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PROXY MEASURES FOR QUEEN CONCH (*STROMBUS GIGAS* LINNÉ, 1758) AGE AND MATURITY: RELATIONSHIPS BETWEEN SHELL LIP THICKNESS AND OPERCULUM DIMENSIONS

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ABSTRACT Estimating age and maturity of the commercially harvested queen conch (*Strombus gigas*) offers fishery managers a unique challenge: How can these variables be determined if only the soft, edible parts of the marine gastropod are landed in port whereas the shells used for aging purposes are discarded at sea? Throughout the greater Caribbean region, including The Bahamas, the age and maturity of *S. gigas* are estimated by measuring the thickness of the flared lip of the shell. Given the traditional fishery practices for queen conch, including at-sea processing, developing proxy measures for *S. gigas* age and maturity would greatly benefit fishery managers. To this end, we used traditional morphometric analysis to find a significant inverse relationship between the ratio of operculum length to operculum width and shell lip thickness. A logistic regression model using the same operculum metric and a breakpoint of 15 mm for shell lip thickness as an indication of *S. gigas* maturity predicted correctly the maturity level for 86% of queen conch sampled in The Bahamas. This study provides the proof of principle for relationships between operculum measures and queen conch age and maturity that can be applied by fishery managers throughout the geographical range of the species.

KEY WORDS: gastropod fishery, Bahamas, age, maturity, opercula, *Strombus gigas*, queen conch

INTRODUCTION

The queen conch, *Strombus gigas* (Gastropoda: Strombidae), is one of the most iconic molluscs throughout the tropical and subtropical western Atlantic Ocean. Valued for both seafood markets and the shell trade, *S. gigas* was exploited heavily in the wider Caribbean region during the late 20th century (Theile 2001), with many fisheries on the verge of collapse at the onset of the 21st century (e.g., Stoner et al. 2012a, Stoner et al. 2012b). Following this trend, during the early 1990s, several nations with management and regulatory authority over fishing activities in the wider Caribbean region worked in concert to list the queen conch in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, thereby restricting imports of the large snail. However, overfishing and poaching contributed to declines in queen conch abundance throughout its natural range (Theile 2001). Last year, the US government was petitioned to list the status of *S. gigas* as threatened or endangered under the Endangered Species Act (Federal Registar 2012), and the National Oceanographic and Atmospheric Administration is conducting the necessary status review for queen conch.

Queen conch fishery practices have been described well by Theile (2001). At-sea processing of queen conch in the wider Caribbean region, where shells are discarded near the point of capture, has occurred for centuries, as evident by the abundant shell middens that occur throughout the gastropod's geographical range (Stoner 1997). Although at-sea processing of queen conch makes economic sense for fishers and likely results in safer passage for small fishing vessels returning to port (Theile 2001), the practice offers fishery managers a unique challenge: How can the size and age of *S. gigas* landed in port be estimated without its shell, the primary structure used to glean this information for management of the species (Theile 2005, FAO 2007, Stoner et al. 2012c)?

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Since the late 1980s, age in queen conch has been estimated reasonably well by measuring the thickness of the flared lip outside the aperture of the *Strombus gigas* shell (Appeldoorn 1988, Stoner & Sandt 1992). The snail is long-lived (25–30 y) and reaches terminal shell length (SL) at about 3.5 y. After this age, subsequent growth of the shell occurs only in thickness (Randall 1964, Appeldoorn 1988). Currently, several Caribbean nations use minimum shell lip thickness (LT) criteria (5–9.5 mm) to indicate sexual maturity in queen conch and to reduce harvest of juvenile and immature *S. gigas* (Theile 2005); however, just recently, Stoner et al. (2012c) were able to link sexual maturation definitively to LT (no less than 15 mm) and concluded that most nations within the wider Caribbean region, even those with LT criteria in place, were inadvertently allowing the harvest of immature queen conch. If landed whole, in the shell, and sampled in port, discrepancies in LTs are easily observed; however, if a queen conch is landed without its shell, there is no easy way to determine its age or maturity because often only the edible meat is landed with no internal organs or other body parts attached, including the gonads (Theile 2001). Given this management conundrum, it is clear that a proxy for LT is needed.

