Negative Consequences of Allee Effect are Compounded by Fishing Pressure on Queen Conch

Las Consecuencias Negativas del Efecto de Allee son Sompuestas Pescando la Presión sobre la Concha de la Reina

Des Conséquencias Negativas de l'éffet d'Allee sont Composés en Pêchant la Pression sur la Lambi

ALLAN W. STONER[1], MARTHA H. DAVIS[2], and CATHERINE J. BOOKER[3]
[1]*NOAA Fisheries Alaska Fisheries Science Center, 2030 S. Marine Science Drive, Newport, Oregon 97365 USA.* allan.stoner@gmail.com.
[2]*Community Conch, 5050 S. Albion St Littleton, Colorado 80121 USA* marthadavis@communityconch.org.
[3]*Community Conch 304 E 49th St. Savannah Georgia 31405 USA.* catherinebooker@communityconch.org.

ABSTRACT

Relationships between density of mature adults and mating frequency in queen conch 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, which is consistent with the established occurrence of a mate-finding Allee effect in queen conch. The unfished reserve site had larger and older conch with 10% of adults mating, and mating frequency increased rapidly with adult density. Logistic modeling showed that a 90% probability of mating occurred at 100 adults/ha. Mating frequencies increased more slowly with density on the fishing grounds, with 5.9% of the adult population mating in the Berry Islands and only 2.4% mating at Andros Island. A 90% probability of mating required 570 and 350 adults/ha, respectively, at those fishing grounds. Higher densities required for successful mating in the fished areas were associated with numerical dominance by small but thick-shelled adults representing a shift in population structure that is likely the result of selection imposed by fishing pressure. Lower mating frequencies were observed in populations dominated by this small adult phenotype, 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.

KEY WORDS: Queen conch, reproduction, Bahamas, fishing effects

INTRODUCTION

The possibility of depensatory mechanisms in queen conch (*Strombus gigas*) reproduction, whereby there might be a critical density for egg production, was pointed out long ago (Appeldoorn 1988a). In fact, 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 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, respectively. Since that time, others have attempted to test density dependence in queen conch reproduction in field experiments (Gascoigne and Lipcius 2004). 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. Complete methods and results for this study are provided by Stoner et al. (2012).

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 (Figure 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 years prior to the first survey in 1995. Observations were made on the island shelf east of Cistern Cay and Warderick 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. Data for the Exuma Park were collected from 12 to 29 July 1995. The Exuma Cays site was surveyed again from 7 to 14 July 2011, exploring a broader range of depth (4 to 29 m; mean = 14 m) on bare sand and hard-bottom. 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 to 13 m (mean = 5 m). 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 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. These two sites represent 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 free-diving from small boats and with increasing use of hookah systems (i.e., surface-supply air) in deeper locations.

Survey Methods and Analysis

Densities of adult conch 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 radius. Fifty-four diver surveys were dispersed evenly over an area of ~40 km^2 in the habitat described above. At the Berry Islands and Andros Island fishing grounds surveys were dispersed systematically over a grid of 1 minute blocks of latitude and longitude (~3.10 km^2 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 km^2 at the Berry Islands and Andros Island, respectively. 2011 surveys in the Exuma Cays site were conducted with a series of belt transects (as above) dispersed evenly over five depth strata in six lines running directly offshore from Warderick Wells Cay.

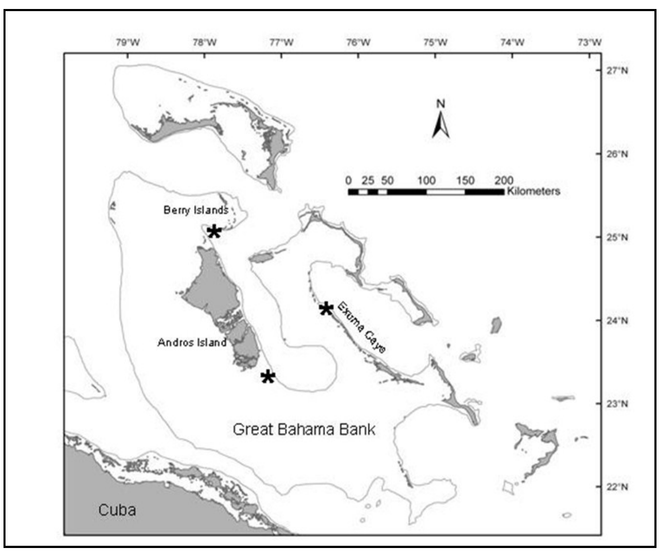

Figure 1. Map of the northern and central Bahamas showing the general locations of three study sites in the Exuma Cays, Berry Islands, and Andros Island. The first site is located in Exuma Cays Land and Sea Park, a no-take marine fishery reserve. The other two sites are historically important fishing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

