Abstract.— A survey of queen conch (Strombus gigas) populations near Lee Stocking Island, Exuma Cays, Bahamas, showed that 74% of all adults were on the narrow island shelf adjacent to the Exuma Sound, in 10-18 m of water. None were found deeper than 25 m, and relatively few adults were found shallower than 10 m. Numbers of juveniles were greatest on the Great Bahama Bank and decreased with increasing depth on the island shelf. No juveniles were found in shelf regions greater than 15 m in depth. Patterns of shell morphology, which were related to growth rates in juveniles, suggest that adults that mature on the Great Bahama Bank rarely move to deep water, and that the most important sources for deep-water stocks are small, nearshore nurseries on the island shelf. The mostly unfished deep-water populations are probably now the primary source of larvae for queen conch in the Exuma Cays. Because virtually all of the conch are within the limits of SCUBA diving, it will be important to identify and to protect critical nursery habitats for reproductive stocks.

Queen conch, *Strombus gigas,* reproductive stocks in the central Bahamas: distribution and probable sources

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Queen conch (Strombus gigas), once abundant throughout the Caribbean region, have been fished to near extinction or to a level at which there is no longer a viable fishery in many localities (Appeldoorn et al., 1987; Berg and Olsen, 1989). This is particularly true in nations where the fisherv has been open to SCUBA divers. Stock depletion resulted in at least temporary closures of the conch fishery in Bermuda, Florida, Cuba, Bonaire, and the U.S. Virgin Islands. Regulations including size limits, catch quotas, gear restrictions, and closed areas have been instituted in other countries.

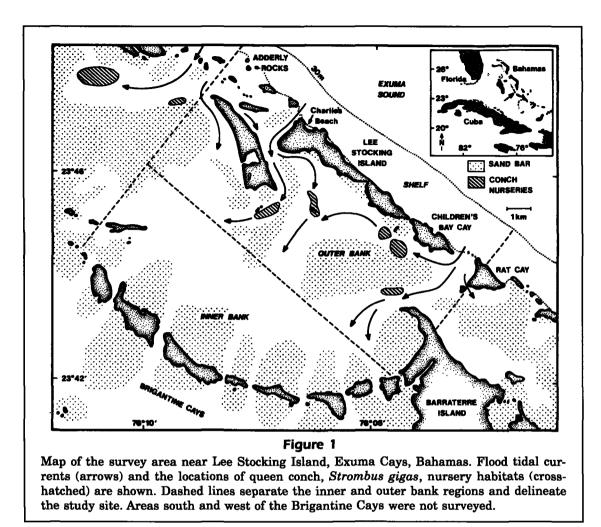
This study was conducted in an attempt to understand reasons for the rapid depletion of queen conch populations in the Caribbean region, and to evaluate the significance of deep-water conch stocks. Several authors have suggested that these deep-water conch, living beyond the normal range of free divers, are the primary source of larvae for shall-water populations and the fishery (Berg and Olsen, 1989; Wicklund et al., 1991; Stoner et al., 1992; Stoner and Sandt. 1992). Therefore, we surveyed the density and age structure of queen conch in the vicinity of Lee Stocking Island in the central Bahamas. Differences in shell morphology and growth rate between conch found on Great Bahama Bank and on the windward island shelf adjacent to Exuma Sound were used as indicators of geographic source for reproductive stocks. The importance of deep-water populations is discussed in terms of fisheries management.

Methods and materials

Study site

An assessment of the adult conch population was conducted between 1989 and 1991 in a 12-km long section of the Exuma Cays, central Bahamas, adjacent to Lee Stocking Island (Fig. 1). To the west and south of the Cays lies the Great Bahama Bank, a shallow, sandand seagrass-covered platform that extends to the Tongue of the Ocean. To the east and north is a narrow (1-2 km) island shelf, a steep shelfbreak beginning at an approximately 30-m depth, and the deep Exuma Sound.

Great Bahama Bank in the region of the study site is characterized by strong tidal currents that carry oceanic water from Exuma Sound onto the bank through channels between the islands. Approximately 90% of the bank area is less than 3.5 m deep; the remainder is tidal channels with depths to 8 m near the inlets and between the Brigantine Cays. For this study the



bank was divided into an inner section from the Brigantine Cays to a line mid-way between the Brigantines and Lee Stocking Island, and an outer section from the mid-line to the cays at the eastern side of the bank (Fig. 1). Each section is approximately 5 km wide. The rationale for this division was that the outer section of the bank is flushed with oceanic water on every tide, while the inner bank is flushed only on extreme tides. Virtually all queen conch nurseries in the Exuma Cays are found within the outer 5.0 km of the bank (Stoner et al., in press.) (Fig. 1).