Lately, biologists have begun to use gastropod opercula to gain new insights into the life history of marine snails. For example, operculum striae (concentric ringlike chitin deposits) have been used to age and estimate growth in large, commercially harvested marine snails from northern Japan (Ilano et al. 2004, Miranda et al. 2008). Although annual rings are apparent in opercula of marine gastropods from temperate latitudes, it is unlikely that the operculum striae of marine gastropods from tropical latitudes will provide as much useful information about snail age and growth (Vasconcelos et al. 2012). However, other morphometric aspects of marine gastropod opercula have received recent attention and have yielded clues to gastropod life history useful to fishery managers. For example, Uneputty (2007) used operculum length and width to demonstrate allometric growth in the tropical marine snail *Nerita undata*, and Vermeij and Williams (2007) contrasted maximum operculum diameter and thickness by species to predict successfully the large-scale spatial distribution of turban snails (Turbinidae).

Compared with other gastropod opercula, the queen conch operculum is relatively long and narrow, curved, and comes to a point at the posterior end of the structure (Little 1965) (Fig. 1). This point makes contact with the seafloor and is used in leaping-type locomotion (Morton 1960). With the recent successes of using opercula in the study of other gastropod fisheries, we surmised that the shape and form of its operculum might provide insight into queen conch age and maturity. To this end, we conducted a traditional morphometric analysis (*sensu* Rohlf & Marcus 1993) of queen conch opercula and the primary shell measurements used in its management: SL and LT. Specifically, we sought to evaluate whether LT, the accepted metric for queen conch age and maturity, could be determined from an analysis of operculum dimensions.

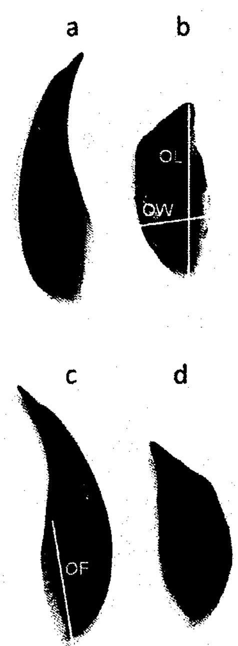

Figure 1. (A–D) Opercula from young and old queen conch with flared shell lips. The upper images (A, B) show the external face of the operculum; the lower images (C, D) show the face that is attached to the queen conch's foot. Operculum length (OL), operculum width (OW), and operculum foot scar (OF) were measured (in millimeters) where indicated by the white lines. The foot scar is the shallow depression where the operculum is attached to the muscular foot (C). Operculum thickness (not pictured) was measured (in millimeters) from the flat external surface to the highest part of the operculum rib, which runs along the longitudinal axis of the operculum on the foot attachment side (C, D). The narrow, pointed end of the operculum is used for leverage on the bottom in queen conch locomotion. The younger specimen (A, C) had a shell length (SL) of 196 mm and a shell lip thickness of 4 mm. The ratio of OL to OW in the younger queen conch was 3.82. The OL:OW in the older specimen (B, D), with a shell length of 193 mm and a shell lip thickness of 42 mm, was 2.60.

METHODS

Study Sites and Queen Conch Collections

Queen conch (n = 147) were collected from two locations within the Exuma Cays, The Bahamas, near Lee Stocking Island (LSI; 23°46′ N, 76°06′ W) and near Warderick Wells (WW; 24°23′ N, 76°38′ W). In both locations, *Strombus gigas* was sampled at depths ranging from less than 3 m to 25 m, from shallow, bank environments to deep, offshore shelf habitats. The bank environment was covered mostly by sand and seagrass (*Thalassia testudinum*), whereas the shelf habitat was comprised of sand, macroalgae-covered hard bottom, and soft corals near shore (depth, ≤15 m) and mixes of sand, hard bottom, and coral reefs offshore (depth, >15 m). Additional site-specific habitat associations of queen conch sampled at these locations can be found in Stoner et al. (2012a).

We collected queen conch with flared shell lips over a wide range of ages and maturities as indicated by the thicknesses of the shell lips. Total SL (in centimeters converted to millimeters) for individuals was measured between the anterior end of the siphonal canal and the posterior end of the spire using large Vernier calipers (SL range, 170–255 mm), whereas LT (in millimeters) was measured along the flared outer lip of the posterior half of the aperture using small Vernier calipers (LT range, 2–42 mm). Additional information on the biological characteristics of the specimens is described in a recent study (Stoner et al. 2012c) of *Strombus gigas* in the region.

