Relationships between Fishing Pressure and Stock Structure in Queen Conch (Lobatus gigas) Populations: Synthesis of Long-Term Surveys and Evidence for Overfishing in The Bahamas

Article *in* Reviews in Fisheries Science & Aquaculture · October 2018

DOI: 10.1080/23308249.2018.1480008

Allan Stoner
Community Conch (non-profit organization)

Martha Davis
Community Conch

Andrew S Kough
Shedd Aquarium

Reviews in Fisheries Science & Aquaculture

ISSN: 2330-8249 (Print) 2330-8257 (Online) Journal homepage: http://www.tandfonline.com/loi/brfs21

Relationships between Fishing Pressure and Stock Structure in Queen Conch (*Lobatus gigas*) Populations: Synthesis of Long-Term Surveys and Evidence for Overfishing in The Bahamas

Allan W. Stoner, Martha H. Davis & Andrew S. Kough

REVIEWS IN FISHERIES SCIENCE & AQUACULTURE
https://doi.org/10.1080/23308249.2018.1480008

Taylor & Francis
Taylor & Francis Group

REVIEW

OPEN ACCESS Check for updates

Relationships between Fishing Pressure and Stock Structure in Queen Conch (*Lobatus gigas*) Populations: Synthesis of Long-Term Surveys and Evidence for Overfishing in The Bahamas

Allan W. Stoner[a], Martha H. Davis[b], and Andrew S. Kough[c]

[a]Community Conch, Lopez Island, Washington, USA; [b]Community Conch, Littleton, Colorado, USA; [c]John G. Shedd Aquarium, Chicago, Illinois, USA

ABSTRACT
Broad-scale surveys for the economically valuable gastropod queen conch in historically important fishing grounds of the Bahamian archipelago provide opportunity to explore the impact of variable fishing intensity on population structures. Visual surveys spanning two decades showed that densities of mature individuals had a significant negative relationship with an index of fishing pressure (FP). Average shell length in a population was not related to FP, but shell lip thickness (an index of conch age) declined significantly with FP. Repeated surveys in three fishing grounds revealed that densities of mature conch have declined in all of those locations and the populations have become younger with time. Densities have also declined significantly in three repeated surveys (over 22 years) conducted in a large no-take fishery reserve. Unlike fished populations, the protected population has aged and appears to be declining for lack of recruitment. In all fishing grounds except those most lightly fished, densities of adult conch are now below that needed for successful mating and reproduction. It is clear that queen conch populations in The Bahamas have undergone serial depletion, nearing fishery collapse, and a wide range of recommendations aimed at stock recovery are offered including a broader network of no-take reserves.

KEYWORDS
Fishing impact; population structure; marine protected area; overfishing; mollusk

Introduction

Growing concern about overfishing

The large gastropod queen conch (*Lobatus gigas*; formerly *Strombus gigas*) is one of the most important fishery resource species in the Greater Caribbean region, exploited for meat and shell products for thousands of years. Unfortunately, because of ever increasing threats caused by heavy fishing and habitat losses in the species' critical shallow-water habitat, queen conch needed to be listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) in 1992. As a result of that action, international trade in queen conch products is regulated under CITES. Fishing regulations associated with queen conch have increased with time but vary substantially over the more than 30 nations where conch are distributed (Appeldoorn, 1994; Theile, 2001, 2005; Boman et al., 2018), ranging from no regulation whatsoever to complete moratoria on fishing in Florida and Bermuda. Despite more than 30 years of moratorium in Florida, the conch population has still not rebounded to a commercially harvestable level (G. Delgado, Florida Fish and Wildlife Conservation Commission, unpubl. data). Harvest regulations in other locations include closed seasons, closed areas, catch quotas, size and age limitations, and gear restrictions designed to promote a sustainable fishery by reducing and containing fishing effort. Despite the various fisheries management measures continued reductions in queen conch densities, decreasing catches per unit effort, and changing age structures throughout the region resulted in a review by the National Oceanic and Atmospheric Administration (U.S. Department of Commerce) to consider queen conch for listing under the Endangered Species Act. Threatened status was declined in 2014; however, the species continues to be severely overfished in many parts of its distribution, and the decision is under appeal. Such a listing would reduce or eliminate import of conch products to the United States.

CONTACT Allan W. Stoner allan.stoner@gmail.com Community Conch, Lopez Island, Washington, USA.
Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/brfs

The Bahamas is a small nation by land area (~11,000 km^2 spread over 700 low islands and cays) but has a vast area of marine banks <50 m deep (~300,000 km^2), much of which is <10 m deep (~136,000 km^2) (Carew and Mylroie, 1997). A large proportion of that shallow bank is characterized by seagrass meadows (especially *Thalassia testudimum*, *Syringodium filiforme*, and *Halodule wrightii*) and macroalgae-covered hard-ground that serve as important habitats for juvenile and adult queen conch (Randall, 1964; Stoner, 2003; Appeldoorn et al., 2011).

The queen conch has high cultural and economic significance in The Bahamas as a traditional food item, and its shell appears on the nation's official seal. This is one of only a few nations where substantial populations of queen conch remain and where a large volume of the conch meats and shell products are exported. Total catch of conch in The Bahamas is difficult to determine because of the dispersed nature of the fishing effort and because much of the catch goes directly from fishers to restaurants and other consumers. The Bahamas Department of Marine Resources (DMR) has reported that total landings reached maximum levels near 858 metric tons of meat weight in the mid-2000s (Gittens and Braynen, 2012); this decreased steadily to 360 metric tons in 2016 (DMR, unpubl. data). A quota for commercial export of conch meats is set by DMR and monitored by CITES. The quota began in 1993 with 250 metric tons and increased to 350 metric tons in 1994. Since then, annual exports have hovered between 92 and 258 metric tons (Gittens and Braynen, 2012). Export weights (clean meats) increased about two-fold between 1995 and 2011 while the values of those exports increased seven times to nearly US$3.3 million in 2011; however, export value in 2016 declined to US$2.1 million. The senior author's direct observations of queen conch populations in the field spanning 30 years substantiate the declining numbers (see also Stoner et al., 2012a; Kough et al., 2017). Other signs of declining stocks include an increasing proportion of juvenile conch in the shells observed at cleaning sites (Stoner, 1997) while the average size and age of queen conch in these shell middens has diminished (Cash, 2013; Community Conch, unpubl. data).

Conch fishing in The Bahamas was restricted to collecting from the surface and by free diving for many decades. This provided a refuge for reproductive-age conch in depths greater than most free divers are willing to work (Stoner and Schwarte, 1994). However, fishers have become increasingly dependent upon surface-supplied air compressors (hookah), allowed with a license and on a seasonal basis (August through March). Unlike most Caribbean nations, The Bahamas has no closed season for conch fishing. There are several marine protected areas, but only the Exuma Cays Land and Sea Park (364 km^2), in the central part of the archipelago, is enforced as a no-take reserve. Outside of closed areas, any queen conch with a flared shell lip may be legally harvested, regardless of size. However, the flared-lip stage, long thought to indicate sexual maturity, in fact, does not guarantee maturity (*Subject Species* below), thus it is legal to harvest conch before they have a chance to reproduce.

The non-profit organization Community Conch was founded in 2009, with the goal of helping to develop a plan for sustainable utilization of queen conch in The Bahamas. Part of that effort has been to conduct surveys and stock assessments for the species over the most important conch fishing grounds in the nation. Research on queen conch in The Bahamas expanded in 2015 to include surveys lead by biologists from Shedd Aquarium that are directly comparable to those of Community Conch. The meta-analysis reported herein was performed to consolidate data for the geographically dispersed surveys conducted by Community Conch and Shedd Aquarium between 2009 and 2017, and to evaluate the effect of fishing pressure (FP) on population structure and reproductive potential. Densities and age structures of adults and large juveniles are reported. Conch surveys were not conducted at most of the fishing grounds prior to 2009, but where possible, comparisons are made with earlier observations, the current condition of the stocks over the Bahamian archipelago is evaluated, and recommendations are offered toward the goal of rehabilitating the overfished stocks.

Life history of the subject species

Queen conch are gonochoristic, and reproduction occurs by copulation during which the female stores sperm, and eggs are fertilized upon laying a benthic egg mass. Each egg mass can hold up to a half million eggs and several egg masses are typically laid in a long summer reproductive season (Davis et al., 1984; Stoner et al., 1992) that varies in duration with geographic position in the Caribbean (Aldana-Aranda et al., 2014; Boman et al., 2018). After developing for about five days, veliger larvae emerge from the egg mass and drift near the surface (Barile et al., 1994) for two to five weeks consuming phytoplankton (Davis, 1998). During the pelagic phase, shell length increases from ~0.2 mm at hatching to ~1.2 mm at the time of settlement to the benthos (Davis, 2005). Newly settled juveniles are rarely observed, but appear to choose shallow seagrass meadows, beds of macroalgae, and coarse-grained sand where diatoms and other small algal foods are abundant in their first benthic habitat. Stoner (2003) reviewed the general subject of queen conch nursery grounds, including larval delivery systems, settlement processes, growth and survival during the first two years of life. Queen conch are herbivorous throughout their entire life cycle, with green macroalgae and seagrass epiphytes being common foods for juveniles and adults (Randall, 1964; Stoner and Waite, 1991).

Although queen conch are known to inhabit depths as great as 50 m on rhodolith reefs of Puerto Rico (García-Sais et al., 2012), the vast majority of queen conch, both juveniles and adults, are found in depths <30 m (Stoner and Ray, 1996) making them highly susceptible to harvest by diving fishers. In The Bahamas, small juveniles are most abundant in water <5 m deep whereas larger and older conch typically increase in numbers with depth. The depth pattern observed today probably results from shallow-water larval recruitment coupled with highest removal of large individuals by free divers in depth <10 m.

At the age of ~3.5 years shell length reaches its maximum dimension (typically 20–25 cm in The Bahamas depending upon location; see below) and the shell lip flares outward from the aperture to form the characteristic pink lip of the queen conch legal for harvest in The Bahamas. Thereafter, the shell grows only in thickness, with nacre laid down on the interior of the shell and the shell lip (Appeldoorn, 1988a). Longevity in queen conch is not known precisely; however, 20 years or more is likely. In The Bahamas shell lip thickness (LT) increases by about 5 mm per year (Stoner and Sandt, 1992), and histological studies show that minimum LT for reproductively mature males and females is 9 and 12 mm, respectively (Stoner et al., 2012b). This means that conch can be legally harvested in The Bahamas before they are sexually mature. Recent logistic analysis shows that ~15 mm represents the LT where there is a 50% probability of maturity for queen conch collected in a variety of Caribbean locations including The Bahamas (Boman et al., 2018), and this threshold is used to define mature conch in field populations discussed in this study.

Survey methods

Survey locations

Locations for queen conch surveys (Figure 1) were proposed by the Bahamas Department of Marine Resources and guided by interviews with fishers on historically important fishing grounds. With the exception of the most remote fishing banks (e.g., Cochinos Bank) and a few other locally important small sites, surveys conducted between 2009 and 2017 covered the most productive and critical fishing grounds in the nation. Apart from one broad-scale survey conducted by Smith and van Nierop (1984), for which few geographic details are available, field work conducted at the Caribbean Marine Research Center beginning in 1991 represents the first fishing-ground-specific data for queen conch populations in The Bahamas. Some comparisons were possible with observations conducted in Berry Islands nursery grounds in the early 1980s (Iversen et al., 1987) and depth-stratified surveys focused near Lee Stocking Island and inside the Exuma Cays Land and Sea Park (ECLSP) in the 1990s (Stoner and Ray, 1996). Follow-up surveys were made in the Park in 2011 and 2016 (Stoner et al., 2012a; Kough et al. 2017). Other temporal comparisons are discussed as possible.

Small-scale maps for each study site were overlaid with a grid of one minute latitude and longitude, yielding blocks approximately one nautical mile on a side. Detailed maps of the actual survey blocks at each location shown in Figure 2 are provided in technical reports available on the Community Conch website (www.communityconch.org). Effort was made to count and observe queen conch in a long survey line (i.e., belt transect; see below) within each block. These broad-scale surveys yielded most of the data for extensive, shallow-water bank areas <10 m deep where queen conch fishing is concentrated in The Bahamas.