The eastern shores of the Exuma Cays are characterized primarily by steep aeolianite cliffs and beach rock interspersed with a few high-energy sandy beaches in coves, particularly on Lee Stocking Island and Children's Bay Cay. The seagrass *Thalassia testudinum* is found on shallow, soft-sediment platforms extending a short distance off the sandy beaches. Most of the shallow nearshore, however, is hard-bottom covered with a short turf of the green alga *Cladophoropsis* sp. The hard-bottom habitat, interspersed with small patches of sand and hard corals, is characteristic to 10-m depth. From 10 to 20 m the bottom comprises mixed hard-bottom and bare sand. Off Lee Stocking Island, corals form a 2-km long steep ledge from 10 to about 18 m, but a gradual slope to 25 m is typical of most of the study area. Patchy sand, coral, and hard-bottom are found between 20 and 30 m.

Detailed hydrographic charts are not available for the Exuma Cays; therefore, shelf bathymetry was mapped with 540 electronic depth-sounder points, corrected for tidal state, and positions acquired with Global Positioning System (GPS) from the RV Challenger during summer 1991. GPS positions taken at close intervals along the eastern shores of the islands were used as zero-depth data points. Threedimensional plotting features of Systat 5.0 software were used to provide a bathymetric chart for the shelf region with 0, 2.5, 5, 10, 15, 20, 25 and 30 m contours for depth at mean low tide. Total surface area for each of the seven depth intervals was calculated with a digitizing board and SigmaScan 3.9 software. The surface area of the inner and outer bank regions was determined in a similar way with the aid of topographic maps.

Survey methods

The shelf region was surveyed in each of seven depth zones between 2.5 and 30 m (described above) along nine transects (perpendicular from the Cays into Exuma Sound) placed at approximately 1.0-km intervals. At each of the 63 shelf stations, divers swam parallel to the isobaths for a distance measured with a calibrated General Oceanics flow meter equipped with a large propeller for low velocity flows. Calibration was performed by towing the meter repeatedly $(n \ge 6)$ through calm water at the side of a small boat over a pre-measured distance of 100 m. Precision was $\pm 2\%$. Current velocity on the shelf adjacent to Lee Stocking Island is generally low (<3 cm/sec) and to the northwest, parallel to the isobaths (Smith, 1992¹). Recognizing the potential effect of current on the calculated distance, each dive included two legs, one up-current and one downcurrent in parallel lines of equal length separated by approximately 20 m.

Two dives were made at most stations for density determinations and shell measurements (described below). For density, all queen conch were counted in an 8-m wide path defined by a line held between two divers. The average swim distance was 380 m, resulting in coverage of just over 3000 m². Conch density was calculated by using only those conch in the 8-m band. Shell measurements were made for animals outside the 8-m band in areas with low conch densities. Underwater visibility was usually high and the area of bottom searched was actually much larger than the swim path alone. Consequently, all conch within approximately 30 m could be collected for measurement. In areas where conch densities were high, one dive was made to collect density data and another to collect only measurement data. An attempt was made to measure at least 100 adults from each depth zone, but this was not possible in the 0-5, 5-10, and 25-30 m zones because of low densities in these zones. Statistical differences in density among the survey zones were evaluated with the non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1969) with stations used as replicates (n=9).

The shallowest depth zone (0-2.5 m) was limited primarily to sandy coves on the major islands of the survey area. Adult queen conch were few in these areas, and juveniles were distributed unevenly; therefore, the important seagrass areas of the shallow coves were thoroughly searched. Density measures were not made but all conch encountered were measured (as described below). Sparse distribution of adult conch and the large surface area of the Great Bahama Bank required the use of different survey methods from those applied on the shelf. Because the bank waters are shallow and conch were easily seen, large areas were surveyed by towing a diver at the surface in continuous lines. The bank region was divided into $95 - 1 \times 1$ km squares oriented along lines of latitude. Then, in a systematic grid of lines running diagonally through the squares, every square was crossed at least once during the survey. Additional tows were made in areas already known to have concentrations of adults, i.e., near nurseries previously mapped (Fig. 1; Stoner et al., in press.). Divers were towed a total distance of 126 km.