Operculum Measurements and Ratios

The opercula for this study were collected ancillary to the biological samples gathered and analyzed by Stoner et al. (2012c). The operculum of each queen conch was excised near the base of the muscular foot, with the remaining tissue removed by peeling or scraping. Queen conch operculum metrics included length, width, thickness, and weight. A 5th metric was the foot scar, the shallow depression where the operculum is attached to the muscular foot. Operculum length (OL) was measured from the tip of the narrowest point to the rounded base of the operculum, whereas operculum width (OW) was measured across the widest section of the operculum (Fig. 1B). Operculum thickness (OT) was measured from the flat external surface to the highest part of the operculum rib (Fig. 1C), which runs along the longitudinal axis of the operculum on the foot attachment side. The operculum foot scar (OF) was measured from its highest point (i.e., the end of the depression toward the narrow tip) to the rounded base of the operculum (Fig. 1C). All length-based measurements were recorded to the nearest 0.1 mm using Vernier calipers, and operculum weight (OWt) was recorded to the nearest 0.01 g using an electronic balance.

Maximum shell length of *Strombus gigas* is variable, ranging from less than 150 mm to more than 300 mm in The Bahamas (Stoner et al. 2012a, Stoner et al. 2012c). Given a direct correlation between SL and operculum dimensions (see Results), several ratios were considered for possible correlation with LT, including OL:OW, OT:OW, OWt:OW, OL:OF, OT:OF, and OWt:OF. The rationale for testing these ratios was that the variables OW and OF would be directly proportional to SL, and that these metrics would be conservative. That is, OW and OF were most likely to remain constant over a wide range of LT, whereas the other metrics (i.e., OL, OT, and OWt) would change over the adult life of an individual queen conch.

Analysis

The basic relationships between shell and operculum measures were examined with standard regression methods using all the data from WW and LSI. Although least squares linear models are the primary results reported in this study, nonlinear models were explored in certain cases for improvements in fit. We report details for only the best correlations, briefly mentioning other findings. Relationships between ratios of operculum measures and LT were explored with a similar approach. Queen conch demonstrate no sexual dimorphism whatsoever in shell morphology, and points representing males and females were fully interspersed for all the operculum measures considered.

When the best linear model for a relationship between ratios of operculum measures and LT was determined, the data were partitioned by site, using WW data as the learning set ($n = 114$) to provide a new regression model. The LSI data were evaluated as an independent test set ($n = 33$) to evaluate the WW model. The quality of the simple regression model for fisheries management purposes was evaluated by the number of correct classifications for mature and immature queen conch based on the established 15-mm LT breakpoint for maturity (Stoner et al. 2012c). After the test set was evaluated, the data were pooled for an overall regression of LT versus operculum measures.

Logistic regression was used to model the probability of queen conch maturity (LT, >15 mm) on the basis of operculum metrics. The model was fitted to all of the data by the method of maximum likelihood for binary data (i.e., mature, ≥15-mm LT; immature, <15-mm LT) using the regression module of Systat 13 (SYSTAT Software, Inc., San Jose, CA) (Peduzzi et al. 1980). This model for maturity was described by the following equation:

$$\log_e\left(\frac{p}{1-p}\right) = \alpha + \beta' x$$

where p is $Pr(y = 1)$, $y = 1$ if mature and $y = 0$ if immature, α is the intercept, x is the model matrix of explanatory variables, and β' is the model coefficient. The maximum likelihood estimates of mortality (p) were calculated as

$$p = \frac{e^{(\alpha+\beta' x)}}{1 + e^{(\alpha+\beta' x)}}$$

After the model was fit, a prediction matrix was used to evaluate its sensitivity. Finally, the logistic model was used to develop the curve showing the probability of maturity based on the operculum metric chosen.

RESULTS

Relationships Between Shell and Operculum Dimensions

Operculum length and OW showed close positive correlations with queen conch SL, whereas OT became increasingly variable with SL (Fig. 2). Length of the foot scar (OF) on the operculum was also closely correlated with SL in a positive linear relationship, whereas OWt increased in an exponential relationship with SL (Fig. 3). Correlations between the operculum measures and

