Slow growth of the overexploited milk shark *Rhizoprionodon acutus* affects its sustainability in West Africa

A. BA*†, K. DIOUF‡, F. GUILHAUMON§ AND J. PANFILI§

Département de Biologie Animale, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, B. P. 5005, Dakar Fann, Dakar, Senegal, ‡Laboratoire de Biologie Marine, LABEP-AO, IFAN-Ch. A. Diop, B. P. 206, Dakar, Senegal and §IRD, UMR MARBEC, Université de Montpellier, cc 093, Place E. Bataillon, 34095, Montpellier Cedex 5, France

Age and growth of *Rhizoprionodon acutus* were estimated from vertebrae age bands. From December 2009 to November 2010, 423 *R. acutus* between 37 and 112 cm total length (L_T) were sampled along the Senegalese coast. Marginal increment ratio was used to check annual band deposition. Three growth models were adjusted to the length at age and compared using Akaike's information criterion. The Gompertz growth model with estimated size at birth appeared to be the best and resulted in growth parameters of $L_\infty = 139.55$ (L_T) and $K = 0.17$ year^{-1} for females and $L_\infty = 126.52$ (L_T) and $K = 0.18$ year^{-1} for males. The largest female and male examined were 8 and 9 years old, but the majority was between 1 and 3 years old. Ages at maturity estimated were 5.8 and 4.8 years for females and males, respectively. These results suggest that *R. acutus* is a slow-growing species, which render the species particularly vulnerable to heavy fishery exploitation. The growth parameters estimated in this study are crucial for stock assessments and for demographic analyses to evaluate the sustainability of commercial harvests.

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Key words: age; chondrichthyan; life-history traits; Senegal; vertebrae.

INTRODUCTION

Chondrichthyans play important functional roles in the top−down control of coastal and oceanic ecosystem structure and function (Ferretti *et al.*, 2010; Heithaus *et al.*, 2012). This group is unintentionally caught as by-catch in many fisheries and those sharks could reach 50% of all shark landings (Stevens *et al.*, 2000; Dulvy *et al.*, 2014). More than 700 000 t of cartilaginous fishes are harvested annually worldwide (Frisk *et al.*, 2001). The responses of sharks to an increased harvest pressure differs between species but there is a considerable concern about shark fisheries around the world as their declining catches are mostly attributed to overfishing (Baum *et al.*, 2003). Shark management and conservation are hindered by a lack of knowledge at the population level (Baum *et al.*, 2003), as well as by the lack of basic biological information (Frisk *et al.*, 2001). One of the most captured genera, *Rhizoprionodon*, is represented worldwide by seven species of small coastal carcharhinids (Compagno,

†Author to whom correspondence should be addressed. Tel.: +221 576 11 81; email: balaye81@gmail.com

1984), although only few studies have given consideration to their importance to fisheries (Castillo-Geniz *et al.*, 1998).

The milk shark *Rhizoprionodon acutus* (Rüppell 1837) is the most widely distributed species of this genus, extending all along the West African coast, in the Indo-Pacific, in the northern part of the Indian Ocean, from the Indonesian to the Philippine archipelagos and from Japan to Australia (Compagno, 1984; Capapé *et al*., 2006; Harry *et al*., 2010). The species is common on the West African continental shelf (Capapé *et al.*, 1994, 2006; Ba *et al.*, 2013*a*, *b*) in water depths up to 200 m (Compagno, 1984). It is the most landed shark species on the Senegalese coasts (Ba *et al.*, 2013*a*) and is also known in many countries, but there are very few available data on their populations status or fisheries (Simpfendorfer, 2003).

The life-history traits of this species vary significantly with its geographic location according to the literature: total length (L_T) at first sexual maturity occurs between 65 and 95 cm, and at birth between 30 and 50 cm (Henderson *et al.*, 2006; Valadou *et al.*, 2006; Ba *et al.*, 2013*a*). The reproductive cycle ranges from seasonal (Bass *et al.*, 1975; Capapé *et al.*, 2006; Ba *et al.*, 2013*a*), partially seasonal (Henderson *et al.*, 2006), to fully aseasonal within northern Australian waters (Stevens & Mcloughlin, 1991).