Although water clarity on the bank was not as high as that on the island shelf, the towed diver could usually see at least 2.5 m on either side of the transect line. Surveys were not conducted on a few days when visibility was restricted. While being towed at approximately 50 cm/sec, the diver signaled numbers of adult queen conch to the boat operator, who recorded position. Positions for the ends of all straight line transects were determined with GPS. tow distance was estimated by chart, and conch density was calculated on the basis of the 5-m wide path examined. During the bank survey, 472 adults were gathered and measured. Presence of juveniles on the bank was noted but not quantified in this study. For comparison with shelf sites, a random collection of 322 juvenile conch was made from a nursery west of Lee Stocking Island during August 1991. These conch were measured for shell length.

The total number of adult queen conch was estimated crudely for each bank and shelf area by extrapolating the average density of conch for an individual zone over the total surface area for the same zone. Because variances in the density data were large, confidence intervals for the extrapolated numbers of conch were not calculated.

Shell measurements

Queen conch reach sexual maturity between 3.5 and 4 years of age, a few months after the shell edge has formed a broadly flared lip (Appeldoorn, 1988). After the lip flares, queen conch stop growing in length but continue to deposit shell material on the inside of the lip (Egan, 1985; Appeldoorn, 1988). Therefore, with certain limitations, thickness of the shell lip is an indicator of approximate age (Stoner and Sandt, 1992). In this study, shell-lip thickness was measured with calipers in the area of greatest thickness, about two-thirds of the distance posterior from the

¹ N. P. Smith, Harbor Branch Oceanography Inst., Fort Pierce, FL, pers. commun. 1992.

siphonal groove and 35 mm in from the edge of the shell, according to the methods of Appeldoorn (1988) and Stoner and Sandt (1992). Shell length was measured from the tip of the spire to the end of the siphonal canal in both adults and juveniles. Repeated measures made by different persons showed that both length and lip thickness measurements were made to ± 1 mm. Differences in length-frequency and thickness-frequency distributions were tested with the non-parametric Kolmogorov-Smirnov test.

Morphological differences between bank and shelf populations were tested with canonical discriminant function analysis from shell length and lip thickness data. This multivariate technique is well suited for differentiating two types where individual characteristics do not separate the types. The analysis computes a third variable Z, which is a linear function of both variables (length and thickness, in this case) such that the equation for the new line maximizes the distance between the two types (Sokal and Rohlf, 1969). The significance of the discriminant function Z was determined with the Hotelling-Lawley trace test statistic (Morrison, 1976). Results of the canonical analysis were then examined to determine what percentage of the individuals were correctly classified according to collection site.

Observations were also made on general shell thickness (particularly in juveniles), length of apical spines and resultant shell diameter, and number of spines per whorl. None of these characteristics were quantified systematically.

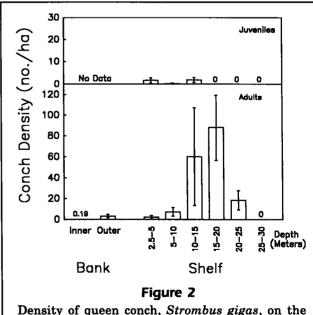
Shell growth experiment

Early observations suggested that shell phenotypes were different between shelf and bank conch. Adults from the shelf appeared to be longer and to have thicker shell lips than those from the bank. Juveniles from the shelf were more narrow, thin-lipped, and had shorter apical spines than those on the bank (Martin-Mora, 1992). To examine the potential relation between shell morphology and growth rates, juveniles were tagged in two different nursery sites: in the well-studied nursery west of Children's Bay Cay and in seagrass areas off Charlie's Beach in the northeast cove of Lee Stocking Island (Fig. 1). Juveniles were individually marked with spaghetti tags (Floy Tag & Manufacturing Co.) tied around the spire and measured to the nearest millimeter with calipers. Charlie's Beach conch between 108 and 150 mm (mean=137 mm, n=281) were measured and released in the last week of August 1990. Children's Bay Cay conch, somewhat smaller than the Charlie's Beach conch (106 to 133 mm, mean=118 mm, n=292), were tagged and released in early September 1990. Conch from both populations were remeasured for shell length five months later, at the end of February 1991. Forty-eight conch were recovered at Charlie's Beach and 135 were recovered at the Children's Bay Cay site. Daily growth rate was calculated for individuals by dividing increase in length by the number of days between measurements. Differences in growth rate between the two sites were evaluated by using the Mann-Whitney *U*test.

