

**Spawning stock density affects reproductive behavior in queen conch: mate-finding  
Allee effects in traditional fishing grounds and a marine protected area**

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**Abstract** Relationships between adult density and mating frequency in queen conch (*Strombus gigas*) were observed at three sites in the central Bahamas including one protected area (Exuma Cays) and two important fishing grounds. No mating was observed at any location with density  $< 56$  adults  $\text{ha}^{-1}$ , consistent with an earlier study suggesting a mate-finding Allee effect in queen conch. The protected site had larger and older conch, and mating at that site increased rapidly with adult density to an average level of 13.7% of the population for locations with densities  $> 100$  adults  $\text{ha}^{-1}$ . Mating frequencies increased more slowly with density at the fishing grounds, to 6.3% in the Berry Islands and just 2.3% at Andros Island. A 90% probability of observing mating occurred at 100, 345, and 570 mature adults  $\text{ha}^{-1}$  in the Exuma Cays, Andros Island and the Berry Islands, respectively. Shifts to the right in mating probability curves for the heavily fished areas were associated with the presence of small, thick-shelled adults. The threshold below which reproduction becomes density dependent may be substantially higher for queen conch in fishing grounds than in protected areas because of disturbances to natural population structure, compounding the density effect.

## Introduction

One of the benefits associated with marine protected areas is the preservation of natural population structures such as density, size, and age distributions. Positive effects of density are often referred to as Allee effects, while negative rates of population growth that occur below a critical population size or density are termed depensation (Stephens and Sutherland 1999; Courchamp et al. 2008). Allee effects are often divided into those related to some directly observed component 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 insure a stable fishery. With the demise of important fishery resource species around the world, we are increasingly aware 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). 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).

Appeldoorn (1988a) pointed out the possibility of depensatory mechanisms in reproduction of the economically important gastropod *Strombus gigas* (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  $\text{ha}^{-1}$ , 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 of 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 areas with an earlier study focused in a large protected area (Stoner and Ray-Culp 2000).

## **Materials and methods**

### Study sites

Surveys for adult conch and their mating behavior were conducted at three different locations in the central Bahamas including the Exuma Cays, Berry Islands, and Andros Island (Fig. 1). The Exuma Cays site was located in the middle of the Exuma Cays Land and Sea Park, 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 years prior to the survey. Stoner and Ray (1996) described the habitat and queen conch distributions (juvenile and adult), and considered the conch population near the Park center to be relatively undisturbed. Observations used in this study were made on the island shelf east of Cistern Cay and Waderick Wells Cay in depths 11 to 19 m (mean = 12 m) on bare sand habitat where queen conch are abundant and where reproductive behavior is commonly observed. The data for this study were collected from 12 to 29 July 1995, and this new investigation represents an expanded and comparative analysis of the collections reported by Stoner and Ray-Culp (2000). Bottom water temperature for this site ranged 27.5 to 28.2°C.

A historically important fishing ground on the south edge of the Berry Islands bank was surveyed during a month-long period from 6 June to 10 July 2009. Adults in this region were abundant on the shallow bank in both sand and hard-bottom habitat in depths of 2 to 13 m (mean = 5 m), and mating behavior was observed over that range of environment. Bottom water temperature ranged from 26.6 to 31.9°C.

A third survey site was located in an important fishing ground at the south end of Andros Island near the Grassy Creek Cays and Pidgeon Cays. Adult conch were surveyed over a depth range of 2 to 9 m (mean = 5 m) in sand, seagrass (primarily *Thalassia testudinum*) and hard-bottom habitats. Andros surveys were conducted 23 May to 5 June 2010, and bottom water temperatures ranged from 26.1 to 28.3°C.

While adult conch were abundant on the broad 11 to 19 m deep shelf east of the Exuma Cays, equivalent habitat near the fishing grounds 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, not on specific habitat features, to yield the best possible assessment of the relationships between spawner density and mating behavior.

Starting dates for the surveys varied by almost seven weeks (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 three survey periods to elicit maximum mating behaviors.

### Survey methods

Densities of adult conch and the frequency of mating behavior were estimated in highly replicated surveys at each of the study sites. Methods for the Exuma Cays site 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 radius. Fifty-four diver surveys were dispersed evenly over an area of ~40 km<sup>2</sup> in the habitat described above. At the Berry Islands and Andros Island fishing grounds surveys were dispersed systematically over a grid of 1° blocks of latitude and longitude (~3.10 km<sup>2</sup> 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 dispersed over

~210 and 180 km<sup>2</sup> in the Berry Islands and Andros Island surveys, respectively. At each location numbers of adults observed by divers were counted in the predetermined survey areas 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 measurements provide insight into the age and sexual maturity of queen conch. Approximately 3.5 years after larval settlement, individuals reach terminal shell length (ranging ~140 to 300 mm) (Appeldoorn 1988b). At about this time, the edge of the shell lip turns outward to form the characteristic flared lip of the species. Following formation of the lip, the shell becomes thicker with time and tagging studies have shown that lip thickness provides a relative index for conch age and maturity (Egan 1985; Appeldoorn 1988b; Stoner and Sandt 1992). While reproductive readiness does not occur until the shell lip reaches 8 to 10 mm, classifying queen conch with flared lips as adults, regardless of shell thickness, is the traditional convention, and legal take of queen conch in the Bahamas and in other nations requires only a flared shell lip.

