Abundance and population structure of queen conch inside and outside a marine protected area: repeat surveys show significant declines

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ABSTRACT: Effectiveness of a marine protected area (MPA) in supporting fisheries productivity depends upon replenishment patterns, both in supplying recruits to surrounding fished areas and having a sustainable spawning stock in the MPA. Surveys for queen conch *Strombus gigas* were made in 2011 at 2 locations in the Exuma Cays, The Bahamas, for direct comparison with surveys conducted during the early 1990s at Warderick Wells (WW) near the center of the Exuma Cays Land and Sea Park (ECLSP) and at a fished site near Lee Stocking Island (LSI). There was no change in adult conch density and abundance in the shallow bank environment at LSI where numbers were already low in 1991, but numbers declined 91% in the deeper shelf waters. At WW, the adult population declined 69% on the bank and 6% on the island shelf. Unlike observations made in the 1990s, queen conch reproductive behavior near LSI is now rare. Average age of adult conch (indicated by shell thickness) at LSI decreased significantly during the 20 yr period between surveys, while average age increased at WW and juvenile abundance decreased. These results show that the LSI population is being overfished and the WW population is senescing because of low recruitment. In 2011, the ECLSP continued to be an important source of larvae for downstream populations because of abundant spawners in the shelf environment. However, it is clear that the reserve is not self-sustaining for queen conch, and sustainable fishing in the Exuma Cays will depend upon a network of MPAs along with other management measures to reduce fishing mortality.

KEY WORDS: Marine protected area · Population structure · Reproduction · Queen conch · Bahamas

INTRODUCTION

No-take marine protected areas (MPAs) have now been established throughout the world with the primary goals of preserving natural community and population structures and helping to sustain fishery productivities for harvested species. The obvious benefits of MPAs including elevated counts, biomass, and sizes of protected fishes and invertebrates are well established (Roberts & Polunin 1991, Halpern 2003, Sobel & Dahlgren 2004). MPAs can contribute to fisheries in the surrounding areas through either spillover of large individuals or export of larvae, and while actual results on these principles are often

lacking, a large amount of literature has accumulated discussing reserve location and size and the role of MPA networks in the context of population connectivity, stock replenishment, and fisheries management (Lubchenco et al. 2003, Jones et al. 2007, Kininmonth et al. 2011).

The efficacy of an MPA for both preservation of a stock and contributions to surrounding fisheries will depend upon either the self-sustaining capacity of the population within the MPA or recruitment from outside. Despite considerable optimism about the role of MPAs as an important tool in fisheries management, the limitations of MPA design and the importance of broader impacts outside the reserves themselves have become clear (Allison et al. 1998, Gaines et al. 2003, Mora et al. 2006, Botsford et al. 2009). Botsford et al. (2001) pointed out a decade ago that the reserve areas likely to be implemented by local governments may not be large enough to sustain natural communities unless fishing and other deleterious effects outside the reserves are limited. Stochastic processes associated with larval transport and population processes including recruitment, along with the human component of fisheries make MPA design especially complex, and modeling efforts show that a single MPA will probably not be able to support a population that is heavily exploited outside the reserve (Stockhausen et al. 2000, Gaines et al. 2003, Kaplan et al. 2009). More specifically, if a population ages and declines from natural mortality without replacement, the population inside the MPA will eventually fail along with the fished parts of the stock (Gaines et al. 2010).

The Exuma Cays Land and Sea Park (ECLSP), established in 1958, is the oldest MPA in The Bahamas. The park is relatively large (456 km^2), enclosing a 40 km long section of the Exuma Cays island chain. It covers the entire island shelf on the east and a broad section of shallow bank to the west of the islands. The ECLSP is a no-take marine fishery reserve that supports large juvenile and adult populations of economically important species including large groupers, spiny lobster *Panulirus argus*, and the large gastropod queen conch *Strombus gigas* (Dahlgren 2004). Fishery resources in the ECLSP had only modest protection during the earliest years, but protection increased gradually with the presence of a local warden and the Royal Bahamian Defense Force.

Several studies of fishery resources have been conducted in ECLSP during the last 25 yr. Sluka et al. (1994) reported that juvenile grouper populations in the shallow coral reef environment of ECLSP were 3 times higher than those of comparable fished locations in the Florida Keys, and densities of Nassau grouper *Epinephelus striatus* were at least 3 times higher than those of any other area surveyed in The Bahamas (Dahlgren 2004). Densities and biomass of large groupers in the Park were substantially higher than those of surrounding areas in the Exumas as well as other sites in the northern Caribbean (Chiappone et al. 2000). In 1994, Stoner & Ray (1996) surveyed adult, juvenile, and larval stages of queen conch at the center of the Park for comparison with a fished area 70 km south in the island chain at Lee Stocking Island. They concluded that 'ECLSP is large enough to protect a large reproductive stock of queen conch in an undisturbed habitat where physical oceanographic features concentrate competent larvae and export them to downstream nurseries and fishing grounds.' Subsequent oceanographic observations and larval surveys in the 1990s resulted in the conclusion that the ECLSP is an important source of larvae for both queen conch (Stoner et al. 1998) and spiny lobster (Lipcius et al. 1997, 2001). However, both Stoner & Ray (1996) and Chiappone & Sullivan-Sealey (2000) warned that the marine resources inside the ECLSP probably depend upon larval transport from up-current areas and that the reserve might not be successful in isolation.

This study was conducted to test for possible changes in the density, abundance, and population structure of queen conch in previously surveyed locations of the Exuma Cays, The Bahamas. Emphasis was placed on determination of the age structure and reproductive potential of the adult component and evaluation of the likelihood of a self-sustaining population in the ECLSP.

MATERIALS AND METHODS

Subject species

The queen conch is a large herbivorous gastropod (up to 30 cm total shell length) representing one of the most important commercially harvested marine animals in the Caribbean region (Berg & Olsen 1989). Populations are declining under intense fishing pressure (Bell et al. 2005, Stoner et al. 2012a) and the species has long been listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) (Daves & Fields 2004). Commercial fisheries and export of queen conch continue in The Bahamas, Turks and Caicos Islands, Honduras, and Belize, and harvest has been completely closed

because of overexploitation in some nations, with little sign of recovery (Theile 2005). In The Bahamas, legal harvest of queen conch requires that they must have a flared shell lip (see below) and can only be collected by free divers or divers that use surface-supplied air, such as a hookah (i.e. not with SCUBA). Additionally, although a quota for the number of conchs exported is set by the government each year, there is no closed season or harvest quota to date.