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. Shell lip thickness is an indicator of 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 7 to 10 mm (Egan 1985, Aldana-Aranda and Frenkiel 2005), as long as six to ten months 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 this study. 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.

Logistic regression was used to evaluate the possible relationships between conch mating and mature conch density. Standard analysis of variance procedures were used to evaluate site differences in conch density and shell dimensions.

RESULTS

Observations on more than 13,000 queen conch with flared shell lips over the three study sites yielded data on conch density, occurrence of mating behavior, and size and age structure (Table 1). 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, and the overall site difference was not significant (ANOVA, p = 0.178). The average density at the Exuma Cays site in 2011 was marginally lower than that in 1995 (Fisher's test, p = 0.055), but a broader different range of habitat was surveyed in the second survey.

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 2.4%, respectively (Table 1). The occurrence of mating behavior was density dependent. In fact, no mating whatsoever was observed in 88 counts where adult density fell below 47 mature adults/ha. 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 in the Exuma Cays and at Andros Island. The occurrence of mating increased rapidly at levels higher than ~100 adults/ha, particularly in the Exuma Cays, but mating frequency was highly variable both within and among the study sites. Little to no mating was observed in many belt transects with high densities, particularly at the Berry Islands and Andros sites.

Logistic regression showed that the probability of mating was highly dependent upon density of mature conch for all of the survey sites (Figure 2). The relationships between adult conch density and the probability of observing mating behavior were described by sigmoid functions at all of the study sites but the shape of the curves varied substantially. During both 1995 and 2011, probability of mating near the Exuma Cays increased rapidly after about 50 adults/ha and reached an asymptote near 110 adults/ha. 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 1). Ninety percent probability occurred at 100, 350, and 570 adults/ha, respectively.

Shell lengths varied significantly across the three study sites (ANOVA, $p < 0.001$) despite a wide range of size at each (Figure 3). Conch in the Exuma Cays averaged 206 and 202 mm in the two surveys and they 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 were all significantly different (Fisher's LSD test, $p < 0.001$), while those at the Exuma Cays site did not change with time ($p = 0.370$). Shell lip thickness also varied significantly across the study sites ($p < 0.001$) (Figure 3). Mean values in the Berry Islands and at Andros Island (15 mm at both) were not different ($p = 0.836$), but

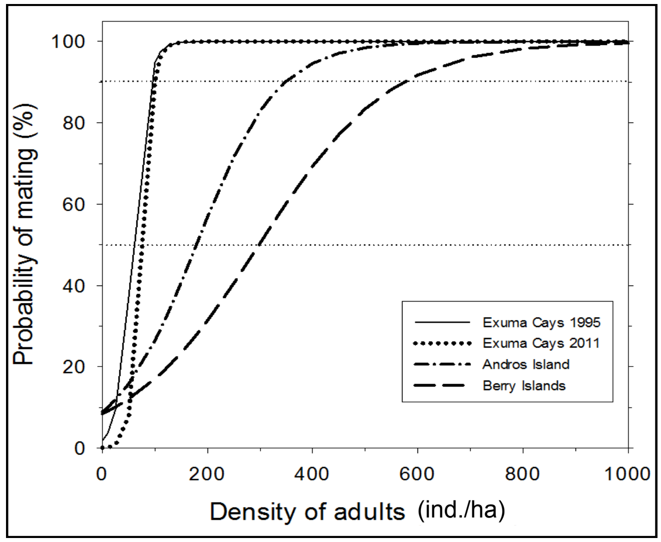

Figure 2. Logistic regression curves showing relationships between the density of mature adult queen conch (shell lip thickness ≥ 10 mm) and the probability of observing mating behavior at the Exuma Cays marine protected area in 1995 and 2011, and at two sites where fishing pressure is high.

significantly lower than the two average values observed in the Exuma Cays (26 - 28 mm) ($p < 0.001$). 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 unfished Exuma Cays study site. These are represented in the cloud of triangles (open and closed) laying on the left side of Figure 2, with shell lengths ranging from 130 to 170 mm and lip thickness ranging from 9 to 25 mm.