Shell lip thickness can not be measured routinely during towed diver surveys for density; therefore, measurements of shell length and lip thickness (see Appeldoorn 1988b) were collected by scuba divers after the adult distributions were characterized for each study site. Measurements were taken with Vernier calipers for 30 to 45 conch with flared shell lips at 9 to 12 locations dispersed throughout each site. Then, densities of conch in the surrounding surveys could be calculated to reflect all adults (by traditional definition) and mature adults (using the proportion of individuals with lip thickness  $\geq 10$  mm). The latter classification eliminated the problem of “delayed functional maturity” identified by Gascoigne and Lipcius (2004b), whereby including immature individuals in a count can result in an underestimate of mating frequency.

## Analysis

The primary purpose of this study was to evaluate the relationship between adult conch density and mating frequency. Conch counts were standardized to numbers of adults (or

mature adults) per hectare and mating frequency was calculated as the percent of adult population engaged in mating behavior.

Logistic regression was used to evaluate possible relationships between conch mating and differences at the protected (Exuma Cays) and unprotected (Berry Islands and Andros Island) sites. 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 12 (SYSTAT Software, Inc., San Jose, CA) (Peduzzi et al. 1980). The model for mating behavior was described by the following equation:

$$\log_e(p/(1-p)) = \alpha + \beta x, \text{ where}$$

$p$  = proportion of  $y = 1$ ,

$y = 1$  if mating occurred, and 0 if no mating occurred,

$\alpha$  = intercept,

$\beta$  = model coefficient (slope), and

$x$  = the independent variable (i.e., adult density values).

The maximum likelihood estimates for mating behavior ( $p$ ) were calculated as

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

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 (i.e., conch density). 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 were tested with standard ANOVA followed by Fishers LSD test for differences among means.

## Results

Observations on more than 13,000 adult queen conch over the three study sites yielded data on both density and mating behavior (Table 1). Overall density of adults was approximately twice as high at the Exuma Cays site (209 adults ha<sup>-1</sup>) as at the two fishing grounds (116 to 117 adults ha<sup>-1</sup>). Shell lengths varied significantly across the three study

sites (ANOVA,  $F_{(2,112)} = 61.303$ ,  $P < 0.001$ ) (Table 1) despite a wide range of size at each (Fig. 2). Conch in the shelf waters of the Exuma Cays, averaging 206 mm, were larger than those at the other sites, 156 mm and 177 mm in the Berry Islands and at Andros Island, respectively. Shell lengths at the three sites were all significantly different (Fisher's LSD test,  $P < 0.001$ ). Shell lip thickness also varied significantly across the study sites ( $F_{(2,112)} = 37.996$ ,  $P < 0.001$ ) (Table 1; Fig. 3). Mean values in the Berry Islands and at Andros Island (15 mm at both sites) were not different (Fisher's LSD test,  $P = 0.854$ ), but significantly smaller than the average value observed in the Exuma Cays (mean = 26 mm) ( $P < 0.001$ ). Only one individual measured in the Exuma Cays had lip thickness  $< 10$  mm, while the proportions of conch likely to be immature 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 never observed at the protected Exuma Cays study site.

Mating behavior was observed in all three survey sites and ranged from 0% to 34% of the adult queen conch at any one count. More than 10% of the conch observed in the Exuma Cays were engaged in mating behavior, while only about 2% of the populations observed at the two fishing grounds were mating (Table 1). When the adult counts were corrected for mature individuals ( $\geq 10$  mm lip thickness), mating frequencies at the Berry Islands and Andros sites rose to 5.3% and 2.4%, respectively. The occurrence of mating behavior was clearly density dependent (Fig. 4). In fact, no mating whatsoever was observed in 89 surveys where adult density was below 56 adults  $\text{ha}^{-1}$ . Lowest density for mating was 56 adults  $\text{ha}^{-1}$  for both the Exuma Cays and Berry Islands spawning grounds and 78 adults  $\text{ha}^{-1}$  for the Andros Island spawning ground. The occurrence of mating increased rapidly at levels higher than  $\sim 100$  adults  $\text{ha}^{-1}$ , particularly in the Exuma Cays, but mating frequency was highly variable both within and among the study sites (Fig. 4). When compared across sites considering only those locations with densities  $> 100$  adults  $\text{ha}^{-1}$  the Exuma Cays had an average mating frequency of 13.7% (SD = 7.6,  $n = 32$ ) which was significantly higher than frequencies observed at the Berry Islands (mean = 5.2, SD = 5.8,  $n = 15$ ) and at Andros Island (mean = 2.2, SD = 2.7,  $n = 23$ ) (ANOVA,

