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Maturation and age in queen conch (*Strombus gigas*): Urgent need for changes in harvest criteria

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ABSTRACT

The queen conch (*Strombus gigas*) is a large economically important gastropod that has been severely depleted throughout much of the Caribbean region. The species has determinate growth and reaches maximum shell length before sexual maturation; thereafter the shell grows only in thickness. In this study, queen conch were collected in the Exuma Cays, Bahamas, to evaluate maturity with respect to shell length (SL) (170–255 mm) and shell lip thickness (LT) (2–42 mm). Soft tissue weight and gonad weight increased with SL, but these same variables, along with the gonadosomatic index (gonad weight/soft tissue weight), all had dome-shaped distributions with LT and decreased slightly with LT > 22 mm. This indicates some loss of fecundity with age; however, no loss of reproductive capability was evident in histological data. Gonad maturity lagged substantially behind first formation of the shell lip. Minimum LT for reproductive maturity was 12 mm for females and 9 mm for males, and 50% maturity for the population was achieved at 26 mm LT for females and 24 mm LT for males, higher than previous estimates. A review of fishing regulations indicates that immature queen conch are being harvested legally in most Caribbean nations, providing at least a partial explanation for widespread depletion. While relationships between shell lip thickness, age, and maturity vary geographically, sustainable management of queen conch will require a minimum shell lip thickness for harvest no less than 15 mm, along with other urgently needed management measures.

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1. Introduction

Sustainable harvest of any exploited species depends upon conserving reproductive stocks. While marine protected areas and harvest quotas are designed to provide for desirable numbers and densities of adults, most fisheries management plans include requirements for minimum size or age at harvest. The importance of large and sexually mature individuals in spawning stocks is evident in studies involving marine fishes (e.g., Berkeley et al., 2004; Froese, 2004; Heupel et al., 2010) and invertebrates (e.g., Perry et al., 1999; Rogers-Bennett et al., 2004; Gorman et al., 2011; Linnane et al., 2011), but regulations for individual species tend to vary among nations. Sometimes the differences are sound, based upon objective biological information, such as differences in age or size at maturity and population modeling. In other cases, harvest-related decisions are based upon best guesses.

Gastropods present certain challenges with respect to criteria for determining sexual maturity. This is because growth is often determinate in gastropods, whereby growth in shell length or weight ends at a time near the onset of sexual maturity (Vermeij, 1980), but size at maturity can be highly variable. Consequently, basic dimensions such as size and weight are not reliable indicators of maturity. Gonadosomatic indices of various forms have been used to determine reproductive maturity and seasonality for a wide range of economically significant gastropods (e.g., Najmudeen, 2007; Cledón et al., 2008; Vasconcelos et al., 2008), but these cannot be determined with living animals. Shell thickness can sometimes be used as an index of sexual maturity because the shell continues to thicken after growth in length or height ends and maturity begins (Appeldoorn, 1988a; Vermeij and Signor, 1992), although various ecological factors such as habitat, food, and presence of predators can also influence shell morphology (e.g., Kemp and Bertness, 1984; Trussell, 2000; Roy, 2002).

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The queen conch (*Strombus gigas*) is a large gastropod (to 30 cm shell length) with high economic and cultural importance, making it iconic throughout most of the Caribbean region (Randall, 1964; Berg and Olsen, 1989). Despite its importance, the queen conch is a good example of a species for which harvest regulations are based upon limited biological information, and those regulations often vary over short distances because of national sovereignties within the region. There is general agreement, however, that no individual should be harvested before it has had the opportunity to reproduce during at least one season. Consequently, most of the Caribbean nations have instituted some minimum shell length or shell lip thickness which reflects queen conch age (Theile, 2005; FAO, 2007). For example, in The Bahamas, legally harvested queen conch must have a flared shell lip (see below), but there is no other size limit. The regulations are more stringent in the United States Virgin Islands and Puerto Rico, where minimum shell length of 9 inches (22.8 cm) and minimum shell lip thickness of 3/8 in. (9.5 mm) are required for harvest (Theile, 2005). Despite attempts to manage the queen conch fisheries, the species continues to be listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) (Daves and Fields, 2004), and numbers continue to decline throughout the geographic range because of ever-increasing fishing pressure (Bell et al., 2005; Posada et al., 2007; Stoner et al., 2012a).

As with many gastropods, growth in queen conch is determinate and strongly influenced by the environment (Alcolado, 1976; Martín-Mora et al., 1995). Queen conch are gonochoristic, the sex ratio is typically 1:1, and individuals reproduce by mating (i.e., fertilization is internal) (Randall, 1964). Approximately 3.5 years after larvae settle to the benthic environment, queen conch reach terminal shell length, and maximum shell length ranges from 140 to 300 mm (Randall, 1964; Appeldoorn, 1988a). At about this time, the outer edge of the shell lip turns outward to form the characteristic flared lip of the “adult” form. Subsequent growth of the shell occurs only in thickness (i.e., not length) and tagging studies show that shell lip thickness provides a relative index for age (Appeldoorn, 1988a, Stoner and Sandt, 1992). Because of these growth characteristics, shell length alone provides no real information about whether or not a queen conch is sexually mature. A flared shell lip indicates a minimum age of 3.5 years, but there have been repeated reminders over the last two decades that a lip flare may not provide ample protection for reproduction. For example, at least some queen conch become mature with relatively thin shell lips (<7 mm) (Egan, 1985; Appeldoorn, 1988a) but recent studies indicate that maturity in many locations occurs at a later time (Avila-Poveda and Baqueiro-Cárdenas, 2006; Bissada, 2011).