Results

Conch densities and abundance

Densities of adult queen conch in the survey area were highest between 15 and 20 m depth on the island shelf (Table 1) with nearly 88 conch/ha (Fig. 2). Density was also high between the 10- and 15-m isobaths. In both of these depth zones densities of adults were highly variable, but there was no apparent pattern across transect lines. There was a highly significant difference in the density of adult conch in the survey zones (Kruskal-Wallis test, $H_{adj.}$ =36.195, P<0.001)(Fig. 2). No conch were found deeper than 25 m, despite an abundance of apparently suitable habitat of sand and algae-covered hard-bottom. Adults were most sparsely distributed



Density of queen conch, Strombus gigas, on the Great Bahama Bank and in six different depth zones of the island shelf hear Lee Stocking Island, Bahamas. Values are \pm mean standard error of the mean.

Table 1

Estimated total number of adult queen conch, *Strombus gigas*, in a 12km section of the Exuma Cays, Bahamas, between Adderly Rocks and Rat Cay.

Region	Total area (ha)	Density (no./ha) (mean ± SE of mean)	Total no. of conch
Bank	· · · · · · · · · · · · · · · · · · ·		
Inner	4,979	0.19 ± 0.14	946
Outer	3,997	3.16 ± 1.69	12,631
Bank total	8,976		13,577
Shelf			
0–2.5 m	161	Low — not qualified	Negligible
2.5–5 m	198	2.24 ± 1.70	444
5–10 m	465	7.21 ± 4.11	3,353
10–15 m	429	60.1 ± 46.8	25,800
15–20 m	454	87.9 ± 31.5	39,902
20–25 m	320	18.3 ± 9.1	5,843
25–30 m	151	0 ± 0	0
Shelf total	3,687		75,342
Grand Total	12,663		88,919

in the inner section of the Great Bahama Bank with only 0.19 conch/ha (SD=0.15, n=28). Density of adult conch in the outer (seaward) section of the bank was close to the value for the 2.5–5 m depth zone on the shelf. Although not quantified, numbers of adults in the nearshore (0–2.5 m) zone of the shelf were negligible.

Few juvenile conch were observed on the shelf between 2.5-and 15-m depth (Fig. 2). A total of 372 juveniles were found in densely aggregated patches on seagrass beds off the eastern beaches of Lee Stocking Island. On the Great Bahama Bank, most juveniles were aggregated in specific nursery locations documented previously (Stoner et al., in press.). None was found deeper than 15 m.

The area between 10 and 20 m depth on the island shelf was a particularly important habitat for adult queen conch (Table 1). Approximately 74% of all conch in the 12-km long survey area reside in this narrow depth zone. It is also clear that large expanses of shallow bank habitat support a relatively small proportion (15.2%) of the adult population. Mating conch and demersal egg masses were very abundant during summer months at shelf sites deeper than 10 m, but none were observed on the bank.

Shell morphology

The shelf sites were characterized by large adult queen conch, primarily between 200 and 260 mm (mean=227, SD=23, n=572), whereas most adult

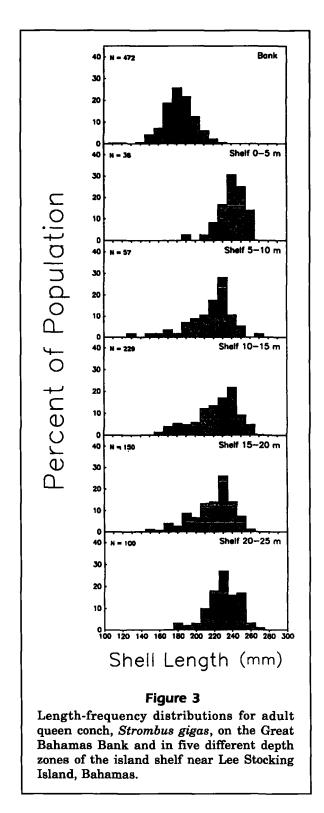
conch on Great Bahama Bank were between 170 and 210 mm shell length (mean=187, SD=16, n=472). Pooling all adults measured, there was a highly significant difference in the length-frequency distribution of conch on the shelf and on the bank (Kolmogorov-Smirnov test, P < 0.001). The distributions (Fig. 3) show clearly the separation in size of adults between bank and shelf sites, particularly when comparing nearshore (0-5 m) shelf zones with those from the bank. The distributions show a decrease in shell length between the nearshore shelf and deeper zones, while those between 5 and 25 m are obviously similar.