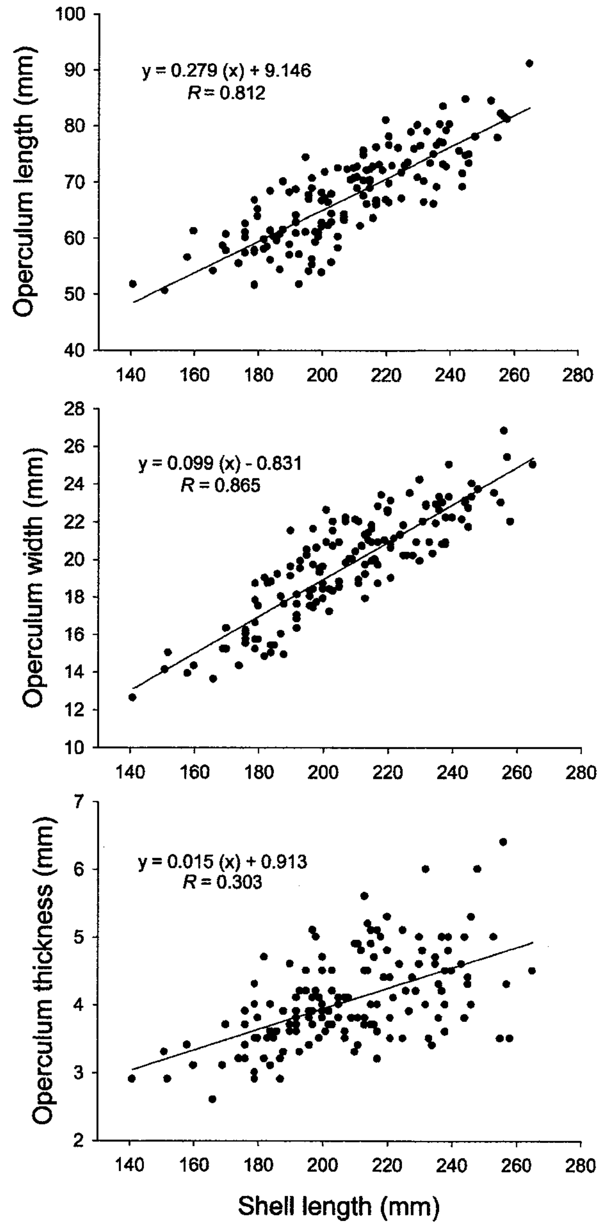

Figure 2. Relationships between shell length and operculum metrics (length, width, and thickness) for queen conch collected in the Exuma Cays, The Bahamas.

LT were all generally weak (R = 0.103–0.310) because of the overwhelming effect of SL, and the coefficients for slope were low or not significant. Thus, direct relationships with LT were considered no further.

Relationships Between Ratios of Operculum Measures and Queen Conch Age

Numerous ratios among the operculum measurements (mentioned earlier) were tested for their possible correlation with the age of queen conch as revealed in their LT measurements. The OL:OW ratio provided the highest significant, albeit negative, correlation with LT ($R = -0.743$, $F_{1,145} = 178.675$, $P <$ 0.0001; Fig. 4). The OL:OF ratio was also correlated negatively

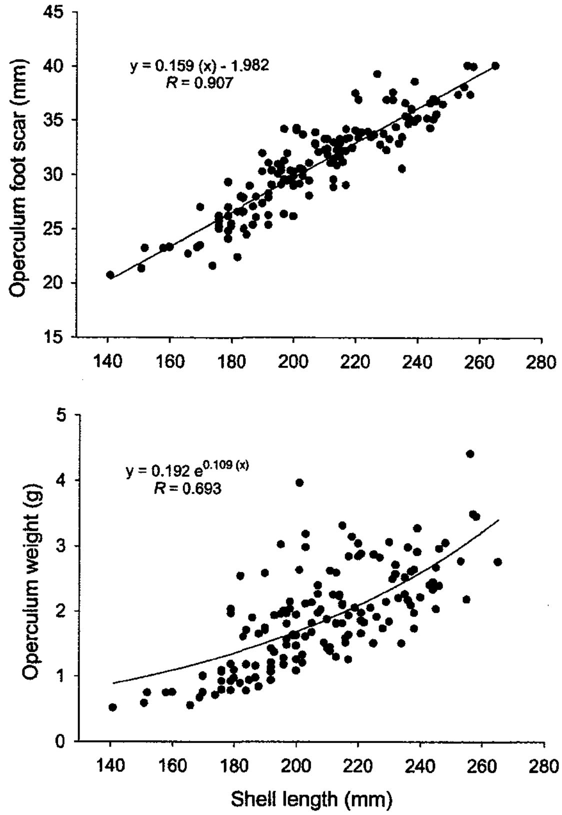

Figure 3. Relationships between shell length and operculum metrics (foot scar and weight) for queen conch collected in the Exuma Cays, The Bahamas.

with LT ($F_{1,145} = 59.046$, $P < 0.0001$); however, the correlation coefficient was less ($R = -0.541$). Ratios using OT measures (i.e., OT:OW and OT:OF) resulted in very poor correlations with LT ($R = 0.018$ and $R = 0.238$, respectively) and insignificant or low slope coefficients; therefore, OT measures were not useful in predicting queen conch age. Ratios incorporating OWt measures (i.e., OWt:OW and OWt:OF) resulted in dome-shaped relationships that also precluded the practical application of predicting *Strombus gigas* age because queen conch at the extreme ends of the curve might have similar ratios.