This study was conducted to provide a detailed analysis of the relationships between queen conch length, shell lip thickness, and reproductive maturity in the Exuma Cays, Bahamas. Two primary approaches were explored to evaluate maturity over a wide range of shell size and shell lip thickness: (1) a gonadosomatic index (GSI) based upon gonad weight and (2) histological evaluation of ovarian and testicular tissues. The overarching goal was to determine whether a minimum shell lip thickness for sexual maturity could be identified and whether or not the oldest queen conch, those with very thick shell lips, might be reproductively senescent. Our findings are discussed in light of current fishery management strategies in The Bahamas and the greater Caribbean region.

2. Methods

2.1. Study sites and queen conch collections

Queen conch for this project were collected near Lee Stocking Island (23°46′N, 76°06′W) and Warderick Wells (24°23′N, 76°38′W) in the Exuma Cays, The Bahamas. Both sites have well-studied populations of both juvenile and adult queen conch (Stoner and Ray, 1996; Stoner et al., 1998; Stoner, 2003), and the reproductive behavior of these populations is known (Stoner et al., 1992; Stoner and Ray-Culp, 2000). An initial collection of 42 queen conch with flared shell lips were made opportunistically near Lee Stocking Island and Warderick Wells to perfect dissections and develop a GSI for maturing males and females. This was followed by a larger collection ($n = 102$) near Warderick Wells from which all of the histological samples were taken. The latter site, in the center of the Exuma Cays Land and Sea Park (a no-take fishery reserve), allowed the best opportunity to select queen conch for the shell criteria desired. The samples were collected in depths 2–30 m on sand, hard-bottom, and seagrass (*Thalassia testudinum*) habitats known to be important for queen conch reproduction.

Queen conch collections were made during peak reproductive season (Stoner et al., 1992) to ensure that the individuals collected would have fully developed gonads. Collections were made at Lee Stocking Island 16–26 June 2011, and at Warderick Wells 7–16 July 2011. To explore the relationship between shell lip thickness (i.e., queen conch age) and sexual maturity, an effort was made at the latter site to collect six females and six males in each of nine lip thickness intervals between 0 and 45 mm. The gender of a living queen conch can be determined underwater by turning the shell aperture up and noting the presence or absence of a verge (penis) when the animal emerges to right itself. This allowed only the necessary number of queen conch to be sacrificed for the analysis. The animals were transported to a temporary laboratory on land for processing.

2.2. Measurements and development of the gonadosomatic index

Several morphological measurements were made for each queen conch. Total shell length (SL, mm), was measured from the anterior end of the siphonal canal to the end of the shell spire with large Vernier calipers. Shell lip thickness (LT, mm) was measured with small calipers on the flared outer lip of the posterior half of the shell aperture following the method of Appeldoorn (1988a).

Measures of soft-tissue parts were made after the animal was anesthetized by chilling in a refrigerator (∼5 °C) for at least one hour. Removal of the soft tissue was done with care because the gonad runs along the length of the terminal part of the body deep inside the shell spire (see Little, 1965; Reed, 1995a,b). This was achieved by carefully chipping the spire off the shell with a small hatchet, and then pulling the queen conch out through the opening. Once removed from the shell, the gender of the conch was determined based upon the presence of a verge (male) or egg groove which runs along the foot (female), and the total weight of the soft tissue (g) (i.e., all tissues except the shell) was determined with a spring balance.

Dissecting the queen conch gonad is complicated by its anatomy. In both females and males the anterior half of the gonad adheres to the stomach, the posterior half tightly saddles the digestive gland, and lateral skirts of the posterior section form an interlaced connection with the digestive gland. As described above, initial collections of queen conch with flared shell lips were used to perfect and streamline the determination of gonad weight. For each individual, the gonad was excised along its margin with the stomach and digestive gland. This material, weighed to the nearest 0.01 g was called the ‘coarse’ gonad weight. However, this coarse weight includes a small but difficult-to-remove wedge of digestive gland between the gonadal skirts in the posterior half of the gonad. To obtain a ‘clean’ gonad weight, the glandular tissue was removed by careful cutting and scraping; this material was weighed (0.01 g), and subtracted from the coarse gonad weight. On average, the residual digestive gland comprised 19% of coarse gonad weight. As expected, this

Table 1
Reproductive phases and area tissue coverage classifications for queen conch gonadal tissue (following Delgado et al., 2004).