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, and Stoner and Ray-Culp (2000) discussed the relevance to queen conch. They also

Table 1. Summary of adult conch densities, mating frequencies, and density-related mating behavior in queen conch at three spawning grounds in The Bahamas. Density values reported in the last 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 Figure 2). Values for percentage of adult densities are mean ± SD.

Study site & survey year	Exuma Cays 1995	Exuma Cays 2011	Berry Islands 2009	Andros Island 2010
Mean density of adult conch (ind./ha)	209 ± 394	60 ± 83	131 ± 272	118 ± 139
% of adults mating	10.4	9.8	5.9	2.4
Lowest density observed for mating	56	74	47	64
50% probability	70	76	300	180
90% probability	100	100	570	350

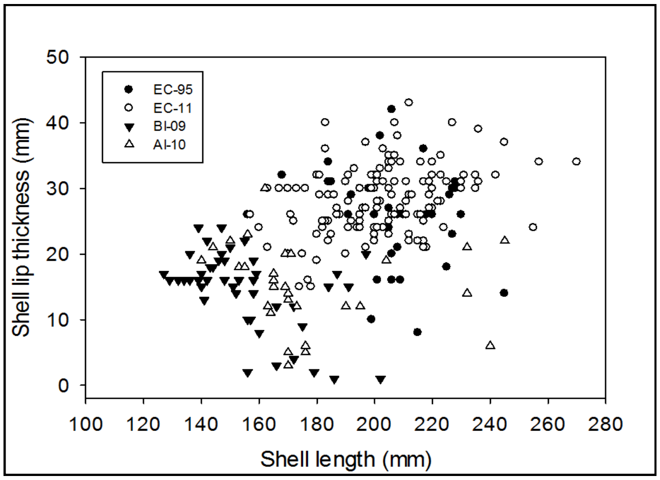

Figure 3. Length and lip thickness plots for the shells of adult queen conch at three study sites in the Bahamas. Shells were measured during two surveys in the Exuma Cays Land and Sea Park, in 1995 and 2011 (EC-95, EC-11), and in important fishing grounds in the Berry Islands in 2009 (BI-09) and near Andros Island in 2010 (AI-10).

reported that 56 mature adults/ha 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, it is more important for management purposes to consider mating behavior at higher levels. Logistic modelling showed that mating increased rapidly with density in the Exuma Cays, reaching the maximum level at just over 100 adults/ha. 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.

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. 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. 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 larger and older.

The obvious differences in mating probability function among the study sites provide strong impetus for future expanded analysis of size- and age-related variation in maturity, reproductive behavior, and fecundity in this important fishery species. More specifically, 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 in the Exuma Cays. We already know that a female conch with the average shell length and thickness observed in the Berry Islands fishing ground has a gonad weight less than one-quarter that of the average Exuma Cays female (Authors, Unpublished data).

Possible Effects of Fishing on Conch Phenotype

Declining average 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. Reflecting that trend, the no-take reserve surveyed in this 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.

i) 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.
ii) 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. Therefore, slow growth to maximum size may provide the most parsimonious explanation for small conch in the two fishing grounds.
iii) 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 at least one gastropod (*Zidona dufresnei*) which showed a significant decrease in size-at-maturity over a 10-year 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.

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. The primary imperative must be to maintain a high 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). However, we also know that a single reserve may not be self-sustaining, and new surveys in the Exuma Cays Land and Park show that adult densities declined significantly between 1994 and 2011 (Stoner et al. 2012). This speaks for a larger proportion of fishing grounds being incorporated into a reserve network 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 environment, and gear that allows deep-diving (e.g., hookah and scuba) should not be used in conch fishing. A long-term ban on 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, 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 2004, Aldana-Aranda and Frenkiel 2005). 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. Preliminary results in the Bahamas indicate that a minimum lip thickness will need to be about 10 mm (Authors, Unpublished data). Finally, fishing quotas that preserve high spawning stock density need to be instituted and enforced. Detailed analysis and simulation modeling (Valle-Esquivel 2003) indicate that the optimal management strategy for queen conch will include legal 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. 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.