In most locations depths increase rapidly from 10 m to great depth around the peripheries of the banks. While the surface area of queen conch habitat at this bank edge is typically small compared with the top of the bank these deeper, open-water locations are often more exposed to high waves, and are less easily exploited by fishers. Therefore, the deep-water habitats often provide refuge for spawning stocks (Stoner and Ray, 1996; Stoner et al., 2012a). Depth-stratified surveys were conducted at the edges of the bank in a few locations to explore conch abundance and size/age structure in the deep-water habitats and to make comparisons with earlier surveys. These included locations around the Berry Islands, east of Lee Stocking Island and the Exuma Cays Land and Sea Park in the Exuma Cays, and on Cay Sal Bank (Figure 1; Table 1). In such cases from 3 to 9 lines running perpendicular to the bank edge were established, and six depth strata (see Survey Protocol) were surveyed, using towed

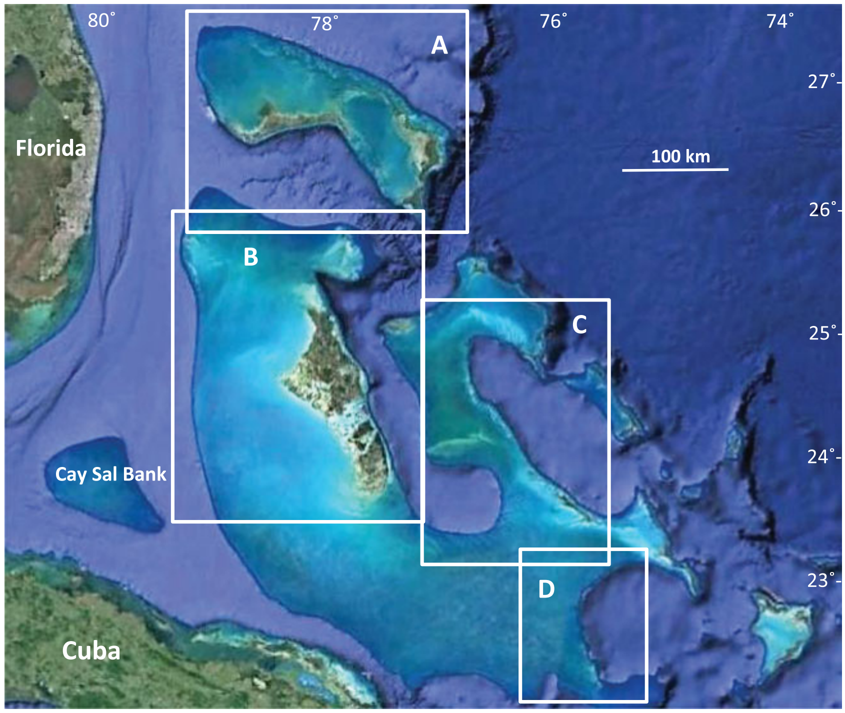

Figure 1. Map of The Bahamas showing the sub-regions where queen conch fishing grounds were surveyed. (A) Northern Bahamas including Grand Bahama Island and the Abaco Cays, located on the Little Bahama Bank. (B) Western Great Bahama Bank – Bimini, Berry Islands and Andros Island. (C) Exuma Cays bordering the Exuma Sound (east) and the southern Tongue of the Ocean (southwest corner). (D) Jumentos Cays and Ragged Islands at the southern end of the Great Bahama Bank. Detailed maps are provided in Figure 2.

snorkelers in depths <10 or 15 m (depending upon underwater visibility) and scuba divers swimming near the bottom in greater depths.

Survey timing

All of the surveys considered in this analysis (1991 through 2017) were conducted between May and September. This corresponds with the height of conch reproductive season in The Bahamas (Stoner et al., 1992; Boman et al., 2018), when adult conch are aggregated more than in the winter season, allowing for best direct comparisons among the study sites. Adult queen conch are long lived, so despite the nine-year span of time needed to cover all of the major fishing grounds in the most recent surveys (2009–2017) the spatial comparisons made are robust in terms of general trends in population structure, density, and reproductive biology.

Survey protocol

Small powerboats (5–7 m length) were used to support the divers who made observations on queen conch density and reproductive behavior at each location. Each boat was fitted with a track-recording GPS unit and depth sounder. For surveys on the banks, positions of grid corners were uploaded into the GPS units for easy location in the field. Coordinates for the beginning and end point of each survey tow, along with depth and temperature data, were downloaded at the end of each day of sampling. Each survey line was assigned to one of the following depth categories: $A = 0–2.5$ m, $B = 2.5–5$ m, $C = 5–10$ m, $D = 10–15$ m, $E = 15–20$ m, and $F = 20–25$ m. For the analysis in this study, the depth strata were consolidated into two zones, <10 m (shallow) and ≥10 m (deep) (see below).

The general approach was to tow the diver from one corner of the block (or the nearest possible point) toward the center of the block, often in the downwind direction, such that the center of the block was always surveyed. A transect 6 m wide was observed for conch, yielding a sample unit of ~6000 m^2. In some cases total distance covered was slightly shorter or longer than the design 1000 m (e.g., because of shoals or land masses, or slight over-runs). Conch densities were calculated on the basis of surface area observed for each tow.

As discussed above, divers equipped with scuba were used to survey conch in areas deeper than 10 or 15 m. In such cases, two or three divers made each dive, descending at the target location and depth

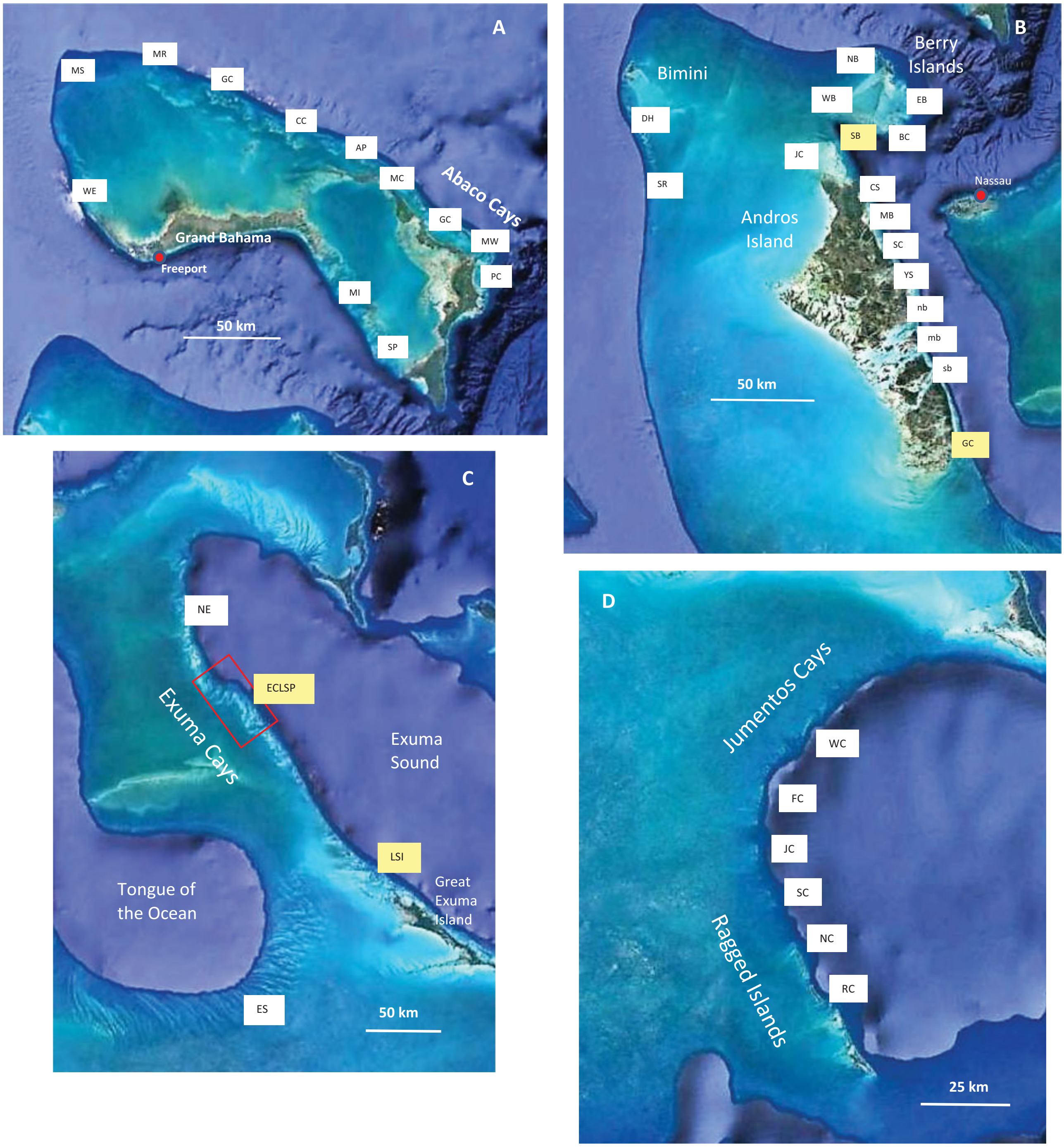

Figure 2. Detailed maps of the four sub-regions (see Figure 1) where queen conch were surveyed. Conch were also surveyed over the eastern part of Cay Sal Bank (Figure 1). (A) Little Bahama Bank survey sites (clockwise from west): West End, Mantanilla Shoal, Mantanilla Reef, Grand Cay, Carter's Cays, Allans-Pensacola Cays, Manjack Cay, Guana Cay, Man-O-War Cay, Pelican Cays, Sandy Point, and More's Island. (B) Western Great Bahama Bank: Near Bimini – South Riding Rock, Dollar Harbor. Berry Islands – North Berry, West Berry, South Berry, East Berry, and the Berry Islands MPA. (C) Central Great Bahama Bank: Northern Exuma Cays, Exuma Cays Land and Sea Park (ECLSP), Lee Stocking Island, and the Eastern Sand Bores. The red rectangle shows the approximate boundaries of ECLSP. (D) Jumentos Cays and Ragged Island: Water Cay, Flamingo Cay, Jamaica Cay, Seal Cay, Nurse Cay, and Racoon Cay. Yellow labels in B and C show sites where repeated surveys were conducted.

interval. The divers swam in parallel near the bottom holding a taut 8-m-long line. The divers swam out from the anchor point, along the pre-determined isobath and returned along a parallel but non-overlapping transect line. Total distance traveled, was measured either with a calibrated low-velocity flow meter carried by one of the divers or with GPS at the dive start and end points. Total distance varied substantially with diving depth, but averaged ~500 m, representing an area of 4000 m^2. Full details for

Table 1: Locations in The Bahamas surveyed for queen conch between 2009 and 2017 and the densities observed for two age classes. Two depth zones include habitats <10 m (S) and >10 m (D). The index of fishing pressure was assigned from 1 to 5 with 1 indicating the least fishing intensity. Densities (numbers per hectare) (mean ± SD) are reported for subadult queen conch (age-3 juveniles) and for individuals with flared shell lips (age-4 and older). The latter are legal for harvest in The Bahamas but not necessarily mature adults. Repeat surveys are indicated after site names where an earlier survey was conducted (see text for further explanations).

