Abstract.—Marine fishery reserves (MFR's) have been set aside in coastal areas throughout the world with the hope of reversing population decreases commonly observed in many marine resources. In this study, a comparison of population structure of the commercially important gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, central Bahamas. There were 31 times more adult conch on the shallow (<5 m) Great Bahama Bank in the MFR, and in a survey at 7 depth intervals (to 30 m) on the island shelf in the Exuma Sound, mean adult density was always higher in the MFR, by as much as 15 times. Shell length and lip-thickness measurements indicated that adults in the MFR migrate with age from bank nursery sites into deeper sound water, whereas those on the bank in the fished area were harvested before reaching water sufficiently deep to protect them from free-diving fishermen. Although sparsely distributed juveniles in shallow-water (<15 m) habitats of the sound were the primary source of adults in the fished area, large juvenile aggregations on the bank also contributed to the deep-water adult stock in the MFR.

Total larval densities in the MFR were frequently an order of magnitude higher than those found in the fished area, and densities of late-stage larvae were 4 to 17 times higher. Because the surface current along the Exuma Cays shelf flows to the northwest, late-stage larvae found inside the reserve must have been spawned outside the reserve; thus the high densities of juvenile and adult conch are the result of natural accumulation of larvae in the area, as well as the result of protection from fishing. Although the fate of larvae dispersed from the reserve is uncertain, it is likely that high numbers of reproductive stock and larvae in the reserve have a significant positive effect on populations in the northern Exuma Sound. Designs of reserves that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production

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In coastal areas throughout the world, tracts of coastline, reef, and banks known to be important spawning or nursery grounds for economically significant species are being set aside as marine fishery reserves (MFR's). Fishing in such areas is either controlled or prohibited to conserve or enhance production of selected species. Bohnsack (1990) listed 21 potential advantages of fishery reserves including important ecological benefits such as 1) protection of reproductive stocks and genetic diversity, 2) maintenance of the age and social structure of populations, 3) maintenance of areas of undisturbed critical habitat, 4) supplemental restocking of fished areas through emigration, and 5) provision for a larval source for recruitment to surrounding areas. Numerous other advantages of reserves relate to data collection and enforcement of regulations. Surveys of the literature (Roberts and Polunin, 1991; Dugan 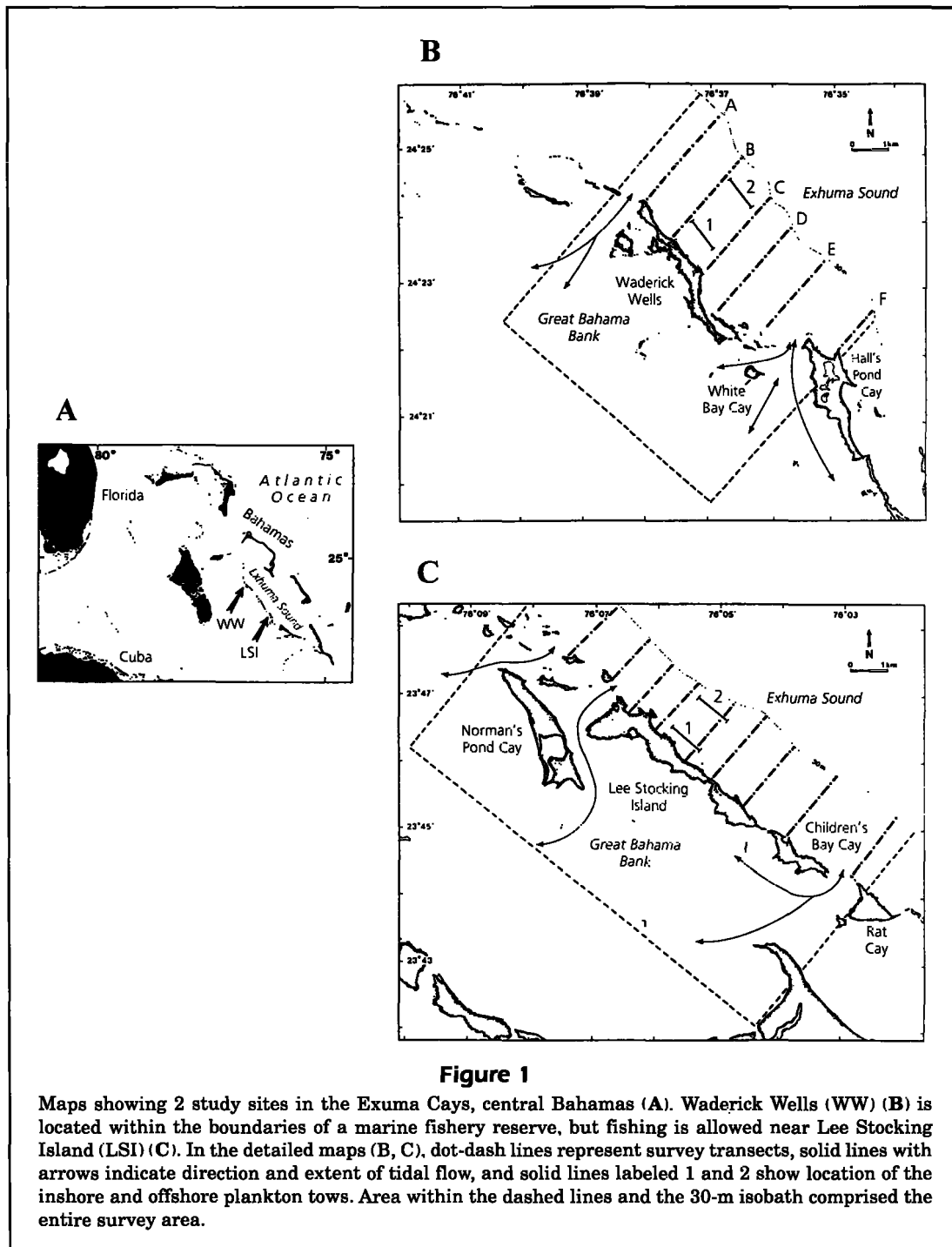and Davis, 1993; Rowley, 1992) have yielded evidence that, in most cases, abundance and size of protected species increase within reserves, but there are few data to support the other predicted advantages (see also Roberts and Polunin, 1991; Polunin and Roberts, 1993).

Many fish and invertebrates produce planktonic larvae; therefore, in order to enhance fishery yields in the surrounding waters, an MFR must be located such that its larval production is exported to suitable habitats and to fished areas. Whether or not reserves are sources of recruitment for areas outside the protected waters is debated by environmental scientists, managers, and user groups. There are virtually no data to speak for or against the larval export benefit (Carr and Reed, 1993), although theoretical models incorporating the concepts of metapopulation dynamics indicate that MFR's should provide for larval recruitment to fished areas (Man et al., 1995). Similarly, there is little information on the emigration of

postsettlement fishes and invertebrates from MFR's into fished areas. A recent study (Rakitin and Kramer, 1996), designed to test for emigration of 24 fish taxa from the Barbados Marine Reserve, did not provide conclusive proof that the reserve allowed for exportation of fishes into the surrounding waters. Without solid data, managers will continue to face criticism from fishermen and other special interest groups that reserves are of no advantage to them or the environment.