ACKNOWLEDGMENTS

This study was supported with funds and logistical assistance from the National Undersea Research Program of NOAA (US Department of Commerce), the Bahamas Department of Marine Resources (DMR), the Bahamas National Trust, and The Nature Conservancy's Northern Caribbean Office. We are grateful to a long list of former employees at the Caribbean Marine Research Center (M Ray-Culp, E Bartels, L Hambrick, R Jones, N Mehta) and volunteers (L Anderson, J Dillet, H Bethel, A Davis, L Davis, K Finalyson, A McLean, T Thompson, and A M Vandenrydt, Vellacott) who assisted with the diving operations.

LITERATURE CITED

Aldana-Aranda, D. and L. Frenkiel. 2005. Lip thickness of *Strombus gigas* (Mollusca: Gastropoda) versus maturity: a management measure. *Proceedings of the Gulf and Caribbean Fisheries Institute* **58**:431-442.

Appeldoorn, R.S. 1988a . Fishing pressure and reproductive potential in strombid conchs: is there a critical stock density for reproduction? *Memoria Sociedad de Ciencias Naturales LaSalle* **48**:275-288.

Appeldoorn, R.S. 1988b. Age determination, growth, mortality, and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fisheries Research* **6**:363-378.

Bell, J.D., P. Rothisberg, J.L. Munro, N.R. Lonergan, W.J. Nash, R.D. Ward, and N.L. Andrew. 2005. *Restocking and Stock Enhancement of Marine Invertebrate Fisheries.* Elsevier Academic Press, San Diego, California USA.

Conover, D.O., S.A. Arnott, M.R. Walsh, and S.B. Munch. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries and Aquatic Science* **62**:730-737.

Daves, N. and J. Fields. 2004. Recent developments in CITES concerning the international trade in queen conch (*Strombus gigas*). *Proceedings of the Gulf and Caribbean Fisheries Institute* **57**:763-770.

Egan, B.D. 1985. Aspects of the reproductive biology of *Strombus gigas*. MS thesis, University of British Columbia, Vancouver, Canada. 147 pp.

Gascoigne, J. and R.N. Lipcius. 2004. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. *Marine Ecology Progress Series* **284**:185-194.

Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science* **62**:824-832.

Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57**:659-668.

Ray, M. and A.W. Stoner. 1994. Experimental analysis of growth and survivorship in a marine gastropod aggregation: balancing growth with safety in numbers. *Marine Ecology Progress Series* **105**:47-59.

Roberts, C.M. and N.V.C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* **1**:65-91.

Stoner, A. and M. Davis. 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., M. Davis, and C. Booker. 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, A.W., M.H. Davis, and C. Booker. 2012. Negative consequences of Allee effect are compounded by fishing pressure: comparison of queen conch reproduction in fishing grounds and a marine protected area. *Bulletin of Marine Science* **88**:89-104.

Stoner, A.W. and R.A. Glazer. 1998. Variation in natural mortality: implications for queen conch stock enhancement. *Bulletin of Marine Science* **62**:427-442.

Stoner, A.W. and M. Ray. 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. *Fishery Bulletin, U.S.* **94**:551-565.

Stoner, A.W. and M. Ray-Culp. 2000. Evidence for Allee effects in an overharvested marine gastropod: density-dependent mating and egg production. *Marine Ecology Progress Series* **202**:297-302.

Stoner, A.W. and V.J. Sandt. 1992. Population structure, seasonal movements and feeding of queen conch, *Strombus gigas*, in deep-water habitats of the Bahamas. *Bulletin of Marine Science* **51**:287-300.

Torroglosa, E.M. and J. Giménez. 2010. Temporal variation in size at maturity of the snail *Zidona dufresnei* from the southwestern Atlantic Ocean after ten years of fishery exploitation. *Aquatic Biology* **11**:163-167.

Valle-Esquivel, M. 2003. *Aspects of the Population Dynamics, Stock Assessment, and Fishery Management Strategies of the Queen Conch,* Strombus gigas*, in the Caribbean.* Ph.D. dissertation, University of Miami, RSMAS, Miami, Florida USA. 338 pp.

Walsh, M.R., S.B. Munch, S. Chiba, and D.O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecological Letters* **9**:142-148.