Survey location	Depth zone	Fishing Pressure	No. of survey lines	Subadults	Flared shell lip
Berry Islands (2009)					
MPA Bank	S	5	42	13.0 ± 30.2	4.4 ± 8.1
MPA Shelf	S	4	16	1.5 ± 2.3	14.1 ± 30.0
	D	2	12	0.3 ± 1.1	5.4 ± 9.3
East Shelf	S	4	6	0.8 ± 1.4	5.8 ± 6.6
	D	2	6	0 ± 0	17.3 ± 37.5
South fishing ground	S	4	73	70.2 ± 140.5	118.4 ± 281.6
	D	2	6	0 ± 0	2.9 ± 7.0
West fishing ground	S	5	70	0.6 ± 1.9	0.7 ± 1.8
North fishing ground	S	2	40	2.9 ± 7.0	1.9 ± 4.8
	D		10	11.7 ± 35.0	25.1 ± 48.5
Andros Island (2010)					
Conch Sound	S	5	8	0 ± 0	0.21 ± 0.59
Mastic Bay	S	5	14	0.95 ± 2.33	0.71 ± 1.08
Stafford Creek	S	5	8	0.63 ± 1.77	0.42 ± 1.18
Young Sound	S	5	6	5.83 ± 6.48	2.50 ± 2.30
North Bight	S	4	19	223.1 ± 601.6	9.99 ± 14.49
Middle Bight	S	4	17	151.4 ± 499.2	2.35 ± 2.57
South Bight	S	4	10	3.50 ± 2.77	3.33 ± 4.44
Grassy Cays	S	2	58	35.2 ± 60.1	117.1 ± 162.4
Exuma Cays (2011)					
LSI bank (repeat)	S	4	70	73.1 ± 158.0	5.8 ± 15.5
LSI shelf (repeat)	S	3	20	1.62 ± 3.03	2.53 ± 7.31
	D	2	30	0.14 ± 0.74	4.29 ± 15.6
ECLSP bank (repeat)	S	2	52	10.8 ± 32.2	16.6 ± 50.4
ECLSP shelf (repeat)	S	1	13	6.9 ± 8.6	113.6 ± 137.8
	D	1	20	2.7 ± 3.9	42.7 ± 74.0
Bight of Abaco (2012)					
More's Island	S	5	115	7.8 ± 20.6	9.8 ± 16.7
Sandy Point	S	5	87	10.1 ± 18.9	6.4 ± 9.6
Jumentos & Ragged Islands (2013)					
Water Cay	S	2	43	9.6 ± 31.8	146.5 ± 151.0
Flamingo Cay	S	1	39	11.2 ± 17.4	168.2 ± 137.1
Jamaica Cay	S	1	22	26.0 ± 54.3	154.3 ± 148.2
Seal Cay	S	1	22	11.9 ± 20.8	126.3 ± 110.1
Nurse Cay	S	2	23	3.9 ± 6.9	91.1 ± 143.4
Raccoon Cay	S	2	27	30.5 ± 105.0	122.0 ± 137.9
Little Bahama Bank (2014)					
West End	S	5	55	8.4 ± 16.1	3.6 ± 4.2
Mantanilla Shoal	S	2	19	0.7 ± 1.5	68.8 ± 115.1
Mantanilla Reef	S	3	41	7.1 ± 12.7	33.9 ± 43.1
Grand Cays	S	4	22	8.1 ± 10.9	25.5 ± 29.2
Carter Cays	S	3	54	10.1 ± 19.9	49.2 ± 77.3
Allan's-Pensacola Cay	S	4	6	1.2 ± 1.6	8.6 ± 5.3
Manjack Cay	S	5	4	0.4 ± 0.8	6.7 ± 6.1
Guana Cay	S	5	5	19.7 ± 39.4	21.7 ± 42.0
Man-O-War Cay	S	5	5	30.3 ± 54.2	15.3 ± 21.6
Pelican Cays	S	2	4	8.3 ± 17.7	22.8 ± 13.8
Eastern Sand Bores (2015)	S	2	114	4.6 ± 11.0	54.2 ± 56.4
	D	2	43	2.0 ± 4.4	46.7 ± 53.6
Western Bahamas (2016)					
Berry Islands (repeat) South fishing ground	S	4	59	39 ± 57	35 ± 85
Dollar Harbor	S	5	46	4.2 ± 8.5	6.9 ± 14.2
South Riding Rock	S	4	42	32 ± 106	39 ± 57
Andros Island					
Grassy Cays (repeat)	S	2	26	6.6 ± 28.5	180 ± 184
Joulter's Cay	S	4	66	57 ± 72	30 ± 128

(*Continued*)

Table 1: Continued.

Survey location	Depth zone	Fishing Pressure	No. of survey lines	Subadults	Flared shell lip
Exuma Cays (2016)					
ECLSP bank (repeat)	S	2	14	14 ± 26	10 ± 18
North Exuma Cays	S	4	101	23 ± 74	4.7 ± 16.4
Cay Sal Bank (2017)					
Shallow Bank	S	1	51	245 ± 547	141 ± 198
Deep Bank	D	1	76	86 ± 247	234 ± 176

diving methods are provided in Stoner and Ray (1996) and Stoner et al. (2012a). Surveys at Cay Sal, all in relatively deep water, followed the same spatial stratification as the towed observer surveys. Four dives were made within each grid proceeding in the direction of the current. Dives were variable in length (mean = 386 ± 362 m; $n = 133$). Otherwise the Cay Sal surveys were carried out as in other locations.

Each transect line was surveyed for:

a. Number of queen conch with flared shell lips. These represent individuals that are legal for harvest in The Bahamas. In some earlier publications, these have been called "adult" conch erroneously (see above). In this report the term "flared-lip conch" is used.
b. Number of "subadults" (also called "rollers" in The Bahamas). These are large juvenile conch (greater than ~15 cm shell length) without a flared shell lip, representing the age-3 year class.
c. Smaller juveniles representing the age-1 and age-2 classes were also observed at certain locations. However, these small conch tend to be highly aggregated and live in somewhat different habitats than subadults and flared-lip conch, and results for small juveniles are not reported here.

Where flared-lip conch were sufficiently abundant, random collections were made to measure for shell length (SL) (±1 mm) with large Vernier calipers. Shell LT (±1 mm) was measured with small Vernier calipers about two-thirds of the way posterior from the anterior siphonal groove of the shell. This is the thickest region of the shell lip and provides a relative index of conch age (Appeldoorn, 1988a; Stoner et al., 2012b; Mueller and Stoner, 2013). For analytical purposes, queen conch with LT ≥ 15 mm were considered to be sexually mature, while those with LT < 15 mm were classified as immature based upon histological studies (see above).

Analytical methods

Densities of flared-lip and subadult queen conch were evaluated for patterns related to location and water depth. Counts were standardized to numbers of conch per hectare (10,000 m^2) for each age group. Density estimates and data on shell dimensions were evaluated on the basis of two depth ranges: 0–10 m (shallow) (pooling the depth zones *A*, *B*, and *C* described above) and 10–25 m (deep) (zones *D*, *E*, and *F*). The break at 10 m was made with the rationale that free divers who harvest queen conch in The Bahamas work in and are most effective at depths <10 m. Additionally, the majority of fishing grounds surveyed for this study were in the shallow range.

A value for "Fishing Pressure" was assigned to each location and depth zone (Table 1). FP was scored with an integer from 1 to 5 (very low to very high pressure), based upon distance from primary fishery landing sites including Nassau (New Providence Island), West End (Grand Bahama Island), Marsh Harbour (Abaco), and Bimini. In some cases substantial landings are also made locally, such as on More's Island in the Bight of Abaco and at Andros Island, then transshipped to Nassau or another major port. A score of 5 (very high FP) was assigned when a major landing site was within 50 km, a score of 4 (high pressure) was assigned when landings occur within 100 km. Scores of 3 and 2 (medium and low pressure) were assigned when conch need to be transported 100–200 km, or more than 200 km, respectively. A score of 1 (very low FP) was given only to survey locations that were distant from landing sites and settlements with commercial fishers, sites protected by fishing closures for queen conch, and/or depths >10 m. For example, the Cay Sal site was assigned a FP score of 1 because of distance from ports, complete lack of settlements, and remote offshore location dangerous to small boats.

The primary statistical tool used in the analysis of FP and conch populations was regression. The goal was to find the best possible fit between variables (e.g., FP and density of mature conch) considering both linear and non-linear (primarily polynomial) models.

Repeated surveys

Repeated surveys were conducted at four locations with between 5 and 22 years of temporal separation.

Three surveys were made in the no-take Exuma Cays Land and Sea Park (1994, 2011, and 2016, and two surveys were made at each of three fished locations: near Lee Stocking Island (1991 and 2011), on the shallow bank west of Chub Cay in the southern Berry Islands (2009 and 2016), and near the Grassy Cays at the south east end of Andros Island (2010 and 2016). Detailed descriptions of field methods for these surveys are provided in earlier analyses (Stoner and Ray, 1996; Stoner et al., 2012a; Kough et al., 2017); for the synthesis reported here data from multiple depth intervals described above were pooled to conform to three broad classifications of habitat: The "bank" habitat represented shallow, seagrass- or sand-covered bottom (mostly <5 m depth) to the west of the islands that separate the Great Bahamas Bank from the Exuma Sound (LSI and ECLSP) and similar shallow bank-top habitat at the Grassy Cays and in the Berry Islands. Also, at LSI and ECLSP, surveys for conch were made on the narrow island shelves to the east of the islands in Exuma Sound. This environment is subject to higher wave energy than the bank and the bottom is algae-covered hard-bottom or bare sand, with small patches of seagrass in the shallowest areas. Two depth intervals (<10 m and >10 m; see above) were considered for the shelf environment. For the most recent surveys in 2016 at the Berry Islands, Grassy Cays, and ECLSP, only the bank habitat was surveyed and analyzed here. Also, these most recent repeat surveys covered less geographic area than the earlier surveys but were centered in the areas with highest conch densities. To accommodate differences in area surveyed only the 1-min blocks of latitude and longitude that were covered in both surveys were used to provide the most robust temporal comparison for the populations. Thus, some of the density values are different from the values used in the analysis of the relationships between FP and density reported above.

Generalized linear models (GLM) were used to describe associations between the densities of flared-lip conch and temporal, geographic, and physical factors in the surveys adjacent to Lee Stocking Island (LSI) and the Exuma Cays Land and Sea Park (ECLSP) comparing surveys in the 1990s and 2011. Abundance patterns of conch associated with the categorical factors of year (1990s vs 2011), depth interval (bank, shallow shelf, and deep shelf) and location (LSI and ECLSP) were examined. The best-fit combination of factors was evaluated using Akaike's information criterion (AIC). A negative-binomial model ("glm.nb"; package MASS; R Core Team 2016) was used for variable abundance because queen conch is a relatively rare species with over-dispersed and zero-inflated counts. A similar modeling approach was used for surveys that were repeated more recently at the Berry Islands (2009 and 2016) and the Grassy Cays (2010 and 2016) but included a random term to account for abundance shifts within individual survey grids and within both fishing grounds ("glmer.nb"; package lme4; Bates et al., 2014).

Differences in shell metrics for flared-lip conch (shell LT and length) were assessed with standard one-way analysis of variance.

Densities of queen conch

Density estimates for queen conch were made for more than 40 locations spread widely over The Bahamas and representing most of the historically important fishing grounds. Over 1700 line transects were surveyed, yielding direct observations on nearly 1 million m^2 (100 ha). Average densities of flared-lip conch were highly variable over the study sites and depth zones ranging from 0.2 to 234 individuals per hectare (Table 1). Not surprisingly, density of flared-lip conch was inversely related to the index of FP. The relationship was strongest when the regression analysis included only the points representing depths <10 m; the best fitting model was polynomial explaining 87% of the density variation ($R^2 = 0.868$, $F = 83.46$, $p < 0.001$, $n = 41$) (Figure 3). When all depth zones were included, the variable FP continued to explain 72% of the variation in flared-lip conch ($R^2 = 0.724$, $F = 39.27$, $p < 0.001$, $n = 49$).

Unlike the density estimates for flared-lip conch, densities of subadult queen conch, those representing the age-3 year class, were independent from FP regardless of whether all depths were used in the analysis ($R^2 = 0.009$, $F = 0.435$, $p = 0.513$) or only the shallow zone ($R^2 = 0.003$, $F = 0.111$, $p = 0.740$).