$F_{(2,67)} = 27.172$ ,  $P < 0.001$ ). Mating frequencies at the latter two sites were not different (Fisher's LSD test,  $P = 0.134$ ). When only mature conch were considered the mating frequencies increased slightly in the Berry Islands (mean = 6.3, SD = 6.0,  $n = 13$ ) and at Andros Island (mean = 2.3, SD = 2.7,  $n = 22$ ), but the statistical outcome was the same ( $F_{(2,64)} = 24.286$ ,  $P < 0.001$ ), with no difference between the two fishing grounds (Fisher's LSD test,  $P = 0.06$ ).

Logistic regression was used to explore the relationship between conch density and the probability of observing mating considering all conch with a flared shell lip and those classified as sexually mature (i.e., shell lip thicknesses  $\geq 10$  mm) (Tables 2 to 4). Mating probability was closely associated with adult density at all of the survey sites. The relationships for mature adults were described by distinctly sigmoid functions at all sites but the shape of the curves varied substantially (Fig. 5). An analogous plot for all adults (not shown) was almost identical to that for mature adults in the Berry Islands, but for Andros conch, the plot for all adults laid to the right of that for mature adults because of the lower density (i.e., slope) parameter (Table 4). Probability of mating near the Exuma Cays increased rapidly after about 56 adults  $\text{ha}^{-1}$  and reached an asymptote near 110 adults  $\text{ha}^{-1}$ . The rise in mating probability was much slower in the two fishing grounds. Fifty percent probability of observing mating occurred at 70, 180, and 300 adults  $\text{ha}^{-1}$  for the Exuma Cays, Andros Island, and Berry Islands sites, respectively. Ninety percent probability occurred at 100, 350, and 570 adults  $\text{ha}^{-1}$ , respectively. Therefore, the logistic models were consistent with obvious thresholds of density-dependent mating frequency seen in Fig. 4.

Quality of the logistic models can be evaluated with prediction success matrices. The best fit occurred with data from the Exuma Cays where 94.4% of the predicted behaviors (presence or absence of mating) were correct (Table 2). Model success was lowest (74.5%) for the Andros Island surveys (Table 4) where incorrect predictions for both the presence and absence of mating occurred. At all three sites, predictions of no mating were more accurate ( $> 87\%$  correct in all cases) than predictions for mating, and the occurrence of mating behavior was under-predicted by the models to varying degrees.

## Discussion

Stoner and Ray-Culp (2000) reported 56 adults  $\text{ha}^{-1}$  as the lower threshold for mating in queen conch in the Exuma Cays, 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 (56 and 78 adults  $\text{ha}^{-1}$ ) were similar to the earlier estimate, and the observed lower threshold for mating appears to be robust. However, these density values represent the absolute minima for reproduction, and it is more important for management purposes to consider mating behavior above the lower threshold. Mating frequencies above the threshold were highly variable at each site, and the apparent asymptotes were substantially different. The most troubling result was that mating frequency at Andros Island and the Berry Islands fishing grounds leveled off at just 6.3% and 2.3% of mature adults, compared with 13.7% in the Exuma Cays. Also, logistic models showed that mating increased rapidly with density in the Exuma Cays where conch fishing is prohibited, reaching maximum level at just over 100 adults  $\text{ha}^{-1}$ . 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  $> 400$  adults  $\text{ha}^{-1}$ .

Density dependence in mating frequency is not surprising for an animal that needs to locate a partner for internal fertilization of eggs. McCarthy (1997) explained the probability of mate encounters in a randomly distributed population, and Stoner and Ray-Culp (2000) discussed likely search areas and how these might be modified by scent trails left by female conch. It is also possible that density affects reproductive behavior through physiological mechanisms. Appeldoorn (1988a) provided circumstantial evidence that contact with males can stimulate gametogenic activity in female strombids, and spawning females are more likely to copulate than non-spawning females. Strongest evidence for this indirect effect of density was provided for populations of milk conch, *Strombus costatus*, and fighting conch, *S. pugilis*. These mechanisms have not been explored quantitatively for *S. gigas*, but it is clear that they are likely and would exacerbate the more direct mate-finding effects of low density on conch reproduction.

The topic of mate-finding Allee effect, including evolutionary implications, was well covered in a recent comprehensive review (Gascoigne et al. 2009).