Queen conch reach sexual maturity at an age of ~4 yr (Egan 1985, Appeldoorn 1988), and they mate and lay demersal egg masses during the warmest months (Stoner et al. 1992). The eggs hatch in ~5 d and the larvae spend 2 to 4 wk in the water column (Davis 1998) before settling in shallow sand and seagrass habitats where the juveniles feed on various forms of algae and detritus (Stoner & Waite 1991). In The Bahamas, juveniles often occur in aggregations covering 1 to 100 ha occupying habitats with specific physical and biological conditions (reviewed by Stoner 2003). With age, large juveniles and adults disperse over a wide range of habitats including seagrass meadows, algae-covered hard ground, and bare sand in depths to ~35 m (Randall 1964, Stoner 2003), consuming primarily green and red macroalgae. An intensive examination of mating behavior conducted in 1995 (Stoner & Ray-Culp 2000) showed that ECLSP was especially valuable in preserving adult conch populations above the critical threshold for successful mating and egg production.

Shell morphology provides important insight into the age and sexual maturity of queen conch. Individuals reach terminal shell length (ranging from ~150 to 300 mm) at about 3.5 yr. At this time, the edge of the shell lip turns outward to form the characteristic flared lip of the 'adult' as traditionally defined. Subsequent growth of the shell occurs only in thickness (i.e. not length), which provides an index of age (Appeldoorn 1988, Stoner & Sandt 1992). Although sexual maturity does not occur until shell lip thickness reaches 8 to 15 mm (Egan 1985, Aldana-Aranda & Frenkiel 2005, Avila-Poveda & Baqueiro-Cárdenas 2006), any conch with a flared lip is legal for harvest in The Bahamas.

Study sites

Surveys were conducted at 2 sites in the Exuma Cays in 2011 (Fig. 1). This island group comprises a chain of about 100 small islands running southeast to northwest in the central Bahamas. The islands are bounded by the deep Exuma Sound on the east and the Great Bahama Bank on the west. The shallow bank environment is covered with sand and seagrass (primarily *Thalassia testudinum*). Water depth over the bank is typically 1 to 3 m at mean low water (tidal range = ~1.0 m), with deeper tidal channels (up to 6 m depth) between the islands and running onto the bank (see Stoner et al. 1996). The vast majority of queen conch juveniles occur on the bank in specific nursery locations that tend to be in direct association with the tidal channels where larvae are concentrated and where there is an abundance of macro-algal foods associated with the seagrasses (Stoner 2003). All along the Exuma Cays, the island shelf
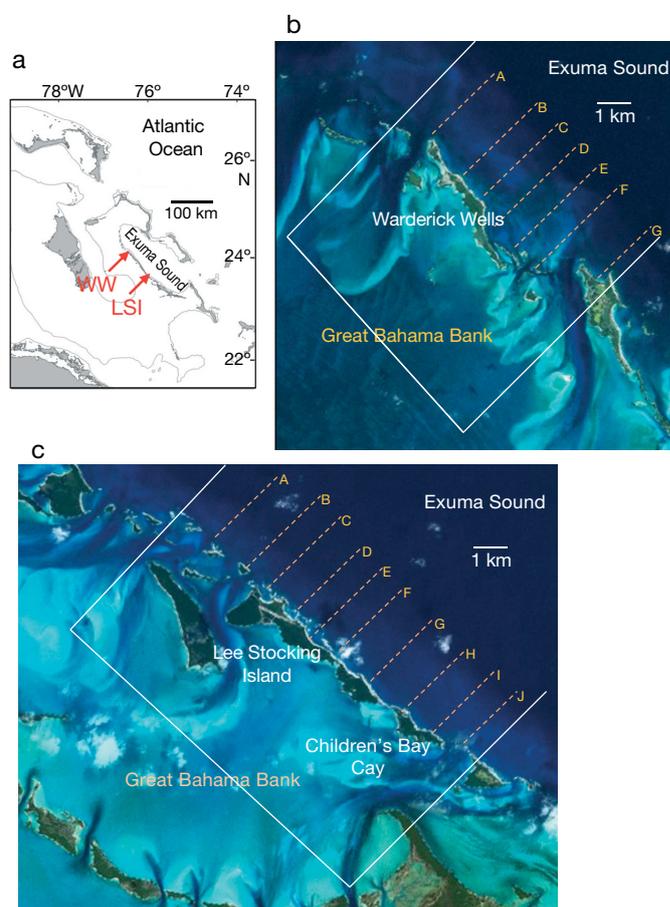

Fig. 1. (a) Survey locations in The Bahamas near Warderick Wells (WW) in the center of the Exuma Cays Land and Sea Park (a no-take marine protected area) and in the fished area near Lee Stocking Island (LSI). The Exuma Cays border the western side of the deep Exuma Sound. (b) WW study site from satellite showing the shallow bank to the west of the islands and (dashed lines) 7 survey transect lines on the island shelf to the east. (c) LSI study site from satellite showing the shallow bank and (dashed lines) 10 survey lines on the island shelf. The shallow shelf areas were surveyed with evenly spaced transect lines running southwest to northeast, 12 lines at WW and 20 at LSI. White lines show the boundaries of the study area

extends 1 to 3 km into Exuma Sound to a steep shelf edge beginning at ~30 m depth. The nearshore environment (<15 m depth) is characterized by shallow sand, hard bottom covered by a short turf of macro-algae (especially *Cladophoropsis* sp.) and sparsely distributed soft corals. Beyond 15 m, the habitat is a mix of sand, patches of hard bottom, and coral reefs. In the past, adult queen conch and a few juveniles have occupied all of these habitats (Stoner & Sandt 1992) except areas covered with hard corals. Most conch mating and egg-laying occurs on the island shelf following an ontogenetic migration from the shallow bank (Stoner 2003).

To repeat surveys exactly as Stoner & Ray (1996) in the early 1990s, queen conch density and abundance were quantified in a 12 km long section of the Exuma Cays adjacent to Lee Stocking Island (LSI) and Childrens Bay Cay and a 7.5 km long section near Warderick Wells at the center of the Exuma Cays Land and Sea Park (ECLSP). The Warderick Wells study site (WW) was chosen by Stoner & Ray (1996) because it is adjacent to ECLSP headquarters, is regularly patrolled by enforcement officials, and is least susceptible to poaching. The WW study site is 15 km from the southern boundary of ECLSP and 70 km north of the LSI study site.