Size and age structures of the populations

Shell length and shell LT were measured for >3000 flared-lip conch at 42 of the survey locations where conch were sufficiently abundant to represent the local population (Table 2). Average shell length ranged from very small (155 mm) in the shallow zone near Joulter's Cays north of Andros Island to >240 mm in the deep-water zone off Lee Stocking Island and south of the Berry Islands. Average shell length increased with depth where measurements were taken in the two primary depth zones at the same general location (paired *t*-test [six pairs]:

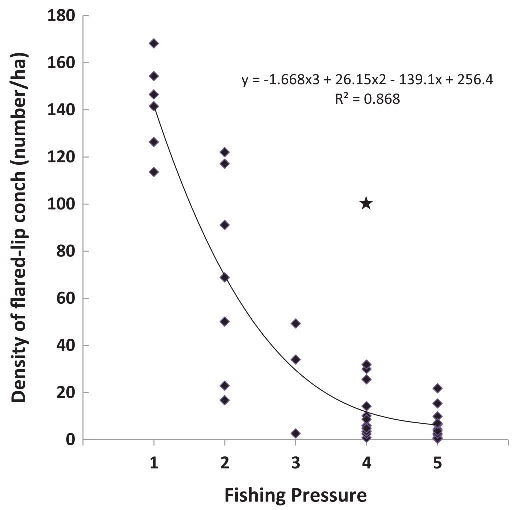

Figure 3. Density of flared-lip queen conch for major queen conch locations in The Bahamas shown as a function of the relative index of fishing pressure for each location. Levels of fishing pressure were scored from 1 to 5 (very low to very high fishing pressure). Data are shown for locations <10 m depth where free-diving fishers are most effective. One location, the south Berry Islands fishing ground (shown as a star) appears as an outlier because the population there is dominated numerically by small, thick-lipped individuals (called "sambas") that have low market value. This point was not included in the regression line or statistics shown in the figure. $n = 41$ for regression.

$t = -4.015$, $p = 0.010$), but there was no significant relationship between shell length and FP ($R^2 = 0.003$, $F = 0.137$, $p = 0.713$).

Like shell length, shell LT was highly variable, with averages ranging from 2 to 29 mm. Shell LT increased with depth in the Berry Islands, in the Exuma Cays (both Lee Stocking Island and ECLSP) and near Sandy Point, Abaco, but not at Cay Sal Bank. Nevertheless, pairwise analysis for six locations with sufficient data showed that the depth-related difference was significant ($t = -3.355$, $p = 0.020$). Unlike shell length, LT decreased in an inverse linear relationship with FP (Figure 4) ($R^2 = 0.697$, $F = 99.81$, $p < 0.001$).

Sexual maturity in queen conch is linked to shell LT as described earlier. When the standard threshold for maturity of 15 mm was set to distinguish mature and immature conch, there was a clear linear relationship between the proportion of populations comprised of mature individuals as might be expected (Figure 5) ($R^2 = 0.744$, $F = 116.20$, $p < 0.001$). Furthermore, the density of mature conch decreased significantly with FP. As observed with the density of all flared-lip conch, the density of mature conch decreased in a polynomial relationship with FP considering both shallow and deep habitats together ($R^2 = 0.797$, $F = 48.38$, $p < 0.001$). The fit was very high ($R^2 = 0.923$, $F = 119.50$, $p < 0.001$) when only the shallow depth range was included in the analysis (Figure 6).

Temporal changes in populations

Nearly 300 follow-up tows were added to those reported above for analysis of long-term trends in queen conch populations at four locations. Comparisons spanning two decades or more were made at two locations in the Exuma Cays: at Lee Stocking Island (LSI) and in the Exuma Cays Land and Sea Park (ECLSP) (Figures 7 and 8). Changes in densities of flared-lip queen conch and shell LT were evaluated for individuals observed on the shallow banks west of the islands (all <10 m depth), and for two depth zones (<10 m and ≥10 m) on the island shelves in Exuma Sound, as described above.

Surveys at LSI provided a 20-year comparison (from 1991 to 2011). Densities in the shallowest habitats (i.e., bank and shallow shelf) were already very low in 1991, with substantial densities of flared-lip conch only in the narrow shelf environment deeper than 10 m (Figure 7A). Densities in the two shallow-water habitats did not change significantly over the 20-year interval; however, densities of flared-lip conch in the deep-water shelf area declined by 92% between 1991 and 2011. Repeated surveys in ECLSP (the no-take fishery reserve) (1994–2011) revealed that densities of flared-lip conch declined 69% in the bank environment, increased on the shallow shelf, and declined 76% in the deep-water habitat (Figure 8A).

Generalized linear models analyses for these comparative surveys show that conch abundance in the two Exuma Cays sites declined between the 1990s and 2011 yet remained progressively greater with increasing depth and within the no-take marine reserve (ECLSP). The best-fit statistical model (negative binomial link) included the factors year (44% decline relative to the earliest surveys) (coefficient $= -0.5427$, $Z = -2.396$, $p = 0.0166$), depth (21% increase at the shallow shelf relative to the bank) (coefficient $= 0.1903$, $Z = 0.621$, $p = 0.5348$), and a 350% increase at the deep shelf relative to the bank) (coefficient $= 1.2734$, $Z = 4.754$, $p < 0.0001$), and location (overall, density at ECLSP was 590% higher than at LSI) (coefficient $= 1.7814$, $Z = 7.833$, $p = <0.0001$). The main effects on the density of flared-lip conch suggest that depth and closure to fishing provide significant refuges to conch over decades of harvest.

Table 2: Shell length and lip thickness for queen conch possessing a flared shell lip at major fishing grounds in The Bahamas between 2009 and 2017. Depth zones are the same as in Table 1, but not all sites are represented with shell measures. Values for shell length and shell lip thickness are means ± SD. Mature individuals are those with shell lip thickness ≥15 mm (see text).

Survey location	Depth zones	No. measured	Shell length (mm)	Shell lip thickness (mm)	Percentage mature
Berry Islands					
MPA Bank	S	30	188 ± 21	2 ± 1	0
MPA Shelf	S	29	224 ± 29	7 ± 6	10.3
	D	16	241 ± 20	17 ± 7	62.5
East Shelf	S	13	224 ± 34	7 ± 5	15.4
South fishing grounds	S	53	167 ± 25	11 ± 7	56.6
West fishing grounds	S	7	196 ± 26	6 ± 8	14.3
North fishing grounds	S	5	211 ± 16	3 ± 2	0
	D	18	224 ± 21	16 ± 7	44.4
Andros Island					
Bight region	S	6	211 ± 40	9 ± 6	16.7
Grassy Cays	S	30	177 ± 27	15 ± 7	53.3
Exuma Cays					
LSI bank	S	100	190 ± 21	9 ± 7	22.0
LSI shelf	S	12	216 ± 27	17 ± 8	75.0
	D	25	243 ± 27	23 ± 7	84.0
ECLSP bank	S	58	200 ± 22	21 ± 10	69.0
ECLSP shelf	S	94	198 ± 19	29 ± 5	98.9
	D	40	214 ± 20	27 ± 6	100
Bight of Abaco					
More's Island bank	S	80	198 ± 24	9 ± 5	10.0
Sandy Point bank	S	66	187 ± 19	6 ± 4	4.5
Sandy Point bank edge	S	25	226 ± 21	17 ± 6	66.7
Jumentos & Ragged Islands					
Water Cay	S	236	195 ± 21	19 ± 5	86.4
Flamingo Cay	S	120	175 ± 17	22 ± 6	74.2
Jamaica Cay	S	99	180 ± 20	18 ± 8	91.9
Seal Cay	S	11	193 ± 17	28 ± 6	100
Nurse Cay	S	116	188 ± 16	23 ± 6	88.8
Raccoon Cay	S	25	192 ± 12	11 ± 7	60.0
Little Bahama Bank					
West End	S	18	196 ± 21	7 ± 5	11.1
Mantanilla Shoal	S	18	201 ± 15	27 ± 5	100
Mantanilla Reef	S	71	219 ± 18	18 ± 8	38.0
Grand Cays	S	37	204 ± 13	7 ± 3	0
Carter Cays	S	87	194 ± 13	12 ± 4	29.9
Allan's-Pensacola Cay	S	22	222 ± 14	5 ± 2	0
Guana Cay	S	27	196 ± 16	5 ± 4	3.7
Man-O-War Cay	S	16	190 ± 16	9 ± 4	12.5
Pelican Cays	S	32	220 ± 14	15 ± 6	53.1
Eastern Sand Bores	S	161	186 ± 15	20 ± 4	90.2
Western Bahamas					
South Riding Rock	S	59	174 ± 10	11 ± 6	32.2
Andros Island					
Joulter's Cay	S	170	155 ± 19	17 ± 5	66.5
Exuma Cays					
North Exuma Cays	S	167	194 ± 29	20 ± 9	68.9
Cay Sal Bank					
Shallow Bank	S	873	171 ± 14	20 ± 5	85.5
Deep Bank	D	853	176 ± 17	18 ± 64	69.9

During the same period of time from the 1990s to 2011, average LT of flared-lip conch at LSI (i.e., conch age) declined significantly on the shallow shelf ($F = 24.84$, $p < 0.001$), but not on the bank ($F = 2.517$, $p = 0.113$) or on the deep-shelf ($F = 1.493$, $p = 0.224$) although average lip shell thickness of conch on the deep shelf declined from 28 to 23 mm (Figure 7B). Unlike the LSI fishing ground, conch in all three

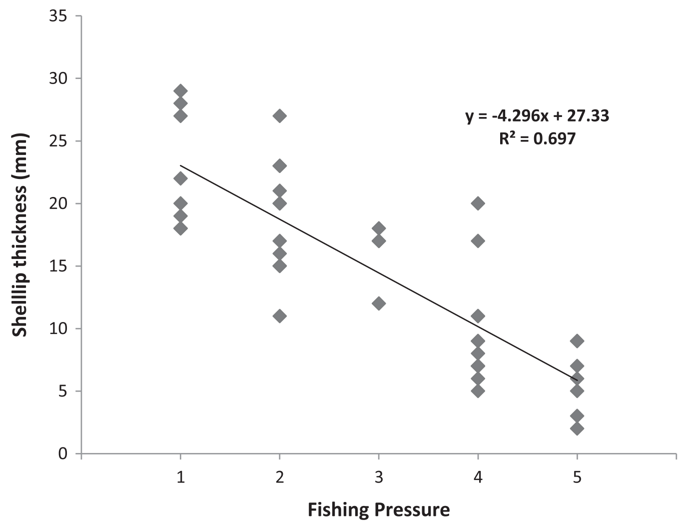

Figure 4. Shell lip thickness observed in queen conch with flared shell lips shown as a function of the fishing pressure index. Data are shown for all 42 sites and depth zones where numbers of conch permitted adequate measures. Values are mean lip thickness for each of the locations.

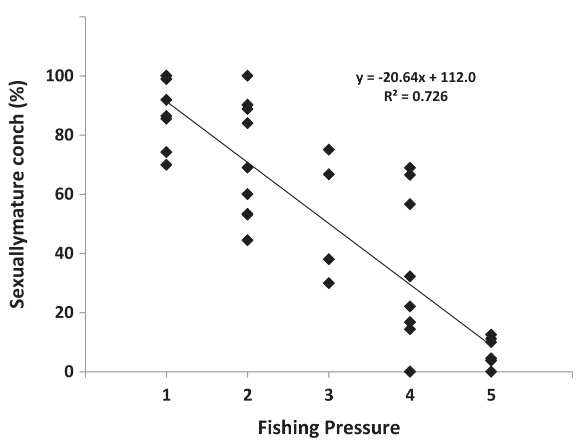

Figure 5. Percentage of queen conch with flared shell lips that are likely to be sexually mature shown as a function of the fishing pressure index. Sexual maturity was considered to occur when a shell lip thickness ≥15 mm was achieved. Data are shown for all 42 sites and depth zones where numbers of conch permitted adequate measures.

protected habitats explored in ECLSP demonstrated increases, rather than decreases, in shell LT (Figure 8B). The increase observed in the bank habitat (from 12 to 21 mm) was particularly significant ($F = 54.24$, $p < 0.0001$) suggesting that the population aged substantially. Differences were smaller in the shelf environment but significant for both the shallow- ($F = 17.44$, $p < 0.001$) and deep-shelf habitats ($F = 4.381$, $p = 0.037$).