While density-dependence in queen conch mating is no longer 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, or maturity structures of the conch populations. Both of the fishing grounds surveyed were shallower than the the Exuma Cays site, and it is possible that variables such as bottom type or wave energy might impact the observed behavioral frequencies. However, all of the study sites offer high abundance of the algal foods typical of queen conch diets, and nutritional differences among them seem unlikely. Similarly, none of the sites surveyed had bottom types that would inhibit locomotion or mate finding.

In the Florida Keys, poor habitat quality associated with pollutants in the nearshore environment of the Florida Keys results in poorly developed gonads in queen conch (Glazer and Quintero 1998; McCarthy et al. 2002). However, poor water quality or polluted sediments are not likely to be a major concern in the relatively isolated and undisturbed habitats that characterize the Andros and Berry Islands fishing grounds. A sporozoan infection (*Coccidian* sp.) that causes histological deficiencies in the reproductive organs has been identified in queen conch in Mexico (Castro-Gonzalez et al. 2007), but the ecological consequences have not been explored.

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 in the contrast between the Exuma Cays and the two fishing grounds. First, the Exuma conch were about 32% larger in shell length than those in the Berry Islands, which are among the very smallest adults known for the species' geographic range (Stoner, pers. observ.). The size, shape, and spination patterns of juvenile queen conch are highly susceptible to local environment (Martín-Mora et al. 1996), and it is possible that conch in Andros and the Berry Islands fishing grounds grow slowly because of cool winter temperatures on the shallow bank habitat (compared with more stable deep-water habitats off the Exuma Cays). Second, the unfished Exuma Cays population had an average shell lip thickness nearly twice that observed at the fishing grounds.

Consequently, the Exuma conch were probably 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 commonly 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 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; Appeldoorn 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. It is equally intriguing to determine whether the small phenotype is related to environmental conditions or might result from long-term fishing pressure.

There is now ample proof that a component Allee effect occurs in queen conch (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004b; this study), but the demographic consequences of the effect are completely unknown. A logical next step will be to test how mating history in individuals and mating frequency in spawning populations translates to numbers of viable eggs 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. Queen conch is an ideal test species for reproductive studies because mating can be quantified precisely and egg masses are large and demersal.

Regardless of the exact mechanisms for density-dependent reproductive behavior in queen conch the fishery management implications are obvious, and we agree with Gascoigne and Lipcius (2004a) that including Allee effects in population models will be critical for precautionary management of this threatened species. The primary imperative must be to increase the density of mature conch over sufficient space to provide progeny for a sustainable fishery. First, it is clear that a no-take fishery reserve in the appropriate

location can help to preserve a naturally high density of spawning stock comprising large adults old enough to yield high reproductive output (Stoner and Ray 1996). Such a reserve should contain both nurseries and spawning grounds as in the Exuma Cays Land and Sea Park. Second, largest and oldest queen conch tend to accumulate in deep-water environment in the Bahamas (Stoner and Schwarte 1994; Stoner et al. 2009) and in other Caribbean locations. Gear that allows deep-diving for conch (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. Third, queen conch are managed by size or shell-lip criteria in most nations of the Caribbean (Aldana-Aranda and Frenkiel 2005), and we have been reminded repeatedly 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. This, of course, would necessitate landing conch in the shell, which is not currently required in most locations. Fourth, 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 and a fishing closure during reproductive season combined with 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 an average abundance of ~18,000 adults in the 1990s to ~34,000 in the 2000s (R.A. Glazer, pers. comm.). In comparison, 208,000 adult conch were estimated for an 8-km-long segment of the shelf edge (22 km<sup>2</sup>) in the center of the Exuma Cays Land and Sea Park (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 and increasing their density to gain a positive 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.

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**Table 1** Summary of surveys made for adult queen conch at three spawning grounds in The Bahamas. Population characteristics and mating frequencies are reported for each study site. Values for conch density, shell length and shell lip thickness are mean  $\pm$  SD. Ranges of values are shown in Figs. 2 and 3

Study site	Exuma Cays	Berry Islands	Andros Island
Total surveys	54	68	58
Surveys with adult conch	54	48	47
No. adult conch observed	4262	4742	4075
Range of density observed (no. ha <sup>-1</sup> )	2 - 2793	0 - 1717	0 - 643
Mean density of adult conch (no. ha <sup>-1</sup> )	209 $\pm$ 394	116 $\pm$ 292	117 $\pm$ 162
Number of mating conch	444	230	80
% of conch mating	10.4	1.9	2.0
% of mature conch mating	10.4	5.3	2.4
No. of shell measurements	40	45	30
Shell length (mm)	206 $\pm$ 18	156 $\pm$ 19	177 $\pm$ 27
Shell lip thickness (mm)	26 $\pm$ 7	15 $\pm$ 6	15 $\pm$ 7

**Table 2** Results of logistic modeling for mating in *Strombus gigas* (queen conch) in the Exuma Cays, Bahamas. The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively. All of the adults at this survey location were sexually mature (see text)