Survey methods

This study was focused primarily on determining the density and abundance of adult queen conch in the 2 study sites for direct comparison with Stoner & Ray (1996). Therefore, the site boundaries and approach were held identical to the earlier study, and all of the 2011 surveys were conducted between June and July to coincide with peak reproductive season in the Exuma Cays (Stoner et al. 1992). As before, 2011 surveys were confined to bank areas within 5 km to the southwest of an imaginary line running along the eastern shore of the islands (Fig. 1) because adult and juvenile conch are rare at greater distances onto the Great Bahama Bank. The bank environment was surveyed along evenly spaced lines running perpendicular to the island chain, with 20 lines at LSI and 12 at WW. A snorkeler was towed behind a small boat (~2 km h^{-1}) over each predetermined line, counting the numbers of adult, subadult, and juvenile conch in a 6 m wide band. A conch was classified as an adult when it had a flared shell lip, compatible with the fishery definition. Sub-adults were 3 yr old conch, as large as adults in shell length but without a flared lip, and juveniles were smaller individuals,

typically <120 mm, representing Age-1 and Age-2 year classes. Towing was stopped at 1 km intervals (or less depending upon the position of islands and intertidal sand bars) and the numbers of conchs were recorded. GPS waypoints, depths, and times were logged for each interval. Total distances surveyed in bank habitat at LSI and WW were 67 and 53 km, respectively. This represents a slightly greater effort than that in the 1990s, when 63 km and 47 km, respectively, were surveyed.

Depths increase over short distances in the shelf area east of the islands. Therefore, depth-stratified surveys were conducted at each site in the shelf habitat. Survey locations were placed along each of 10 lines running offshore from LSI and 7 lines running offshore from WW (Fig. 1). Precisely as performed by Stoner & Ray (1996), conch density determinations were made in 6 depth intervals (0–2.5, 2.5–5, 5–10, 10–15, 15–20, 20–25 m) placed on each line. This excluded a narrow band at depths of 25–30 m surveyed by Stoner & Ray (1996), which yielded no conch at LSI and relatively few at WW. At the 2 shallowest intervals a snorkeler was towed for 1 km in a direction parallel to the adjacent island shore, recording conch counts and navigational data as described above. At the deeper intervals, 2 SCUBA divers swam transects parallel to the bathymetry, holding a line (8 m) between them and counting the conch that lay below the line. One diver carried a calibrated flow meter to calculate the distance traveled. To compensate for possible effects of current on distance measured, the divers swam from the boat's anchor into any discernible current and back, covering 2 parallel but non-overlapping paths. Although not by design, the total effort at each site was increased somewhat between the early surveys and those in 2011. Total distances covered on the shelf at LSI were 21 and 31 km for 1991 and 2011, respectively. At WW, distances surveyed increased from 13 to 18 km total.

Adult conch were measured for shell length and shell lip thickness. At LSI, where adults were rare, divers returned to locations on the bank where conch were abundant to gather a total of 100 measures for that habitat. On the shelf, conch were measured as encountered during the diving surveys, with just 37 adults found. A similar sub-sampling was conducted at WW, with 58 conch representing the bank environment and 134 measured on the shelf. Also, shells of dead conch were relatively common in deep water near both LSI and WW. These appeared to be old individuals based upon their lip thickness and the extent of erosion on the shell exterior, and measure-

ments were made to evaluate their size and thickness (i.e. relative age) compared with living adults. At LSI, 38 individuals were collected near Line I of the survey. At WW along Lines D, E, and F off the island shelf, 33 shells of dead conch were collected for measurement. All shells measured were those likely to have resulted from natural mortality and not those obviously opened by fishers.

Observations of reproductive behavior in queen conch were recorded for each survey line. This included numbers of mating pairs and egg-laying females (see Stoner & Ray-Culp 2000). Egg masses were also observed upon occasion, but counts were not quantitative because the masses are not always detected. Observations made near WW during this study were plotted with results obtained in 1995 by Stoner & Ray-Culp (2000) for direct comparison.

Juvenile queen conch (Age-1 and Age-2, see above) in the Exuma Cays are highly aggregated (Stoner 2003), and broad-scale transecting offers only qualitative data about the abundance of these youngest juveniles. However, in 2011, visits were made to locations known for aggregations of Age-1 and Age-2 juveniles in the 1990s at both LSI and WW. Divers were towed through 3 historically important nursery grounds near LSI for a qualitative determination of juvenile presence or absence and extent of dispersion. Five additional nurseries mapped in 1993 (Stoner & Ray unpubl. data) near WW and at the southern boundary of the ECLSP were similarly explored in July 2011.

Analysis

Densities of adult conch were reported in numbers per hectare, and total abundances for each LSI and WW depth zone were estimated using the surface area for each depth interval and bank habitat reported by Stoner & Ray (1996). Density values were compared across survey years and sites using standard 1- and 2-way analysis of variance (ANOVA) tests following log_{10}-transformation as necessary. Levene's test was used to evaluate homogeneity of variance and Kolmogorov-Smirnov tests were used for evaluating normal distribution. A similar ANOVA approach was used to examine differences in shell length and shell lip thickness among the populations over both time and location. While adult densities and abundance could be compared directly with the surveys made in the 1990s, subadults were not counted in the earlier surveys and temporal comparisons are not possible.

Reproductive behavior was analyzed with respect to the surrounding density of adults and compared with earlier studies of reproductive frequency at LSI and WW (Stoner & Ray-Culp 2000) and other locations in The Bahamas (Stoner et al. 2012a).

RESULTS

Densities and abundance of adult conch

During the 2011 surveys just 280 adult conch were observed in nearly 100 km of transect lines at LSI. While the average density of adult conch was somewhat higher on the bank in 2011 than in 1991 (Table 1, Fig. 2), the difference was not significant (ANOVA, $F_{1,119} = 2.596$, p = 0.110), and average densities were low (<6 adults ha^{-1}). In strong contrast with the pattern observed in 1991, density values on the LSI island shelf in 2011 were lower than those on the bank, except for the deepest depth interval (20–25 m). Two-way ANOVA showed a Year × Depth interaction ($F_{4,81} = 3.560$, p = 0.010) because year differences in density were not significant for the depth intervals 2.5–5 and 5–10 m (p = 0.671 and 0.190), but highly significant in all of the other inter-annual comparisons (p < 0.05). The most notable declines in conch density and abundance occurred in the depth range of 10–20 m where densities were highest in 1991 (Table 1).

In the 1990s, density of adult conch on the WW bank was ~17 times higher than that at LSI. The difference was substantially lower in 2011 (2.9 times). This occurred because of the small but nonsignificant increase in density at LSI paired with a highly significant 69% decrease at WW ($F_{1,85} = 9.080$, p = 0.003; Table 1).

Surveys conducted on the WW shelf showed that differences in densities observed between 1994 and 2011 varied with depth zone (Table 1), and the Year × Depth interaction was marginally significant ($F_{4,53} = 2.157$, p = 0.087). There was an increase in density in the 5–10 m zone, but substantial decreases occurred in the deeper range (10–25 m) where adult densities had been especially high in 1994.