Phase	Scale	Definition
Early developing	1	Females: only primary growth and cortical alveolar oocytes present Males: only spermatogonia and spermatocytes present
Developing	2	Females: early vitellogenic oocytes present Males: all stages of spermatogenesis present, no vas deferens present
Spawning capable	3	Females: late stage vitellogenic oocytes predominant Males: vas deferens present, spermatozoa in vas deferens
Regressing	4	Females: resorption of vitellogenic oocytes; atresia common Males: only residual spermatozoa, lobules degenerating, atresia present
Immature	6	Females: only primary oocytes present Males: only spermatogonia present
No germ tissue	7	No evidence of germ tissue in gonad; “holes” in tissue
Undifferentiated	8	Undifferentiated gonial cells—cannot determine if are spermatogonia or oogonia

Cover	Scale	Definition
<25%	1	None to small amounts of germ tissue present
25–50%	2	Moderate amount of germ tissue present
51–75%	3	Large amount of germ tissue present
>75%	4	Germ tissue in majority of gonad section

proportion diminished with increasing gonad weight and a correction was developed for each gender. The best fit occurred for females using an exponential function ($R = 0.675$):

$$y = 0.2359(e^{-0.026x})$$

For males, a power function provided the best fit ($R = 0.660$):

$$y = 0.2946(x^{-0.258})$$

In both cases, x is the coarse gonad weight and y is the proportion of non-gonad tissue.

These same measures were made for the larger collection of queen conch collected at Warderick Wells except that coarse weights only were measured for the gonads, and gender-specific corrections were applied to calculate clean gonad weights from the coarse weights. A GSI, equal to clean gonad weight divided by soft tissue weight (×100), was calculated for each individual to explore the relationship between shell lip thickness and reproductive maturity.

Relationships between SL, LT, and other morphological measures were evaluated with regression analysis, and analysis of covariance was used to test for a gender difference in the relationship between gonad weight and SL. Obvious dome-shaped relationships between LT and both gonad weight and GSI were examined with a nonlinear regression approach, applying a Gaussian three parameter peak equation to the results for each gender:

$$y = a \times \exp\left[-0.5\left(\frac{x - x_0}{b}\right)^2\right]$$

where y is gonad weight or GSI, x is shell lip thickness, and x_0 is the parameter estimate for peak location. All regression analyses were carried out with SigmaPlot 12.0.

2.3. Histological preparations and analysis

A subsample of gonadal tissue (∼10 mm cube) was removed from the middle section of each gonad for histological preparation. This was preserved in 10% neutral buffered formalin for a period of at least 7 days. Following fixation, the tissue was rinsed overnight in fresh water, dehydrated in a series of graded ethanols, cleared with xylene, and embedded in paraffin following standard histological techniques. Paraffin blocks were sectioned at 4 μm, mounted on glass slides and stained with hematoxylin and eosin for histological analysis.

All samples underwent two types of histological analysis. Initially, each section was inspected for stages of gametogenesis and percent cover of gametogenic tissue and given a reproductive classification following procedures adapted from Delgado et al. (2004) (Table 1). These results were tabulated for percentages of each lip thickness class. For direct comparison with earlier studies, the minimum size at maturity (SL_{min}) and the size at which 50% of the queen conch were mature (SL_{50}) was determined graphically for females and males. Similar overall statistics were determined for shell lip thickness criteria (LT_{min} and LT_{50}).

A more detailed analysis of gonadal tissue was made from digitized images. An entire histological section was photographed in a series of non-overlapping views (two to nine views per slide, depending on the amount of gonadal tissue) for determination of a Gonadal Maturity Index (GMI) following a modification of procedures in Tomkiewicz et al. (2011). Briefly, the estimation of area fractions for different gametogenic tissue categories was carried out by placing a point grid (70–88 points) on two randomly selected images (photomicrographs) with the plug-in ‘Analyze’ for the ‘Grid’ function of ImageJ software (Abramoff et al., 2004). The cell type at each intersection of the grid lines (i.e., each point) was categorized as somatic cells (Ts), atretic germ cells (A) or germ cells (G1-G4) (Table 2), excluding areas with no tissue. The area fraction per cell type was estimated as the sum of points identified per category divided by the total number of grid points that intersected gonadal tissue in the photomicrograph. Calculation of the GMI was based upon the area fractions for each tissue category weighted by a factor (Table 2) that increases with gamete development:

$$\mathrm{GMI} = 0.0F\mathrm{Ts} + 0.2F\mathrm{A} + 0.4F\mathrm{G1} + 0.6F\mathrm{G2} + 0.08F\mathrm{G3} + 1.0F\mathrm{G4},$$

where F is the area fraction for the indicated cell type. The index ranges from 0 when only Ts cells are present to 1.0 when all germinal cells are spermatozoa in males or late vitellogenic in females. The GMI was not calculated for queen conch that had no discernible gonadal tissue (i.e., phases 7 and 8, Table 1).