Bank conch had thin shell lips (mean=10, SD=6); conch

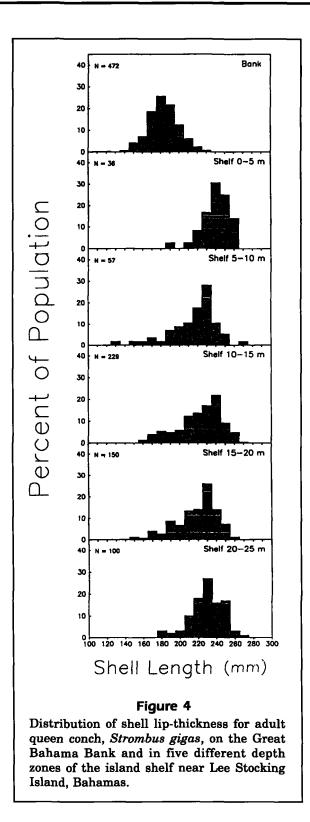
from nearshore (2.5-5 m) regions of the shelf were intermediate in lip thickness (mean=18, SD=5); and deep-shelf (5-25 m) conch had the thickest shell lips (mean=30, SD=7)(Fig. 4). All three of these groups were significantly different from one another in terms of lip thickness distribution (Kolmogorov-Smirnov tests, P<0.01). There was obvious similarity in the thickness distributions of shells in depth zones between 5 and 25 m; therefore, these four depth categories were pooled.

Distinctness of the morphs collected on the bank and shelf is further suggested by a plot of shell length and lip thickness for 250 randomly chosen individuals from each of the two regions (Fig. 5). Also, when length and lip thickness data for all 1,029 conch measured in the survey were used in canonical discriminant function analysis, a highly significant separation was found between conch collected in the two different regions (Hotelling-Lawley Trace, F=1,854, P<0.001). Less than 5% of the conch in the survey were not collected in the region predicted by the multivariate equation. Bank conch were small and had thin shell lips, whereas conch from the island shelf were large and had thick shell lips. Results of the analysis, however, do not rule out the possibility that the smallest adult conch from the shelf region, particularly apparent in the 5-10 m depth zone, could be older animals from the bank.

Length-frequency distributions of juvenile queen conch were different on the Great Bahama Bank and island shelf (Fig. 6). Both the bank and nearshore

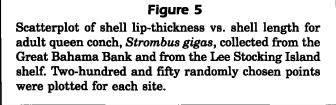


(0-2.5 m) shelf had juveniles less than 100 mm in shell length; however, these were rare in the shelf environment, and few juveniles less than 160 mm were found on the shelf between 2.5- and 15-m depth. None of the juveniles on the bank were near the 227-mm average length of adults on the shelf,



but many juveniles collected in deeper water were close to adult size.

Other differences were observed in the shells of queen conch from bank and shelf regions. Juvenile conch from the bank differed from shelf juveniles because of thicker shells and longer lateral spines



20

Shell Length (cm)

25

30

(5-6 spines/whorl vs. 7-9 spines/whorl in shelf juveniles). Bank conch had a maximum shell diameter between 80 and 90% of shell length at 100 mm length, whereas juveniles from the shelf had diameters between 50 and 60% of shell length. These characteristics persisted to adult stages with bank conch having longer spines. The outer whorls of shelf adults, even young individuals, were often nearly smooth.

Growth rates

50

40

30

20

10

0

10

Lip Thickness (mm)

Bank

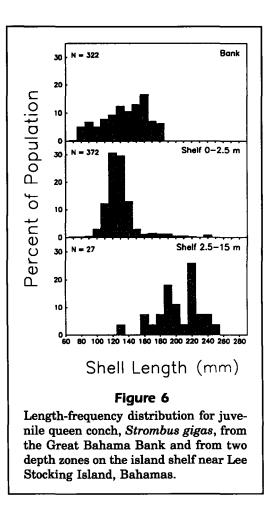
Shelf

15

Juvenile queen conch on the island shelf at Charlie's Beach grew in length at a rate approximately 2.4 times the rate observed at the Children's Bay Cay site. Conch recovered at Charlie's Beach grew 0.139 mm/day (SD=0.025, n=135). At Children's Bay Cay, mean growth rate was 0.058 mm/day (SD=0.021, n=48). The differences in growth rate between bank and shelf juveniles were highly significant (Mann-Whitney U-test, P<0.001).