The age and growth estimations are fundamental components of fisheries management, and maximizing their accuracy is critical for stock assessment (Cailliet *et al.*, 2006). The age of chondrichthyan species is usually estimated when interpreting growth increments deposited in calcified structures such as vertebrae, dorsal spines or caudal thorns (Goldman *et al.*, 2012). The timing and periodicity of growth increment deposition must be validated but periodicity is typically annual for chondrichthyans (McAuley *et al.*, 2006) as the mean birth dates are well defined most of the time by the viviparous type of reproduction (Cailliet & Goldman, 2004).

Very few data on the life history of *R. acutus* are available despite the fact that this species is heavily exploited (Simpfendorfer, 2003). Given the importance of life-history information in the development of age structured population models (Goldman *et al.*, 2012), the first objective of this study was to gather information about the age and growth of the *R. acutus* landing along the West African coast using interpretation of growth marks on vertebrae. These data will be useful for designing an effective management strategy for fisheries.

MATERIALS AND METHODS

SPECIMEN COLLECTION

From December 2009 to November 2010, *R. acutus* were sampled monthly from the artisanal fishery catches along the Senegalese coast (Fig. 1). Individuals were captured by using drift nets, surface longlines, sole gillnets and purse seines. Once fishermen landed the *R. acutus*, L_T (cm, stretched total length, from the tip of the snout to the extremity of the caudal fin, along the main axis of the body), total mass (*W*, g), sex and maturity information were recorded. Maturity of males and females were determined macroscopically (Ba *et al.*, 2013*a*). Afterwards, the five largest vertebrae were removed in each individual from the region just below the first dorsal fin, stored on ice and then frozen before treatment at the laboratory.
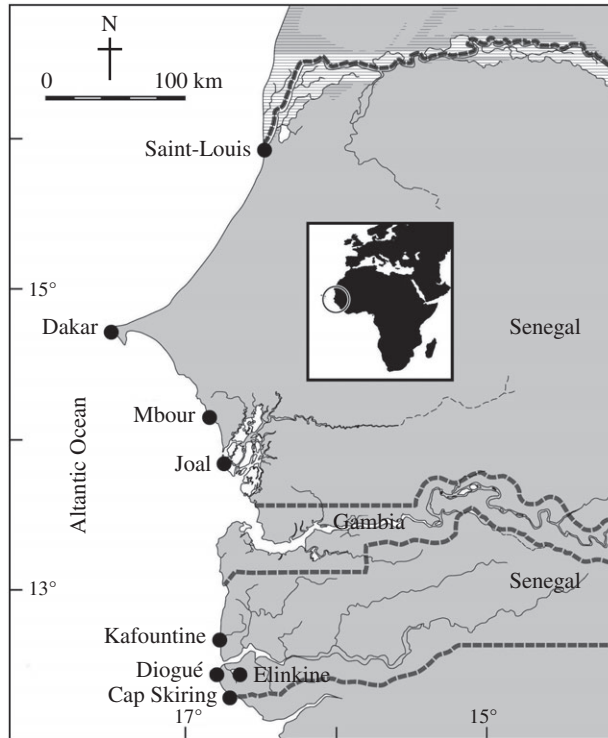
Fig. 1. Sampling locations of *Rhizoprionodon acutus* in Senegal.

PREPARATION AND INTERPRETATION OF VERTEBRAE GROWTH MARKS

In the laboratory, vertebrae were cleaned by immersion in a solution of 5% sodium hypochlorite and by removing adhering tissues under a stereoscope (Huveneers *et al.*, 2013). The minimum immersion time was 30 min in duration and varied depending on the vertebra size, and each one was then washed with water for 30–60 min and air-dried for 24–48 h also depending on its size. The preparation method of vertebrae was specifically developed for this study after different tests. Vertebrae were embedded in polyester resin before being sectioned along the sagittal axis with a low speed diamond saw (Isomet, Buehler; www.buehler.com). Vertebrae sections were then etched with 5% acetic acid for 2 min and then stained with toluidine blue for 5 min before being gently rinsed with water The stained vertebra sections were observed with a stereomicroscope under transmitted light coupled with a 3CCD video camera (Sony DXP; www.sony.com) and a calibrated image of each section was recorded. Vertebral radius (V_R in mm) was measured from the focus along the vertebral body to the edge using the TNPC software (http://www.tnpc.fr/en/visilog.html).