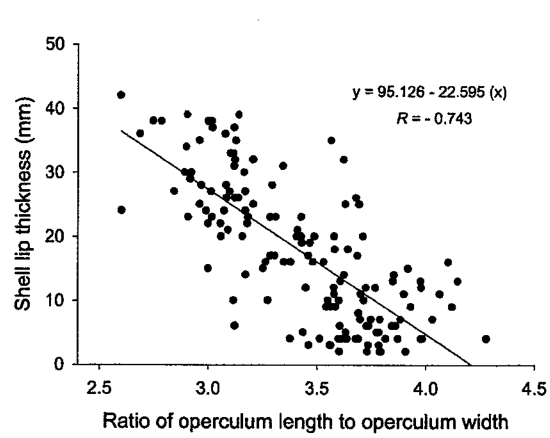

Figure 4. Relationship between the ratio of operculum length to operculum width (OL:OW) and shell lip thickness in queen conch collected in the Exuma Cays, The Bahamas.

Predicting Queen Conch Maturity from Operculum Dimensions

As described earlier, 15 mm was used as the minimum LT for classifying a queen conch as a sexually mature individual. When the combined data set (LSI and WW) was evaluated with the linear regression model for LT based on OL:OW, 88.4% of the queen conch (130 of 147) were classified correctly as being more than or less than 15 mm in LT. Only 8 *Strombus gigas* were classified incorrectly as being less than 15 mm in LT (immature), and 9 individuals were classified incorrectly as being ≥15 mm in LT (mature).

Binary logistic regression provided another good way to examine the robustness of the relationship between operculum metrics and maturity as defined by 15-mm LT. The OL:OW ratio was a highly significant predictor of maturity, with the logistic model correctly predicting maturity for 85.8% of the cases (Table 1). The logistic curve developed for the relationship followed the actual proportions of individuals that were mature in 13 data bins based on the OL:OW ratio (Fig. 5), and the curve shows that an OL:OW ratio less than ~3.2 yields a probability of 0.9 that a queen conch is mature. Opercula with OL:OW ratios more than 3.5 are most likely to represent immature queen conch.

DISCUSSION

In this study, we examined the relationships between several sets of variables corresponding to measured lengths and widths on the queen conch operculum and shell in The Bahamas. Our intent was to identify proxy measures of *Strombus gigas* age and maturity using traditional morphometrics. Not all combinations of the measured variables were successful in achieving this goal. For example, OT appeared to remain in constant proportion with OW and OF. Furthermore, OT was difficult for us to measure accurately because subtle differences in positioning the Vernier calipers across the operculum resulted in variation of the metric. This effectively rendered the ratios OT:OW and OT:OF useless for age determination. Similarly, the dome-shaped relationship between LT and the ratios using OWt made the latter metrics useless for age determination. This pattern probably resulted from an increase in OWt during early adult life, followed by a decrease in OWt related to erosion of the

TABLE 1.

Results of binary logistic modeling for maturity in queen conch using the ratio of operculum length to operculum width (OL:OW) as a predictor for individuals ≥15 mm in shell lip thickness.

Parameter	Estimate	Z value	*P* value
Constant	23.516	5.809	<0.001
OL:OW	–6.701	–5.800	<0.001

Prediction matrix for the logistic model

	Mature predicted	Immature predicted	Actual total
Mature	69	13	82
Immature	8	58	66
Total predicted	77	71	148
Correct (%)	84.1	87.8	
False (%)	10.4	18.3	
Total correct (%)			85.8