In this study, a comparison of population structure of the commercially and culturally significant gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, an island chain in the central Bahamas (Fig. 1A). The fished area was near Lee Stocking Island,

Figure 1

Maps showing 2 study sites in the Exuma Cays, central Bahamas (A). Waderick Wells (WW) (B) is located within the boundaries of a marine fishery reserve, but fishing is allowed near Lee Stocking Island (LSI) (C). In the detailed maps (B, C), dot-dash lines represent survey transects, solid lines with arrows indicate direction and extent of tidal flow, and solid lines labeled 1 and 2 show location of the inshore and offshore plankton tows. Area within the dashed lines and the 30-m isobath comprised the entire survey area.

at the southern end of the chain (Fig. 1C), and the MFR was 87 km north near Waderick Wells in the Exuma Cays Land and Sea Park (Fig. 1B). Our objectives were 1) to test the perceived benefits of an MFR by quantifying differences in densities of adults, juveniles, and larvae; 2) to consider physical-oceanographic mechanisms for such differences with respect to the open nature of the population; 3) to compare abundance patterns with data reported from other regions; 4) to determine sources of adult conch; and 5) to make management recommendations for a species that has been heavily exploited in many Caribbean locations.

Subject species

The natural history of the queen conch is relatively well known. The species is indigenous to subtropical and tropical waters of the western Atlantic from Bermuda and southern Florida to Venezuela and Trinidad (Abbott, 1974). Several egg masses, each containing ~400,000 eggs, are laid by females on clean sand during the summer season (Robertson, 1959; Stoner and Sandt, 1992). Larvae hatch in 3–5 d and live in the upper 5–10 m of the water column for 16–28 d, feeding on phytoplankton (Brownell, 1977; Davis et al., 1993; Stoner and Davis, in press, a). Vertical migration appears to be slight (Barile et al., 1994), and the larvae drift passively on near-surface currents (Stoner and Davis, in press, b). Genetic studies (Mitton et al., 1989; Campton et al., 1992) and analysis of queen conch larval life history and ocean currents in the Caribbean region (Davis et al., 1993) suggest that larvae can travel long distances to colonize seagrass nursery grounds where they settle and feed.

Young conch feed on seagrass detritus and algae (Randall, 1964; Stoner and Waite, 1991) and migrate into deeper water with age (Weil and Laughlin, 1984; Stoner and Schwarte, 1994). At 3.5–4 yr, queen conch reach sexual maturity, cease to grow in shell length, and begin to form the characteristic flared shell lip that thickens with age (Egan, 1985; Appeldoorn, 1988). Longevity is at least 6–7 yr (Berg, 1976) and may reach 26 yr in deep-water habitats (Coulston et al., 1987). Fishing regulations in the Bahamas prohibit the taking of any nonlipped (i.e. juvenile) queen conch and the use of SCUBA gear for any kind of fishing. A general lack of conch at depths >30 m has been attributed to low abundance of plant foods at such depths (Randall, 1964; Adams, 1970).

In 1990, the economic value of queen conch taken from the Caribbean region was estimated at $40 million (US) (Appeldoorn, 1994a). However, as a result of severe overfishing throughout its range (Berg

and Olsen, 1989; Appeldoorn, 1994a), queen conch was considered commercially threatened worldwide in 1983 (Wells et al., 1983) and, in 1992, it was added to Appendix II of the Convention on International Trade in Endangered Species (CITES). Fisheries have been closed seasonally or for multiyear periods in areas of Venezuela, Colombia, Belize, Mexico, Cuba, and the U.S. Virgin Islands. Despite closure in Florida (since 1985) and Bermuda (since 1978), stock recovery has been slow (Appeldoorn, 1994a).

Methods

Study sites

The Exuma Cays island chain comprises more than 100 small islands that extend northwest to southeast in the central Bahamas, separating Exuma Sound from the Great Bahama Bank (Fig. 1). The bank is a shallow platform covered with sand and seagrass meadows. In the sound, the island shelf extends from land out 1–3 km to a steep shelf edge beginning at ~30 m depth. At both Lee Stocking Island (LSI) (Fig. 1C), where fishing is allowed, and at Waderick Wells (WW) (Fig. 1B), within an MFR, habitats in the depth range of 2.5–15 m include sand, coral rubble, algal-gorgonian hard-bottom, and seagrass. The hard-bottom is covered with the short turf of the green alga *Cladophoropsis* sp. in many subtidal locations. Beyond 15 m, the habitat is mostly sand and large coral ridges with some hard-bottom. Most of the rocky eastern shore of WW lacks beaches, and water depth close to shore is typically 2 m. At LSI, small sandy beaches lie in protected coves at certain locations between rocky headlands.

Water exchange between the bank and sound occurs through numerous passes that separate the islands, creating extensive tidal flow fields on the bank. At LSI (Fig. 1C), most queen conch reproductive activity occurs in the sound on the island shelf, where adults live in highest densities and juveniles are rare (Stoner and Schwarte, 1994). Larvae are carried through the tidal passes and settle onto the bank (Stoner et al., 1994; Stoner and Davis, in press, b) (Fig. 1, B and C). Discrete juvenile aggregations, with densities of 0.1–1.3 conch/m^2 (most >80 mm shell length), occur on the bank in the same general locations year after year (Wicklund et al., 1991; Stoner and Ray, 1993; Stoner et al., 1996) and may cover 5–600 ha. Most aggregations are located within 5 km of inlets on the Great Bahama Bank in beds of the seagrass *Thalassia testudinum* (Stoner et al., 1994).

The Exuma Cays Land and Sea Park, recognized as a protected area in 1958, extends 40 km along the

Exuma Cays and 13 km across the bank and sound to comprise 456 km². A full-time warden enforces park regulations, which strictly prohibit the collection of any plants or animals. This investigation was conducted near the island of Waderick Wells (Fig. 1B) where the park headquarters are located and fishing regulations are best enforced. The study area was well within the park boundaries, 10 km from the southern boundary of the park and 24 km from the northern boundary.

Adult surveys

For a comparison of fished and unfished areas, density surveys for adult queen conch were conducted on the bank and the island shelf, from beach to shelf edge, in the Exuma Sound near LSI between March and September 1991 (Stoner and Schwarte, 1994) and near WW in 1994 in this study. Annual surveys for adult conch conducted at selected sites off LSI, where fishing is allowed, showed little interannual variation in population size (Stoner and Sandt, 1992) and provide justification for the comparison of population densities in different years. Between 1988 and 1991, maximum variation from the mean population size was just 19%; the population was 4% above average in 1991. Adult densities at an important reproductive site at 18 m depth off LSI (Stoner and Sandt, 1992) differed only 8% between 1991 and 1994. Given the relative stability of adult conch populations at LSI and the long adult life (probably >20 years; Coulston et al., 1987), we concluded that surveys from WW and LSI could be compared. In addition, intrasite comparisons of conch density and age structure provided some of the most compelling evidence for the effects of fishing on the recruitment and population size. For direct comparison, survey methods for this study were similar to those used by Stoner and Schwarte (1994).