AGE ESTIMATION AND VALIDATION

To avoid bias interpretation, growth increments (thin stainable bands) were interpreted and counted without prior knowledge of the L_T or sex of the specimens. The same reader interpreted all vertebrae sections twice. The average percentage of error (E) between readings was calculated using the Beamish–Fournier (1981) formula: $E = 100R^{-1} \sum\limits_{i=1}^{R} \left| X_{ij} - \overline{X}_j \right| \overline{X}_j^{-1}$,

where X_{ij} is the ith age estimation of the jth fish, $\overline{X}_j$ is the mean age of the jth fish and R is the number of times each fish is aged. Chang (1982) suggested incorporating the S.D. in the previous equation rather than the absolute deviation from the mean age. The resulting equation produces an estimate of the coefficient of variation (C.V., X) of consecutive readings:

$$X = 100 \left[\left(\sqrt{\sum_{i=1}^{R} \left(\left(X_{ij} - \overline{X}_j \right) (R-1)^{-1} \right)^2} \right) \overline{X}_j^{-1} \right].$$

Each growth cycle included a thin dark-stained band (translucent and more chromophilic band) and a large band (opaque and less chromophilic band) that were considered together as one annual cycle before the subsequent validation. The thin dark-stained band, ring, was counted for age estimation. The radius along the vertebral body was measured starting from the focus to the edge, the number of rings was counted along this axis and the distance between the vertebra focus and each ring was also measured. The 0+ year age class corresponding to the first distinct stained band defined as the birthmark was excluded from this analysis to ensure that growth from the birthmark did not affect the results. The distance from the last stained band to the vertebra edge was measured along the vertebral body in order to validate the timing of the band deposit. The mean marginal increment ratio (I_M) for each month was plotted for females and males to determine if there was a yearly pattern in margin width (Natanson *et al.*, 1995; Liu *et al.*, 1999) using the following equation: $I_M = (V_R - R_n)(R_n - R_{n-1})^{-1}$, where V_R is the distance between the focus and the edge of the vertebra (in mm), R_n the distance between the focus and the last chromophilic band (in mm) and R_{n-1} is the distance from the centra to the penultimate band. Differences among monthly mean I_M were tested for heteroscedasticity by Bartlett's test and a non-parametric Kruskal–Wallis one-way ANOVA was used to test for differences in I_M by months (Simpfendorfer *et al.*, 2000; Sulikowski *et al.*, 2005). Monthly mean size was compared by one-way ANOVA. A Kolmogorov–Smirnov test was used to compare L_T frequency distributions between males and females. The relationship between L_T and V_R was calculated using linear regression analysis. An ANCOVA was used to compare the allometric relationships between sexes.

GROWTH MODELS

Since the parturition season of *R. acutus* may occur from May to June along the Senegalese coast (Capapé *et al.*, 2006; Ba *et al.*, 2013*a*), the mean birth date was set as 1 May in this study. Three growth models were adjusted to the length-at-age data for comparison and selection, and one to mass-at-age data. All models were fitted separately for males and females as sex differentiation is recognized for shark species. The first model was the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938): $L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right]$, where L_t is the predicted length-at-age t, L_∞ is the asymptotic length, K is the growth coefficient and t_0 is the x-intercept. Two Gompertz models (Mollet *et al.*, 2002), one with fixed size at birth (GGF1) and the other with estimated size at birth (GGF2), were fitted to length-at-age data for comparison, and given by the following equation: $L_t = L_b e^{\left[\ln \left[L_\infty L_b^{-1} \right] \left[1 - e^{(-Kt)} \right] \right]}$, where, in the first version of the Gompertz model (GGF1), L_b is the published size at birth 39 cm (L_T) (Capapé *et al.*, 2006), and the other parameters are as described above. In the second version of the Gompertz model (GGF2), the estimated size at birth (L_0) replaced the published birth length (L_b), and was calculated from the published length at birth (L_b) using the estimated parameters (L_∞, K and t_0) of the VBGF, and given by the formula: $L_b = L_\infty \left[1 - e^{(K \times t_0)} \right]$, where K is the growth coefficient and t_0 is the x-intercept. Bias between published size at birth and estimated size at birth was defined as the ratio of L_b and L_0 (*i.e.* $L_b L_0^{-1}$) (Pardo *et al.*, 2013).

