

Evidence for a Significant Decline in Queen Conch in the Bahamas, Including the Population in a Marine Protected Area

Evidencia de una Déclinación Significativa en Concha de Reina en las Bahamas, Incluyendo la Población en un Área Protegida Marina

Evidence pour un Déclin Significatif dans la Lambi en Bahamas, y Compris la Population dans une Zone Protégée Marine

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ABSTRACT

Twenty years ago, surveys conducted in the Exuma Cays, Bahamas, showed that the density of adult queen conch in the shallow bank habitat at the Exuma Cays Land and Sea Park (ECLSP) (> 50 adults/ha²) was 17 times higher than in a fished area near Lee Stocking Island (LSI). Differences in deeper shelf environment (10 - 30 m) were about three times. When identical surveys were repeated in 2011, it was discovered that the density of conch in the bank habitat of LSI had increased slightly, but numbers in shelf habitat had declined 91%, to densities below capacity to support reproduction. At ECLSP, bank densities declined by 69% to just 16 adults/ha. The population in shelf environment declined a smaller amount (6.4%), but the ECLSP population is also becoming older, indicating recruitment limitation. Histological studies on reproductive readiness in ECLSP revealed that males and females were not spawning capable until at minimum 10 - 15 mm lip thickness, respectively. Although these surveys represent two specific areas in the Exuma Cays, it is clear that queen conch populations have declined precipitously since the 1990s, that conch inside even a large protected area like ECLSP are vulnerable to fishing that occurs outside the reserve, and that in the Bahamas conch are legally allowed to be harvested before reaching sexual maturity. We propose that a single marine reserve cannot work in isolation for species with pelagic larvae. We recommend that a network of reserves and a minimum lip thickness criteria of 10 - 15 mm be implemented for sustainable harvest of queen conch (and other species with pelagic larvae) in the Bahamas and other nations of the Caribbean.

KEY WORDS: Queen conch, reproduction, Bahamas, MPA management

INTRODUCTION

The Exuma Cays Land and Sea Park (ECLSP), established in 1958, is the oldest marine protected area (MPA) in The Bahamas. The Park is relatively large (456 km²), 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. 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 queen conch (*Strombus gigas*) (Dahlgren 2004). Fishery resources in the Park had only modest protection during the earliest years, but in 1986 the Park was made an official no-take zone and protection increased gradually with a local warden and increased enforcement (Chiappone and Sealey 2000). At present, the Park is protected with a fleet of small boats and permanent presence of the Royal Bahamian Defense Force.

In 1994, Stoner and Ray (1996) surveyed adult, juvenile, and larval stages for queen conch at Warderick Wells (WW) in the center of the Park for direct comparison with surveys conducted three years earlier near the moderately fished waters of Lee Stocking Island (LSI) 70 km south. They concluded that densities of adults on the shallow bank around WW were 17 times higher than densities in comparable habitats with moderate fishing pressure near (LSI) and that the Park was "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 ECLSP is an important source of larvae for both queen conch (Stoner et al. 1998) and spiny lobster (Lipcius et al. 1997). However, both Stoner & Ray (1996) and Chiappone & Sealey (2000) warned that the marine resources inside 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 the two previously surveyed locations at WW and LSI in the Exuma Cays. Emphasis was placed upon the age structure and reproductive potential of the adult component and evaluating the likelihood of a self-sustaining population in the ECLSP.

METHODS

Study Sites

Surveys were conducted at two sites in the Exuma Cays in 2011 (Figure 1a), repeating surveys that were conducted by Stoner and Ray (1996) in the early 1990s. 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*). Depths over the bank are typically 1 - 3 m at mean low water (tidal range = ~1.0 m), with deeper tidal channels (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 which tend to be in direct association with the tidal channels where larvae are concentrated and where there is an abundance of macroalgal foods associated with the seagrasses (Stoner 2003). All along the Exuma Cays, the island shelf extends 1-3 km offshore from land 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 macroalgae (especially *Cladophoropsis* sp.) and sparsely distributed soft corals. Beyond 15 m, the habitat is a mix of sand and large coral ridges with patches of hard bottom. In the past, adult queen conch and a few juveniles have occupied all of these habitats (Stoner, Personal observation) except the coral areas.

To repeat surveys exactly as made by Stoner and Ray (1996) in the early 1990s, queen conch density and abundance were explored in a 12 km long section of the Exuma Cays adjacent to Lee Stocking Island and Childrens Bay Cay, and a 7.5 km long section near Warderick Wells at the center of the ECLSP (Figures 1b and c). The Perry Institute for Marine Science requests no fishing within one-half mile of LSI. The Warderick Wells study site (WW) was chosen by Stoner and Ray (1996) because it is adjacent to ECLSP headquarters, is regularly patrolled by enforcement officials, and has probably been least susceptible to poaching over the last 20 years. The WW study site is 15 km from the southern boundary of ECLSP and 70 km north of the LSI study site.

Survey Periods

The survey periods for 2011 and the earlier surveys are as follows:

| | <u>1991/1994</u> | <u>2011</u> |
|------|------------------------|-------------------|
| LSI: | March - September 1991 | 16 - 26 June 2011 |
| WW: | 12 - 29 July 1994 | 7 - 16 July 2011 |

Comparisons in reproductive behavior were made during peak mating season (summer) for the two sites described above. Water temperatures on the bottom were

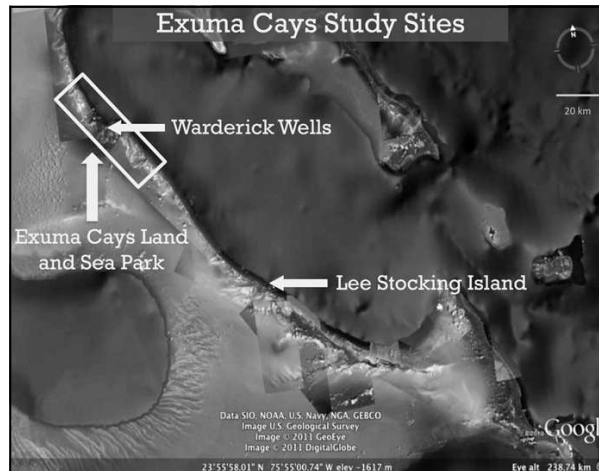


Figure 1 (a). Map of study sites in the Exuma Cays of The Bahamas including Warderick Wells (WW) in the Exuma Cays Land and Sea Park, and Lee Stocking Island (LSI).