Near WW in the MFR, the bank survey area extended 7.5 km along the long axis of the island and 5 km southwest from the channels north and south (Fig. 1B), comprising 3,245 ha. Throughout this area, a snorkeler was towed behind a small boat for a total of 47 km while counting the number of adult conch within a 6-m-wide field of view and recording the locations in which adults were abundant. Tows were made along a total of 12 transects which ran perpendicular to WW. These transects started near the western shores of the primary islands and were less than 1 km apart. Latitude and longitude for the beginning and end of each transect were recorded with Global Positioning System (GPS). This resulted in direct observation of a surface area of 28.0 ha. Densities of adult conch were calculated for the transects,

and the number of conch was extrapolated for the entire area.

To test the hypothesis that depth distribution of adults differed between the 2 sites, depth-stratified surveys for adult conch were conducted in Exuma Sound along 6 transects which ran perpendicular to WW. Transect A ran northeast from the north tip of WW, and transect F ran northeast from the north end of Hall's Pond Cay (Fig. 1B). Other transects were spaced as uniformly as possible between A and F, 1–2 km apart. Along each transect, estimates of conch density were made at 7 depth intervals: just off the beach (when present), 2.5–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, and 25–30 m. Within each interval, two SCUBA divers swam for 8–30 minutes, depending on depth, holding a line (8 m) between them and counting the number of adult conch that lay beneath the line. One diver carried a calibrated flow meter to calculate the distance traveled. To compensate for the potential influence of current on distance measured, the divers swam from the boat anchor into any discernible current and back, covering two parallel, nonoverlapping paths that normally ran parallel to the isobaths. Thirty-six dives were made during this shelf survey for adult conch density. The mean swim distance was 360 m (SD=6 m). Sampling effort was lowest for the 25–30 m interval because of diving limitations imposed by depth; however, the surface area of this deepest sampling zone was relatively small (Table 1). Again, results were directly comparable with Stoner and Schwarte (1994).

A bathymetric chart of the island shelf east of WW (to 45 m) was created from 250 points for which depth (corrected for tidal state) and position (determined with GPS) were recorded from a small boat. Computer-generated contour lines (1 m) were resolved with normal smoothing algorithms. Surface areas for each contour interval were calculated, and the mean density of conch found during the dive surveys was extrapolated to determine total number for each depth interval.

To examine age distribution and to evaluate potential migration patterns at WW, shell length and shell lip thickness were measured for at least 50 individuals at each depth interval on the shelf and for 213 individuals collected from several locations on the bank. Although young adults laid down lip material faster than older adults and although shells are subject to erosion, shell thickness at the lip provides a relative indication of conch age (Appeldoorn, 1988; Stoner and Sandt, 1992).

To test for differences in size and age distribution associated with depth, frequency distributions of shell length and shell lip-thickness data were analyzed by depth interval with the nonparametric Kolmogorov-Smirnov test. Several aspects of shell

Table 1

Comparison of the total abundance and density of adult queen conch. *Strombus gigas*, in the marine fishery reserve near Waderick Wells and in the fished area near Lee Stocking Island. Estimates for total abundance were extrapolated from bathymetric data and conch density surveys conducted in each habitat and range of depth. Values for adult density are mean ±SE; numbers in parentheses are the number of surveys at each depth.

Habitat and depth (m)	Marine fishery reserve			Fished area		
	Adults (no./ha)	Area (ha)	Total no. of conch	Adults (no./ha)	Area (ha)	Total no. of conch
Bank	53.6	3,245	174,080	1.7	3,997	6,816
Shelf						
0–2.5	0 ±0 (2)	158	0	0 ±0 (4)	161	0
2.5–5	34 ±22 (6)	200	6,871	2.2 ±1.7 (7)	198	444
5–10	49 ±18 (7)	1,035	51,138	7.2 ±4.1 (9)	465	3,353
10–15	270 ±85 (6)	375	101,187	60 ±47 (9)	429	25,800
15–20	104 ±58 (6)	193	20,113	88 ±32 (9)	454	39,902
20–25	148 ±72 (5)	136	20,108	18 ±9 (9)	320	5,843
25–30	122 ±70 (6)	71	8,635	0 ±0 (9)	151	0
Shelf total		2,167	208,053		2,178	75,342
Overall total		5,412	382,133		6,175	82,158

shape, including shell length, are induced by habitat characteristics of juvenile queen conch (Martín-Mora et al., 1995) and are conserved in adults (Stoner and Schwarte, 1994). For example, juvenile conch that develop in shallow seagrass beds of the bank cease to grow in shell length at a smaller size in comparison with conch developing on the shelf in Exuma Sound.

To test for differences in the density of adult queen conch among depth zones and between sites, 2-way analysis of variance (ANOVA) was performed on log-transformed data ($\log_{10}(n+1)$: there were numerous zeros in the data) in accordance with the guidelines of Day and Quinn (1989). Prior to analysis, variances were tested for heterogeneity with Cochran's test ($P>0.05$). The 2-way ANOVA was followed by Tukey's HSD multiple comparison test.

Because the comparison between the MFR near WW and the fished area near LSI constitutes an important aspect of this study, basic results from LSI (modified from Stoner and Schwarte, 1994) are reported in some figures and tables.

Juvenile surveys

To estimate abundance of juvenile queen conch at the two sites, we calculated the areal extent of juvenile aggregations at both WW and LSI. Aggregations of juvenile conch have abrupt boundaries and high densities are found adjacent to habitats without conch (Stoner and Ray, 1993). To estimate the

size of aggregations in the study areas, divers were towed systematically over these areas to determine the boundaries within which density was ≥0.1 conch/m^2. Boundaries were marked with buoys, and buoy positions were determined with GPS. The potential error in positions measured with GPS is variable and can be as large as 150 m. However, when the points were plotted on a small-scale chart, they characterized accurately the shapes defined by the buoys in the field, and any error was uniform in direction and magnitude. Absolute position was not critical for the calculation of aggregation sizes. Surface areas of the aggregations were determined with the plots and a digitizing board. Surveys of juvenile queen conch have been conducted each summer since 1988 at LSI and were conducted in 1991 at WW. Juvenile conch were infrequently encountered on the island shelf; consequently, densities there were determined in conjunction with the adult survey.