In 2011, the density of adult conch in the shelf environment was about 28 times higher at WW (89.8 adults ha^{-1}) than at LSI (3.2 adults ha^{-1}) considering the entire shelf areas at each site. This represents a substantial change from the 1990s when the difference between WW and LSI in overall adult density in shelf habitat was just 2.8 times. The obvious site difference (Table 1) was highly significant

Table 1. *Strombus gigas.* Abundance of queen conch with flared shell lips near (a) Lee Stocking Island (fished area) and (b) Warderick Wells (marine protected area) in the Exuma Cays, Bahamas, by overall habitat and depth intervals within the shelf habitat. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner & Ray 1996). Values for densities are mean ± SE

Habitat (m)	1991 or 1994				2011		
	No. of lines surveyed	Habitat area (ha)	Adult density (ind. ha^{-1})	Estimated no. of adults	No. of lines surveyed	Adult density (ind. ha^{-1})	Estimated no. of adults
(a) Lee Stocking Island (1991)							
Bank	51	3997	3.16 ± 1.69	12 631	70	5.78 ± 1.85	23 103
Shelf, combined	56	2178		75 342	50		7026
Shelf depth intervals (m)							
0–2.5	4	161	0	0	2	1.85 ± 1.85	298
2.5–5.0	7	198	2.24 ± 1.70	444	8	1.25 ± 0.82	248
5–10	9	465	7.21 ± 4.11	3353	10	3.69 ± 3.24	1920
10–15	9	429	60.1 ± 46.8	25 782	10	1.70 ± 1.09	729
15–20	9	454	87.9 ± 31.5	39 907	10	1.80 ± 0.85	817
20–25	9	320	18.3 ± 9.1	5856	10	9.42 ± 8.48	3014
25–30	9	151	0	0	Not surveyed		–
Total numbers		6175		87 973			30 129
(b) Warderick Wells (1994)							
Bank	35	3245	53.6 ± 19.2	174 080	52	16.6 ± 7.0	53 867
Shelf, combined	36	2167		208 053	33		194 698
Shelf depth intervals (m)							
0–2.5	2	158	0	0	0	Not surveyed	0
2.5–5.0	6	200	34.4 ± 22.4	6871	7	35.5 ± 12.1	7100
5–10	7	1035	49.4 ± 18.3	51 138	6	144.5 ± 45.5	149 557
10–15	6	375	269.8 ± 85.0	101 187	7	85.1 ± 41.3	31 912
15–20	6	193	104.2 ± 58.4	20 113	7	7.59 ± 3.61	1464
20–25	5	136	147.8 ± 72.5	20 108	6	34.3 ± 17.1	4665
25–30	6	71	121.9 ± 70.2	8635	0	Not surveyed	–
Total numbers		5412		382 133			248 565

(2-way ANOVA, $F_{1,71}$ = 45.518, p < 0.001), with no Site × Depth interaction ($F_{4,71}$ = 1.542, p = 0.157). Considering all habitats together (bank and shelf), average density of adult conch was 5.0 times higher at WW than LSI in the 1990s and 9.4 times higher at WW in 2011.

The overall population estimate for adult conch at LSI declined 63.3% from 1991 to 2011 (Table 1). Whereas most of the adults (91.7%) were found east of the island in the shelf environment in 1991, the pattern was reversed in 2011, when just 23.3% of the adults were located on the shelf. This occurred primarily because the shelf segment of the population declined 91%. At WW adult populations declined 35%, with most of the change occurring on the shallow bank.

Conch size and shell lip thickness

Shell lengths of adult queen conch were shorter in the bank environment than on the island shelf at both LSI and WW during both early and recent surveys (Table 2), although the bank–shelf difference was relatively small at WW in 2011. Some apparent changes in average shell length occurred between survey years. In 2011, the average adult conch on the LSI shelf was 6 mm larger than 2 decades earlier, but the difference was not significant (ANOVA, $F_{1,592}$ = 2.668, p = 0.103). Inter-year difference on the LSI bank was even smaller (3 mm). At WW, a 12 mm increase in average shell length observed in the bank environment between 1994 and 2011 was significant ($F_{1,269}$ = 15.379, p < 0.001), but the small increase in shelf environment was not ($F_{1,593}$ = 1.137, p = 0.287).

Shell lip thickness varied both spatially and temporally over the 2 survey sites (Table 3). Conch with thinnest shells occurred in the bank environment at LSI with mean values between 9 and 10 mm during the 2 survey years. Shells were thicker on the LSI island shelf, and those measured in 2011 were significantly thinner (mean = 21 mm) than shells measured in 1991 (mean = 28 mm) (ANOVA, $F_{1,269}$ = 38.320, p < 0.001). A similar analysis at WW revealed a different
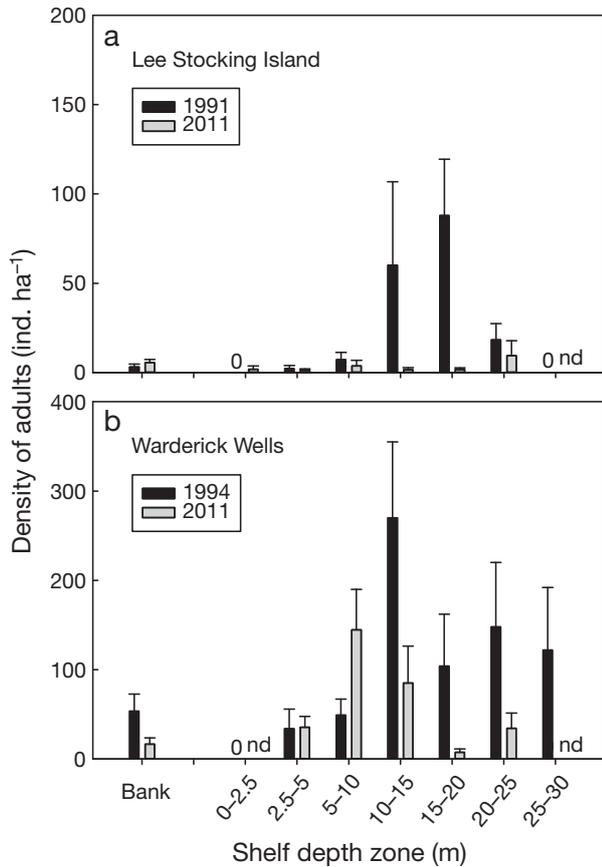
Fig. 2. *Strombus gigas.* Densities of adult queen conch near (a) Lee Stocking Island and (b) Warderick Wells, Exuma Cays in the 1990s and in 2011. Densities (mean + SE) are shown for the shallow bank environment west of the islands and for 7 depth zones of the shelf environment east of the islands bordering Exuma Sound. Note the different *y*-axis scales for the 2 sites. nd = no data