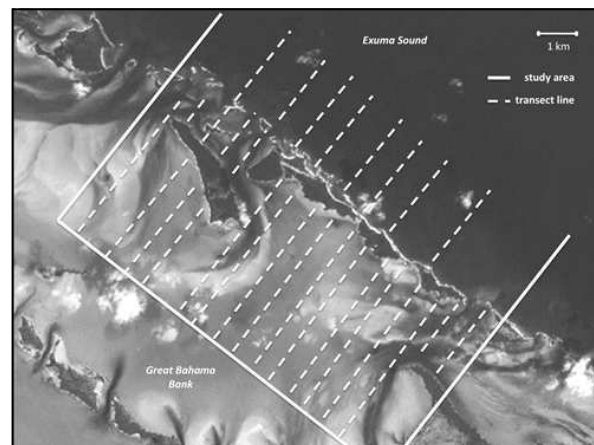


Figure 1 (b). Lee Stocking Island study site.

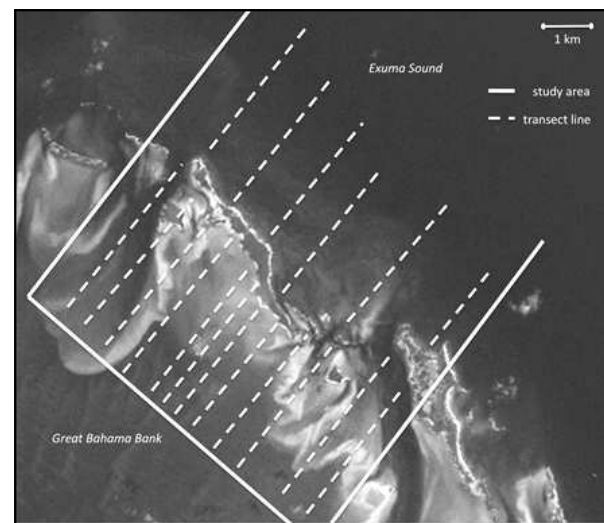


Figure 1 (c). Warderick Wells study site.

relatively similar for each of the surveys and it is unlikely that this variable caused any differences in spawning behavior.

| | <u>Observation period</u> | <u>Range of water temperature</u> |
|-----|---------------------------|-----------------------------------|
| WW: | 12-29 July 1995 | 27.5 to 28.2 °C |
| WW: | 7-16 July 2011 | 27.8 to 29.9 °C |

Survey Methods

This study was focused primarily on determining the density and abundance of adult queen in the two study sites for direct comparison with Stoner and Ray (1996). Therefore, the site boundaries and approach were held identical to the earlier study. As before, 2011 surveys were confined to bank areas within 5 km of an imaginary line running along the eastern shore of the islands (Figures 1b and c) 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/hr) over each pre-determined line, counting the numbers of adult, subadult, and juvenile conch (see below) in a 6 m wide band. Towing was stopped at 1 km intervals (or less depending upon the position of islands and intertidal sand bars), and the numbers 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 was a slightly greater effort than that in the 1990s, when 63 km were surveyed at LSI and 47 km at WW.

Depths increase over short distances in the shelf area east of the islands. Therefore, depth-stratified surveys were conducted at each site. Survey locations were placed along each of 10 lines running offshore from LSI and six lines running offshore from WW. As performed by Stoner and Ray (1996), conch density determinations were made in six depth intervals (0 - 2.5, 2.5 - 5, 5 - 10, 10 - 15, 15 - 20, and 20 - 25 m) placed on each line. This excluded a narrow band at depths 25 - 30 m surveyed by Stoner and Ray that yielded no conch at LSI and relatively few at WW. At the two 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, two 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 two 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.

A queen conch was classified as an adult when it had a flared shell lip, compatible with the fisheries management definition. Subadults were three year old juveniles, typically called "rollers"; these are individuals as large as adults in shell length but without the flared shell lip. One and two-year old juveniles were also counted when observed. These were generally < 120 mm shell length and represented the age-1 and age-2 year classes. While adult densities and abundance could be compared directly with the earlier surveys, only adult data were recorded in the 1990s; therefore, direct comparisons with the younger conch are not possible. Also, juvenile distributions are highly aggregated (Stoner 2003), and broad scale transecting offers only qualitative data about the abundance of the younger (age-1 and age-2) juveniles. Stoner and Ray mapped queen conch nurseries in the ECLSP for the Bahamas National Trust in 1993 and the conch research team at the Caribbean Marine Research Center mapped nurseries in the vicinity of LSI over an 8 year period (Stoner 2003). To gauge the current extent of three of these historic nurseries in the study area at LSI and five nursery areas in and outside of the study area at WW, a refined grid of transect lines was towed over each area to locate nursery populations of juveniles.

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 extent of erosion on the shell exterior. Therefore, collections were made to evaluate their relative size and age. At LSI, 38 individuals were collected and 33 shells of dead conch were collected for measurement at WW. In all cases the shells measured were those likely to have resulted from natural mortality and not those obviously "knocked" by fishers.

Observations of reproductive behavior in queen conch were recorded for each survey line. This included numbers of mating pairs and numbers of egg-laying females. Egg masses were also observed upon occasion, but counts were not quantitative because the masses alone are not always detected.

Collections for Gonad Weights and Histology

Collections of conch with flared shell lips were made at LSI and WW to explore the relationship between reproductive maturity and shell lip thickness, a surrogate indicator of conch age. This evaluation included both quantitative and qualitative measures of gonad development in both males and females. First, gonads were

extracted to determine their weights relative to total soft body weight (proportion of soft tissue). Second, samples of the gonads were preserved for histological examination to evaluate the actual reproductive maturity (or readiness) of the tissues.

Methods for dissecting and measuring gonad weights for both males and females were standardized at LSI. This entailed carefully breaking away the spire so that the entire soft body of the conch could be extracted in one piece through the top of the shell. The gonad tissues and associated duct structures were then dissected away from the surrounding digestive gland. During the process, weights were taken for the whole animal (including shell), the entire soft body, and the gonad, along with total shell length and shell lip thickness as described above. These numbers provided opportunity to examine relationships among the various metrics including derived measures such as ratios of gonad weight to soft tissue weight. Standard linear regression techniques were used to evaluate the relationships. An effort was made to collect equal numbers of male (identified by the presence of a verge) and female conch over a range of shell lip thickness ranging from 1 to 42 mm in nine bins of 4 mm each (0 - 4, 5 - 9, 10 - 14, etc). Thirty-two and 112 queen conch were collected for this purpose at LSI and WW, respectively.