An obvious sigmoid relationship between the GMI and LT was examined with a nonlinear regression approach, applying a Gompertz three parameter sigmoid equation:

$$y = a \times \exp\left[-\exp\left(\frac{-(x - x_0)}{b}\right)\right]$$

Table 2
Calculations of tissue area fractions (F) and the Gonadal Maturity Index (GMI) based on the histological image of queen conch ovary or testis and point counts (n) per cell type in the point grid. The GMI is the product of the weighting factor (w) and estimated F (see text). Cell types are somatic cells (Ts), atresia (A), primary growth oocytes (PG), cortical alveolar oocytes (CA), early vitellogenic oocytes (EV), late vitellognic oocytes (LV), spermatogonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz).

Cell type	Females	Males	Weighting factor (w)
Ts	Non-gamete tissue	Non-gamete tissue	0
A	Atretic oocytes	Atretic vas deferns or Sz	0.2
G1	PG	Sg	0.4
G2	CA	Sc	0.6
G3	EV	St	0.8
G4	LV	Sz	1.0

where y is GMI, x is shell lip thickness, and x_0 is the parameter estimate for the location of upward inflection in the curve. We also tested for a possible correlation between GSI and GMI with standard regression methods.

3. Results

3.1. Weight relationships and GSI

Queen conch collected at LSI and WW were combined for analysis of soft weight relationships. As expected, there was a significant linear relationship between soft tissue weight and SL (Fig. 1a). In contrast, a peaked function was evident in the relationship between soft tissue weight and LT (Fig. 1b), and a three-parameter Gaussian curve yielded a reasonable fit for the data. This analysis shows that the soft tissue weight decreased as LT increased beyond ∼22 mm.

Gonad weight increased with SL (Fig. 2a), corresponding closely with the relationship observed for soft tissue weight. The regression lines were nearly identical for females and males, and analysis of covariance showed that the effect of SL was highly significant ($F = 2.613$, $p < 0.0001$), but gender was not ($F = 0.007$, $p = 0.932$). The overall correlation was significant ($R = 0.699$, $F = 102.13$, $p < 0.0001$). As with soft tissue weight, gonad weight (both female and male) showed a dome-shaped relationship with LT (Fig. 2b), with gonad weight declining as LT increased above ∼23 mm.

A dome-shaped pattern was also observed for the relationship between LT and GSI for queen conch regardless of gender (Fig. 3).

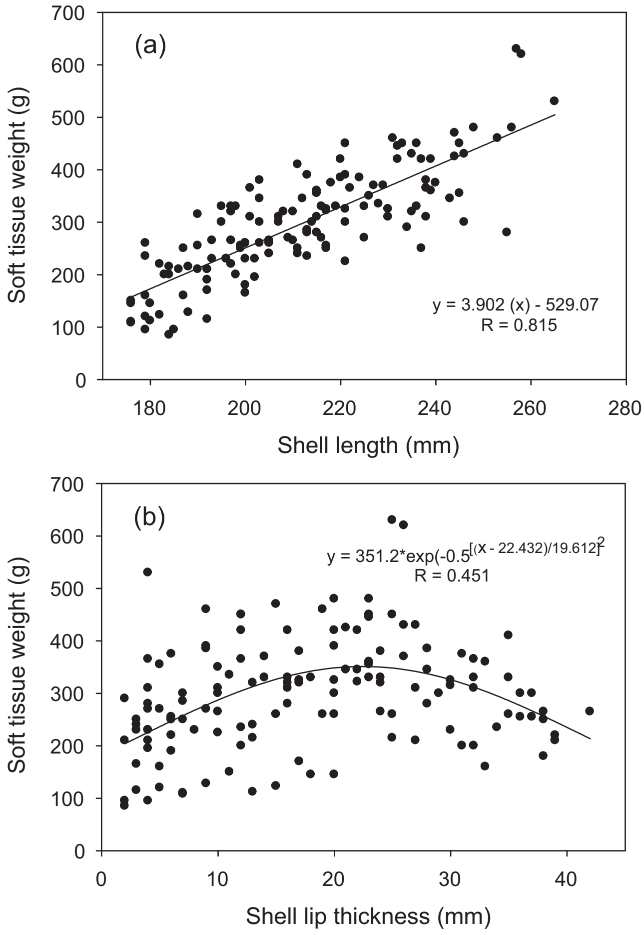

Fig. 1. Soft tissue weights of queen conch plotted as a function of (a) shell length and (b) shell lip thickness. Linear regression is shown for the shell length relationship and a Gaussian curve for shell lip thickness (see supplemental materials). Data for females and males were combined.