More recent surveys allowed an examination of temporal shifts in population structure at three locations, including a five-year extension of observations on the bank at ECLSP (Figure 9). At that site, comparing identical sections of the bank between 2011 and 2016, densities of flared-lip conch continued to decline from 32/ha to just 10/ha. The number of grids where conch were resurveyed ($n = 14$) was not sufficiently high for interpretation with GLM, but the latest survey revealed another 69% decrease in the protected population, for a total loss of population near 90% over the 22-year period of observation. Shell LT on the ECLSP bank continued to increase significantly ($F = 19.90$, $p < 0.0001$) (Figure 9B). As of 2016, the average LT for conch measured in the ECLSP was very high at 29 mm, an increase of 140% since 1994. During the same interval average shell length decreased from 202 to 186 mm; the 8% change was significant ($F = 92.26$, $p < 0.0001$).

Recent comparative surveys at the Berry Islands (2009 and 2016) and the Grassy Cays (2010 and 2016) revealed 74 and 24% declines in densities of flared-lip conch, respectively in identical survey grids (Figure 9A). The best-fit GLM statistical model (negative binomial link) was the full model which included a random factor of grid and the main factors of year and location. The main effects were a negative association with year (71% overall decline) (coefficient = −1.242, $Z = -6.043$, $p < 0.0001$), and a significant positive association with location (Grassy Cays having higher density than the Berry Islands) (coefficient = 2.631, $Z = 6.428$, $p < 0.0001$). There was no significant change in shell LT of flared-lip conch at either the Berry Islands ($F = 0.130$, $p = 0.720$) or the Grassy Cays ($F = 1.20$, $p = 0.274$), with all of the averages between 15 and 16 mm (Figure 9B). However, most of the flared-lip individuals were very small thick-lipped “samba” conch (see Randall, 1964) with

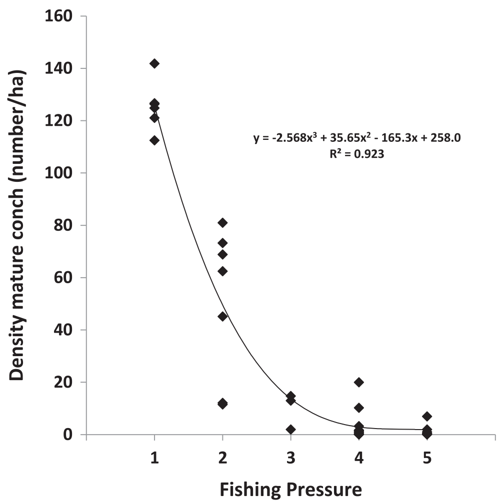

Figure 6. Density of sexually mature queen conch shown as a function of the relative index of fishing pressure. Data are shown for locations <10 m depth where free-diving fishers are most effective. About 34 sites provided sufficient data on shell lip-thickness to evaluate sexual maturity.

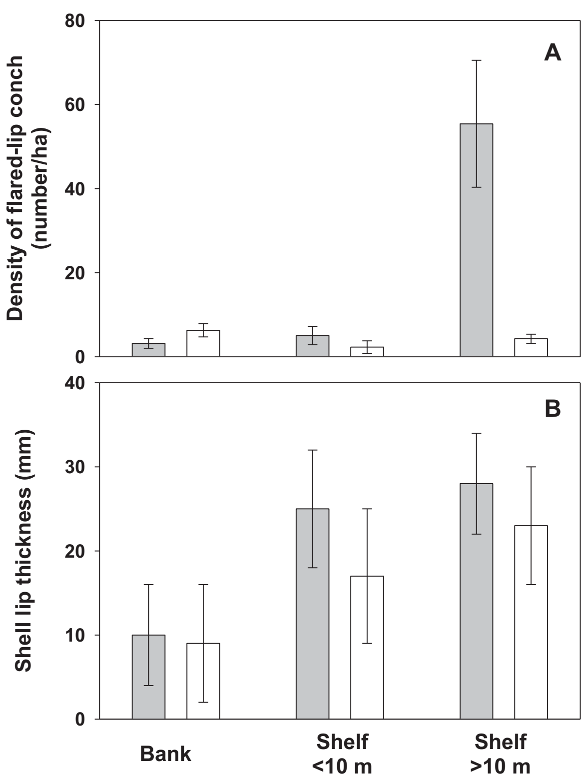

Figure 7. Population structure of queen conch observed near Lee Stocking Island in the central Exuma Cays during two identical surveys conducted in 1991 (grey) and 2011 (open bars). (A) Densities of flared-lip conch (mean ± SE) for three types of habitat: the shallow bank west of the island chain, and two depth intervals on the narrow island shelf east of the islands. (B) Shell lip thickness data (mean ± SD) for the same habitats.

average lengths of 156 mm and 164 mm, at the Grassy Cays and Berry Islands, respectively, in 2016. These small conch are not considered valuable by fishers.

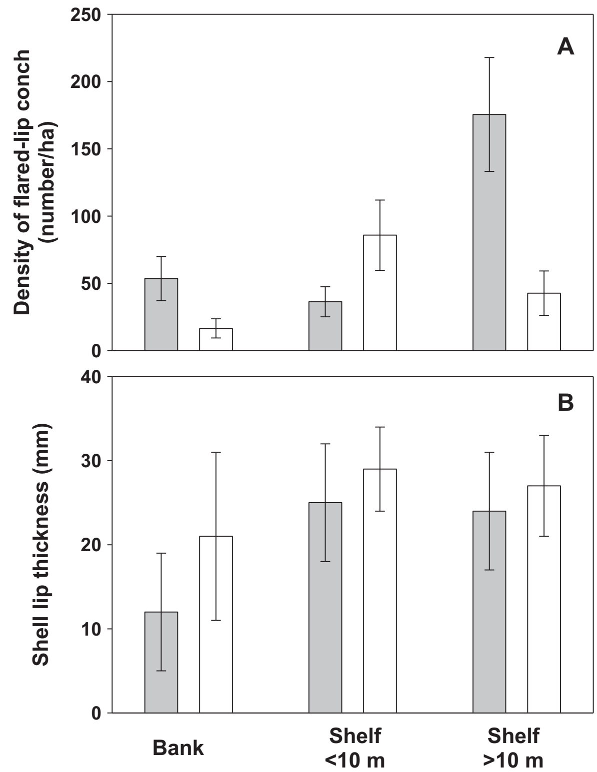

Figure 8. Population structure of queen conch observed in the central sector of the Exuma Cays Land and Sea Park (ECLSP), a no-take fishery reserve in the central Exuma Cays. Two identical surveys were conducted in 1994 (grey) and 2011 (open bars). (A) Densities of flared-lip conch (mean ± SE) for three types of habitat: the shallow bank west of the island chain, and two depth intervals on the narrow island shelf east of the islands. (B) Shell lip thickness data (mean ± SD) for the same habitats.

Current status of Bahamian conch populations

New surveys for queen conch show that densities of legal-to-harvest flared-lip queen conch are well below the minimum threshold for reproductive success (~56 flared-lip conch/ha) (Stoner and Ray-Culp, 2000; Stoner et al., 2012c) except in the most remote areas. Areas with densities near the 100/ha value suggested for sustainable fishing by a panel of experts on queen conch (UNEP, 2012) included Cay Sal Bank and the Jumentos Cays. Cay Sal Bank is a deep, open-ocean site with very little shelter in the Strait of Florida. Only large vessels can visit that location in relatively settled weather. The Jumentos Cays are a long chain of small islands which offer little protection except in light winds, and only one small village (<100 people) lies within a radius of ~80 km from the central Jumentos. Nassau, the primary market for queen conch is ~300 km away. There were also substantial densities of queen conch near the Grassy Cays at the southern end of Andros Island; however, the majority of these conch are the small, thick-shelled "samba" phenotype which have low market value as discussed above. This site is distant from Nassau and a vessel landing conch there would need to travel >100 km over deep, open-water environment. The island shelf habitat on the eastern boundary of the Exuma Cays Land and Sea Park also had densities of flared-lip conch >100/ha in the earliest surveys. Because surveys were conducted near the center of the large no-take fishery preserve, near the warden's office, high densities are expected there. Nevertheless, in 2011, densities of flared-lip conch on the deep shelf had declined to less than 50/ha, and it is clear that even those protected stocks are changing rapidly.

The overall pattern of queen conch density, however, was inversely related to the score systematically assigned to each location for FP. Fewer conch were observed where the primary landing sites and high human populations were located nearby. Also, locations with water depths >10 m had higher conch densities than shallow-water locations. Increasing numbers of older conch associated with increasing depth can result from two factors. First, queen conch settle primarily in shallow waters in The Bahamas (typically <5 m depth) and disperse to greater depths with age (Stoner and Schwarte, 1994; Stoner 2003); however, this migration can take many years and spawning adults are often found in shallow water habitats protected from fishing. A more likely explanation for low numbers of flared-lip conch in depths <10 m is that they are being removed by fishers.

A common effect of fishing mortality on the demographics of long-lived species is that age distribution becomes truncated (Leaman, 1991; Huntsman and Schaff, 1994; Heppell et al., 2005); that is, the older age groups are lost from the population. This was evident in shell LT data for queen conch, the proxy measure for conch age. Locations with high FP were characterized by low average values for LT. In four high pressure locations the average was ≤5 mm; these represent very young conch, well below the threshold for sexual maturity (Stoner et al., 2012b; Boman et al., 2018). Further, the negative impact of FP on queen conch population structure is clearly shown by the negative correlations with both shell LT and the percentage of mature conch among flared-lip individuals.

There was no significant relationship between the densities of subadult conch and FP. This is not surprising because, the subadult classification represents just one year class and is, therefore, highly susceptible to variable recruitment. Further, subadult conch receive at least some relief from FP since this age group is not legal for harvest, and have lower market value. Nevertheless, large juvenile conch are increasingly harvested where flared-lip conch have become scarce and where fisheries enforcement is low (see below).

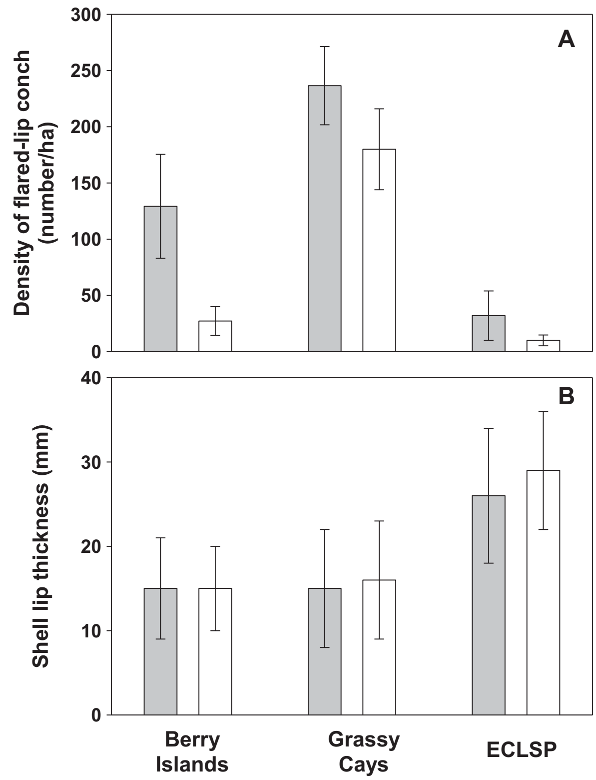

Figure 9. Population structure of queen conch observed in the most recent repeated surveys at two fishing grounds, one on the southern edge of the shallow bank near the Berry Islands (2009 and 2016), and one near the Grassy Cays at the south end of Andros Island (2010 and 2016). Also, repeated surveys (2011 and 2016) were conducted in the central sector of the Exuma Cays Land and Sea Park (ECLSP), a no-take fishery reserve in the central Exuma Cays. Results for the earliest surveys are shown in grey and 2016 surveys are shown with open bars. The two surveys for each site covered identical areas near the center of the populations and, hence, the results for ECLSP in 2011 in Figures 7 and 8 do not match (i.e., this figure represents a smaller survey area). All of the results are for shallow bank areas depth interval <10 m deep. (A) Densities of flared-lip conch (mean ± SE). (B) Shell lip thickness data (mean ± SD).