A large subset of the conch collected at WW for gonad weights were also sampled for histological evaluation of the gonads. For this a 1 cm cube of gonad tissue was removed from the center of the gonad and preserved in a 10% solution of buffered formalin. Samples taken from 102 conch, representing equal numbers of males and females with shell lip thicknesses ranging from 2 to 42 mm, were prepared for examination. After at least 7 days in formalin, the samples were transferred to 70% ethanol and shipped to Nancy Brown-Peterson at Ecofish Consulting for analysis. Then, the tissues were loaded into an automatic tissue processor (Shandon Hypercenter XP) for dehydration, clearing, and paraffin infiltration. Tissues were embedded in Paraplast Plus and sectioned at 4 micrometers with a rotary microtome. Two serial sections

from each tissue sample were mounted on glass slides, allowed to dry overnight, and stained with hematoxylin-1 and eosin Y. A detailed histological inspection of each sample was made to assess the stage of gonadal maturity and the percentage of gametogenic tissue. Each animal was given a score from 0 to 5 to quantify maturity (Table 1). In addition, the percentage of ovarian or testicular tissue present was visually estimated by using the following index (< 25%, 25 - 50%, 51 - 75%, and > 75%).

RESULTS

Adult Density and Abundance

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 (5.78 adults/ha²) than in 1991 (3.16 adults/ha²) (Table 2; Figure 2), the difference was not statistically significant. 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), and the effects of survey year were highly significant. The most notable declines in conch density and abundance occurred in the depth range of 10 - 20 m where densities were highest in 1991.

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 insignificant increase at LSI and a large (69%) decrease in the density and numbers of conch at WW. Unlike the small change at LSI, the decrease in density on the WW bank was highly significant.

Surveys conducted on the WW shelf showed that densities there both increased and decreased between 1994 and 2011, depending upon the depth interval. However, at depth intervals where adult conch had been particularly abundant in 1994, such as 10 - 25 m, densities declined substantially and the overall shelf population decreased about 6%.

Table 1. Index and definitions used to quantify gonadal maturity in queen conch (following Egan 1985).

| Gonad condition | Score | Definition |
|------------------|-------|---|
| No germ tissue | 0 | Holes in the gonadal area with some epithelial tissue, but no germinal tissue |
| Immature | 1 | Oogonial nests in females, spermatogonial nests in males; no other germinal tissue present |
| Early developing | 2 | Only spermatogonia and spermatocytes in males; only primary growth and cortical alveolar oocytes in females |
| Late developing | 3 | All stages of spermatogenesis in males, including spermatozoa. No vas deferens present, or, if present, no spermatozoa in them. Early vitellogenic oocytes present in females, with a few vitellogenic oocytes. Conch in this phase are not capable of releasing gametes. |
| Spawning capable | 4 | All stages of spermatogenesis in males, with spermatozoa in the vas deferens. In females, late vitellogenic oocytes predominate. If oviducts are present, vitellogenic oocytes in oviducts. Conch in this phase are capable of releasing gametes. |
| Regressing | 5 | In males, lobules degenerating, atresia and resorption of all stages of spermatogenesis; macrophages and macrophage aggregates common. In females, oocyte atresia common, macrophage aggregates present. Conch in this phase are not capable of releasing gametes. |

In 2011, the density of adult conch in the shelf environment was about 28 times higher at WW (89.8 adults/ha²) than at LSI (3.2 adults/ha²) considering the entire shelf areas at each site (Table 2). The overall difference in density was highly significant as was the difference at every comparable depth interval. This represents a substantial change from the 1990s when the difference between WW (96.0 adults/ha²) and LSI (34.5 adults/ha²) in overall adult density in shelf habitat was just 2.8 times. Considering all habitats together (bank and shelf), average density of adult conch was 5.0 times higher at WW than LSI in 1990s and 9.4 times higher at WW in 2011.

The overall population estimate for adult conch at LSI declined 65.7% from 1991 to 2011 (Table 2). Whereas most of the adults (85.6%) 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 population declined 90.7%. At WW adult populations declined 35.0%, with most of the change occurring on the shallow bank where adult conch numbers had decreased 69.1%.

Adult Size and Shell Lip Thickness

The shell lengths of adult queen conch were shorter in the bank environment than on the island shelf at LSI and WW during both early and recent surveys (Table 3), although the bank-shelf difference was relatively small at WW in 2011. Some apparent changes in average shell length occurred between survey years. At LSI, the largest inter-year difference was observed in shelf environment, where adult conch in the 2011 surveys were 6-mm larger than two decades earlier, but the difference was not statistically significant. Inter-year difference on the LSI bank was even smaller (3 mm). At WW, a 12 mm increase in average shell length observed in bank environment between 1994 and 2011 was highly significant, but the small increase (2 mm) in shelf environment was not.

Shell lip thickness varied both spatially and temporally over the two survey sites (Table 4). Conch with thinnest shells occurred in the bank environment at LSI with mean values between 9 and 10 mm during the two survey years. Shells were thicker on the LSI island shelf, and analysis of variance showed that shells measured in 2011 were significantly thinner (mean = 21 mm) than those measured

Table 2. Abundance of adult queen conch with flared shell lips near Lee Stocking Island (fished area) and Warderick Wells (marine protected area) in the Exuma Cays, Bahamas. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner and Ray, 1996). Values for densities are mean \pm SD, and number of survey lines (n).