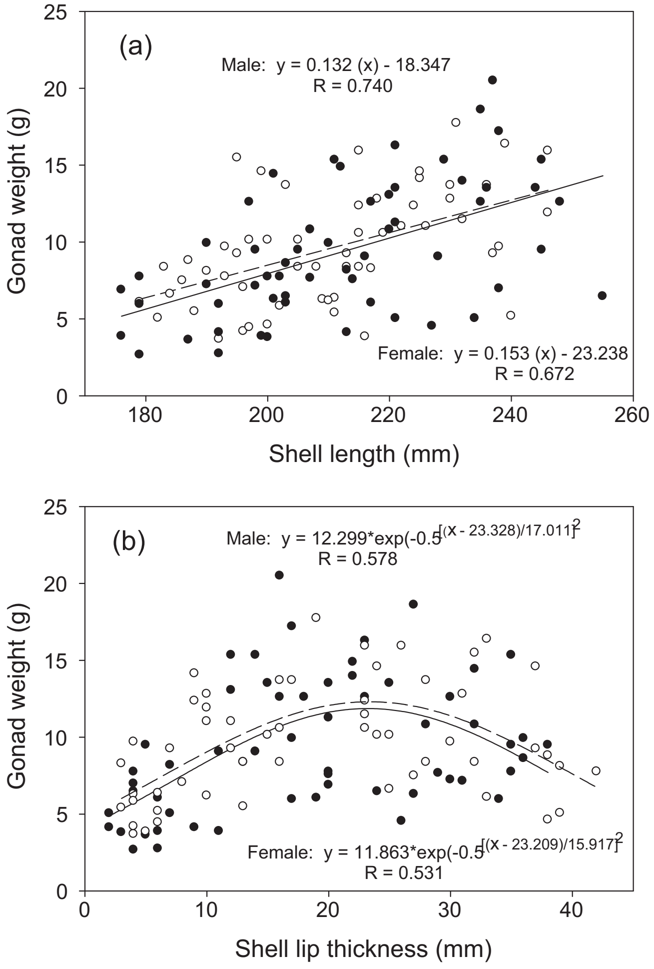

Fig. 2. Gonad weights of queen conch plotted as a function of (a) shell length and (b) shell lip thickness. Linear regressions are shown for shell length relationships and Gaussian curves for shell lip thickness (see supplemental materials). Data for females are shown with closed circles and solid lines. Males are represented with open circles and dashed lines.

Table 3
Percentage of gonadal tissue containing germ cells present in testes and ovaries by size class (mm shell lip thickness, LT) for female (F) and male (M) queen conch.

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

Table 4
Reproductive phases (percent) present in gonads of female and male queen conch by shell lip thickness (LT).

LT (mm)	*n*	No germ tissue	Immature	Early developing	Developing	Spawning capable	Regressing
Female							
<5	7	100	0	0	0	0	0
5–9	8	62.5	37.5	0	0	0	0
10–14	6	0	0	16.7	33.3	50.0	0
15–19	6	0	0	0	0	100	0
20–24	6	0	0	0	0	100	0
25–29	6	0	0	0	0	100	0
30–34	6	0	0	0	0	100	0
35–39	6	0	0	0	0	100	0
Male							
<5	7	71.4	14.3	14.3	0	0	0
5–9	7	42.8	0	14.3	28.6	14.3	0
10–14	6	0	0	0	16.7	83.3	0
15–19	6	0	0	0	0	100	0
20–24	6	0	0	14.3	0	85.7	0
25–29	6	0	0	0	12.5	75.0	12.5
30–34	6	0	0	0	0	100	0
35–39	6	0	0	0	0	83.3	16.7
40+	1	0	0	0	0	100	0

However, GSI was maximum for females with LT = 24.6 mm and for males at LT = 26.6 mm.

3.2. Histological relationships

Overall, females with LT < 10 mm had little to no ovarian tissue and can be considered reproductively inactive (Table 3). High numbers of individuals with >50% ovarian tissue occurred only among females with LT ≥ 15 mm. In contrast, while all males <5 mm LT were reproductively inactive, most had a high percentage of spermatogenic tissue in the testis by 10 mm LT (Table 3).

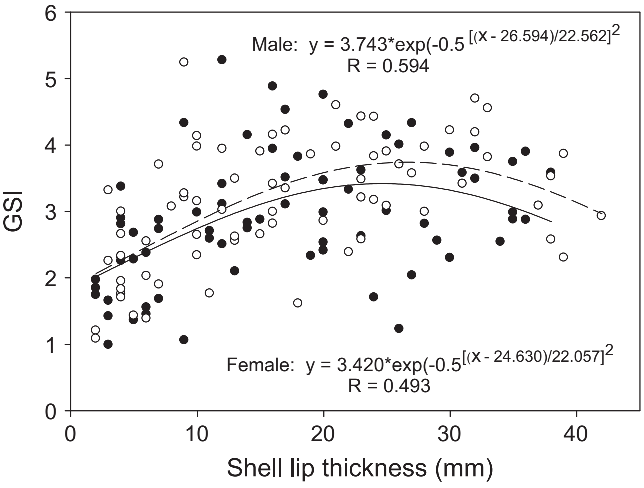

Fig. 3. Gonadosomatic Index (GSI) for queen conch plotted as a function of shell lip thickness. Gaussian curves are shown for females (closed circles and solid lines) and males (open circles and dashed lines) (see supplemental materials).