Parameter	Estimate	Z	P value
constant ( $\alpha$ )	-3.978	-2.636	0.008
adult density ( $\beta$ )	0.069	3.011	0.003

Field observation	Predicted observation			Actual total
	No mating	Mating		
No mating	39	1		40
Mating	2	12		14
Total predicted	41	13		54
Correct (%)	95.7	85.7		
Total correct (%)				94.4

**Table 3** Results of logistic modeling for mating in *Strombus gigas* (queen conch) in the Berry Islands, Bahamas. Logistic regressions were performed including all of the adults defined by a flared shell lip and for sexually mature adults (i.e., with lip thicknesses  $\geq 10$  mm). The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively, for mature adults

Parameter	Estimate	Z	P value	
All adults				
constant ( $\alpha$ )	-2.428	-4.128	<0.001	
adult density ( $\beta$ )	0.008	2.945	0.003	
Mature adults				
constant ( $\alpha$ )	-2.382	-4.122	<0.001	
adult density ( $\beta$ )	0.008	2.939	0.003	
Predicted observation				
Field observation	No	mating	Mating	Actual total
No mating	34		2	36
Mating	6		6	12
Total predicted	40		8	48
Correct (%)	94.4		50.0	
Total correct (%)				83.3

**Table 4** Results of logistic modeling for mating in *Strombus gigas* (queen conch) at Andros Island, Bahamas. Logistic regressions were performed including all of the adults defined by a flared shell lip and for sexually mature adults (i.e., with lip thicknesses  $\geq 10$  mm). The percentages of correctly predicted mating and non-mating observations (based upon observed counts) represent indices of model sensitivity and specificity, respectively, for mature adults

Parameter	Estimate	Z	P value	
All adults				
constant ( $\alpha$ )	-2.321	-3.617	<0.001	
adult density ( $\beta$ )	0.011	3.177	0.001	
Mature adults				
constant ( $\alpha$ )	-2.321	-3.617	<0.001	
adult density ( $\beta$ )	0.013	3.176	0.001	
Predicted observation				
Field observation	No	mating	Mating	Actual total
No mating	27		4	31
Mating	8		8	16
Total predicted	35		12	47
Correct (%)	87.1		50.0	
Total correct (%)				74.5

## List of Figures

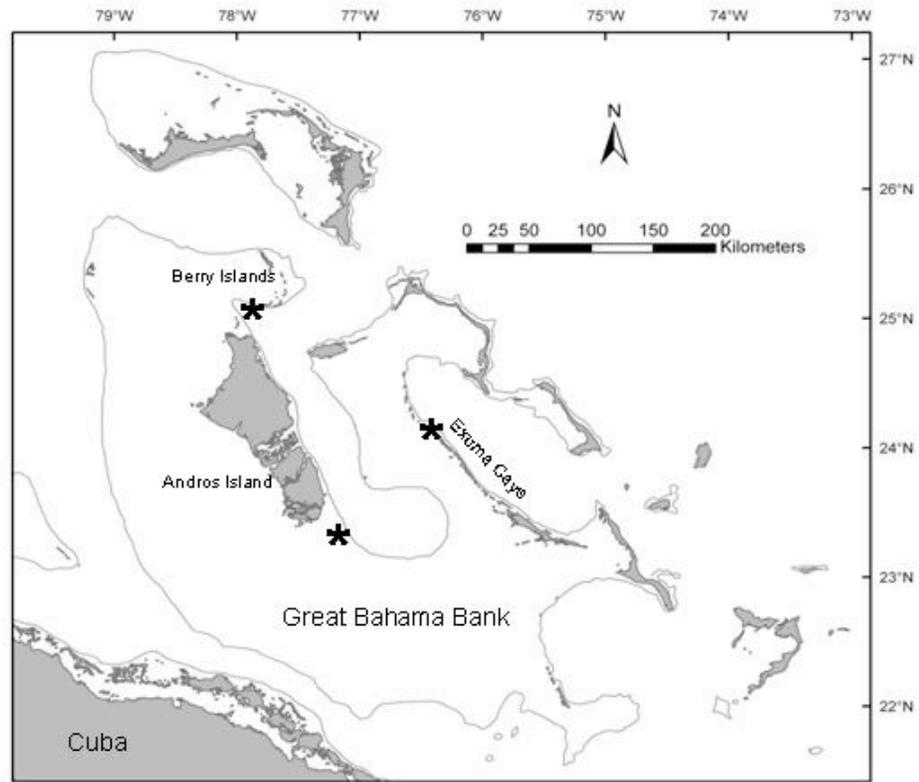
**Fig. 1** Map of the northern and central Bahamas showing the general locations of three study sites in the Exuma Cays, Berry Islands, and Andros Island. The first site is located in Exuma Cays Land and Sea Park, a no-take marine fishery reserve. The other two sites are historically important fishing grounds. 200-m isobaths surrounding the shallow banks are shown