Long-term changes in conch populations

Substantial decreases in densities of flared-lip queen conch (to 74%) observed in repeated surveys in three fishing grounds indicate that the conch populations are collapsing. In fact, in 2011 and 2016, when the most recent repeat surveys were completed in areas with historically abundant populations of queen conch, only one of the locations had densities of flared-lip queen conch that exceeded the minimum threshold for reproduction discussed earlier. Furthermore, high density of flared-lip conch observed at the Grassy Cays and the remaining low-density population at the Berry Islands site were comprised of low-value “samba” conch. Mating behavior has been observed in these small-form queen conch, but thick shells and small overall body size necessarily result in low fecundity (see Stoner et al., 2012b), and their relative role in reproduction is essentially unknown. Densities of flared-lip conch at LSI were far below the mating threshold in all depth zones in 2011, and declining numbers of subadults in all of the fished areas suggest that recruitment is failing.

One additional comparison is possible. In 1993, the senior author conducted a depth-stratified survey of queen conch at the northwest corner of Cape Eleuthera (Stoner et al., 1998). That survey was repeated in 2014 (Thomas et al., 2015), and there were highly significant decreases in conch densities in all five depth strata. For example, conch densities in the 0-5 m depth stratum declined from 228 flared-lip conch/ha to just 10.6/ha. The average decrease for all of the strata was 88.1%. This indicates another location where the population of queen conch has diminished substantially.

While changes in densities of flared-lip conch in the ECLSP varied somewhat with depth interval, the very large decreases observed on the shallow bank between 1994 and 2011 was highly significant, and a 90% loss in the shallow bank habitat (1994–2016) is remarkable for a marine protected area, noting that the flared-lip class of queen conch normally represents many year classes. Changes in the deep-water environment were lower, but significant, suggesting that the population in the ECLSP is in general decline. In fact, all of the surveys in ECLSP were conducted near the Park headquarters in the well patrolled center of the 44 km long chain of islands encompassing the Park, and poaching cannot explain the decrease in conch numbers. A reasonable explanation for declining numbers and increasing age of the population is failure of recruitment from upstream sources of larvae. Hydrographic studies in Exuma Sound (Stockhausen et al., 2000) and analysis of likely queen conch larval transport (Stoner et al., 1998; Kough et al., in prep) have indicated that recruitment in the Park depends upon reproduction in populations to the southeast. It is clear by the example offered at Lee Stocking Island, that upstream populations have probably diminished to a point where mating and larval production cannot be expected, and the adult conch in ECLSP represent a remnant, senescing population.

Other less quantitative observations on changing queen conch populations are available for some nursery ground locations observed over several decades. In the 1980s biologists from the University of Miami conducted surveys and experiments with juvenile conch in nursery grounds identified at Vigilant Cay and Bird Cay in the southern Berry Islands. In 1980–1981, there were thousands of juvenile queen conch at these two sites, with densities between 12 and 20 individuals/10 m^2 (Iversen et al., 1987). In 2009, spatially comprehensive surveys conducted by Community Conch biologists in and around these two nurseries revealed that the Vigilant Cay nursery had a few hundred individuals (Stoner et al., 2009) and only 21 individuals were found at the Bird Cay nursery ground. While it is known from long-term surveys near Lee Stocking Island that juvenile aggregations are subject to large inter-annual shifts in conch recruitment (Stoner, 2003), nurseries are typically inhabited by three year classes or more at any one time, the near total loss of conch at these sites suggests multi-year recruitment failure or heavy illegal fishing on the nursery grounds.

Other losses in juvenile populations were reported near Lee Stocking Island where aggregations associated with nursery grounds were estimated to have decreased by more than half between surveys conducted in the early 1990s and 2011 (Stoner et al., 2011). Within the Exuma Cays Land and Sea Park, juvenile populations at two locations near the Park headquarters in 2011 were about one-quarter those observed in 1993 (Stoner et al., 2011).

Changes in mollusc populations can be inferred from the piles of shells that accumulate where they are harvested and landed (Meehan, 1982; Kidwell, 1991); such studies include strombid gastropods (Torres and Sullivan-Sealey, 2002; O’Dea et al., 2014). In the case of queen conch, shell middens represent catches spanning at least 500 years based upon carbon dates (Stoner, 1997) and provide valuable insight into the changing age structure of conch harvested by fishers over the long term. Recently harvested conch (representing a two- to three-year history) can be identified by the presence of brown peristracum on the outside of the shell, while older harvest are identified by an absence of peristracum, weathering of the shells to a white or black color, and increasingly broken shell lips and spires. Two studies of shell middens conducted near Cape Eleuthera in the central Bahamas show that illegal under-age conch are being harvested in increasing numbers. Clark et al. (2005) reported that >62% of conch in middens had no flared shell lip. Subsequently for the same general area Cash (2013) explored 12 midden sites and found that shells in "fresh" harvests were "primarily juveniles" while old middens had "few to no juveniles". Among conch with flared shell lips the average thickness of "fresh" catches was <6 mm, while old middens had average shell thickness values near 12 mm. This means that a very large proportion of the conch landed in recent years at Cape Eleuthera were not sexually mature.

Also, since 2013, Community Conch biologists have partnered with the Bahamas National Trust and the Bahamas Reef Environment Educational Foundation to use conch shell middens as a teaching resource for school-aged children in The Bahamas, while providing data on the abundance of illegal and immature conch in recent harvests. Almost 2000 shells were measured from recent shell middens over six island groups ranging from Grand Bahama and the Abaco Islands in the north to Crooked and Acklins Islands in the south. Preliminary analysis shows that 20.6% of recently harvested queen conch over all six sites were younger than the legal standard (with a flared shell lip). Further, ~64% of the conch had shell LT values less than the 15 mm breakpoint for 50% likelihood of sexual maturity (C. Booker, Community Conch, unpubl. data). This contrasts strongly with measurements of "old" shell landings which are comprised of larger and older flared-lip individuals, comporting with the long-term harvest regulations. From these observations, it is clear that young conch are being harvested in recent years, most likely because of dwindling numbers and decreasing age structure in the local populations and providing further evidence that the stocks are severely overfished.

Likely mechanisms for the population declines observed

Over-exploitation is the most likely mechanism for declining populations of queen conch in The Bahamas, both in terms of spawner densities and average age. Losses or poor health in queen conch attributed to habitat destruction and pollution in other locations (Glazer and Quintero, 1998; Spade et al., 2010; Appeldoorn et al., 2011; Titley-O'Neal et al., 2011) is not a large problem on the scale of national fisheries in The Bahamas. Pollutants are probably a localized problem in the heavily populated centers such as Nassau and Freeport where tourism and deeply dredged harbors have greatest impact. The large banks where conch were historically abundant have relatively high water quality and unaltered benthic habitat (authors' personal observations). Seagrass meadows and algal beds that serve as conch habitat can be adversely affected by hurricane events, but significant storms in The Bahamas were rare between 1992 (Hurricane Andrew effecting the western Bahamas primarily) and 2017 when Hurricane Irma had widespread impacts on the shores of the southern and central Bahamas. Hurricane damage to conch habitat in The Bahamas has not been evaluated.

There are two important impacts of overfishing on queen conch biology that can be discussed with the results presented in this study:

a. Queen conch reproductive behavior is highly subject to density dependence (Allee effect) observed empirically in The Bahamas (Stoner and Ray-Culp, 2000; Stoner et al., 2012c). That is, when densities of adults fall below a threshold near 56/ha, queen conch have a low probability of finding appropriate mates and egg-laying is diminished to near zero. Furthermore, Appeldoorn (1988b) speculated that oogenesis in queen conch might be stimulated by mating, compounding the role of density dependence. This would help to explain the observed sigmoid increase in egg-laying associated with conch density observed in The Bahamas (Stoner and Ray-Culp, 2000). Most of the Bahamian fishing grounds now have densities of adult queen conch below the mating threshold, and egg and larval production may have diminished since the first surveys for veliger larvae in the 1990s (Stoner and Smith, 1998; Stoner et al., 1998). Similar to conclusions drawn here regarding queen conch demographics, Hobday et al. (2001) concluded that the demise of another large motile gastropod, the white abalone (*Haliotis sorenseni*) on the Pacific coast of Mexico and California, was directly related to loss of densities sufficient for reproduction. That species was listed as an endangered species in 2001 and the once valuable fishery is completely closed at this time.
b. Legal harvest of queen conch in The Bahamas is limited to individuals with a "well-formed shell lip". It is now well established that the species does not reach sexual maturity until at least 6–12 months past the time when the flare of shell lip is developed (Stoner et al., 2012b; Boman et al., 2018). Histological studies show that males reach maturation earlier than females and that the 50%

probabilities for maturation vary somewhat over the geographic range of queen conch. Authors of both studies have proposed that allowing harvest only after a 15 mm shell LT has formed would provide for at least one mating season to occur before legal harvest. Survey data provided in this study show that the distribution of shell LT for a conch population is inversely related to FP on that population, and that the average LT of conch in many of the populations surveyed was well below 15 mm. Prominent exceptions to this were populations in very remote or difficult to access locations. Furthermore, studies of shell middens show that landings of illegal conch (individuals without a flared shell lip) are increasing.

The spatial and temporal patterns of reduced queen conch densities and changing age structures over The Bahamian archipelago indicates that serial depletion of the population is occurring. That is, there is a progressive over-exploitation of the resource in space and time which will likely lead to depletion throughout the region. A similar pattern of population decline was observed for white abalone before the species was listed under the Endangered Species Act (Hobday et al., 2001). Similar to queen conch, the white abalone is a large, slow-growing gastropod that matures at four to six years. While abalone do not copulate like queen conch their gametes have a very short span in the water column and the spawning males and females must be within a few meters of one another for fertilization to occur (Levitan, 1991). Reproduction in the two species are similarly subject to Allee effect.

Hobday et al. (2001) concluded that the loss of white abalone in California and Mexico occurred in large part because of failure to recognize serial depletion. Similarly, this synthesis of survey results shows that serial depletion is occurring in queen conch. By necessity, fishers are diving deeper and traveling farther for their catches while landings and export data show rapidly declining abundance of queen conch. For example, fishers from south Andros Island are now traveling to the Cay Sal Bank (150–200 km) to harvest from one of the last well-functioning conch grounds.

The overall conclusion from this study is that the majority of queen conch populations in The Bahamas, with the exception of the one large closed area (Exuma Cays Land and Sea Park) and two of the most remote bank fishing grounds, are too sparsely distributed and too young to reproduce effectively. Also, the numbers of conch capable of mating and egg-laying are declining with time. Even the population within the closed area is declining in terms of conch density and a rapidly aging structure. The primary populations of queen conch in The Bahamas are near collapse, and there is urgent need for additional protection and changes in fishery regulations to provide any chance of a sustainable future fishery.