Table 2. *Strombus gigas.* Mean ± SD (n) shell lengths (mm) for queen conch with flared shell lips near Lee Stocking Island and Warderick Wells in the Exuma Cays, Bahamas for (a) overall habitats and (b) depth intervals within the shelf habitat. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner & Ray 1996). Significant differences in mean values between years are indicated for overall habitats only. Significant values in **bold** (p < 0.001). Data are reported for depth intervals where there were comparable data, but these were not compared statistically

| | —— Lee Stocking Island —— | | —— Warderick Wells —— | |
	1991	2011	1994	2011
(a) Habitat				
Bank	187 ± 17 (472)	190 ± 21 (100)	**188 ± 20 (213)**	**200 ± 22 (58)**
Shelf, combined depths	228 ± 22 (557)	234 ± 30 (37)	201 ± 21 (461)	203 ± 20 (134)
(b) Shelf depth intervals (m)				
2.5–5.0	247 ± 10 (21)	No data	195 ± 20 (39)	No data
5–10	201 ± 26 (57)	216 ± 27 (12)	200 ± 20 (144)	198 ± 19 (94)
10–15	226 ± 24 (229)	242 ± 20 (4)	194 ± 19 (148)	214 ± 20 (36)
15–20	222 ± 23 (150)	240 ± 45 (8)	209 ± 20 (60)	227 ± 0 (1)
20–25	233 ± 17 (100)	245 ± 14 (13)	209 ± 20 (70)	201 ± 16 (3)

pattern. Shell lip thickness increased from 1994 to 2011, particularly on the bank, where average lip thickness increased by 9 mm (Table 3). The effect of year was significant for both bank ($F_{1,592}$ = 54.238, p < 0.001) and shelf environments ($F_{1,593}$ = 26.310, p < 0.001).

Some important differences in shell metrics (mean ± SD) between living and dead conch at the 2 study sites are evident in scatterplots (Fig. 3). Thickness for empty shells at LSI (33 ± 4 mm; range = 23 to 41) was significantly higher ($F_{1,72}$ = 67.416, p < 0.001) than that for living adults (21 mm; Table 3) at the same site. The difference at WW was minor and not significant ($F_{1,164}$ = 1.599, p = 0.208), with a mean of 30 ± 5 mm (range = 20 to 42) for empty shells versus 28 mm for living adults. However, lengths of empty shells found on the island shelf were in ranges similar to those of the living adult conch at each of the 2 sites (Fig. 3). Lengths of empty shells were 201 ± 18 mm (range = 170 to 224) at LSI, and 194 ± 25 mm (range = 159 to 245) at WW.

Subadult and juvenile populations

Subadult conch, representing the 2008 year class during 2011 surveys, were most abundant on the shallow banks west of both LSI and WW (Table 4). Highest average density (73 subadults ha^{-1}) occurred on the bank near LSI, and this was significantly higher than the density observed on the bank near WW (10.8 subadults ha^{-1}) ($F_{1,120}$ = 15.110, p < 0.001), although densities at both sites were highly variable.

On the LSI bank, subadults were 12 times more abundant than adults, whereas adults were more abundant than subadults at WW.

Subadults were relatively uncommon in the shelf environment, particularly at LSI where densities were < 2.0 subadults ha^{-1} in all depth zones and none were found deeper than 15 m depth (Table 4). Densities ranged from 2.5 to 8.8 subadults ha^{-1} on the WW shelf and were present in all of the depth zones sampled.

Small juveniles (Age-1 and Age-2) were found primarily on the bank at both LSI and WW. They were present in 20 of the 70 bank transects surveyed near LSI (28.6%) and 17 of 52 surveyed near WW (32.7%).

Table 3. *Strombus gigas.* Mean ± SD (n) shell lip thickness (mm) for queen conch with flared shell lips near Lee Stocking Island and Warderick Wells in the Exuma Cays, Bahamas for (a) overall habitats and (b) depth intervals of the shelf environment. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner & Ray 1996). Significant differences in mean values between years are indicated for overall habitats only. Significant values in **bold** (p < 0.001). Data are reported for depth intervals where there are comparable data, but these were not compared statistically

| | —— Lee Stocking Island —— | | —— Warderick Wells —— | |
	1991	2011	1994	2011
(a) Overall habitats				
Bank	10 ± 6 (472)	9 ± 7 (100)	**12 ± 6 (213)**	**21 ± 10 (58)**
Shelf, com- bined depths	**28 ± 7 (557)**	**21 ± 8 (37)**	**25 ± 7 (461)**	**28 ± 6 (134)**
(b) Shelf depth intervals (m)				
2.5–5.0	18 ± 5 (21)	No data	23 ± 5 (39)	No data
5–10	28 ± 6 (57)	17 ± 8 (12)	26 ± 8 (144)	29 ± 5 (94)
10–15	30 ± 7 (229)	27 ± 6 (4)	25 ± 7 (148)	27 ± 6 (36)
15–20	27 ± 6 (150)	18 ± 10 (8)	21 ± 5 (60)	26 ± 0 (1)
20–25	28 ± 6 (100)	24 ± 5 (13)	23 ± 5 (70)	29 ± 6 (3)

Fig. 3. *Strombus gigas.* Total shell length against shell lip thickness for adult queen conch near (a) Lee Stocking Island (LSI) and (b) Warderick Wells (WW). Data are shown for conch from the shelf and bank habitats and for empty shells representing natural mortalities at each site

Only 1 juvenile was observed on the island shelf (3 m depth) near LSI. On the WW island shelf, 8 juveniles were widely scattered over a range of depths from 5 to 23 m. More importantly, in 2011 juveniles were present in all of the nursery locations at LSI and WW identified in the 1990s; however, the juvenile aggregations had diminished substantially in most of them. The 3 nurseries at LSI all supported juveniles in 2011 but areal extent of the aggregations had declined by more than half since the 1990s. Two aggregations near WW were about one-quarter of their 1993 dimensions. Two juvenile aggregations just inside the southern boundary of ECLSP were about the same or reduced slightly since 1993, and 1 large aggregation just south of the boundary was about one-half of its 1993 extent.

Reproductive behavior

Reproductive behavior was observed at only 1 location at LSI. Three mating pairs were found on Line F at 23 m depth on 21 June 2011. This was coincident with the highest adult density recorded for the LSI island shelf environment (85.5 adults ha^{-1}). Neither egg-laying females nor egg masses were observed at any location during surveys at LSI. This contrasts substantially with observations during the 1980s and 1990s (see 'Discussion').

In contrast with LSI, reproductive behavior at WW was observed on both the bank and shelf (Table 5). Fifteen mating pairs were observed at 4 of the 52 tow locations on the bank in depths ranging from 3 to 5 m near the island passes. All of these observations occurred in the 9 transect segments with highest adult densities (13 to 155 adults ha^{-1}). Thirty-six mating pairs were observed on 9 of the 33 counts made on the island shelf, and 15 egg-laying females were observed in 6 of the counts. Mating was observed at every shelf location where density was >100 adults ha^{-1}. Egg-laying was also associated with high adult density, ranging from 94 to 219 adults ha^{-1}, and just 1 high-density site lacked egg-laying behavior (Table 5).