**Fig. 2** Frequency distribution of shell length for queen conch at three sites in the Bahamas. Each vertical bar represents a 10-mm range of lengths (e.g., 120 to 129 mm, 130 to 139 mm, etc.). The data represent all individuals possessing a flared shell lip in the traditional definition of adults, but this includes some sexually immature individuals (see text).  $n$  is the number of measurements for each of the study sites

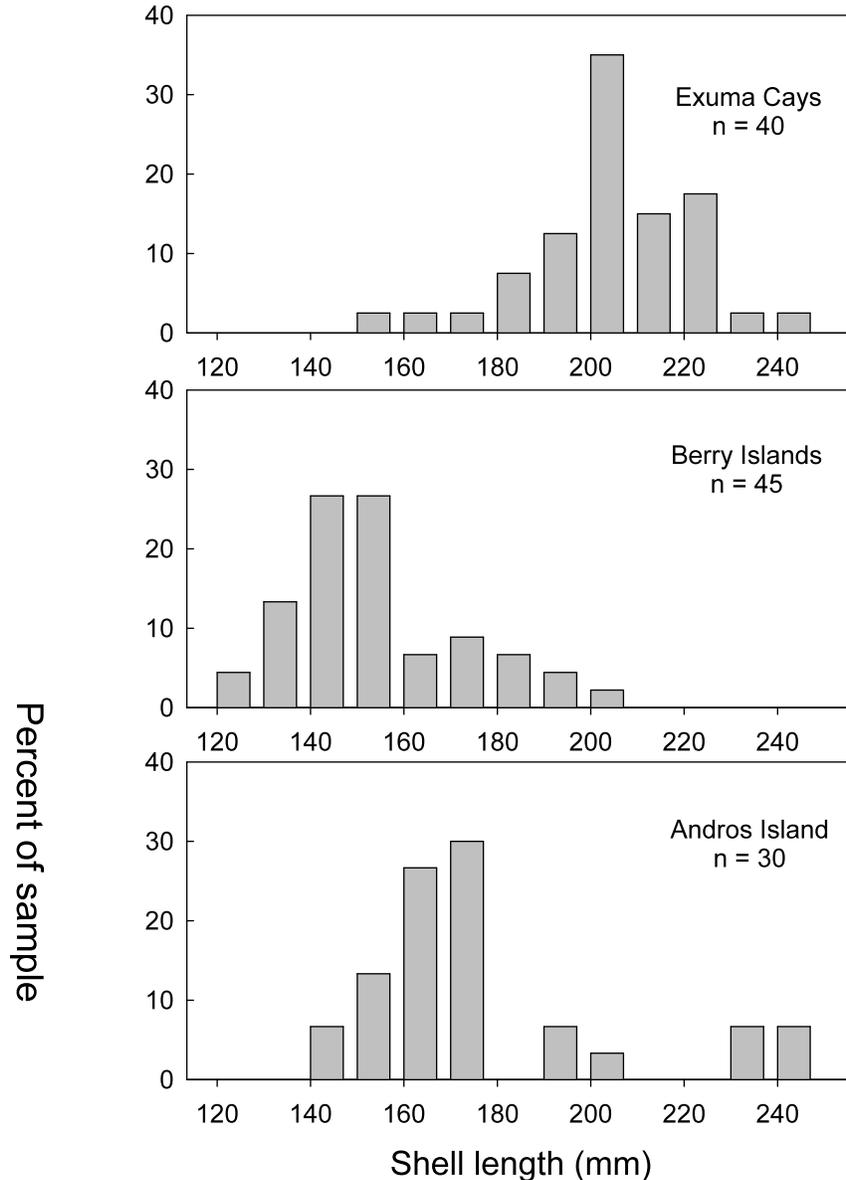
**Fig. 3** Frequency distribution of shell lip thickness for queen conch at three sites in the Bahamas. Each vertical bar represents a 4-mm range of thickness values (e.g., 0 to 3 mm, 4 to 7 mm, etc.). Growth in shell length ends at sexual maturity, and lip thickness provides a relative index of conch age. Some thin-shelled individuals were not sexually mature (see text).  $n$  is the number of measurements for each of the study sites

**Fig. 4** Association between mating frequency in queen conch and density of adults (defined by a flared shell lip) 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