Mass-at-age data was modelled with a modified VBGF (Ricker, 1979): $W_t = W_\infty \left[1 - e^{-K(t-t_0)} \right]^3$, where W_t is the mass-at-age t, W_∞ represents theoretical asymptotic mass and the other parameters are as previously defined.

Coefficient of determination values (r^2) were used in order to compare the fit of non-linear regression models described above with that of a linear intercept-only model, and as indicators
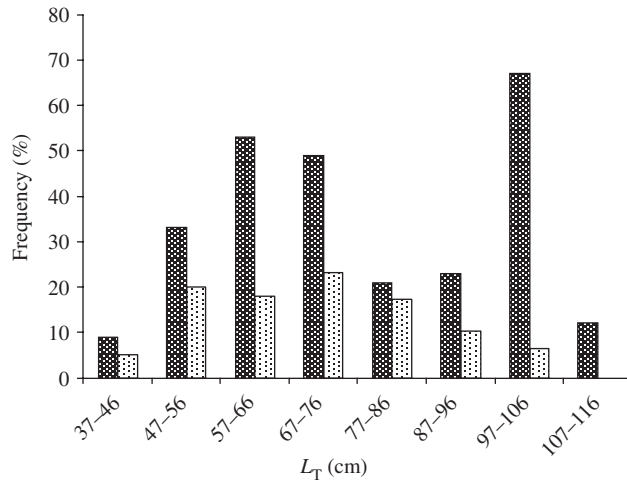
FIG. 2. Total length (L_T) frequency for *Rhizoprionodon acutus* sampled during this study [▨, females, $n = 267$; ▨, males, $n = 156$].

of the proportion of the total variation in L_T that is explained (or accounted for) by regressions with age (Kvalseth, 1985): $r^2 = 1 - \left[\sum \left(y - \hat{y} \right)^2 \right] \left[\sum \left(y - \bar{y} \right)^2 \right]^{-1}$.

The three growth models fitted to length-at-age data were discriminated within a model selection framework using the small-sample corrected Akaike's information criterion (AIC$_c$) (Burnham & Anderson, 2002). AIC$_c$ (X) is given by the following equation: $X = n \log(Z)n^{-1} + 2p[n(n - p - 1)^{-1}]$, where Z is the residual sum of squares, p is the number of fitted parameters in the model (plus one for the estimated variance) and n is the sample size. The model with the lowest AIC$_c$ is considered to fit the data best. All models were fitted separately for males and females as sex differentiation is recognized for shark species and all statistical analyses and model adjustments were preformed with the Statistica software (www.statsoft.com).