| Site and Habitat | Habitat Area (ha) | Adult Density (no./ha ²) | Estimated Total Number | Adult Density (no./ha ²) | Estimated Total Number | % Change |
|----------------------------|-------------------|--------------------------------------|------------------------|--------------------------------------|------------------------|----------|
| Lee Stocking Island | | 1991 | | 2011 | | |
| Bank | 3,997 | 3.16 \pm 1.69 (51) | 12,631 | 5.78 \pm 1.85 (70) | 23,103 | 45.3 |
| Shelf | | | | | | |
| 0 - 2.5 m | 161 | 0 \pm 0 (4) | 0 | 1.85 \pm 1.85 (2) | 298 | |
| 2.5 - 5.0 m | 198 | 2.24 \pm 1.70 (7) | 444 | 1.25 \pm 0.82 (8) | 248 | |
| 5 - 10 m | 465 | 7.21 \pm 4.11 (9) | 3,353 | 3.69 \pm 3.24 (10) | 1,920 | |
| 10 - 15 m | 429 | 60.1 \pm 46.8 (9) | 25,782 | 1.70 \pm 1.09 (10) | 729 | |
| 15 - 20 m | 454 | 87.9 \pm 31.5 (9) | 39,907 | 1.80 \pm 0.85 (10) | 817 | |
| 20 - 25 m | 320 | 18.3 \pm 9.1 (9) | 5,856 | 9.42 \pm 8.48 (10) | 3,014 | |
| 25 - 30 m | 151 | 0 \pm 0 (9) | 0 | not surveyed | -- | |
| Shelf total | 2,178 | 34.5 | 75,342 | 3.2 | 7,026 | -90.7 |
| Total numbers | 6,175 | 14.2 | 87,973 | 4.9 | 30,129 | -65.6 |
| Warderick Wells | | 1994 | | 2011 | | |
| Bank | 3,245 | 53.6 \pm 19.2 (35) | 174,080 | 16.6 \pm 7.0 (52) | 53,867 | -69.1 |
| Shelf | | | | | | |
| 0 - 2.5 m | 158 | 0 \pm 0 (2) | 0 | not surveyed | 0 | |
| 2.5 - 5.0 m | 200 | 34.4 \pm 22.4 (6) | 6,871 | 35.5 \pm 12.1 (7) | 7,100 | |
| 5 - 10 m | 1035 | 49.4 \pm 18.3 (7) | 51,138 | 144.5 \pm 45.5 (6) | 149,557 | |
| 10 - 15 m | 375 | 269.8 \pm 85.0 (6) | 101,187 | 85.1 \pm 41.3 (7) | 31,912 | |
| 15 - 20 m | 193 | 104.2 \pm 58.4 (6) | 20,113 | 7.59 \pm 3.61 (7) | 1,464 | |
| 20 - 25 m | 136 | 147.8 \pm 72.5 (5) | 20,108 | 34.3 \pm 17.1 (6) | 4,665 | |
| 25 - 30 m | 71 | 121.9 \pm 70.2 (6) | 8,635 | not surveyed | -- | |
| Shelf total | 2,167 | 96 | 208,053 | 89.8 | 194,698 | -6.4 |
| Total Numbers | 5,412 | 70.6 | 382,133 | 45.9 | 248,565 | -35.0 |
| Ratio WW:LSI | | | | | | |
| Bank | | 17.0 | | 2.9 | | |
| Shelf | | 2.8 | | 28.1 | | |
| Total | | 5.0 | | 9.4 | | |

in 1991 (mean = 28 mm). A similar analysis at WW revealed a different pattern. Shell lip thickness increased from 1994 to 2011, particularly on the bank, where average lip thickness increased by 9 mm. The year differences were significant for conch from the bank and the shelf habitats.

Differences in shell length and lip thickness between the bank and shelf habitats and between living and dead conch at each of the two sites are evident in the scatterplots

shown in Figure 3. Shells of dead conch found on the island shelf had average lengths in ranges similar to the living adult conch at each of the two sites. However, the average shell thickness for dead conch (33 mm; SD = 4; range = 23 - 41) was significantly higher than that for living adults at LSI which averaged just 21 mm (Table 3). The difference at WW was minor, with a mean of 30 mm (SD = 5; range = 20 - 42) for dead shells and 28 mm (SD = 5; range = 15 - 43) for living adults.

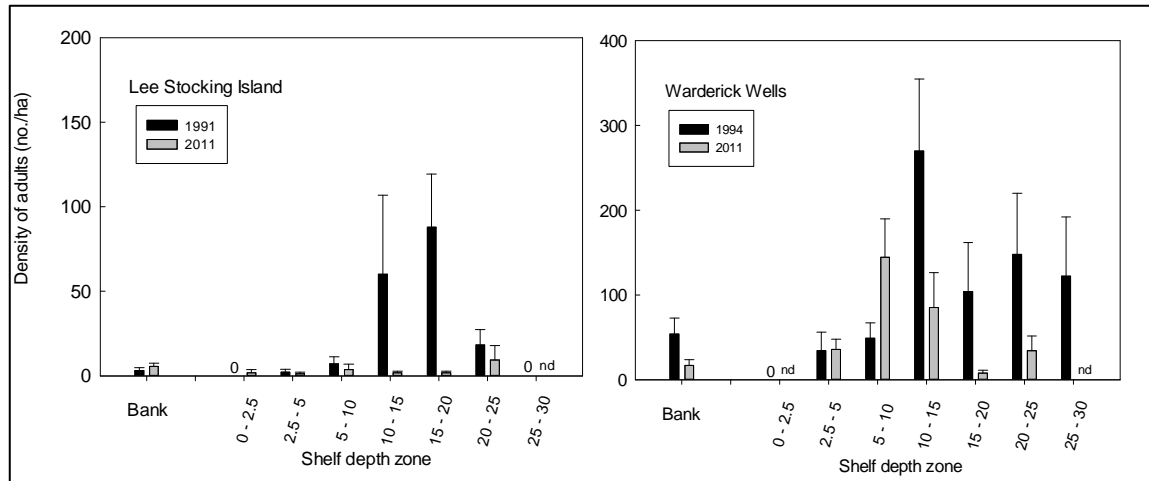


Figure 2. Densities of adult queen conch near Lee Stocking Island and Warderick Wells, Exuma Cays in the 1990s and in 2011. Densities are shown for the shallow bank environment west of the islands and for seven depth zones (shown in meters) in shelf environment east of the islands bordering Exuma Sound. Values are mean ± standard deviation. nd = no data. Note the different scales for the two sites.

Table 3. Shell length data for adult queen conch with flared shell lips near Lee Stocking Island and Warderick Wells in the Exuma Cays, Bahamas. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner and Ray, 1996). Data are reported for depth intervals where there are comparable data. Values (mm) are mean ± SD, and number of samples (n).