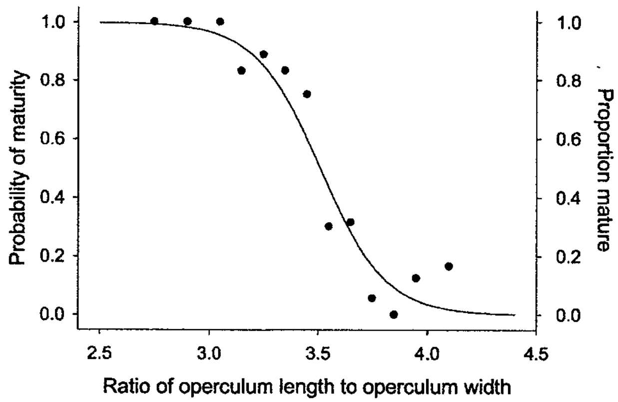

Figure 5. Results of binary logistic regression for queen conch maturity (shell lip thickness, ≥15 mm; see text) based on the ratio of operculum length to operculum width (OL:OW). The curve represents the probability of observing a mature individual with the respective OL:OW value. Individual points show the actual proportion of mature queen conch for bins of data based on OL:OW (n = 147).

operculum during the normal life span of the queen conch. Despite these shortcomings, at least 1 relationship proved very useful: that between LT and the ratio OL:OW.

The inverse correlation between the OL:OW ratio and LT is probably related to the unique way that *Strombus gigas* propels itself over the bottom. Typical of strombids, a queen conch does not glide over the bottom like most gastropods; rather, it moves forward in a series of short leaps, using its strong foot to lift the forward edge of the shell off the substratum and lunge ahead (Morton 1960). With each thrust, the foot is extended and the narrow, pointed end of the operculum provides leverage on the coarse sand or hard bottom that comprises typical queen conch habitat (Stoner et al. 2012a). Often appearing translucent brown, in The Bahamas, the queen conch operculum is appropriately referred to as the horn. In older individuals, the tip of the horn may appear worn down or chipped from years of hopping along the bottom (Fig. 1). Indeed, after the shell and operculum reach maximum size near sexual maturity, neither hard part grows more in external dimensions (Randall 1964, Appeldoorn 1988, Savazzi 1991, Checa & Jiménez-Jiménez 1998) and erosion begins. Ostensibly, while the external surface of the shell is reduced by bioeroders such as cyanobacteria, green and red algae, and microendolithic heterotrophs (Vogel et al. 2000), the operculum is eroded by constant contact with the sea bottom. Throughout the adult life span of *S. gigas*, possibly 25–30 y (Randall 1964, Appeldoorn 1988), the narrow, pointed end of the operculum is gradually worn down, reducing the OL:OW ratio, whereas OW and OF remain constant.

Fishery Management Implications

The relationship we describe between LT and the ratio OL:OW provides fishery managers with an alternative to measuring LT to estimate age and maturity in *Strombus gigas* and may obviate the need to land or process queen conch shells in port for management purposes. For example, fishery managers could permit at-sea processing of *S. gigas* and the disposal of shells, easing the transfer of product and improving fishing vessel safety, and could require that the catch be landed with opercula intact (i.e., with horns on). Measuring OL and OW would be easy and straightforward for both fishers and management personnel, whether at sea or in port.

Sexual maturity in queen conch varies throughout the Caribbean region. In this study, we used a 15-mm LT as the conservative test for The Bahamas (Stoner et al. 2012c), but other breakpoints could be applied. For example, 50% of the females sampled in selected areas of Colombia were mature at an LT of 17.5 mm, whereas 50% of the males were mature at a 13-mm LT (Avila-Poveda & Baqueiro-Cárdenas 2006). In Barbados, 50% of the *Strombus gigas* population sampled was sexually mature at ~19-mm LT regardless of gender (Bissada 2011). Our analytical methods could be used by fishery managers with these breakpoints just as easily as that used for The Bahamas. Put into practice, to determine whether a queen conch meets minimum age or maturity criteria for a given management area in the wider Caribbean region, sampling staff would simply measure OL and OW, calculate the ratio between the 2, and look up where this value lies on the curve developed for that area (Fig. 5).

In summary, we provided proof of principle that a simple morphometric analysis of opercula can be used to determine proxy measurements of *Strombus gigas* age and maturity. With an LT of 15 mm as the breakpoint for maturity (Stoner et al. 2012c), we predicted successfully the level of maturity in ~86% of queen conch sampled in The Bahamas merely by using the ratio of OL:OW and the analytical methods outlined here. We are confident that the relationships we describe will be further strengthened with additional testing in other fishing areas and commercial ports throughout the wider Caribbean region.

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