At LSI, the juvenile surveys were concentrated in the flow field that begins just north of the island and runs south of Norman's Pond Cay onto the Great Bahama Bank and in the flow field that runs between Children's Bay Cay and Rat Cay (5 km) (Fig. 1C). Although most conch were associated with these tidal channels, the entire bank between Rat Cay and the north end of LSI was searched. At WW, the survey area comprised the flow field south of the island which extended onto the bank toward the south end of Hall's Pond Cay (6 km) and the surrounding bank areas (Fig.

1B). These particular tidal flow fields were emphasized because adults on the island shelf probably originated from nurseries in adjacent bank and shelf areas.

To compare juvenile conch abundance at WW and LSI, the percentage of the bank survey area occupied by juvenile aggregations was calculated (ha of aggregation/ha of bank area surveyed). Although this index provides only a crude comparison of juvenile abundance without quantitative data on animal density within the aggregations, our long experience with juvenile aggregations in the Exuma Sound has shown that aggregations rarely have <0.1 or >1.5 conch/m². General observations on densities were noted in our 1991 surveys at both sites.

Larval surveys

Surveys for queen conch larvae were conducted during the primary spawning season (June through August) at WW and LSI in order to provide information on the production of larvae in the two areas and to evaluate the supply of late-stage larvae. In 1993, samples were collected on 5 dates (12 June, 30 June, 15 July, 4 August, and 22 August) at each site over the island shelf at 1 inshore station (5-m isobath) and at 1 offshore station (20–30 m isobath) (Fig. 1, B–C). In 1994, samples were collected on 3 dates (22 June, 20 July, and 18 August) at only the offshore stations, where highest concentrations of adults occurred and where highest concentrations of late-stage larvae were collected in 1993. Simultaneous studies of spawning behavior at LSI and WW in 1995 showed that egg-laying is synchronous in the two areas (Stoner and Ray, unpubl. data).

Conical plankton nets (202-µm mesh, 0.5-m mouth diameter) were towed behind a 20-m vessel at 100 m/sec for replicated ($n=2$) 15-min tows. Because queen conch larvae are found in the upper water column during the day (Stoner and Davis, in press, a), nets were towed in the upper 1–2 m of the water column at inshore sites. At offshore sites, replicated 15-min tows were made for ~5 min at each of the following depths: 1 m, 2–3 m, and 5 m. The volume of water filtered on each tow was calculated from a calibrated flow meter (General Oceanics) secured in the mouth of the net. Samples were preserved in 5% formalin-seawater mixture. Strombid veligers were sorted from the plankton with a dissecting microscope and identified according to Davis et al. (1993). The number of queen conch veligers per 10 m³ of water was calculated, and subsamples of veligers from each tow were measured for shell length. The veligers were classified as early-stage (≤500 µm), mid-size (500-900 µm), or late-stage (>900 µm). Late-stage larvae were metamorphically competent or nearly so.

Results

Adult surveys

Variation in density and abundance There were an estimated 208,500 adult conch in Exuma Sound near WW within the MFR survey area, which comprised 2,167 ha (Table 1). Two-way ANOVA of the 5 depth intervals from 2.5 to 25 m revealed significant differences both between the two different areas ($F_{1, 63}$ =16.62, $P<0.001$) and among zones ($F_{4, 63}$=3.87, P =0.007). The deepest interval (25–30 m) was excluded from analysis because adult conch were never observed at that depth in the fished area. Interaction between the two variables was not significant ($F_{4,63}$=1.48, P=0.218).

Mean adult density was always higher, by as much as 15 times, in the MFR than in the fished area for each depth interval (Table 1). Maximum mean density (270 conch/ha) occurred at 10–15 m in the MFR. This value was three times higher than the highest density observed in the fished area near LSI (88 conch/ha at 15–20 m) and was significantly higher than densities at all LSI depth intervals (Tukey test, $P\leq0.03$) except 15–20 m ($P=0.58$).

Although nearly half the survey area in the MFR was 5–10 m deep (Table 1), adult densities were relatively low at depths <10 m (0–49 conch/ha) and high (≥104 conch/ ha) at all deeper intervals, even at greatest depth (122 conch/ ha at 25–30 m). No adults were observed at the two beach locations surveyed.

Variation in conch density within depth intervals was high and apparently related to island shelf structure. For example, density at 25–30 m was ≤6 conch/ ha along transects D and E where the slope to the shelf edge increased sharply from 15 m, whereas density was 432 conch/ha farther north in transect C, where the slope to 30 m was more gradual.

The density of adult queen conch on the bank adjacent to WW and Hall's Pond Cay in the MFR (53.6 conch/ha) was 31 times higher than that in the fished area near LSI (1.71 conch/ha). Seventy-four percent of all adult conch encountered on the bank near WW were within 2 km of inlets; this general distribution pattern was also evident at LSI.

There was an estimated total of 174,100 adult queen conch on the bank in the entire MFR survey area (3,245 ha) (Table 1). This was 45.6% of the overall total for the shelf and bank. In the fished area, there were only 6,816 adults in the bank area surveyed (3,997 ha), and this number comprised a relatively small portion of the overall total for the site (8.3%). Most adult conch in the fished area (>87%) were found in depths >10 m, whereas only 39% of adult conch in the MFR were in depths >10 m.

Shell structure Pairwise Kolmogorov-Smirnov tests showed differences in frequency distributions of shell length in the MFR between adult conch on the bank and those at each depth interval ($P \le 0.002$ in all cases) except 2.5–5 m ($P=0.14$). Adult conch from the sound, always ≥ 150 mm, tended to be longer than those from the bank (Fig. 2). The length mode for sound conch ranged from 180–189 mm (at 5–10 m and 10–15 m) to 210–219 mm (at 15–20 m and at 25–30 m, where the largest individual [265 mm] was found). Conch at the deepest interval were relatively large, and mean shell length increased 18 mm between the 10–15 m and 25–30 m intervals. A bimodal distribution was observed in the three deepest intervals, with a low frequency of 200–209 mm conch in all cases. Mean shell length for all conch from the sound was 202 mm (SD=21 mm, $n=524$), compared with 188 mm (SD=20 mm, $n=213$) for conch on the bank. An intersite comparison showed significant differences in frequency distributions of shell length between the MFR and the fished area for conch living at each depth interval but not for those on the bank (Fig. 2). Adult conch from the shelf in the fished area had longer shells than those from the shelf in the MFR.

Pairwise Kolmogorov-Smirnov tests also showed differences in frequency distributions of shell lip thickness in the MFR between adult conch on the bank and those at each depth interval ($P<0.001$ in all cases) because those on the bank had relatively thin shell lips. All bank adults had shell lips ≤ 28 mm thick, and 31% were ≤ 8 mm (Fig. 3). Lip thickness values were >16 mm for most adults in the sound, and $<5\%$ of the conch at each of the three depth intervals to 15 m had lip thickness ≤ 8 mm. Beyond 15 m no thin-lipped conch were measured. Mean lip thickness for all conch from the sound was 24 mm (SD=7 mm, $n=524$), compared with 12 mm (SD=6 mm, $n=213$) on the bank.