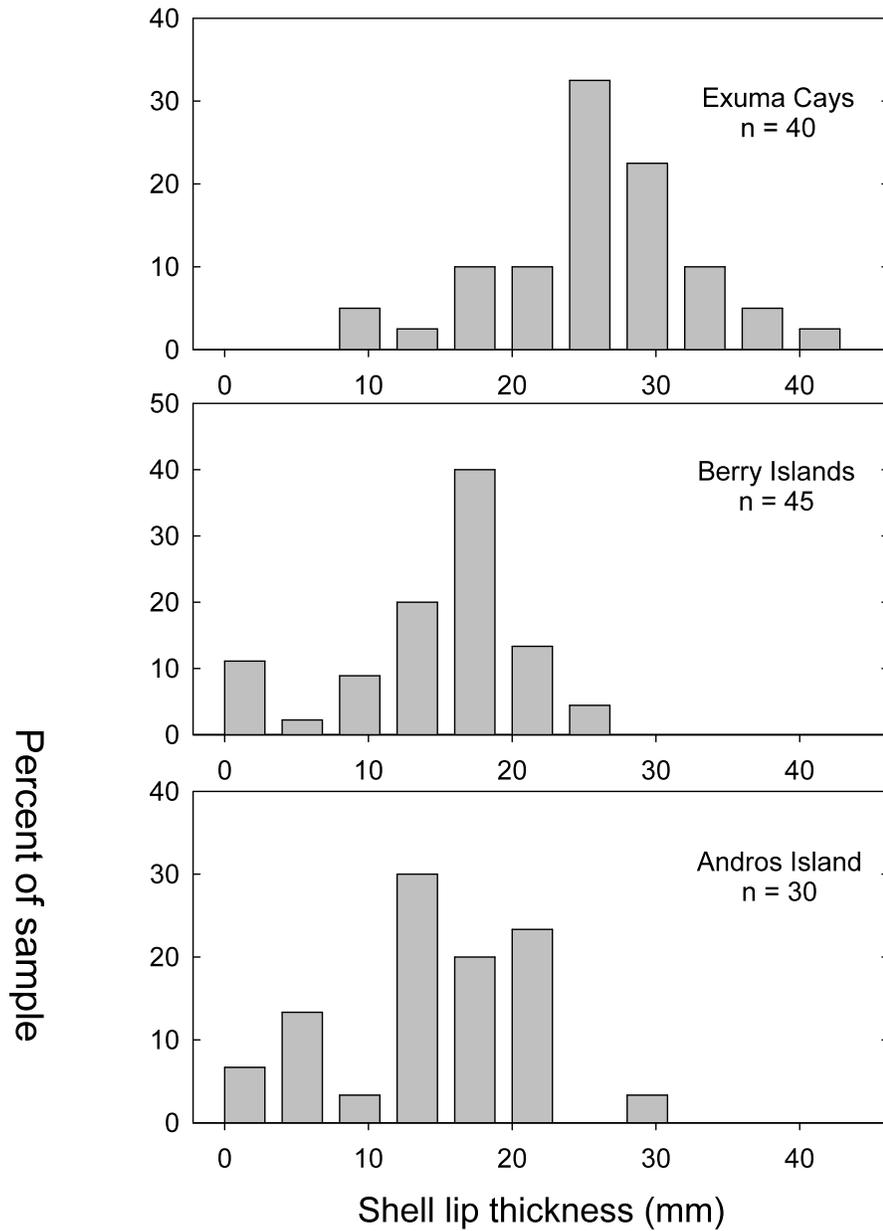
**Fig. 5** Logistic regression curves showing relationships between the density of mature adult queen conch (shell lip thickness  $\geq 10$  mm) and the probability of observing mating behavior. Results are shown for three different study sites in the Bahamas. The Exuma Cays site was surveyed in the center of a no-take marine reserve, and the other two sites represent historically important fishing grounds where fishing pressure is high