RESULTS

MORPHOLOGICAL MEASUREMENTS

A total of 267 females and 156 males of *R. acutus* were sampled. The L_T of females (63·1% of the total sample) was comprised between 38 and 112 cm and that of males (36·9% of the total sample) between 37 and 104 cm (Fig. 2). Mean $\pm$ S.E. L_T for the whole sample was $78·14 \pm 19·86$ cm for females and $70·26 \pm 14·86$ cm for males. A significant difference was found in the monthly comparison of female sizes (ANOVA, $F_{1,11} = 4·76$, $P < 0·05$) and male sizes (ANOVA, $F_{1,11} = 3·11$, $P < 0·05$). The L_T frequency distributions were different between males and females, females being generally larger (Kolmogorov–Smirnov, $P < 0·05$). The relationship between L_T and V_R for males and females was significantly different (ANCOVA, $F_{2,425} = 1·03$, $P < 0·05$); therefore, all subsequent models were fitted separately for males and females. The linear regression was $L_T = 6·843V_R + 28·276$ ($r^2 = 0·87$) for females and $L_T = 6·364V_R + 29·872$ ($r^2 = 0·76$) for males.
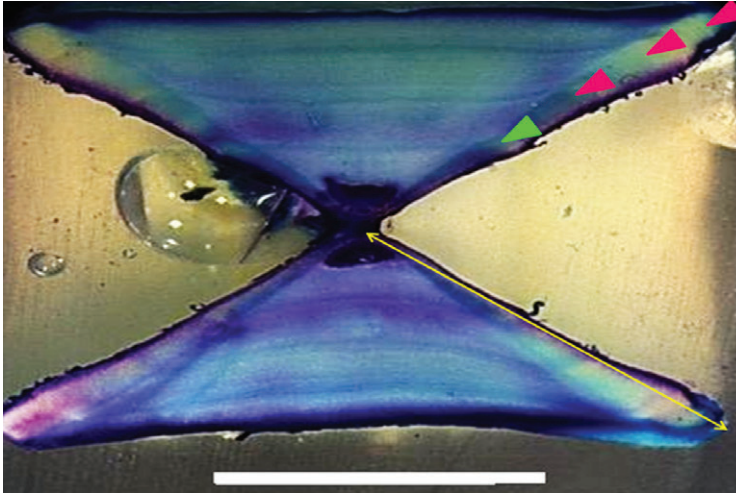
FIG. 3. Sagittal stained section of a vertebrae from a male *Rhizoprionodon acutus* (total length, $L_T = 66$ cm) with three interpreted growth bands. This individual was estimated to be 3 years old. ➤, birthmark; ➤, interpreted growth bands for age estimation; ↔, the vertebral body. White scale bar = 5 mm.

VERIFICATION OF GROWTH BAND PERIODICITY AND AGE ESTIMATION

Stained growth bands were visible on the vertebrae and were numbered along the vertebral body (Fig. 3). If bands were not clearly visible and interpretable, the corresponding vertebrae were excluded from the analysis. The average per cent error (APE) value ranged from 2·99% (for the 2+ year class, $n = 45$) to 1·61% (for the 4+ year class, $n = 69$), with a mean APE of 1·55% for the whole sample between the two readings. The C.V. value ranged from 4·22% (for the 2+ year class, $n = 45$) to 2·28% (for the 4+ year class, $n = 69$) with a mean C.V. of 2·20% for the whole sample between the two readings. These values gave enough precision of the results and then allowed age estimation using the chromophilic growth bands.

Significant differences were found in the marginal increment I_M among months for females (Kruskal–Wallis, $H = 47·98$, d.f. = 11, $P < 0·05$) and males (Kruskal–Wallis, $H = 30·50$, d.f. = 11, $P < 0·05$). The distance between the last stained band and the vertebra edge showed an annual increase until May for females and June for males followed by a decrease until August for females and September for males (Fig. 4). The lowest I_M was recorded in August and September for females and males, respectively, assuming that the stained band was formed annually in this period for both sexes.