Fisheries management recommendations

The primary requirements for rebuilding a rapidly declining queen conch stock in The Bahamas are to reduce fishing mortality and to rebuild densities of spawning stocks. In 2012, a panel of conch experts met in Miami to provide fishery management recommendations for queen conch (UNEP, 2012). The recommendations made here are compatible with those in the UNEP report, and are discussed briefly in the context of the conch fishery challenge in The Bahamas and in order of likely applicability to that nation:

a. Increase the number of locations truly closed to queen conch fishing and expand the total area of closures in locations known to serve as conch nurseries and spawning grounds. An extensive array of closed areas has been delineated in The Bahamas, but only the Exuma Cays Land and Sea Park has fishery enforcement in place. As always, a network of closed areas should consider the adult, juvenile, and larval ecology of the target species, and take advantage of likely connection pathways and avenues of replenishment. Recent genetic studies indicate that conch populations in The Bahamas are relatively independent from the surrounding nations (Truelove et al., 2017), and biophysical models designed to explore likely flow of conch and other larvae over the archipelago are currently in development (Kough, unpubl. data). Closed areas will allow at least some populations to have adult densities near the 100/ha recommended in the UNEP report for successful queen conch reproduction and a relatively natural age structure.
b. Establish a closed season for queen conch fishing in harmony with the rest of the Caribbean region. Unlike most of the region, The Bahamas has no closed season for queen conch. A summer closed season would release conch from harvest during at least a few months in the critical reproductive period, and might allow first year spawners to mate and lay eggs before they become vulnerable

to FP. The optimal period would run from 1 June through the end of September (see Stoner et al., 1992 and Boman et al., 2018).

c. Establish a "size" limit for legal harvest of queen conch. This should be based upon shell LT (not shell length), and the suggestion for 15 mm was advocated earlier (Stoner et al., 2012b; Boman et al., 2018). This is not a new concept. Foley and Takahashi (2017) proposed a 16 mm LT limit in Belize, and other nations have imposed fishery requirements based upon LT for queen conch harvest ranging from 5 to 9.5 mm (i.e., Antigua and Barbuda, Cuba, St. Barthelemy, and federal waters of Puerto Rico and the US Virgin Islands) (Boman et al., 2018). This will require that conch are landed in the shell or another proxy for age or maturity will need to be formulated. Mueller and Stoner (2013) explored the possibility of using metrics associated with the chitinous opercula which could remain attached to conch meats; however, the relationship to age appears to vary strongly with location (Stoner, unpubl. data; R. Appeldoorn, University of Puerto Rico, unpubl. data). A harvest strategy employing presence and absence of the primary sexual structures including verge and egg groove might also be possible (R. Appeldoorn, pers. comm.). In this case, the meats would need to be landed with skin intact. The difficulty associated with a size or maturity requirement in The Bahamas is that the fishery is diffuse over the large archipelago, and enforcing such regulations is already difficult as observed in the numbers of illegal juvenile conch in shell middens. It should be noted, however, that size limits did not prevent white abalone from reaching endangered status (Hobday et al., 2001).

   In lieu of a new regulation on shell LT, a requirement to land conch in the shell might help to reduce illegal harvest of young conch.

d. Limited entry and licensing. Many fisheries management plans around the world limit the number of fishers who are licensed to harvest for commercial purposes. A well designed plan for The Bahamas would reduce the total fishing mortality of queen conch.

e. End the use compressed-air diving systems by conch fishers. Given that queen conch are relatively uncommon at depths >30 m and that most reproductive conch now exist deeper than 10 m, it is important to protect the reproductive stock in the deeper parts of the distribution. That is, conch fishing should be limited to free-diving fishers. Ending compressor use is difficult to enforce and may be considered unacceptable politically.

f. End export of queen conch from The Bahamas. Currently, export creates an important market for queen conch fishers but the price to fishers is low, compared with profits to middlemen. Over time, export has ranged from 33 to 50% of landings, and impact on the stock may be large. A ban on export would reduce fishing mortality for the species. Furthermore, given the cultural significance of queen conch in The Bahamas, perhaps greater than any other Caribbean nation, it seems only logical to reserve the dwindling conch stock for the domestic market including that for the enormous demand created by millions of visitors to The Bahamas each year.

   In lieu of ending export, a substantial tax could be imposed on exported conch products, which could be used to provide sorely needed financial support for fisheries management and enforcement. Such taxes are used in other nations (e.g., Jamaica) to help manage conch stocks.

g. Numerous Caribbean nations use a quota-based system to manage their queen conch resources. These include Jamaica (Pedro Bank), Belize, and Honduras. Naturally, any quota-based system requires a certain amount of routine population monitoring and modeling to determine sensible quotas as well as systematic collection of landings data. This is a particularly large challenge for a small nation with a very large and diffuse network of fishing grounds, coupled with very limited budget for fishery management. The fishery operates over thousands of square miles and landings data have been notoriously difficult to assemble in The Bahamas. Clearly a much larger budget would be needed for a quota system even without extensive survey-based modeling.

h. Since earliest efforts in the 1970s and 1980s to culture and release queen conch (Berg, 1976; Appeldoorn and Ballantine, 1983; Laughlin and Weil, 1983) there has been interest in restocking conch populations with hatchery-reared juveniles. Natural mortality rates in the field, however, are very high (Stoner and Glazer, 1998) and, a major hatchery and release effort made by the State of Florida ended more than a decade ago. Interest in hatchery releases continues (Shawl et al., 2007), but to date no successes in field survival have been recorded. Therefore, it seems unwise to rely upon unproven potential for hatchery-based restocking of queen conch except in cases where stocks have been lost entirely. Despite great challenges diligent fishery management for natural stocks of queen conch is the better choice.

i. Barring successful application of at least several of the above mentioned fishery management measures and if conch populations continue to decline in The Bahamas, it may be necessary to close the queen conch fishery entirely for a period of at least five years. The goal would be to allow at least one complete generation of conch to reach maturity with no fishing mortality whatsoever.

All of these fishery management recommendations require compliance and enforcement to achieve success in conserving queen conch. Again, because of the far-flung nature of the conch fishery in The Bahamas, enforcing fishery regulations presents a large challenge and increased budget seems critical for success. The Bahamas National Trust and the Bahamas Defense Force, as well as the Department of Marine Resources, are already involved in monitoring and enforcement of fishery regulations, but increased numbers of fishery officers and patrol vessels for these activities will be required over the geographic range of fishing activity and closed areas.

Conclusions

Visual surveys for queen conch in The Bahamas spanning more than 40 fishing grounds show that densities of adults decreased in direct proportion to increases in FP indexed on the basis of distance from major markets and water depth. Fishing did not appear to have an effect on average shell length in a population, but average age in a population (determined on the basis of shell LT) had a strong negative relationship with FP. As a result of age truncation the proportion of mature conch in a population declined in an inverse linear relationship with FP, and the converse was observed for immature individuals, with FP explaining more than 70% of the variation in each function. At all but the most remote and difficult to access locations, densities of sexually mature conch are now well below the well-established levels (56–100 adults/ha) necessary for successful reproduction, and widespread recruitment failure observed over the archipelago is most likely related to the negative Allee effect of low population density on mate-finding behavior. Reduced density and truncation of age structure are clear signs of overharvest.

Repeated surveys in three fishing grounds revealed that densities of flared-lip conch (age-4+ year classes) declined in all of those locations and that the populations have become progressively younger. The vast majority of these conch are below the age required for sexual maturity. That is, very few conch had shell LT values >15 mm. These results, coupled with the observations described above, show that queen conch populations are experiencing serial depletion over the Bahamian archipelago.

The Exuma Cays Land and Sea Park is the largest no-take fishery reserve (364 km^2) in The Bahamas. Despite well-enforced protection for queen conch in ECLSP, three repeated surveys spanning 22 years in the center of the Park show that the conch population, as in unprotected locations, is declining rapidly (by as much as 90% in the shallow bank habitat). Notably the observed changes in age structure are completely opposite those observed in unprotected locations; the conch population in ECLSP has aged significantly, with the remaining conch having average shell lip thicknesses near 30 mm. In 2016, very few individuals had lip thicknesses <10mm, and the Park population is moving toward reproductive senescence. It is clear from the results reported here that the ECLSP is not large enough to hold a self-sustaining queen conch population and that a network of protected areas will be required to sustain a long-term population of conch in The Bahamas.

All of the research on population structure and reproductive biology of queen conch conducted over the last decade indicates that most populations of queen conch in The Bahamas are currently at or below critical densities and age-structures for successful mating and reproduction, and we conclude that overfishing is the primary cause for the serial depletion observed. Also, despite sampling limitations, landings and export data suggest a downward pathway for the fishery, and we conclude that a viable fishery for queen conch might last only another 10 or 15 years unless significant measures are taken to reduce fishing mortality.

While new fishery management options can be guided by modelling exercises there are obvious actions that can help to preserve a natural stock of queen conch. These include a greatly expanded network of areas closed to conch fishing, a season closed to conch fishing, an end to conch export, consideration of a shell-lip-thickness criterion for harvest, and greatly expanded enforcement of fishing regulations. Unfortunately, any management measures designed to reduce fishing mortality will impact the near-term ability of conch fishers to make a living wage, and it will be important to assist displaced fishers in finding other sources of income. This is not an easily solved problem but, as in all overfishing cases, survival of a long-term queen conch fishing industry will hinge upon management with a long view for sustainability.

Acknowledgments

This project was funded primarily by the non-profit organizations Community Conch between 2009 and 2015 and the John G. Shedd Aquarium between 2014 and 2017. Small boat support and funding for some of the surveys was provided by the Bahamas Department of Marine Resources, with constant encouragement from Michael Braynen and Lester Gittens. The Andros Island survey was funded in part by The Nature Conservancy (Bahamas), and research in the Exuma Cays had generous logistical support from the Bahamas National Trust. Surveys conducted in the 1990s were funded by NOAA's National Undersea Research Program to the Caribbean Marine Research Center. Catherine Booker was a critical participant in all of the Community Conch surveys, assisting with logistics, coordinating volunteers, and managing the many databases. Mark van den Rydt also participated in most of the surveys, serving as boat captain for the vessel DeerDancer, operating and repairing small boats, diving, and assisting with vessel instrumentation and navigation databases. The field work for this project would not have been possible without several dozen volunteers from The Bahamas, United States and Canada, who participated in logistical support, and boating and diving operations.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Aldana-Aranda, D., H. A. Oxenford, C. Bissada, M. Enriquez-Díaz, T. Brulé, G. A. Delgado, I. Martinez-Morales, and L. Frenkiel. Reproductive patterns of queen conch, *Strombus gigas* (Mollusca, Gastropoda), across the wider Caribbean region. *Bull. Mar. Sci.*, **90:** 283–298 (2014).

Appeldoorn, R. S. Age determination, growth, mortality and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fish. Res.*, **6:** 363–378 (1988a).

Appeldoorn, R. S. Fishing pressure and reproductive potential in strombid conchs: Is there a critical stock density for reproduction? *Mem. Soc. Nat. LaSalle*, **48:** 275–288 (1988b).

Appeldoorn, R. S. Queen conch management and research: Status, needs and priorities, pp. 301–319. **In:** *Queen Conch Biology, Fisheries and Mariculture* (Appledoorn, R. S., and B. Rodriquez, Eds.) Caracas: Fundacion Científica Los Roques (1994).

Appeldoorn, R. S., and D. L. Ballantine. Field release of cultured queen conch in Puerto Rico: Implications for stock restoration. *Proc. Gulf. Carib. Fish. Inst.*, **35:** 89–98 (1983).

Appeldoorn, R. S., E. R. Castro-Gonzalez, R. A. Glazer, and M. Prada. Applying EBM to queen conch fisheries in the Caribbean, pp. 177–186. **In:** *Towards Marine Ecosystem-Based Management in the Wider Caribbean* (Fanning, L., R. Mahon, and P. McConney, Eds.) Amsterdam: Amsterdam Univ. Press (2011).

Barile, P. J., A. W. Stoner, and C. M. Young. Phototaxis and vertical migration of the queen conch (*Strombus gigas* Linne) veliger larvae. *J. Exp. Mar. Biol. Ecol.*, **183:** 147–162 (1994).

Bates, D., M. Maechler, B. Bolker, and S. Walker. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7. Available from http://CRAN.R-project.org/package=lme4 (2014).

Berg, Jr., C. J. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. *Mar. Biol.*, **34:** 191–199 (1976).

Boman, E. M., M. de Graaf, L. A. J. Nagelkerke, A. W. Stoner, C. E. Bissada, O. H. Avila-Poveda, E. R. Baqueiro-Cardanas, and A. C. Smaal. Variability in size at maturity and reproductive season of queen conch, *Lobatus gigas* (Gastropoda: Strombidae) in the wider Caribbean region. *Fish. Res.*, **201:** 18–25 (2018).