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

Subadult Density and Abundance

Subadult conch, representing the 2008 year class during the 2011 surveys, were most abundant on the shallow banks west of both LSI and WW (Table 5; Figure 4). Highest average density (73.1 subadults/ha²) occurred on the bank near LSI, and this was significantly higher than the density value on the bank near WW (10.8 subadults/ha²), 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 shelf environment, particularly at LSI where densities were < 2.0 subadults/ha² in all depth zones and none were found deeper than 15 m depth (Table 5). Densities ranged from 2.4 to 8.8 subadults/ha² on the WW shelf and were present in all of the depth zones sampled.

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

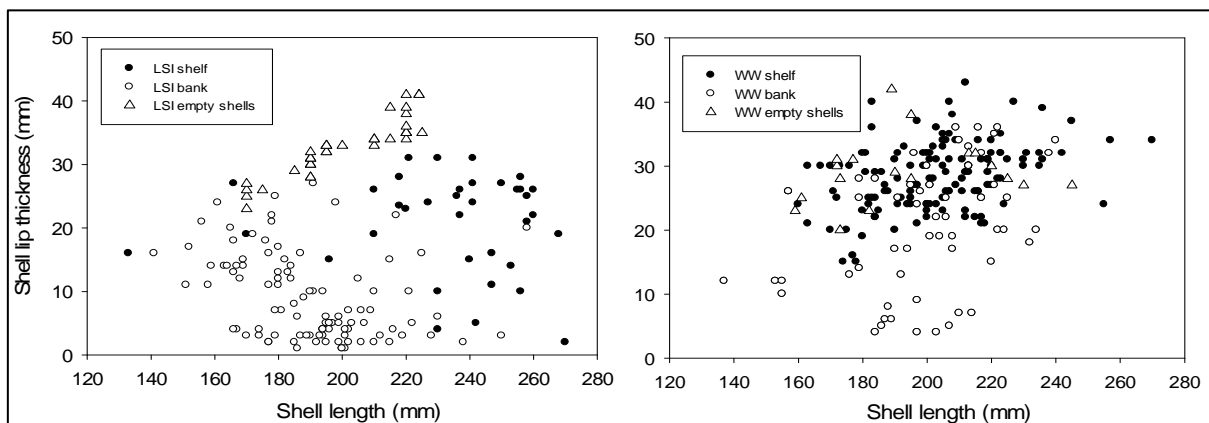


Figure 3. Plots of total shell length and shell lip thickness for adult queen conch near Lee Stocking Island (left) and Warderick Wells (right) in 2011. Data are shown for conch from the shelf and bank habitats, and for empty shells representing natural mortalities at each site.

Table 4. Shell lip thickness data for queen conch with flared shell lips near Lee Stocking Island and Warderick Wells in the Exuma Cays, Bahamas. Surveys conducted in 2011 are compared with those for LSI in 1991 and WW in 1994 (adapted from Stoner and Ray, 1996). Data are reported for depth intervals where there are comparable data. Values (mm) are mean ± SD, and number of samples (n).

| Lee Stocking Island | 1991 | 2011 |
|---------------------|--------------|--------------|
| Bank | 10 ± 6 (472) | 9 ± 7 (100) |
| Shelf | | |
| 2.5 - 5.0 m | 18 ± 5 (21) | no data |
| 5 - 10 m | 28 ± 6 (57) | 17 ± 8 (12) |
| 10 - 15 m | 30 ± 7 (229) | 27 ± 6 (4) |
| 15 - 20 m | 27 ± 6 (150) | 18 ± 10 (8) |
| 20 - 25 m | 28 ± 6 (100) | 24 ± 5 (13) |
| Shelf total | 28 ± 7 (557) | 21 ± 8 (37) |
| Warderick Wells | 1994 | 2100 |
| Bank | 12 ± 6 (213) | 21 ± 10 (58) |
| Shelf | | |
| 2.5 - 5.0 m | 23 ± 5 (39) | no data |
| 5 - 10 m | 26 ± 8 (144) | 29 ± 5 (94) |
| 10 - 15 m | 25 ± 7 (148) | 27 ± 6 (36) |
| 15 - 20 m | 21 ± 5 (60) | 26 ± 0 (1) |
| 20 - 25 m | 23 ± 5 (70) | 29 ± 6 (3) |
| Shelf total | 25 ± 7 (461) | 28 ± 6 (134) |

near WW (32.7%). Only one juvenile was observed on the island shelf near LSI, in 3 m depth. On the WW island shelf, eight juveniles were widely scattered over a range of depth 5 to 23 m. Because of the highly aggregated distribution of small juveniles, the broad-scale surveys for adults and subadults do not provide robust values for the smaller individuals, and there are no comparable data for the 1990s. Rather, transects were run through three historic nursery sites at LSI and five sites at WW to confirm their current status. The three nurseries at LSI, near Tug and Barge, Shark Rocks and Children’s Bay Cay were all still functioning but their areal extent had declined by more than one half since the 1990s. At WW, there were only two

historic nurseries in the study area, near Riding Rocks and White Bay, and both were about a quarter of the sizes mapped in 1993. At two other nurseries, located south of the study area but within ECLSP, the Sandy Cay nursery was much reduced while the Channel Rocks nursery appeared to be similar to that observed in 1993. The historic nursery at Compass Cay, just south of the park boundary, was about one-half its historic extent.

Reproductive Behavior

At LSI, reproductive behavior was observed at only one location. Three mating pairs were found on transect F in 23 m depth on 21 June 2011 (Table 6). This was