An intersite comparison showed significant differences in frequency distributions of shell lip thickness for conch living on the bank and at each depth interval ($P \le 0.001$ in all cases) except for those at 5–10 m ($P=0.08$) (Fig. 3). Compared with conch in the
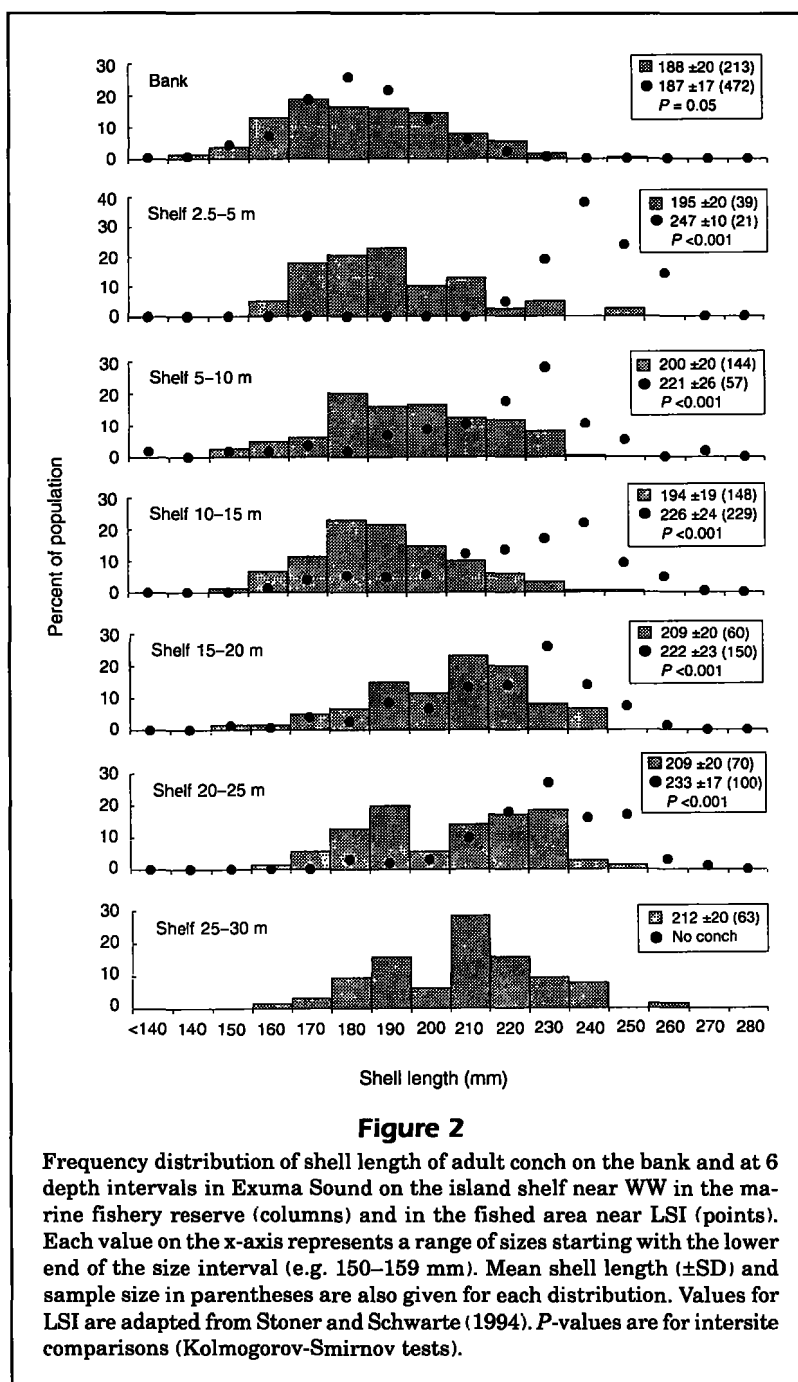

Figure 2

Frequency distribution of shell length of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 150–159 mm). Mean shell length (±SD) and sample size in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). P-values are for intersite comparisons (Kolmogorov-Smirnov tests).

MFR, conch in the fished area tended to have thinner lips in shallow water (bank, and sound <5 m) and thicker lips in deeper water.

Juvenile surveys

Juvenile conch were never observed at depths >15 m in the Exuma Sound at either study area, and they were infrequently observed (mean <6/ha) in shallower water in the MFR (Fig. 4). Highest density of

juveniles in the sound (33.3 juveniles/ha) occurred in the MFR at 5–10 m, but the standard deviation for this depth interval was more than twice the mean (all other densities were 0, except 1 at 5.1 juveniles/ ha). In contrast with adults, intersite differences for juvenile densities in Exuma Sound were not significant (Student's t-test, P>0.2 for 2.5–5 m, 5–10 m, and 10–15 m).

The majority of juvenile conch at both sites were found on the Great Bahama Bank. On the bank in the fished area, interannual variation in the surface area occupied by juvenile aggregations was high, ranging from 8 to 44 ha in the flow field north of LSI and from 2 to 87 ha in the Children's Bay Cay flow field (Table 2). In the MFR in 1991, juveniles occupied 125 ha. Although data for the MFR are available for only 1 yr, the surface area was nearly twice a large as the average surface area occupied in two flow fields over 6 yr in the fished area. In the MFR, juvenile aggregations covered 3.84% of the bank area surveyed, compared with a mean value of 1.62% in the fished area.