Females with LT < 5 mm had no germ tissue present, and all with LT < 10 mm were immature (Table 4). However, all females with LT ≥ 15 mm were spawning capable. No females in any thickness category were found in the regressing phase, generally seen at the end of the reproductive season. The LT_{min} and LT_{50} were 12 and 26.2 mm, respectively, for female queen conch. The SL_{min} and SL_{50} were 176 and 206 mm, respectively (Fig. 4).

Some male queen conch with LT < 5 mm showed spermatogenic activity, but none of the thin-shelled males were reproductively active, and the majority had no germ tissue present at all (Table 4). Some males in the 5–9 mm LT category were spawning capable and the majority of males with LT ≥ 10 mm were reproductively active. Some males in the thicker classes were found in the regressing phase, but the oldest (i.e., thickest) male was still reproductively active. The LT_{min} and LT_{50} were 9 and 24 mm, respectively, for male. The SL_{min} and SL_{50} were 179 and 210 mm, respectively (Fig. 4).

The GMI was calculated for each individual and plotted as a function of shell lip thickness (Fig. 5). All of the female queen conch <10 mm LT had GMI values equal to zero, following the results above. The index then rose rapidly between 12 and 20 mm LT with wide variation among individuals. A Gompertz three-parameter sigmoid curve yielded a good fit to the data for females. A similar pattern was apparent for males (Fig. 5) except that the first non-zero GMI value occurred at 7 mm LT and, despite wide variation in GMI among thicker-shelled individuals, an asymptote near 0.4 was lower than that observed for females. The GMI data taken in combination with results on coverage of gamete tissue and reproductive phase indicate that few male and female queen conch with

Table 5
Shell length (SL) and shell lip thickness (LT) parameters observed for maturity in queen conch in different parts of the greater Caribbean region. Values represent the minimum measures where maturity was observed (SL_{min}, LT_{min}) and where 50% of the population sampled was sexually mature (SL_{50}, LT_{50}) (see text) based upon histological evaluation of ovaries and testes.

Location	SL_{min} – female (mm)	SL_{min} – male (mm)	LT_{min} – female (mm)	LT_{min} – male (mm)	Reference
San Andres Archipelago, Providencia, & Santa Catalina, Colombia	205	~214	2	8	Avila-Poveda and Baqueiro-Cárdenas (2006)
San Andres Archipelago, Colombia	>170	>170	>5	>5	Aldana-Aranda and Frenkiel (2007)
Barbados	~260	~260	3	3	Bissada (2011)
Exuma Cays, Bahamas	176	179	12	9	This study

Location	SL_{50} – female (mm)	SL_{50} – male (mm)	LT_{50} – female (mm)	LT_{50} – male (mm)	Reference
San Andres Archipelago, Providencia, & Santa Catalina, Colombia	249	234	17.5	13.0	Avila-Poveda and Baqueiro-Cárdenas (2006)
Barbados	282	280	18.8	19.2	Bissada (2011)
Exuma Cays, Bahamas	206	210	26.2	24.0	This study

LT < 10 mm LT are reproductively active, and that individuals with LT > 15 mm contribute most to reproductive output.

GMI increased generally with GSI for both females and males; however, the correlations were weak and probably not meaningful. Pearson correlation coefficients for females and males were 0.409 and 0.494, respectively.

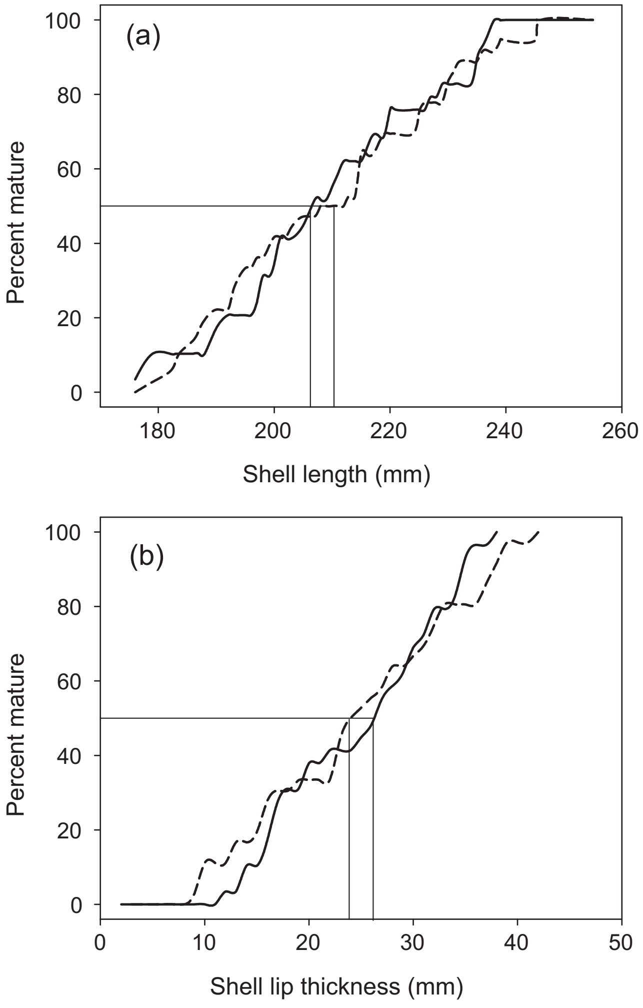

Fig. 4. Maturity of queen conch plotted as a function of (a) shell length (SL) and (b) shell lip thickness (LT). Cumulative curves are shown for females (solid lines) and males (dashed lines).