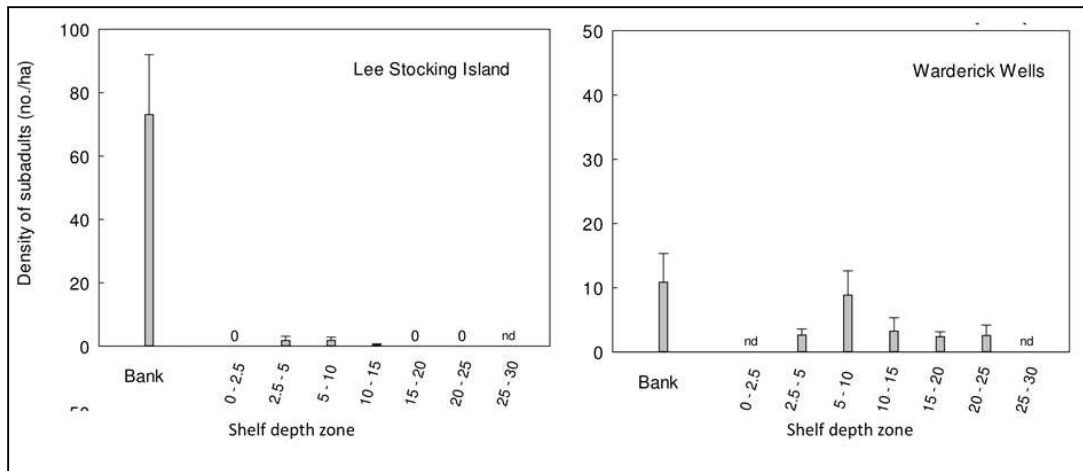


Figure 5. Densities of subadult queen conch (3-year old juveniles; 2008 year class) near Lee Stocking Island and Warderick Wells, Exuma Cays in 2011. Densities are shown for the shallow bank environment west of the islands and for seven depth zones (shown in meters) in shelf environment east of the islands bordering Exuma Sound. Values are mean ± standard deviation. nd = no data. Note the different scales for the two sites.

Table 5. Abundance of subadult queen conch (2008 year class) near Lee Stocking Island (fished area) and Warderick Wells (marine protected area) in the Exuma Cays, Bahamas in June/July 2011. Values for densities are mean ± SD, and number of survey lines (n).

| Site and Habitat | Habitat Area | Subadult density |
|----------------------------|--------------|------------------------|
| | (ha) | (no./ha ²) |
| Lee Stocking Island | | |
| 2011 | | |
| Bank | 3,997 | 73.1 ± 18.9 (70) |
| Shelf | | |
| 0 - 2.5 m | 161 | 0 ± 0 (2) |
| 2.5 - 5.0 m | 198 | 1.81 ± 1.31 (8) |
| 5 - 10 m | 465 | 1.90 ± 1.03 (10) |
| 10 - 15 m | 429 | 0.41 ± 46.8 (10) |
| 15 - 20 m | 454 | 0 ± 0 (10) |
| 20 - 25 m | 320 | 0 ± 0 (10) |
| Warderick Wells | | |
| 2011 | | |
| Bank | 3,245 | 10.85 ± 4.47 (52) |
| Shelf | | |
| 0 - 2.5 m | 158 | not surveyed |
| 2.5 - 5.0 m | 200 | 2.62 ± 0.95 (7) |
| 5 - 10 m | 1,035 | 8.83 ± 3.80 (6) |
| 10 - 15 m | 375 | 3.24 ± 2.10 (7) |
| 15 - 20 m | 193 | 2.37 ± 0.78 (7) |
| 20 - 25 m | 136 | 2.56 ± 1.62 (6) |

coincident with the highest adult density recorded for the LSI island shelf environment (85.5 adults/ha²). Just one other survey line yielded a higher adult density (120.6 adults/ha²) on bank line 15, but no reproduction was observed there. At this bank location, about half of the conch classified as adults had thin shell lips (< 10 mm) and were probably not sexually mature (see Relationship between shell dimensions and maturity). 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 in both the bank and shelf environment. Fifteen mating pairs were observed at four of the 52 tow locations on the bank in depths 3 to 5 m deep near the island passes. All of these observations occurred among the nine transect segments with highest adult densities (13 - 155 adults/ha²). Thirty-six mating pairs were observed on nine of the 33 surveys on the island shelf, and 15 egg-laying females were observed on six surveys. Mating was observed at every shelf location where density was > 100 adults/ha². Egg-laying was also associated with high adult density, ranging from 94 to 219 adults/ha², and just one high-density site lacked egg-laying behavior (Table 6).

Relationships Between Shell Dimensions and Maturity

Gonad weight increased with shell length for both female and male conch with a broad spread of points (Figure 5). The gonads of conch less than 160 to 180 mm were very small, generally < 5 g. The highest gonad weights were ~25 g in females and 20 g in males. Gonad weights also increased generally with shell lip thickness, but the relationships were more scattered (Figure 6) because of the confounding effect of shell length. For example, large thick lipped conch had higher gonad weights than equally thick small conch. A better predictor

of gonad weight was possible when shell length and shell lip thickness were considered together. In fact, multiple regressions showed that gonad weight was closely correlated with a combination of the two variables, with correlation coefficients of 0.800 for female conch and 0.843 for males. Histological analysis of the gonad tissues showed that lip thickness (LT) had a large effect on the maturity of both male and female conch (Tables 7 & 8). For example, 71.4% of the tissues in males < 5 mm had no germ tissue at all, and no male in this age category had gonad development beyond early stages. Fourteen percent of the tissue in males 5 - 9 mm LT showed signs of spawning capability (Table 7); while much higher spawning capabilities occurred in individuals with thickness higher than 9 mm. Also at this lip thickness, at least 50% of the tissues observed had a high percentage of gonad tissue (i.e., > 75% of the tissue was actual gonadal tissue) (Table 8). Females appear to have later development with respect to shell lip thickness. No females thinner than 10 mm had tissues capable of spawning (Table 7), and at 10 - 14 mm LT only 16.6% of the tissue had a high proportion of germ cells (Table 8). The majority of females did not have large, fully developed ovaries until 15 mm LT. Although all females > 15 mm LT were spawning capable, conch with thicker lips had more ovarian tissue than those with thinner lips. There was no evidence of female or male senescence with increasing lip thickness, although some males > 25 mm LT showed significant regression of testes, probably following mating (Table 7).