Larval surveys

Densities of queen conch larvae were consistently higher in the MFR near WW than in the fished area near LSI. In 50 plankton tows made at the two sites between 1993 and 1994, densities in the fished area were always <6 larvae/10 m^3 and typically near 1–2 larvae/10 m^3 (Table 3). Densities in the MFR were frequently an order of magnitude higher, reaching a maximum of 55 larvae/10 m^3 in July 1994. Intrasite differences were most notable in the MFR on 22 August 1993 when the offshore station had 184 times the density of veligers as the inshore station. However, results were variable, and during both June cruises in 1993, the inshore station at the MFR had
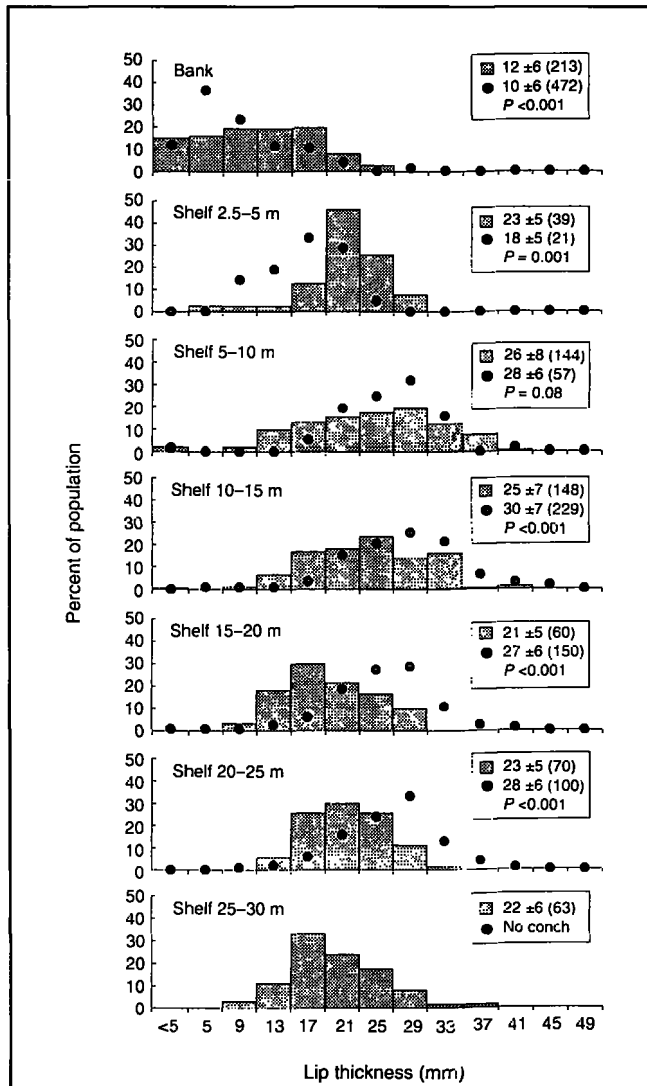
Figure 3

Frequency distribution of shell lip thickness of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 5–8). Mean lip thickness (±SD) and sample sizes in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). P-values are for intersite comparisons (Kolmogorov-Smirnov tests).
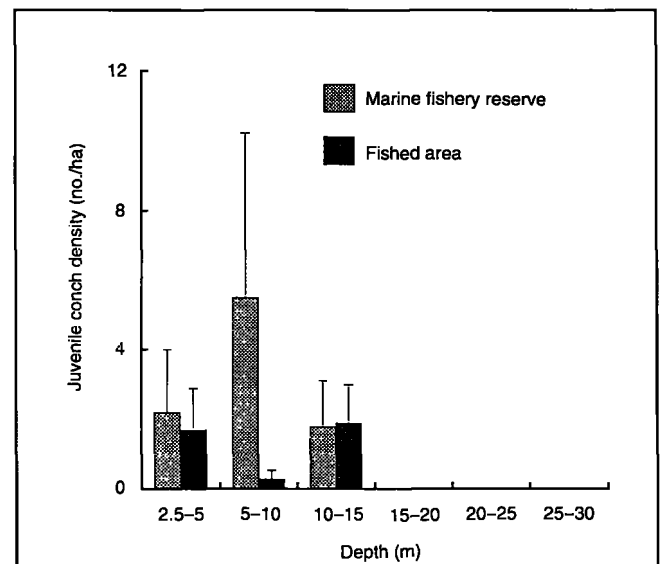
Figure 4

Juvenile conch density at 6 depth intervals in Exuma Sound on the island shelf at the fished area near LSI (Stoner and Schwarte, 1994) and at the marine fishery reserve near WW (this study). Values are mean (+SE).

higher mean larval densities than the offshore station (Table 3).

Early-stage larvae (≤500 μm SL) represented the most abundant size class in collections made at both areas (>90%) (Table 4). Late-stage larvae (≥900 μm SL) were always present in the MFR, except on 22 June 1994, and always occurred at higher densities in the MFR than in the fished area. The highest observed density was 1.9 late-stage larvae/10 m³ on 4 August 1993. Late-stages were also more abundant offshore than inshore at both sites.

Discussion

Comparisons with earlier investigations

Although direct comparisons of LSI/WW density data with data from other studies are made difficult because of different sampling strategies, incomplete data in some reports, and failures to distinguish between adult and juvenile densities, a review of the literature suggests high regional variability in adult queen conch densities, ranging over three orders of

Table 2

Surface area occupied by juvenile queen conch in two tidal flow fields, one originating north of Lee Stocking Island (LSI), and the second originating between Rat Cay and Children's Bay Cay (CBC) (see Fig. 1C). Surface areas for LSI and CBC were standardized to percent of bank surface area occupied by juvenile aggregations.

| Year | Surface area (ha) | | | % of bank |
	LSI	CBC	Total	
1989	31.7	32.2	63.9	1.60
1990	14.5	7.4	21.9	0.55
1991	19.4	1.7	21.1	0.52
1992	8.3	51.7	60.0	1.50
1993	42.2	86.8	129.0	3.23
1994	44.3	49.2	93.5	2.34
Mean	26.7	38.2	64.9	1.62
SD	14.9	31.6	41.8	1.05

Table 3

Larval densities (no. 10/m³) (mean ±SD) in a marine fishery reserve near Waderick Wells (WW) and in a fished area near Lee Stocking Island (LSI). Samples were collected inshore and offshore for 5 days in 1993 and offshore for 3 days in 1994. *P*- and *t*-values are from Student's *t*-test using pooled variances when data were homogeneous (Cochran's test, *P*>0.05) and from separate variances when data were not (0.01<*P*<0.05).

1993	12 Jun	30 Jun	15 Jul	4 Aug	22 Aug
Inshore					
WW	50.0 ±5.1	43.6 ±5.4	0.65 ±0.33	4.42 ±0.52	0.22 ±0.21
LSI	0.52 ±0.21	2.70 ±0.45	0.63 ±0.44	no data	1.58 ±0.77
t	−13.83	−10.66	−0.06		2.41
P	0.005	0.009	0.96		0.14
Offshore					
WW	36.3 ±2.7	7.26 ±1.12	0.91 ±0.62	1.87 ±0.19	40.4 ±15.4
LSI	0.62 ±0.19	1.00 ±0.10	1.22 ±0.09	0.74 ±0.44	0.43 ±0.24
t	−18.42	−7.85	0.71	−3.33	−3.66
P	0.003	0.02	0.55	0.08	0.17

1994	22 Jun	20 Jul	18 Aug		
Offshore					
WW	27.8 ±5.09	54.7 ±9.35	0.98 ±0.18		
LSI	5.94 ±1.44	0.25 ±0.23	0.06 ±0.08		
t	−5.86	−8.23	−6.73		
P	0.03	0.08	0.02		

Table 4

Densities of queen conch veligers (no. /10 m³) in three size classes in a marine fishery reserve near Waderick Wells and in a fished area near Lee Stocking Island. Samples were collected inshore and offshore in 1993 and offshore in 1994. Values are mean ±SD; the numbers in parentheses are the number of sampling dates for each site.