4. Discussion

4.1. Relationships between shell metrics and maturity

In this study, we examined both quantitative and qualitative aspects of sexual maturity in queen conch and the relationships with external features of the shell morphology. Among the quantitative metrics both soft tissue weight and gonad weight increased with SL. However, relationships between LT and internal structures were more complex. Shell thickness increases with queen conch age because nacre is continuously deposited on the inside of the shell, resulting in the reduced internal space for soft tissue (Randall, 1964). Concordantly, our analyses show that soft tissue weights, gonad weights, and the GSI all decrease slightly with LT values >22–25 mm. This suggests that the oldest queen conch may have reduced numbers of eggs, although the histological results revealed no reduction in egg quality with age as has been observed in red abalone (*Haliotis rufescens*) (Rogers-Bennett et al., 2004).

Overall, large queen conch will have higher reproductive potential than small individuals up to the point that internal space

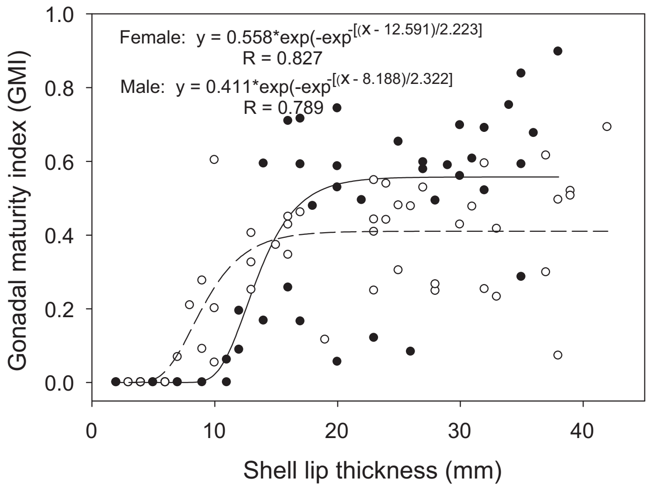

Fig. 5. Gonadal Maturity Index (GMI) for queen conch plotted as a function of shell lip thickness. Gompertz sigmoid curves are shown for females (closed circles and solid lines) and males (open circles and dashed lines) (see supplemental materials).

becomes limiting for soft tissue and gonads in the oldest individuals. It is clear that the small, thick-shelled “samba” queen conch observed in some heavily fished areas in the Caicos Islands (Clerveaux et al., 2005), The Bahamas (Stoner et al., 2012b), and Cuba (Cala et al., in press) almost certainly have small gonads and low fecundity.

Histological results provide critical insight into the qualitative aspects of queen conch reproductive biology, most notably the relationship between actual gonad maturity and LT. In fact, indications that maturity lags substantially behind formation of the flared shell lip in queen conch emerged more than 25 years ago. The first histological evaluations made by Egan (1985) showed that earliest maturity in queen conch in Belize occurred at 4 mm LT for females and 3 mm LT for males. Soon thereafter, population growth models developed by Appeldoorn (1988a) indicated an LT_{min} of 5 mm in Puerto Rico, 5–10 months following initial shell lip formation. Similarly, histological observations on queen conch with different shell lip thicknesses in St. Christopher and Nevis led Buckland (1989) to conclude that sexual maturity was not achieved until at least 10 months after the shell flare first forms. More detailed recent studies of gonad development make it clear that LT is the critical metric in evaluating sexual maturity in queen conch (Table 5). Studies from the Colombian islands (Avila-Poveda and Baqueiro-Cárdenas, 2006) and Barbados (Bissada, 2011) show that the LT_{50} for maturity is higher than previously thought, between 13 and 19 mm, and our study in the Exuma Cays indicates that LT_{50} can be >20 mm (Table 5). Reasons for differences among the study sites are unknown but most likely associated with differences in the nutritional environments, water temperature, and overall growth rates.

On the reproductive grounds near Lee Stocking Island shell thicknesses of tagged queen conch increased 4.2–5.2 mm per year (Stoner and Sandt, 1992). Given those values, 20 mm LT would occur no less than 4 years after initial formation of the shell flare, to yield 50% maturity in the population. Growth in LT, however, can vary with location. Appeldoorn (1988a) reported that queen conch in Puerto Rico accumulated thickness at a rate of 17–18 mm per year, and noted the likely importance of site-specific differences. Although maturity has been observed in the gonads of queen conch with relatively thin shell lips as discussed above, it seems likely that relatively few queen conch are reproductively mature anywhere in the greater Caribbean region in less than 1 or 2 years following formation of the shell lip flare (i.e., in their fifth or sixth year of life).