Discussion

The rapid increase in adult queen conch density at depths greater than 10 m is probably a direct function of fishing, which is limited to free-diving on the bank and shallow nearshore shelf areas around Lee Stocking Island. This conclusion is substantiated by observations of conch depth distribution in other localities. In unfished areas of Islas Los Roques, Venezuela, Weil and Laughlin (1984) found that



density of queen conch was highest in 4.0 m of water and density decreased with depth to 18 m. This may represent the natural distribution of queen conch. In comparable 4-m deep habitats not protected from fishing, densities were 5 times less than those in the protected area. Similarly, in the Exuma Land and Sea Park, a 500-km² fishery reserve 90 km north of Lee Stocking Island, there are large numbers (unquantified) of adult conch at 2-4 m depth, and many of these shallow-water conch have been observed laying eggs (Stoner, pers. observ.); whereas adults are uncommon in shallow water near Lee Stocking Island and spawning has never been observed at less than 5 m depth. Similar to the pattern reported in this study for Lee Stocking Island, Torres-Rosado (1987) found maximum density of adult queen conch between 10 and 20 m in Puerto Rico, where fishing is heavy in shallower waters.

It is recognized that queen conch move to greater depths with age and size (Randall, 1964; Weil and Laughlin, 1984); this has been confirmed in the Lee Stocking Island area by the recovery of individuals that were tagged as juveniles at Charlie's Beach and subsequently found in deeper offshore waters (Stoner, unpubl. data). However, our morphological analyses of conch suggest that very few conch using the bank for a nursery actually reach the offshore spawning sites. Furthermore, similarities in length frequency and shell morphology between juveniles found immediately off the east (windward) side of the Cays on isolated seagrass beds and adults in deep water suggest that the small aggregations of juveniles found on the shelf serve as the primary source for the offshore reproductive stocks. Given that mating and egg-laying are rare on the Great Bahama Bank, it is likely that recruitment to bank nurseries is sustained by deep-water reproductive populations (Wicklund et al., 1991; Stoner et al., 1992; Stoner and Sandt, 1992).

Differences in shell morphology between bank and shelf conch are not well understood but appear to be related to growth rate. Alcolado (1976) reported that large, thin shells and short spines in queen conch in Cuba were associated with rapid growth. A similar phenomenon may explain the shell differences observed in this study. Juveniles in the nearshore shelf environment of Charlies' Beach grew rapidly and had the large, thin-shelled, shortspined morphotype typical of the shelf adults. The small, thick-shelled, long-spined conch on the bank had growth rates less than half of those on the shelf. A recent transplant experiment at Lee Stocking Island demonstrated that shell form and spination in juvenile conch is an environmentally mediated characteristic associated with habitat type and individual growth rate (Martin-Mora, 1992).

The large size of the deep-water reproductive stock may explain high productivity of queen conch in the Exuma Cays. It is likely, however, that abundance of conch in the region is now dependent upon the small, isolated pockets of fast-growing juveniles that inhabit the nearshore shelf habitat during the first two or more years of life then recruit to deepwater reproductive populations. Stoner and Sandt (1992) found that the adult population at an 18-m deep site off Lee Stocking Island was relatively stable between 1988 and 1991, but most individuals were old and thick-lipped. The predominance of old conch in deep water may or may not be a function of low recruitment rates from shallow water in recent years, and the significance of shallow-water spawning to conch abundance is unknown.

In an comparison of data from Glazer and Berg (in press.), densities of queen conch in the Exuma Cays are 10 to 100 times higher than those reported for many other localities in the Caribbean region. This may be related to geographic differences in habitat quality, recruitment processes, and fishing methods. The Exuma Cays probably represent a particularly efficient system for retaining conch larvae because of unique geographic and oceanographic conditions such as an alongshore current and numerous tidal inlets leading to nursery grounds (Stoner et al., in press), but fishing methods can play a large role in the population structure of queen conch. Fishing in the Bahamas is restricted to freediving and limited diving with surface-supply air for adults with flared shell lips; therefore, conch deeper than 10 m are rarely exploited. Depth distribution of queen conch near Lee Stocking Island suggests that virtually every conch in the Exuma Cays is within the range of SCUBA divers and that populations of S. gigas could be decimated quickly if the fishery were opened to this latter gear. On the other hand, if the source of deep-water conch is shallowwater nurseries, protection of deep-water reproductive stocks only delays the effects of overfishing, and certain nurseries should be protected as well. Analysis of larval transport and recruitment processes will be crucial to the sound management of this already threatened commercial species.

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