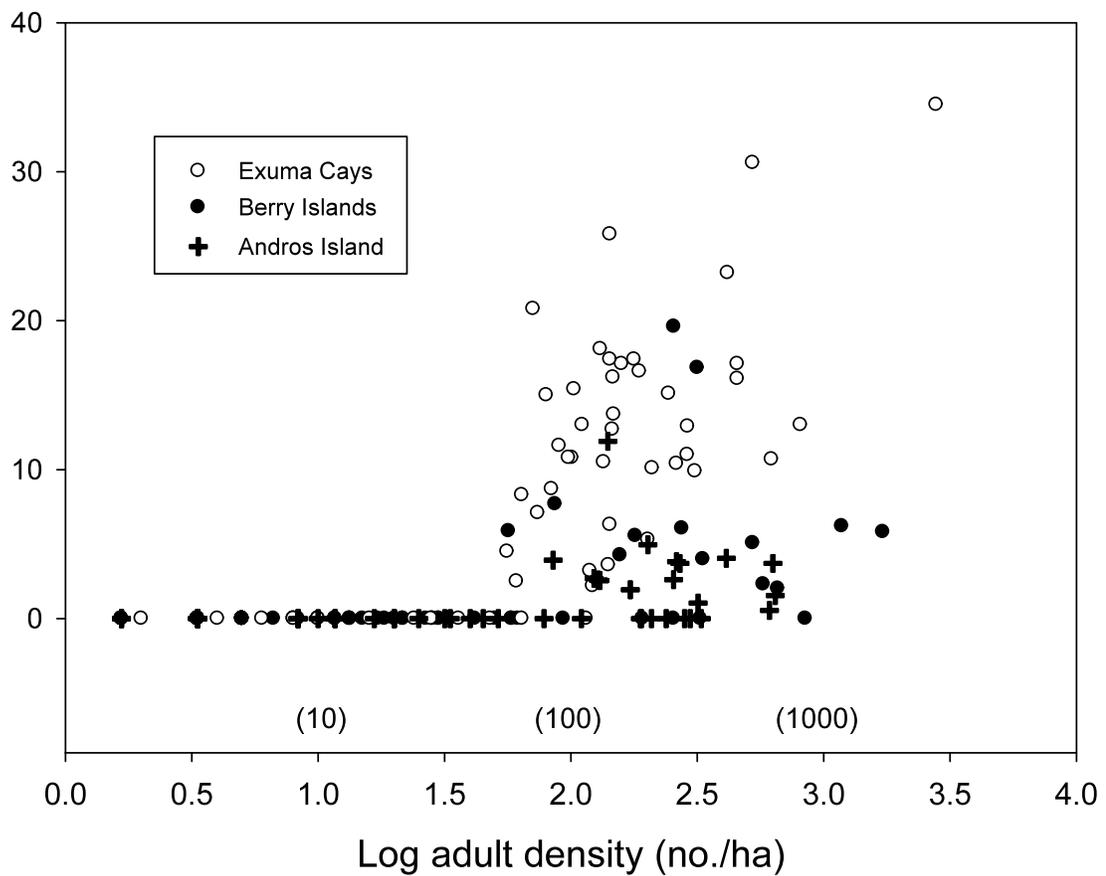
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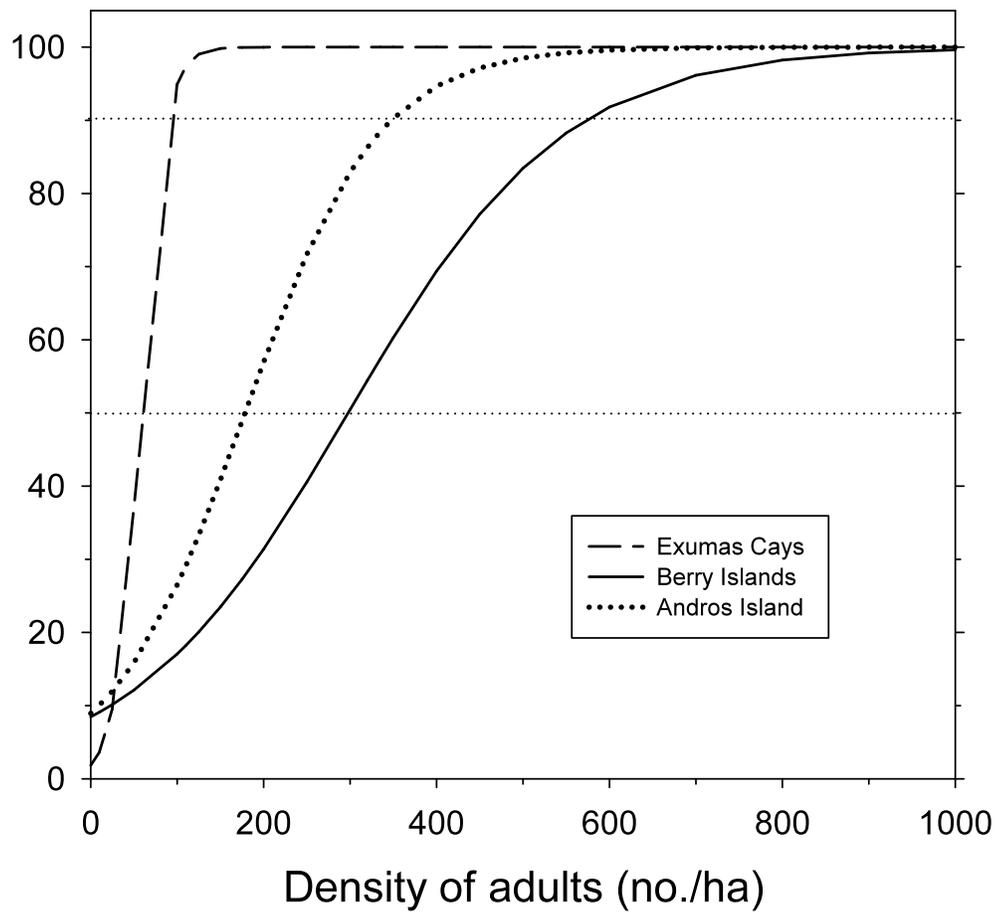
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