A critical link to actual reproductive output for queen conch, beyond sexual maturation, is reproductive behavior. While there have been good observations on mating and egg-laying behavior (Davis et al., 1984; Delgado et al., 2004) and analyses of reproductive frequency in different populations (Stoner and Ray-Culp, 2000; Gascoigne and Lipcius, 2004; Stoner et al., 2012b), we are not aware of data on relationships between reproductive behavior and morphological characteristics such as queen conch size or shell thickness. Earlier studies have shown that spawning behavior in the abalone *Haliotis laevigata* parallels histological maturity (Wells and Mulvay, 1995); new observations on egg-laying frequency and actual fecundity by SL and LT criteria would be particularly useful in evaluating reproductive capacity of queen conch. This will be especially critical in light of increasing numbers of small phenotype adults observed in heavily fished populations (Stoner et al., 2012a), but density-dependent oogenesis observed in strombids (Appeldoorn, 1988b) and density-dependent mating behavior in queen conch (Stoner et al., 2012b) will complicate any analysis of reproductive output.

4.2. Fishery management implications

The queen conch has enormous economic and cultural significance throughout the 30+ nations that encompass its geographic range, and the desire for sustainable fisheries is nearly universal. Toward that goal, most nations have imposed at least some explicit harvest regulations including size requirements, shell lip criteria, gear restrictions, and quotas for landings and export. Among the 27 Caribbean nations with open queen conch fisheries (Theile, 2005), 18 have some minimum shell length required for harvest (ranging from 180 to 250 mm SL), and 14 require a flared shell lip.

It is now clear that size at maturity in queen conch is variable and site specific, as is true for other gastropods (Pernet, 2007). In southern Mexico (Aldana-Aranda and Frenkiel, 2007) and The Bahamas (this study) shell length at first maturity is about 170 mm while in the Colombian islands (Avila-Poveda and Baqueiro-Cárdenas, 2006) and Barbados (Bissada, 2011) maturity occurs in queen conch >200 mm SL. Sizes required to observe 50% maturity in the populations, of course, are higher (Table 5). We also know that size at maturity may change with time and with fishing pressure, as has been observed for the commercially harvested volutid gastropod *Zidona dufresnei* (Torroglosa and Giménez, 2010) as well as queen conch (Stoner et al., 2012a). Consequently, regulations on shell length do not provide for the conservation of mature individuals.

We have known for two decades that shell thickness should be the criterion for legal harvest of queen conch and that a flared shell lip does not guarantee sexual maturity (Appeldoorn, 1994; Clerveaux et al., 2005; Cala et al., in press; this study). At the time of Theile's review (Theile, 2005), Cuba and Venezuela required a 5 mm minimum LT, Colombia required 7 mm, and the US Caribbean (Puerto Rico and the US Virgin Islands) required 9.5 mm. However, with three recent studies (Table 5) showing LT_{50} values for females ranging from 17.5 to 26.2 mm and males ranging from 13.0 to 24.0 mm, it is clear that a minimum LT of at least 15 mm should be established for legal harvest throughout the Caribbean region.

Imposition of a shell-lip-thickness criterion for legal harvest of queen conch where such does not already exist is likely to be unpopular with fishers for two primary reasons. First, a minimum lip thickness obviously decreases the number of queen conch available for legal harvest. This is complicated by the fact that high exploitation rates on queen conch typically result in declining average LT in fished populations (Stoner et al., 2012a), and we observe only thin-lipped individuals (<5 mm) in many Bahamian locations where harvest rates are highest. Second, an LT requirement will require landing queen conch in the shell. This means that fewer conch can be carried on a boat safely, and fishers will need a higher price for their catches to offset the increased effort and transportation costs.

Queen conch have been depleted to the extent that fisheries for this species are no longer economically viable in many nations (Theile, 2005; Bell et al., 2005; Posada et al., 2007), and numerous fishing regulations and quotas have been imposed with the hope of rebuilding stocks. However, it is now clear from this and earlier studies that immature queen conch are being harvested legally throughout the Caribbean region, and this is one likely reason for rapid declines observed in the populations. Still, we believe that recovery of sustainable fisheries is possible with strong management action. For example, conserving large or older spawners often has a positive effect on population growth in gastropods (Rogers-Bennett and Leaf, 2006), and successful management for another large gastropod, the Australian greenlip abalone (*Haliotis laevigata*), has been accomplished through regulating numbers of fishing licenses, suitable size limits, appropriate quotas, and effective enforcement of the regulations (Mayfield et al., 2011). For queen conch, simulation models developed by Valle-Esquivel (2003) show that the optimal management strategy for queen conch will include strictly enforced limits on shell lip thickness, a fishing closure during the reproductive season, and control of total fishing effort. However, the need for change is urgent.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2012.07.017.

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