary effects of fishing on size at maturation. ICES J Mar Sci. 67:412–425. http://dx.doi.org/10.1093/icesjms/fsp248

Peduzzi PN, Holford TR, Hardy RJ. 1980. A stepwise variable selection procedure for nonlinear regression models. Biometrics. 36:511–516. PMid:7213912. http://dx.doi.org/10.2307/2530219

Ray M, Stoner AW. 1994. Experimental analysis of growth and survivorship in a marine gastropod aggregation: balancing growth with safety in numbers. Mar Ecol Prog Ser. 105:47–59. http://dx.doi.org/10.3354/meps105047

Roberts CM, Polunin NVC. 1991. Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fish. 1:65–91. http://dx.doi.org/10.1007/BF00042662

Shelton PA, Healey BP. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? Can J Fish Aquat Sci. 56:1521–1524. http://dx.doi.org/10.1139/cjfas-56-9-1521

Sobel J, Dahlgren C. 2004. Marine reserves: a guide to science, design, and use. Washington DC: Island Press.

Stephens PA, Sutherland WJ. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol. 14:401–405. http://dx.doi.org/10.1016/S0169-5347(99)01684-5

Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is the Allee effect? Oikos. 87:185–190. http://dx.doi.org/10.2307/3547011

Stoner A, Davis M. 2010. Queen conch stock assessment: historical fishing grounds, Andros Island, Bahamas, June 2010. Technical report to The Nature Conservancy, Northern

Caribbean Office, Nassau, The Bahamas. 15 p., plus appendices. Available from: http://www.communityconch.org.

Stoner A, Davis M, Booker C. 2009. Queen conch stock assessment: Proposed MPA and fishing grounds, Berry Islands, Bahamas. Technical report to the Department of Marine Resources, Nassau, The Bahamas, October 2009. 49 p. Available from: http://www.communityconch.org

Stoner AW. 2003. What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. Mar Ecol Prog Ser. 257:275–289.

Stoner AW, Glazer RA. 1998. Variation in natural mortality: implications for queen conch stock enhancement. Bull Mar Sci. 62:427–442.

Stoner AW, Ray M. 1996. Queen conch (*Strombus gigas*) in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. Fish Bull. 94:551–565.

Stoner AW, Ray-Culp M. 2000. Evidence for Allee effects in an overharvested marine gastropod: density-dependent mating and egg production. Mar Ecol Prog Ser. 202:297–302. http://dx.doi.org/10.3354/meps202297

Stoner AW, Sandt VJ. 1992. Population structure, seasonal movements and feeding of queen conch, *Strombus gigas*, in deep-water habitats of The Bahamas. Bull Mar Sci. 51:287–300.

Stoner AW, Sandt VJ, Boidron-Metairon IF. 1992. Seasonality of reproductive activity and abundance of veligers in queen conch, *Strombus gigas*. Fish Bull. 90:161–170.

Torroglosa EM, Giménez J. 2010. Temporal variation in size at maturity of the snail *Zidona dufresnei* from the southwestern Atlantic Ocean after ten years of fishery exploitation. Aquat Biol. 11:163–167. http://dx.doi.org/10.3354/ab00306

Valle-Esquivel M. 2003. Aspects of the population dynamics, stock assessment, and fishery management strategies of the queen conch, *Strombus gigas*, in the Caribbean. PhD dissertation, University of Miami. 338 p.

Walsh MR, Munch SB, Chiba S, Conover DO. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecol Lett. 9:142–148. PMid:16958879. http://dx.doi.org/10.1111/j.1461-0248.2005.00858.x

Zheng J. 2008. Temporal changes in size at maturity and their implications for fisheries management for Eastern Bering Sea Tanner crab. J Northw Atl Fish Sci. 41:137–149. http://dx.doi.org/10.2960/J.v41.m623

Addresses: (AWS) *Fisheries Behavioral Ecology Program, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 2030 S. Marine Science Drive Newport, Oregon 97365.* (MHD) *Community Conch, 5050 S. Albion Street, Littleton, Colorado 80121.* (CB) *Community Conch, 304 E 49th Street, Savannah, Georgia 31405.* Corresponding Author: (AWS): *E-mail: <Al.Stoner@noaa.gov>.*

BMS