The relationship between the percentage of adult conch mating and adult density in the shelf environ-
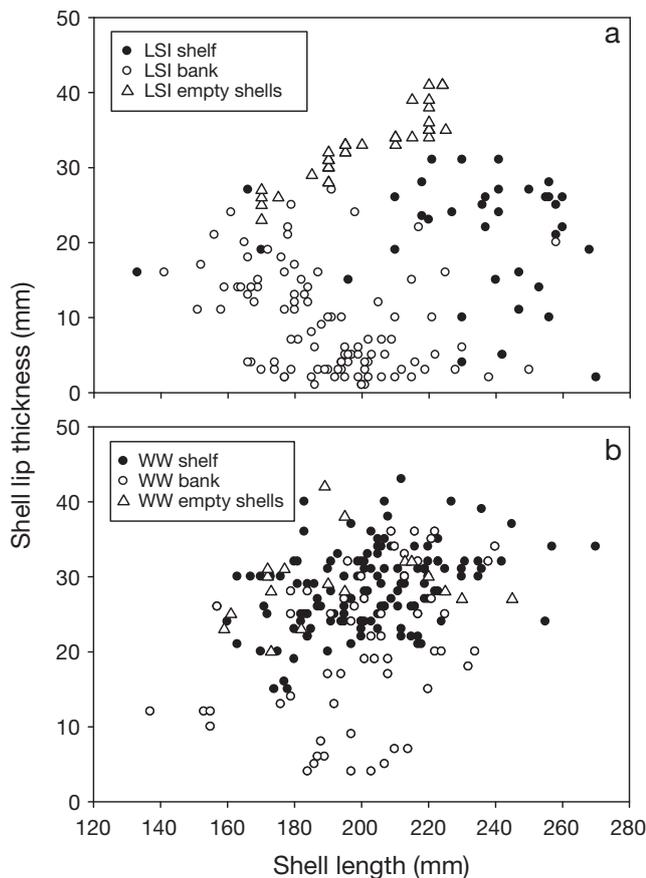
Table 4. *Strombus gigas.* Density (mean ± SE) of subadult queen conch (2008 year class) near (a) Lee Stocking Island (fished area) and (b) Warderick Wells (marine protected area) in the Exuma Cays, Bahamas in June/July 2011

Site and habitat	No. of lines surveyed	Habitat area (ha)	Subadult density (ind. ha^{-1})	Estimated no. of subadults
(a) Lee Stocking Island				
Bank	70	3 997	73.1 ± 18.9	292 181
Shelf, combined	50	2 178		1418
Shelf depth intervals (m)				
0–2.5	2	161	0	0
2.5–5.0	8	198	1.81 ± 1.31	358
5–10	10	465	1.90 ± 1.03	884
10–15	10	429	0.41 ± 46.8	176
15–20	10	454	0	0
20–25	10	320	0	0
Total numbers		6 175		293 599
(b) Warderick Wells				
Bank	52	3 245	10.85 ± 4.47	35 208
Shelf, combined	33	2 167		11 683
Shelf depth intervals (m)				
0–2.5		158	Not surveyed	
2.5–5.0	7	200	2.62 ± 0.95	524
5–10	6	1 035	8.83 ± 3.80	9139
10–15	7	375	3.24 ± 2.10	1215
15–20	7	193	2.37 ± 0.78	457
20–25	6	136	2.56 ± 1.62	348
Total		5 412		46 891

Table 5. *Strombus gigas.* Reproduction observed in queen conch during 2011 surveys at (a) Lee Stocking Island and (b) Warderick Wells, Exuma Cays. Letter and number codes refer to the survey transect lines on the shelf and bank, respectively (see Fig. 1)

Survey transect	Date	Depth (m)	Adult density (ind. ha^{-1})	No. of mating pairs	No. of egg-laying females
(a) Lee Stocking Island					
Shelf F	21 June	23	85.5	3	0
(b) Warderick Wells					
Bank 1	10 July	5	314.4	6	0
Bank 7	11 July	4	98.3	5	0
Bank 11	9 July	3	40.4	1	0
Bank 11	9 July	4	20.4	3	0
Shelf A	7 July	25	106.6	3	3
Shelf A	7 July	14	94.3	0	2
Shelf A	10 July	8	225.2	9	4
Shelf B	10 July	9	225.7	3	1
Shelf B	10 July	12	255.1	2	3
Shelf C	11 July	13	219.0	1	2
Shelf D	12 July	24	74.0	1	0
Shelf D	16 July	4	90.0	5	0
Shelf E	14 July	8	275.6	10	0
Shelf F	14 July	8	84.5	2	0

ment at WW during surveys conducted in 1995 and 2011 is shown in Fig. 4. No mating whatsoever was observed when densities were <56 adults ha^{-1} (1.75 on the log$_{10}$ scale) in either of the surveys. Mating frequency increased rapidly at higher densities, with a maximum of 34% of the population mating in 1 count in 1995 where the density was ~2500 adults ha^{-1}.

DISCUSSION

Changing function of a marine reserve

More than a decade ago, Allison et al. (1998) pointed out that where threat to a fishery has a broad scale, a marine reserve cannot be effective in preventing decline without other forms of management. In fact, persistence will depend critically upon the health and fishery status of the population outside the MPA and how fishing effort is redistributed after implementation (Gerber et al. 2002, Botsford et al. 2009, Kaplan et al. 2009). Also, when larvae of a marine species are transported between sites for recruitment, a single isolated MPA is unlikely to ensure persistence of a marine metapopulation (Mora et al. 2006, Kininmonth et al. 2011). Concordant with theory, speculation that ECLSP might not conserve its fishery resource species because of heavy fishing in up-current areas (Stoner & Ray 1996, Chiappone & Sullivan-Sealey 2000) appears to have been correct for queen conch. Further, Gaines et al. (2010) predicted that if a population inside a marine reserve ages and declines from natural mortality without replacement, that population will eventually fail along with the fished parts of the stock. This also appears to be happening with queen conch in the Exuma Cays. Below we consider the changing structure of queen conch populations at the study sites, their reproductive potential and possible solutions to the fisheries management challenge for this key species.