	Early-stage (<500 μm)	Mid-size (500–900 μm)	Late-stage (>900 μm)
1993			
Marine fishery reserve			
Inshore	19.7 ±24.9 (5)	0.037 ±0.073 (5)	0.042 ±0.060 (5)
Offshore	15.9 ±18.8 (5)	0.646 ±0.874 (5)	0.768 ±0.701 (5)
Fished Area			
Inshore	1.25 ±1.07 (4)	0.093 ±0.134 (4)	0.011 ±0.008 (4)
Offshore	0.740 ±0.348 (5)	0.018 ±0.017 (5)	0.045 ±0.058 (5)
1994			
Marine fishery reserve			
Offshore	27.4 ±27.0 (3)	0.322 ±0.206 (3)	0.110 ±0.111 (3)
Fished Area			
Offshore	2.05 ±3.33 (3)	0 ±0 (3)	0.029 ±0.025 (3)

magnitude (Table 5). Mean values in the MFR near WW for each depth interval were always ≥34/ha, well above those reported for Bermuda, Florida, Puerto Rico, and the U.S. Virgin Islands. Densities in the MFR in depths >10 m were comparable to those observed before 1984 at Cabo Cruz, Cuba, in the Turks and Caicos Islands, and at a fished area of Venezuela. Only two other studies quantified adult conch densities by depth (Table 6). In Puerto Rico, maximum adult density occurred at 20–25 m, but the value was only 0.05 adults/ha (Torres Rosado, 1987), three orders of magnitude lower than that for our MFR, and two orders of magnitude lower than that at our fished area near LSI. In the U.S. Virgin Islands, adult density was maximum (17.1 adults/ha) at 18–24 m (Friedlander et al., 1994), and nearly identical to densities (18.3 adults/ha) observed in 20–25 m in our fished area.

Highest densities reported in the literature were observed >20 years ago in Cuba and >10 years ago in Venezuela. The highest single density estimate in our study (568 adults/ha) represented only 30–36% of the highest densities reported for Diego Perez, Cuba (1,582/ha), and for a fishery reserve at Islas Los Roques in Venezuela (1,886/ha) (Table 5). This protected area in Venezuela was subsequently depleted of adult conch through illegal fishing (Rodríquez and Posada, 1994), and declines in population density throughout the Caribbean are well documented (Appeldoorn, 1994a). Densities of conch in the Exuma Cays are now among the highest in the region.

Low numbers of adults found in shallow water have been attributed directly to fishing off the Turks and Caicos Islands (Hesse, 1979), Venezuela (Weil and Laughlin, 1984), Puerto Rico (Torres Rosado, 1987), the U.S. Virgin Islands (Friedlander et al., 1994), and the Bahamas (Stoner and Schwarte, 1994). In this investigation there were >31 times the number of adult conch on the bank in the MFR compared with the number in the fished area. Because any adult conch living in water <10 m deep near LSI can be collected easily by abundant free-diving fishermen, we also attribute density differences between our sites at least partly to fishing, although other explanations are also plausible (see below).

Densities of queen conch larvae have been reported in only two published studies. Our estimates of density near WW, commonly >30 veligers/10 m³, were much higher than these studies. The highest density from a cruise in the eastern Caribbean in 1988 was only 1.2 veligers/10 m³ (mid- and late-stages) near the Grenadines (Posada and Appeldoorn, 1994), and the highest value found near Puerto Rico in 1993 was only 0.68 veligers/10 m³ (Appeldoorn and Rodriquez[1]). The highest single value recorded for a site outside the Exuma Sound was 2.0 veligers/10 m³ (including newly hatched larvae) in the Florida Keys in 1994, with all other values one or two orders of magnitude lower (Stoner et al., in press; Stoner and Mehta, unpubl. data). High larval densities in the Exuma Cays, particularly in the MFR, appear to be directly associated with abundance of spawning stocks.

[1] Appeldoorn, R. S., and L. Rodriquez. 1995. Department of Marine Sciences, University of Puerto Rico, P.O. Box 908, Lajas, Puerto Rico 00667. Unpubl. data.

Table 5

Adult queen conch densities reported throughout the Caribbean and arranged by decreasing latitude.

Location	Density (no/ha)	Depth (m)	Survey date	Reference	Survey methods
Bermuda	0.52	0–20	1988	Berg et al. (1992a)	Towed-diver transects
Florida Keys, United States	0.50	0–25	1987–1988	Berg et al. (1992b)	Stratified towed-diver transects
Bahamas			1983–1984	Smith and van Nierop[1]	Swim transects
Little Bahama Bank	28.50	0–18			
Great Bahama Bank	20.79	0–18			
Cuba			1972–1974	Alcolado (1976)	Swim transects
Diego Perez	1582	3–4			
Cabo Cruz	130	0–5			
Turks and Caicos Islands	255	0–4	1974–1975	Hesse (1979)	Swim transects
Puerto Rico, United States	2.62	0–30	1985–1986	Torres Rosado (1987)	Swim transects
Virgin Islands, United States		—	1981	Wood and Olsen (1983)	Sled transects
St. Thomas	9.7				
St. Croix	7.6				
Virgin Islands, United States			1990	Friedlander et al. (1994)	Scooter transects
St. Thomas	11.79	5–30			
St. John	12.64	5–30			
Los Roques, Venezuela			1981–1983	Weil and Laughlin (1984)	Fixed quadrats
Fished	160[2]	1–4			
Unfished	1886[2]	1–18			

[1] Smith, G. B., and M. van Nierop. 1984. Distribution, abundance, and potential yield of shallow-water fishery resources of the Little and Great Bahama Banks. UNDP/FAO Fish. Dev. Proj. BHA/82/002, p. 1–78.
[2] Assuming conch >210 mm in shell length were adults (Laughlin and Weil, 1983).

Distribution processes in the Exuma Cays

In terms of both density and extrapolated total numbers there were more adult conch in the MFR near WW than in the fished area near LSI. The two sites were similar in terms of habitat, and they lie relatively close together in the same oceanographic basin, yet there were density differences, most notably in the shallow bank waters. We recognize that no unreplicated comparison of two field sites can provide indisputable proof that an MFR is advantageous to a stock unless the analysis includes long time series or data before and after closure of a fishing area, or both (Stewart-Oaten et al., 1986; Osenberg et al., 1994; Underwood, 1994). Unfortunately we know of no biological data for the Exuma Cays Land and Sea Park collected before the fishing closure. This is a common problem associated with studies of MFR's (see Roberts and Polunin, 1991), and future studies should use control sites and replication in both time and space for definitive answers regarding the impact of closing fisheries in reserve areas. On the other hand, it is not surprising when stocks of exploited species increase in closed areas. A more important

Table 6

Adult queen conch densities reported for two locations in the Caribbean by depth interval. Data for Puerto Rico were collected in 1985–86 (Torres Rosado, 1987) and data for the United States Virgin Islands were collected in 1990 (Friedlander et al., 1994). See Table 1 for comparison with the Exuma Cays sites.