GROWTH ESTIMATION

Age estimation showed that the young individuals dominated the whole sample (Fig. 5). The three growth models used in this study (VBGF, GGF1 and GGF2) fitted the data well for growth in length ($0·65 < r^2 < 0·85$; Table I). Based on the AIC_c values incorporating separate parameter estimates for each sex, the GGF2 outperformed the GGF1 and the VBGF (Table I) and fitted the best model length-at-age data. For both the sexes, the standard VBGF-estimated L_∞, 152 and 117 cm for females and
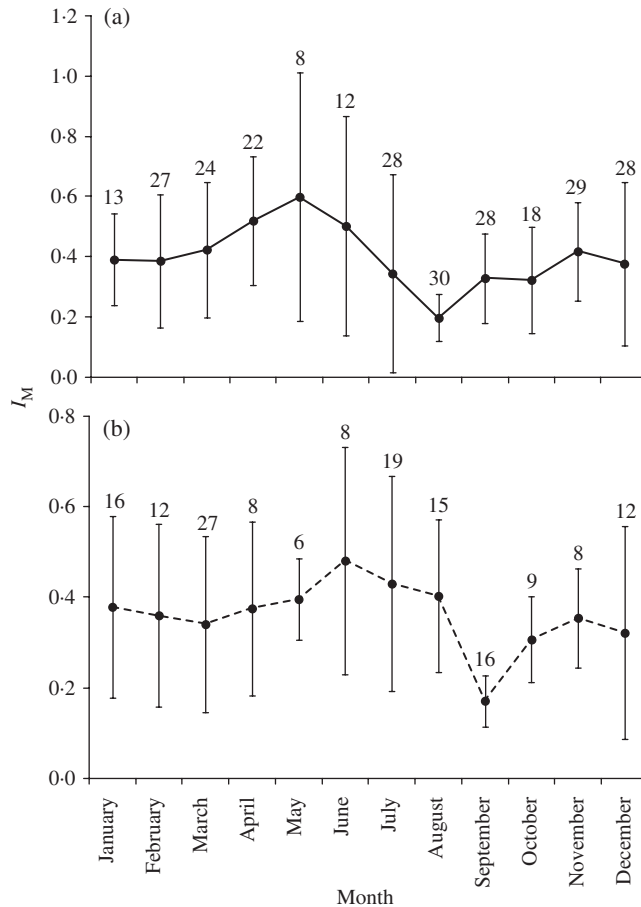
FIG. 4. Mean ± s.e. monthly marginal increment ratio (I_M) for (a) female ($n = 267$) and (b) male ($n = 156$) *Rhizoprionodon acutus*. Numbers indicate sample size,

males, was higher than the observed maximum, 112 and 104 cm for females and males [Table I and Fig. 6(a)]. The GGF models produced a larger asymptotic size for females than males [Table I and Fig. 6(b), (c)]. For females, both estimated and fixed size at birth in the GGF models, L_∞ (139 and 125 cm), were significantly higher than the observed maximum length of 112 cm. For males, the L_∞ estimated with GGF2 (126 cm) was significantly larger than the observed maximum length of 104 cm, while for the GGF1 (105·06 cm), it was almost similar to the observed maximum length. The maximum observed age was 9 years for females (106 cm L_T) and 8 years for males (104 cm L_T) (Fig. 6). Bias between published size at birth and estimated size at birth given by the ratio $L_b L_0^{-1}$ were 0·86 and 0·82 for females and males.

For both forms of the GGF model, the growth coefficient in length at age was higher for males (0·29 and 0·18 for GGF1 and GGF2) than females (0·23 and 0·17 for GGF1 and GGF2; Table I). The growth model used in this study fitted the data well for growth in mass (0·68 < r^2 < 0·70; Table I). The mass asymptotic value of females was 9150 g, whereas that of males was 7755 g (Fig. 7). For both sexes, asymptotic mass estimated
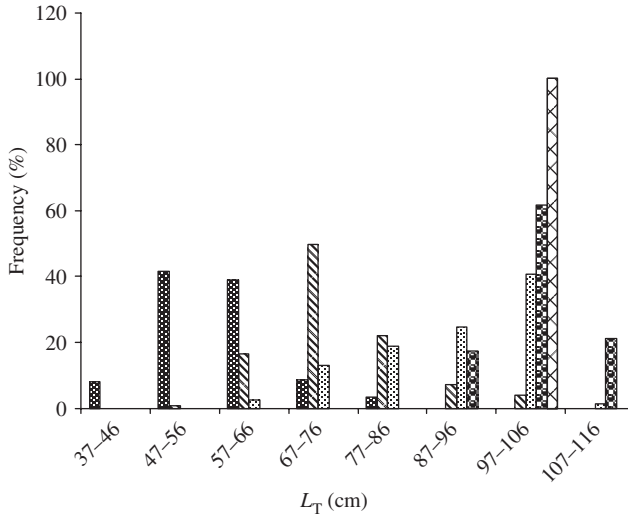
FIG. 5. Total length (L_T)–frequency of *Rhizoprionodon acutus* by age classes (▨,1 + 2 years; ◫, 3 + 4 years; ▩, 5 + 6 years; ▨, 7 + 8 years; ▧, 9 + years; $n = 423$).