Population changes

Queen conch populations throughout the Caribbean region are under increasing threat from over-fishing (Posada et al. 2007). While The Bahamas continues to be one of the small group of nations with a viable conch fishery and export market, this study
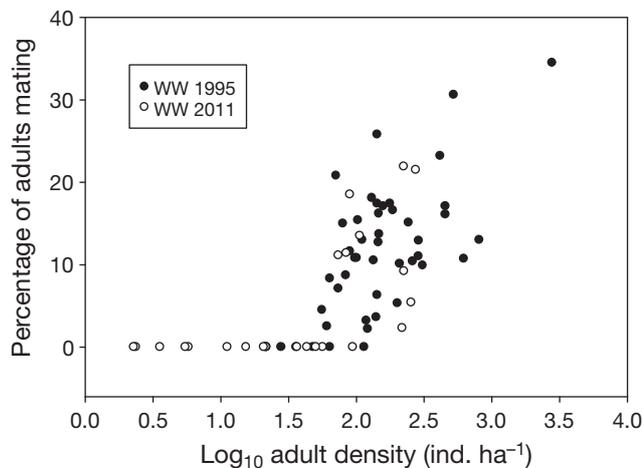
Fig. 4. *Strombus gigas.* Association between mating frequency in queen conch and density of mature adults (shell lip thickness ≥ 10 mm) observed near Warderick Wells (WW) in this study (2011) and during earlier surveys conducted in 1995 (Stoner & Ray-Culp 2000). Density is shown on a $\log_{10}$-transformed axis. Mating frequency is shown as the percentage of the adult population engaged in mating behavior

clearly shows that numbers have declined significantly at 2 important sites over the last 2 decades. Abundance of adult conch on the heavily fished island shelf near LSI declined 91%, and that population is now younger than it was in the early 1990s, as shown by a significantly thinner average shell lip thickness and declining numbers of juveniles. Also, given that queen conch live 20 yr or more empty shells of conch found on the island shelf represent animals recruited to the populations many years earlier. In 1991, the average shell lip thickness of living adults observed at LSI was similar to the empty shells collected in 2011, suggesting that at least some members of the population lived to maximum age. In 2011, the average lip thickness of living adults was significantly thinner than that of the empty shells. The increasing proportion of young adult conch shows that adults are being removed well before they reach an age of natural mortality, and the deep-water refuge for spawning stock at this site discussed by Stoner & Schwarte (1994) is in obvious decline. All of these observations suggest that queen conch near LSI are over-harvested.

Substantial changes in adult density also occurred in the MPA near WW, in both bank and shelf environments. While the shelf population declined only 6% between 1994 and 2011, the 69% decrease in conch density in shallow bank habitat was highly significant. Also, the bank population had an average shell thickness that was 75% greater in 2011 than in

1994. In sharp contrast with the adult population at LSI, increasing shell lip thickness at WW reveals an aging population. In fact, relatively few thin-lipped individuals were observed in shelf waters near WW, and the average living adult is very old, only slightly younger (thinner) than empty shells found in the shelf habitat. Furthermore, subadults were uncommon in shelf waters at just 2 to 9 ind. ha^{-1}, and populations of 1 and 2 yr old conch have diminished substantially since the 1990s. These demographic characteristics suggest that recruitment to the reserve population is low and that the population is in decline. While poaching might be considered a likely reason for any decline in overall adult density near the boundaries of the ECLSP, both the 1994 and 2011 surveys were conducted near the park headquarters where protection has been good for at least 2 decades.

Juvenile conch were not counted in the early surveys, so direct comparisons are not possible. However, the abundance of Age-3 subadults was high on several bank survey lines near LSI, suggesting substantial recruitment in 2008. The presence of a strong 2008 year class at LSI provides some encouragement that an occasional strong year class might help to replenish conch populations if the spawning stock can be protected, but declining nursery aggregations both inside and outside ECLSP is worrisome.

Declining reproductive potential

Mating behavior and egg-laying in queen conch are both directly related to the density of mature adults (Stoner & Ray-Culp 2000, Gascoigne & Lipcius 2004, Stoner et al. 2012a). More specifically, below a certain critical density, reproductive behavior will rarely occur. The minimum density where mating can occur is ~50 mature adults ha^{-1} at WW; however, a density of ~100 adults ha^{-1} is required for high mating frequency. In fact, the shelf waters at LSI were known for abundant reproductive conch in the 1990s (Stoner & Sandt 1992), and the 15 to 20 m depth zone was a routine source of egg masses for larval culture at the LSI field station during that time. However, in 2011, mating behavior was observed at just 1 LSI location, and neither egg masses nor egg-laying females were found during peak reproductive season. It is clear that average densities of adult conch at LSI are now well below the lower critical threshold for reproduction, and LSI can no longer provide significant numbers of larvae to support downstream populations.

In the 1990s, the ECLSP had very large quantities of adult queen conch and reproduction was high (Stoner & Ray-Culp 2000). In 2011, mating and egg-laying conch were observed frequently in both shelf and bank habitats near WW, and the relationship between adult density and mating frequency was identical to that observed in 1995 (Stoner et al. 2012a). However, densities have declined significantly, along with total abundance, suggesting that reproductive potential has also decreased. Queen conch densities and mating frequencies in ECLSP should be monitored for future reference while stronger fishery management practices are instituted outside the reserve (see below).

Based upon larval surveys for queen conch in Exuma Sound and concurrent studies of physical oceanography in the Exuma Sound conducted between 1992 and 1995 (Smith & Stoner 1993, Stoner et al. 1996, 1998) larvae were concluded to be transported northwest along the Exuma Cays and drawn through the island passes on flood tide to settle on shallow sandbars and seagrass meadows within a few kilometers of the inlets (Stoner 2003). Larval densities were especially high in the northernmost Exuma Cays, probably concentrated by the combination of northward flow and mesoscale gyres that appear to advance from south to north in the Sound (Lipcius et al. 1997, Stoner et al. 1998). The new adult surveys reported here show that the number of spawners on the LSI shelf has diminished by 91% since the mid-1990s, and the same may be true for a large portion of Exuma Sound beyond the boundaries of ECLSP. We expect that larval densities will reflect that decrease and speculate that the park may now be the primary source of larvae for the Exuma Sound system. In 1994, densities of queen conch veligers in ECLSP were the highest ever recorded in the species' range (Stoner & Ray 1996). New larval surveys would be useful in understanding the population decline in the Sound, the role of the ECLSP in supplying larvae to the surrounding fishing grounds, and possible conservation strategies.

Lockwood et al. (2002) calculated that to have a persistent population in an isolated marine reserve, the reserve needs to span ~2 times the mean dispersal distance of the subject species to ensure that it is substantially self-recruiting. While ECLSP continues to produce large numbers of conch eggs and larvae and is relatively large compared with other marine reserves around the Caribbean region, it is not large enough to retain larvae. Surface currents (1.3 to 2.9 km d^{-1}) that flow northwest along the Exuma Cays (Stoner & Ray 1996) can easily carry most of the larvae away from the 40 km long protected area over the 16 to 28 d period of larval development before settlement. Even at the lowest current velocities and shortest developmental periods, the requirement of 2 times larval dispersal distance is not met, and the ECLSP will depend upon upstream sources of eggs and larvae for benthic recruitment. If conch populations to the southeast of the park no longer have the reproductive capacity to produce eggs and larvae, as observed at LSI, the conch population in ECLSP will decline.