Puerto Rico		Virgin Islands	
Depth (m)	Density (no/ha)	Depth (m)	Density (no/ha)
0–5	0	0–6	5.2
5–10	0.04	6–12	4.2
10–15	0.035	12–18	17.1
15–20	0.035	18–24	10.9
20–25	0.05	24–30	11.0
25–30	0.023		

issue may be whether or not the reserves contribute to long-term conservation of species or whether or not they preserve or enhance stocks in the surrounding waters. Answers to such questions require data

on mechanistic issues such as reproductive output, recruitment dynamics, and larval import and export. Our data on adult shell size and age, juveniles, and larval size and abundance make this analysis unique and allow considerable insight into distribution mechanisms in the Exuma Cays. An understanding of such mechanisms is critical for making effective management policies.

Site-specific differences in shell size and shape described for queen conch (Stoner and Schwarte, 1994; Martín-Mora et al., 1995) are useful in explaining adult recruitment patterns at WW and LSI. Juveniles in the shelf environment of Exuma Sound grow rapidly, produce shells that are long and slender, and reach sexual maturity (hence terminal length) at a larger size than conch developing on the Great Bahama Bank. On the basis of shell size and shape, low numbers of adults on the bank and near inlets, and high fishing pressure, Stoner and Schwarte (1994) concluded that little migration occurred between bank and sound at LSI and that small numbers of juveniles in shallow regions of the sound were the primary source of deep-water reproductive stock. Adults on the bank were mostly young (i.e. thin-lipped), and most were removed by fishing before they could migrate offshore to the primary reproductive grounds in the deeper shelf environment.

Adults on the bank in the MFR near WW had a length-frequency distribution virtually identical to those on the bank at LSI (i.e. small adults). However, unlike the LSI shelf where large adults dominated the population, adult length-frequency in the shelf environment of WW was bimodal. The smaller WW adults originated on the bank and were able to migrate to deeper shelf waters in the absence of fishing. Therefore, although there was only one primary source of adults for the sound population at LSI, there were two sources at WW, and migration from the unfished bank provides at least a partial explanation for higher densities and the bimodal distribution observed on the adjacent Exuma Sound shelf. Although, in some areas, fishing may result in removal of large individuals and in artificial selection for small conch (Appeldoorn, 1994b), this does not appear to be a problem near LSI, where adults were relatively large.

On the basis of shell lip thickness, it appears that conch were removed from the bank near LSI at an early age, whereas older, thick-lipped conch accumulated on the bank in the MFR near WW. The reverse was evident in deep shelf waters where the average age of conch was higher at LSI than at WW. It is possible that harvesting of young adults from shallow bank and shelf waters near LSI has reduced recruitment to the deep-water spawning population.

It has been assumed that, by allowing fishermen to collect conch only by free-diving, a deep-water refuge is secured for conch spawning stock. Although this is true in general, virtually all juveniles and first-year adults in the Exuma Cays live in shallow (<15 m) water and all are available to free-diving fishermen until after reaching adulthood. Protection of habitat used as a migratory pathway is critical in the management of conch stocks.

Patterns of abundance for queen conch juveniles and larvae suggest that differences in recruitment processes, in addition to fishing pressures, may affect differences in the numbers of adult conch between the two study sites. In 1991, juvenile aggregations in the MFR were an order of magnitude larger than those in the fished area, where the aggregations were relatively small in all six annual surveys. The large juvenile aggregations in the MFR can be explained by relatively high densities of competent larvae arriving at the site. In 1993, the mean concentration of late-stage larvae at the offshore shelf stations at the MFR was 17 times higher than the concentration in the fished area. In 1994, the difference was approximately fourfold. The supply of larvae to the MFR nurseries appears to be much higher than the supply to nurseries in the fished area.

Differences in larval supply to a site are affected by three primary processes—production, survival, and transport. Virtually nothing is known about the predators of queen conch larvae or about the survival of queen conch in the plankton. There is little doubt, however, that site differences in larval production, demonstrated by the density of early-stage larvae, reflect local spawning stock size and density. In terms of transport, near-surface flow along the Exuma Cays shelf is to the northwest at LSI, at WW, and at a station midway between the two sites. From June through September 1993, the current on the shelf at WW flowed to the northwest at 1.6–3.4 cm/s (1.4–2.9 km/day (Hickey[2]). Given a larval life of 16–28 d (Davis et al., 1993), late-stage queen conch larvae arriving in the MFR near WW must originate well to the south, and their high densities most likely reflect a natural accumulation of larvae produced by spawning stocks all along the Exuma Cays. This abundance of recruits must also contribute to high densities of juveniles and adults observed in the MFR. Larvae of a closely related, but unfished strombid, *Strombus costatus*, were also highly concentrated in the MFR in 1994 (Stoner, unpubl. data). We conclude, therefore, that the high density of adult conch at WW results not only from reduced fishing

pressure but also from natural accumulation of larvae. Furthermore, given the surrounding current patterns, the reserve is probably not large enough to hold a self-sustaining conch population; conch at WW are derived from up-stream spawning stocks located outside the reserve. With a northwest current along the Exuma Cays shelf, an MFR located farther to the south might actually allow better downstream conservation of queen conch. However, exact transport distances are unknown, and calculations are complicated by the potential effects of numerous tidal passes and plumes. Because preservation of external sources of larvae will be critical to the maintenance of populations within any park, managers establishing all such reserves must consider the broad metapopulation context (Carr and Reed, 1993; Man et al., 1995).

It is likely that the high densities of larvae exported from the Exuma Park on the northwest current represent a significant recruitment source for conch populations in the northern Exuma Sound. Very large aggregations of juvenile conch (>600 ha) were measured in the northern Exuma Sound near the Schooner Cays in 1993 (Stoner, unpubl. data). These populations appear to have increased since the establishment of the Exuma Cays Land and Sea Park (Higgs[3]). Future modeling of larval transport will be particularly valuable in estimating the actual significance of enhanced larval production in this and other marine fishery reserves. Although the significance of larval export is difficult to prove experimentally (Dugan and Davis, 1993), the value of reserves located upstream may be especially high.

Clearly, the Exuma Cays Land and Sea Park 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. Because of the potential fishery value of exported larvae, a good understanding of the strategic locations of reserves and of the general oceanographic conditions within the dispersal range of the larvae is necessary. Our observations provide support that fishery reserves can indeed enhance fishery populations in the downstream direction through export of larvae, although only if the sources of larvae for the reserves are maintained. Furthermore, reserves need to incorporate design features that protect habitats required by each life stage. Legal prohibition of the use of SCUBA gear prevents immediate depletion of adult queen conch because

those individuals that survive the migration to deep-water constitute an unfished deep-water reproductive stock, even outside a reserve. However, every young adult is vulnerable, and multiple well-placed reserves that protect the tidal inlets, which serve as pathways between nurseries and important reproductive grounds on the shelf, could be particularly valuable. Reserve designs that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

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