DISCUSSION

Changing Populations

The overall abundance of adult queen conch declined substantially over the last two decades at both LSI and WW. Although the density and abundance of adults on the shallow bank near LSI did not change significantly since

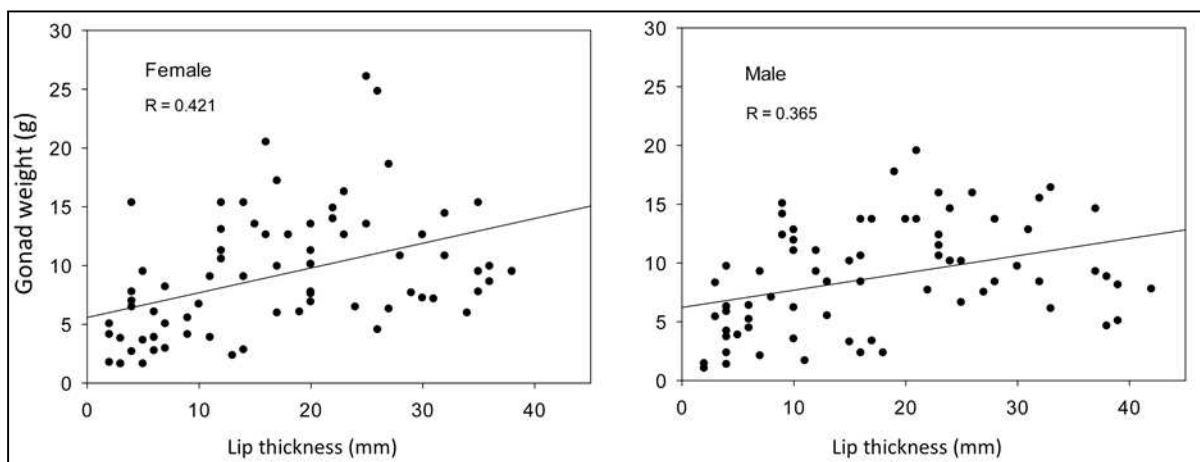


Figure 6. Relationship between gonad weight and shell lip thickness for female and male queen conch collected in the Exuma Cays near Lee Stocking Island and Warderick Wells in June/July 2011. 72 individuals were sampled for each gender.

the early 1990s, the densities observed in the early surveys were already very low (Stoner and Schwarte 1994). More importantly, abundance on the island shelf declined more than 90% during the interval between 1991 and 2011. It is clear that fishing pressure or some other variable is severely reducing the abundance of queen conch in the region. However, two other variables strongly support that the LSI population is overfished. First, the adult population is now younger than it was in the early 1990s, as shown by a significantly thinner average shell lip thickness. Second, the average shell lip thickness of living adults are significantly thinner than the shells of conch found dead of natural causes in deep water. The latter represent animals from years to decades past, and the age structure was

similar to that observed in the early surveys. Consequently, it is apparent that the population of adults at LSI is becoming younger, a universal signal of overfishing.

Changes in adult density also occurred at WW, in both bank and shelf environments. While the shelf population has declined only 6% since 1994, the 69% reduction in shallow bank habitat is highly significant. Given that queen conch have long lives (at least 20 years or more), the failure represents a general decline in recruitment over the long term, and not failure of a single year class or two. Also, the bank population had an average shell thickness 75% greater in 2011 than in 1994. This represents a significant aging of the population. A smaller but signifi-

Table 6. Reproduction observed at during 2011 surveys at Lee Stocking Island (LSI) and Warderick Wells (WW), Exuma Cays. Letter and number codes refer to the survey transect lines on the shelf and bank, respectively. Under observations, M = number of mating pairs, E = number of egg-laying females.

| Location | Date | Depth | Adult density | Mating pairs | Egg-laying females |
|------------|--------|-------|---------------|--------------|--------------------|
| | | (m) | (no./ha) | | |
| LSI | | | | | |
| Shelf F | 21-Jun | 23 | 85.5 | 3 | 0 |
| WW | | | | | |
| Bank 1 | 10-Jul | 5 | 314.4 | 6 | 0 |
| Bank 7 | 11-Jul | 4 | 98.3 | 5 | 0 |
| Bank 11 | 9-Jul | 3 | 40.4 | 1 | 0 |
| Bank 11 | 9-Jul | 4 | 20.4 | 3 | 0 |
| Shelf A | 7-Jul | 25 | 106.6 | 3 | 3 |
| Shelf A | 7-Jul | 14 | 94.3 | 0 | 2 |
| Shelf A | 10-Jul | 8 | 225.2 | 9 | 4 |
| Shelf B | 10-Jul | 9 | 225.7 | 3 | 1 |
| Shelf B | 10-Jul | 12 | 255.1 | 2 | 3 |
| Shelf C | 11-Jul | 13 | 219 | 1 | 2 |
| Shelf D | 12-Jul | 24 | 74 | 1 | 0 |
| Shelf D | 16-Jul | 4 | 90 | 5 | 0 |
| Shelf E | 14-Jul | 8 | 275.6 | 10 | 0 |
| Shelf F | 14-Jul | 8 | 84.5 | 2 | 0 |

Table 7. Percentage of gonadal developmental phases present in testes and ovaries by size class (mm lip thickness, LT) for male (M) and female (F) conch (Brown-Peterson, 2011).

| LT (mm) | No germ tissue | | Immature | | Early Developing | | Developing | | Spawning Capable | | Regressing | |
|---------|----------------|------|----------|------|------------------|------|------------|------|------------------|-----|------------|----|
| | M | F | M | F | M | F | M | F | M | F | M | F |
| < 5 | 71.4 | 100 | 14.3 | 0 | 14.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 - 9 | 42.8 | 62.5 | 0 | 37.5 | 14.3 | 0 | 28.6 | 0 | 14.3 | 0 | 0 | 0 |
| 10 - 14 | 0 | 0 | 0 | 0 | 0 | 16.7 | 16.7 | 33.3 | 83.3 | 50 | 0 | 0 |
| 15 - 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 100 | 0 | 0 |
| 20 - 24 | 0 | 0 | 0 | 0 | 14.3 | 0 | 0 | 0 | 85.7 | 100 | 0 | 0 |
| 25 - 29 | 0 | 0 | 0 | 0 | 0 | 0 | 12.5 | 0 | 75 | 100 | 12.5 | 0 |
| 30 - 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 100 | 0 | 0 |
| 35 - 39 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 83.3 | 100 | 16.7 | 0 |
| 40+ | 0 | -- | 0 | -- | 0 | -- | 0 | -- | 100 | -- | 0 | -- |

cant change in shell lip thickness also occurred in the shelf environment at WW. Furthermore, the average living adult had an age not much less than the average age of dead conch recovered from the shelf habitat. This demographic characteristic suggests that the population has very low recruitment, is aging, and is likely to decline rapidly over the next few decades.