Recruitment limitation has been shown for other mollusks. For example, by transplanting bay scallops *Argopecten irradians concentricus*, Peterson et al. (1996) showed a close spatial relationship between spawner density and local recruitment of spat, and mtDNA data for the same species show that net dispersal distances are short, resulting in closed populations over a much larger geographic range (Marko & Barr 2007). Therefore, spawner transplants can serve as a potential solution to local depletions for bay scallop. The larvae of queen conch, however, can disperse great distances over the open banks of The Bahamas during a larval period of several weeks, and the available genetic data indicate that there is little differentiation among conch populations over the greater Caribbean region (Mitton et al. 1989). Consequently, queen conch will probably need to be managed as a metapopulation (Stoner 1994). Transplants to increase the density of adult conch and to place them in good spawner habitat in the Florida Keys have led to increases in reproduction (Delgado et al. 2004), but substantial increases in local recruitment are dubious.

Looking forward

Answers to questions on mechanisms causing the decline of queen conch in the Caribbean region and how to best structure a network of marine reserves will depend upon more research on larval dispersal, biophysical modeling, and new tools related to stock identification and movement such as molecular genetics and micro-constituent analysis of veliger statoliths or shells of newly settled juveniles. However, these promising approaches require 'prodigious effort or a serious list of assumptions to turn raw data into discernable patterns' (Palumbi 2004). While more research on larval connectivity and network design for marine reserves in The Bahamas would be useful, immediate fundamental changes in fisheries management are needed to stop the decline in conch

numbers and to rebuild the stocks. Experience in the Florida Keys over the last 25 yr shows that queen conch populations are very slow to rebuild naturally once the spawning stock falls below a critical threshold. Since the complete closure of fishing in the Florida Keys in 1986, the conch population has gradually increased with time; however, the gains are modest, from an average abundance of ~18 000 adults in the 1990s to ~34 000 in the 2000s (R. Glazer pers. comm.). Consequently, 2 basic changes clearly need to be made: (1) reduce total fishing mortality and (2) protect the density and age structure of the spawning stocks. Both will require a significant reduction in fishing effort and demand. This can be affected by changes in allowable fishing gear and fishing seasons, new closed areas, lip thickness criteria for legal harvest, and establishing a total allowable catch.

Large, old queen conch tend to accumulate in deep water (Stoner & Schwarte 1994), and a long-term ban on SCUBA diving for conch in The Bahamas may be one of the reasons that the fishery remains viable. Unfortunately, the legal use of hookah for conch fishing is increasing because shallow-water stocks are declining. We believe that the fishery should be open to free-diving only. Also, a closed season during the summer mating and egg-laying season would allow young adults to spawn at least once. Queen conch are managed by size or shell-lip criteria in most nations of the Caribbean (Aldana-Aranda & Frenkiel 2005, Clerveaux et al. 2005), and there have been repeated reminders that thin-lipped adults are not functionally mature (Egan 1985, Appeldoorn 1988, Stoner et al. 2012a). Shell length requirements do not adequately protect reproduction, and lip-thickness measures would clearly provide the best criterion to ensure that conch are allowed to mature and reproduce before harvest. Based upon earlier study of gonadal maturation in queen conch and new information from Warderick Wells (Stoner et al. 2012b), we recommend that the shell lip thickness required for harvested conch should be at least 15 mm. Also, fecundity appears to increase with conch age (i.e. shell lip thickness) and marine reserves can help to conserve a population of the most fecund individuals.

Expanding the MPA system in The Bahamas is an attractive option because all of the other measures mentioned above require either close enforcement throughout the enormous Bahamian archipelago or landing queen conch in the shell, which is dangerous for the small-boat fishery. While results from this study substantiate the growing body of literature suggesting that a single marine reserve cannot protect a species when its population outside the reserve

is heavily exploited (Stockhausen et al. 2000, Gaines et al. 2003, Kaplan et al. 2009), maintaining the required connectivity of populations may be possible with a network of MPAs (Palumbi 2004, Cowen et al. 2006, Jones et al. 2007) carefully designed for location, number, size, and total area (Botsford et al. 2001, Sala et al. 2002, Kaplan et al. 2009, Kininmonth et al. 2011). Network design is beyond the scope of the present study; however, a large and extensive system would likely be needed to be effective. Gaines et al. (2010) reviewed 57 case studies finding that the benefits of marine reserves for fisheries accrue best when the networks are large, comprising ~30% of the total area of the region.

Given the limitations of all of the management tools discussed above, it seems likely that specific controls on total fishing mortality will be required for a sustainable queen conch fishery. Currently, an export quota for conch exists in The Bahamas, and while accurate records for total catch are not available because of the dispersed nature of the conch fishery, conch intended for export are estimated to make up about one-half of the total catch, elevating the already high demand for conch. For long-term sustainability, ending the export market might be wise, leaving the product for domestic consumption only. Finally, a total allowable catch may need to be determined and enforced to preserve the spawning stock. Recent simulation modeling indicates that the optimal management strategy for queen conch would include limits on shell lip thickness, a fishing closure during the reproductive season, and control of total fishing effort (Valle-Esquivel 2003). Successful management for another gastropod species, the Australian greenlip abalone *Haliotis laevigata* was affected by limited access regulated by the number of fishing licenses, suitable size limits, appropriate individual transferable quotas, effective enforcement of the management arrangements, and responsive and adaptive management established before over-exploitation (Mayfield et al. 2011). Of course these management tools require high quality, long-term fishery-independent and fishery-dependent data sets.

CONCLUSIONS

Marine protected areas provide one important tool in the conservation of exploited species. However the conservation goals of a reserve system will not be met if that system is poorly designed, implemented, or protected (Allison et al. 1998). Worse yet, the presence of reserves can lead to a false sense of security

about the state of marine resources (Carr & Reed 1993, Rowley 1994). Low efficacy of MPAs can also tarnish the legitimacy and future adoption of closed areas by stakeholders. In fact, changes in the population structure of queen conch in the ECLSP suggest that this population is not self sustaining. The overall population of adults has declined 35 % over the last 17 yr (69 % in shallow bank habitat), and the adult population was significantly older in 2011 than it was in 1994. Declining numbers and aging of the adult population means that larval recruitment to the ECLSP has diminished, and surveys for queen conch upstream from the park at LSI show that the spawning stock has reached reproductive failure. At present, the ECLSP probably continues to be an important source of larvae for nurseries downstream in the Exuma Sound, but declining numbers and changing age structure indicates that queen conch in The Bahamas will need to be managed on a larger geographic scale. As with world abalone species (Mayfield et al. 2011), there are few if any examples of queen conch recovery in the Caribbean region and, to date, no rehabilitation effort releasing hatchery-reared juveniles has been successful (Stoner & Glazer 1998, Bell et al. 2005). Consequently, more aggressive preservation of natural stock structure is clearly required for a sustainable queen conch fishery. An MPA system is but one of the management tools needed.

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