Carew, J. L., and J. E. Mylroie. Geology of the Bahamas. Chap. 3A, pp. 98–139 **In:** *Geology and Hydrogeology of Carbonate Islands. Developments in Sedimentology 54* (Vacher, H. L., and T. Quinn, Eds.). Amsterdam: Elsevier (1997).

Cash, E. *Assessment of queen conch, Lobatus gigas, density, middens and permitting requirements, in south Eleuthera, Bahamas*. M.S. Thesis, Auburn University, Auburn, AL, pp. 68 (2013).

Clark, S. A., A. J. Danylchuk, and B. T. Freeman. The harvest of juvenile queen conch (*Strombus gigas*) off Cape Eleuthera, Bahamas: Implications for the effectiveness of a marine reserve. *Proc. Gulf Carib. Fish. Inst.*, **56:** 705–714 (2005).

Davis, M. *The effects of natural foods, temperature and salinity on the length of larval life for the tropical gastropod Strombus gigas*. Ph.D. Dissertation, Florida Institute of Technology, Melbourne, FL, pp. 136 (1998).

Davis, M. *Species profile: Queen conch, Strombus gigas*. Southern Regional Aquaculture Center, Publ. no. 7203, pp. 12 (2005).

Davis, M., B. A. Mitchell, and J. L. Brown. Breeding behavior of the queen conch *Strombus gigas* Linne held in a natural enclosed habitat. *J. Shellfish Res.*, **4:** 17–21 (1984).

Foley, J. R., and M. Takahashi. Shell lip thickness is the most reliable proxy to sexual maturity in queen conch (*Lobatus gigas*) of Port Honduras marine reserve, Belize; informing management to reduce the risk of growth overfishing. *Front. Mar. Sci.*, **4:** 179 (2017).

García-Sais, J. R., J. Sabater-Clavell, R. Esteves, and M. Carlo. Fishery independent survey of commercially exploited fish and shellfish populations from mesophotic reefs within the Puerto Rican EEZ. Final Report to the Caribbean Fisheries Management Council, San Juan, Puerto Rico (2012).

Gittens, L. G., and M. T. Braynen. *Bahamas national report -CFMC/OSPESCA/WECAFC/CRFM working group on* *queen conch*. Report to the Caribbean Fisheries Management Council, pp. 4 (2012).

Glazer, R., and I. Quintero. Observations on the sensitivity of queen conch to water quality: implications for coastal development. *Proc. Gulf Carib. Fish. Inst.*, **50:** 78–93 (1998).

Heppell, S. S., S. A. Heppell, A. J. Read, and L. B. Crowder. Effects of fishing on long-lived marine organisms, pp. 211–231. **In:** *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity* (Norse E. A., and L. B. Crowder, Eds.). Washington: Island Press (2005).

Hobday, A. J., M. J. Tegner, and P. L. Haaker. Over-exploitation of a broadcast spawning marine invertebrate: Decline of the white abalone. *Rev. Fish Biol. Fish.*, **10:** 493–514 (2001).

Huntsman, G. R., and W. E. Schaff. Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby. *N. Amer. J. Fish. Manage.*, **14:** 41–52 (1994).

Iversen, E. S., E. S. Rutherford, S. P. Bannerot, and D. E. Jory. Biological data on Berry Islands (Bahamas) queen conchs, *Strombus gigas*, with mariculture and fisheries management implications. *Fish. Bull.*, **85**: 299–310 (1987).

Kidwell, S. M. The stratigraphy of shell concentration, pp. 211–290. **In:** *Taphonomy: Releasing the Data Locked in the Fossil Record* (Allison, P. A., and D.E.G. Briggs, Eds.) New York: Plenum (1991).

Kough, A. S., H. Cronin, R. S. Skubel, C. A. Belak, and A. W. Stoner. The efficacy of an established marine protected area at sustaining a queen conch *Lobatus gigas* population during three decades of monitoring. *Mar. Ecol. Prog. Ser.*, **573:** 177–189 (2017).

Laughlin, R. A., and E. Weil. Queen conch mariculture and restoration in the Archipielago de Los Roques: Preliminary results. *Proc. Gulf Carib. Fish. Inst.*, **35**: 64–72 (1983).

Leaman, B. M. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environ. Biol. Fish.*, **30:** 253–271 (1991).

Levitan, D. R. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.*, **181:** 261–268 (1991).

Meehan, B. *Shell Bed to Shell Midden*. Melbourne, Australia: Australian Institute of Aboriginal Studies, Globe Press, pp. 189 (1982).

Mueller, K. M., and A. W. Stoner. Proxy measures for queen conch (*Strombus gigas*, Linné 1758) age and maturity: Relationships between shell lip thickness and operculum dimensions. *J. Shellfish Res.*, **32:** 739–744 (2013).

O'Dea, A., M. L. Shaffer, D. R. Doughty, T. A. Wake, and F. A. Rodriguez. Evidence of size-selective evolution in the fighting conch from prehistoric subsistence harvesting. *Proc. Biol. Sci.*, **281(**1782**):** 20140159 (2014).

Randall, J. E. Contributions to the biology of the queen conch, Strombus gigas. *Bull. Mar. Sci.*, **14:** 246–295 (1964).

Shawl, A., M. Prada, E. Casro, E. Taylor, and M. Davis. Queen conch ranching and educational outreach as part of the Seaflower Biosphere Reserve, Colombia. *Proc. Gulf. Carib. Fish. Inst.*, **59:** 79–83 (2007).

Smith, G. B., and M. van Nierop. *Distribution, abundance and potential yield of the shallow-water fishery resources of the Little and Great Bahama Banks*. Rome: Final report to Food and Agriculture Organization of the United Nations (1984).

Spade, D. J., R. J. Griffitt, L. Liu, N. J. Brown-Peterson, K. J. Kroll, A. Feswick, R. A. Glazer, D. S. Barber, and N. D. Denslow. Queen conch (*Strombus gigas*) testis regresses during the reproductive season at nearshore sites in the Florida Keys. *Plos One.*, **5(9):** e12737 (2010).

Stockhausen, W. T., R. N. Lipcius, and B. M. Hickey. Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. *Bull. Mar. Sci.*, **66:** 957–990 (2000).

Stoner, A. W. Shell middens as indicators of the long-term distributional pattern in *Strombus gigas*, a heavily exploited marine gastropod. *Bull. Mar. Sci.*, **61:** 559–570 (1997).

Stoner, A. W. What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. *Mar. Ecol. Prog. Ser.*, **257:** 275–289 (2003).

Stoner, A., M. Davis, and C. Booker. *Queen conch stock assessment – Proposed MPA and fishing grounds Berry Islands, Bahamas*, p. 49. Technical report to the Department of Marine Resources, Government of The Bahamas. Available from www.communityconch.org (2009)

Stoner, A., M. Davis, and C. Booker. *Surveys of queen conch populations and reproductive biology at Lee Stocking Island and the Exuma Cays Land and Sea Park, The Bahamas*, pp. 28. Technical report to the Department of Marine Resources, Government of The Bahamas. Available from www.community conch.org (2011).

Stoner, A. W., M. H. Davis, and C. J. Booker. Abundance and population structure of queen conch inside and outside a marine protected area: Repeat surveys show significant declines. *Mar. Ecol. Prog. Ser.*, **460:** 101–114 (2012a).

Stoner, A. W., M. H. Davis, and C. J. Booker. Negative consequences of Allee effect are compounded by fishing pressure: comparison of queen conch reproduction in fishing grounds and a marine protected area. *Bull. Mar. Sci.*, **88:** 89–104 (2012c).

Stoner, A. W., and R. A. Glazer. Variation in natural mortality: Implications for queen conch stock enhancement. *Bull. Mar. Sci.*, **62:** 427–442 (1998).

Stoner, A. W., N. Mehta, and M. Ray-Culp. Mesoscale distribution patterns of queen conch (*Strombus gigas* Linne) in Exuma Sound, Bahamas: links in recruitment from larvae to fishery yields. *J. Shellfish Res.*, **17:** 955–969 (1998).

Stoner, A. W., K. W. Mueller, N. J. Brown-Peterson, M. H. Davis, and C. J. Booker. Maturation and age in queen conch (*Strombus gigas*): Urgent need for changes in harvest criteria. *Fish. Res.*, **131:** 76–84 (2012b).

Stoner, A. W., and M. Ray. Queen conch (*Strombus gigas*) in fished and unfished locations of the Bahamas: Effects of a marine fishery reserve on adults, juveniles, and larval production. *Fish. Bull.*, **94:** 551–565 (1996).

Stoner, A. W., and M. Ray-Culp. Evidence for Allee effects in an over-harvested marine gastropod: Density-dependent mating and egg production. *Mar. Ecol. Prog. Ser.*, **202:** 297–302 (2000).

Stoner, A. W., and V. J. Sandt. Population structure, seasonal movements and feeding of queen conch *Strombus gigas*, in deep-water habitats of the Bahamas. *Bull. Mar. Sci.*, **51:** 87–300 (1992).

Stoner, A. W., V. J. Sandt, and I. F. Boidron-Metairon. Seasonality in reproductive activity and larval abundance of queen conch *Strombus gigas*. *Fish. Bull.*, **90**: 161–170 (1992).

Stoner, A. W., and K. C. Schwarte. Queen conch, *Strombus gigas*, reproductive stocks in the central Bahamas: Distribution and probable sources. *Fish. Bull.*, **92:** 171–179 (1994).

Stoner, A. W., and N. P. Smith. Across-shelf transport of gastropod larvae in the central Bahamas: Rapid responses to local wind conditions. *J. Plankton Res.*, **20:** 1–16 (1998).

Stoner, A. W, and J. M. Waite. Trophic biology of *Strombus gigas* in nursery habitats: diets and primary food sources in seagrass meadows. *J. Moll. Stud.*, **57:** 451–460 (1991).

Theile, S. *Queen conch management in the Caribbean*. Technical Report to the CITES Secretariat A-2000/01. TRAFFIC, Europe, pp. 91. (2001).

Theile, S. Status of the queen conch *Strombus gigas* stocks: Management and trade in the Caribbean: A CITES review. *Proc. Gulf. Carib. Fish. Inst.*, **56:** 675–694 (2005).

Thomas, C., S. Auscavitch, A. Brooks, and A. Stoner. Assessing essential queen conch habitat in Eleuthera: Population declines suggest the urgent need for changes in management. *Proc. Gulf. Carib. Fish. Inst.*, **67:** 344–347 (2015).

Titley-O'Neal, C. P., B. A. McDonald, E. Pelletier, R. Saint-Louis, and O. S. Phillip. The relationship between imposex and tributyltin (TBT) concentration in *Strombus gigas* from the British Virgin Islands. *Bull. Mar. Sci.*, **87:** 421–435 (2011).

Torres, R. E., and K. M. Sullivan-Sealey. Shell midden surveys as source of information about fished queen conch (*Strombus gigas*) populations: A case study in Parque Nacional del Este, Dominican Republic. *Proc. Gulf Carib. Fish. Inst.*, **53:** 143–153 (2002).

Truelove, N., S. J. Box, C. J. Aiken, A. Blythe-Mallett, E. M. Boman, C. J. Booker, T. T. Byfield, C. E. Cox, M. H. Davis, G. A. Delgado, B. A. Glazer, S. M. Griffiths, K. Kitson-Walters, A. S. Kough, R. Pérez-Enríquez, R. F. Preziosi, M. E. Roy, I. Segura-García, M. K. Webber, and A. W. Stoner. Isolation by distance and spatial genetic structure in an overharvested international fishery. *Divers. Distrib.*, **2017:** 1–9 (2017).

UNEP. Report of the Queen Conch Expert Workshop. May 22–24, Miami, FL, USA, pp. 16. (Accessed January 12, 2018) Available from: www.cep.unep.org/content/about-cep/spaw/additional-output-on-the- clme-project/queen-conch-expert-workshop.pdf (2012).