Subadult conch were not classified and counted in the early surveys, so direct comparisons are not possible. However, the abundance of subadults was very high on several bank survey lines near LSI, suggesting high recruitment to the benthic population in 2008. The source of recruitment is unknown, but this may offer some reason for optimism that an occasional strong year class may be able to replenish conch populations if spawning stocks upcurrent are protected (see below). Subadults were relatively uncommon in shelf environment at WW and rare on the LSI shelf. This is not unexpected because most queen conch nursery grounds in the Exuma Cays occur on the shallow bank (Stoner 2003).

Populations of juveniles (age-1 and age-2) were still intact at most of the Exuma Cays nurseries re-visited in 2011. However, declining recruitment is evidenced by the decreases in sizes of juvenile aggregations near both LSI and WW. Low recruitment to nurseries helps to explain the failing population of adults at LSI and the aging population at WW. The nurseries depend upon upstream spawning stocks and larval recruitment (see below).

Reproduction Biology

Histological evaluation showed that the males were not ready for actual mating until they had reached a lip thickness of at least 5 mm. The testes for males at 5 - 9 mm LT had a relatively low proportion of actual gonad tissue and only about 14% of the male tissue contained spermatozoa. Much higher spawning readiness occurred above 10 mm LT. For females, spawning readiness was even more delayed, with high proportions of gonad tissue and mature eggs in the ovaries not occurring until 15 mm LT. Based upon histological studies for queen conch in Colombia, Aldana Aranda and Frenkiel (2005) suggested that queen conch require at least 7 mm in lip thickness to be mature (both males and females). This corresponds relatively well with our findings for males in the ECLSP, but not with our findings for females. In fact, we conclude that high spawning capability for conch in The Bahamas requires 10 mm LT in males and 15 mm LT in females. Clearly, this is well after the age the conch are subject to legal fishing.

Mating behavior was observed at just one LSI location in 2011. Three mating pairs were found in 23 m depth in a location with 85.5 adults/ha². Neither egg masses nor egg-laying females were found during the two week survey period in peak reproductive season. While mating and egg laying was observed infrequently in the bank environment during intensive field work near LSI during the 1990s (Stoner, pers. observ.), the shelf waters offshore from the

island were known for abundant reproductive conch (Stoner and Sandt 1992) and the 15 to 20 m zone was a routine source of egg masses for larval culture conducted by the Caribbean Marine Research Center during that time (Davis et al. 1993, Davis 1998). It is clear that that scenario has changed substantially, and it is unlikely that LSI provides significant numbers of eggs and larvae for downstream populations at this time.

Production of Larvae

Larval surveys for queen conch were conducted close to LSI and WW in 1993 and 1994 (Stoner and Ray 1996) and in the broader context of Exuma Sound in 1995 (Stoner et al. 1998). Based upon those collections and studies of physical oceanography in the Sound it was concluded that larvae are 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 transport 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 90% since the mid-1990s, and the same may be true for a large portion of Exuma Sound beyond the boundaries of the 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 conch veligers in ECLSP were the highest ever recorded in the Caribbean region (Stoner and Ray 1996). New larval surveys would be useful in understanding the population decline in the system and the role of the Park in supplying larvae to the surrounding fishing grounds.

Conservation Role of ECLSP

Changes in the population structure of queen conch in the ECLSP suggest that the Park population is not self sustaining. First, the total population of adults has declined ~35% over the last 17 years. While poaching might be considered a potential reason for a decline near the boundaries of the Park, both the 1994 and 2011 surveys were conducted near the Park headquarters where protection is high. The largest decline in adults (69.5%) occurred in shallow bank habitat. This represents the adults closest to the primary nursery grounds (which occur primarily on the bank), and the decline in adults probably means that larval recruitment to the site has diminished.

Further evidence for recruitment limitation near WW is provided by changes in age structure as revealed by shell lip thickness. An exploited population generally gets younger with time because adults are removed, and this was the observed result at LSI. However, at WW the adult population was significantly older in 2011 than it was in

Table 8. Percentage of gonadal tissue containing germ cells present in testes and ovaries by size class (mm lip thickness, LT) for male (M) and female (F) conch (Brown-Peterson, 2011).

| LT (mm) | <25% gonadal tissue | | 25-50% gonadal tissue | | 51-75% gonadal tissue | | >75% gonadal tissue | |
|------------|------------------------|------|--------------------------|----|--------------------------|------|------------------------|------|
| | M | F | M | F | M | F | M | F |
| < 5 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 - 9 | 42.8 | 100 | 18.6 | 0 | 28.6 | 0 | 0 | 0 |
| 10 - 14 | 0 | 16.7 | 16.7 | 50 | 33.3 | 16.7 | 50 | 16.6 |
| 15 - 19 | 0 | 0 | 16.7 | 0 | 0 | 50 | 83.3 | 50 |
| 20 - 24 | 0 | 0 | 0 | 20 | 28.6 | 0 | 71.4 | 80 |
| 25 - 29 | 0 | 0 | 0 | 0 | 37.5 | 0 | 62.5 | 100 |
| 30 - 34 | 0 | 0 | 0 | 0 | 20 | 14.3 | 80 | 85.7 |
| 35 - 39 | 0 | 0 | 0 | 0 | 0 | 20 | 100 | 80 |
| 40+ | 0 | -- | 0 | -- | 0 | -- | 100 | -- |

1994, in both bank and shelf habitats. This is the expected result when the adult population is not being exploited but where recruitment has slowed.

ECLSP is relatively large compared with other marine reserves around the Caribbean region. However, based on the observed changes in density and age structure of queen conch near WW and the reduction in size of historic nurseries outside the study area, we conclude that the Park is not large enough to hold a self sustaining conch population. While substantial numbers of eggs and larvae are produced in the Park, alongshore northwest currents (1.3 to 2.9 km/day) (Stoner and Ray 1996) could carry most of the larvae away from the protected area over the 16 to 28 day period of larval development before settlement. 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 over time. This would substantiate the growing body of literature suggesting that a single marine reserve cannot protect a species with pelagic larvae when the population outside the reserve is heavily exploited (Stockhausen et al. 2000, Gaines et al. 2003, Kaplan et al. 2009). Rather, a network of marine reserves is needed to provide a chain of reproductive sources. More specifically, if a population ages and declines from natural mortality without replacement, the population inside a marine reserve will eventually fail along with the fished parts of the stock (Gaines et al. 2010).

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Contributors

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Project Volunteers

At both study locations, volunteers collected data under the direction of Community Conch scientists. Volunteers at both sites included:

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