values were higher than the maximum observed masses (7000 g for females and 5300 g for males). The growth coefficients in mass for both males and females were almost similar (Table I). After the fifth year, mass gain of females was higher than males (Fig. 7). The evolution of the monthly mean mass showed the smaller increase during the months of June and July. This period of reduced overall growth corresponded with the deposition of a stainable band in the vertebrae in August and September.

DISCUSSION

RHIZOPRIONODON ACUTUS AGE ESTIMATION AND VERIFICATION

This study has provided estimates of age and growth for *R. acutus*, a coastal shark species, which is the most landed shark species along the Senegalese coast and easily accessible to small-scale fisheries (Capapé *et al.*, 2006; Ba *et al.*, 2013*a*). This is the first comprehensive study of age and growth for age estimation in this species in West African waters. It used stained growth bands on vertebrae for this purpose.

The values of indices comparing consecutive interpretations of vertebrae growth bands (APE and C.V. in this study) indicated a very good precision for the age estimation of *R. acutus* with stained bands distinguishable on vertebrae. Cailliet & Goldman (2004) mentioned that there has been an increase in the use of both verification and validation methodologies in chondrichthyan age and growth estimation studies, such as the use of the marginal increment ratio. The hypothesis of annual growth increment deposition has been supported in this study by the marginal increment ratio on the vertebrae edge. This method demonstrated that a unique growth band, consisting of one thin stained band, was formed annually. The minimal width of the marginal

TABLE I. Growth model parameters [asymptotic length (L_∞) and mass (W_∞), growth coefficient (K)]: von Bertalanffy growth function (VBGF) for total length (L_T, cm) and mass (g), and Gompertz growth model (with fixed size at birth (GGF1) and estimated size at birth (GGF2) for L_T, for male and female *Rhizoprionodon acutus*

Models	Sexes	Parameters	Estimation	S.E.	*t*-values	*P*	r^2	AIC_c
VBGF	Females	L_∞	152·21	15·89	9·58	<0·001		1098·90
		K	0·11	0·03	4·42	<0·001	0·85	
		t_0	−2·72	0·44	−6·24	<0·001		
	Males	L_∞	116·83	13·29	8·79	<0·001	0·76	627·11
		K	0·17	0·05	3·27	<0·001		
		t_0	−2·27	0·59	−3·82	<0·001		
GGF1	Females	L_∞	125·98	4·05	31·03	<0·001	0·85	480·87
		K	0·23	0·01	16·97	<0·001		
	Males	L_∞	105·06	4·64	22·631	<0·001	0·77	478·99
		K	0·29	0·02	11·00	<0·001		
GGF2	Females	L_∞	139·55	6·9	20·05	<0·001	0·85	469·49
		K	0·17	0·01	12·87	<0·001		
	Males	L_∞	126·52	12·52	10·10	<0·001	0·78	466·34
		K	0·18	0·02	6·63	<0·001		
Mass VBGF	Females	W_∞	9148·59	1809·37	5·06	<0·001	0·68	1739·36
		K	0·19	0·04	4·47	<0·001		
		t_0	−0·51	0·55	−0·93	>0·05		
	Males	W_∞	7756·27	2528·27	3·07	<0·001	0·70	1621·19
		K	0·20	0·07	2·94	<0·001		
		t_0	−0·57	0·73	−0·78	>0·05		

AIC_c, Akaike information criteria.

increment was recorded for *R. acutus* captured in August for females and in September for males. The edge analysis supported the hypothesis that bands were formed at the end of the rainy season (May to September). An annual periodicity for growth band formation is common in temperate and subtropical shark species (Branstetter, 1987*a*; Simpfendorfer *et al.*, 2002; Wintner *et al.*, 2002; Joung *et al.*, 2004; McAuley *et al.*, 2006). This was also verified for different species of the *Rhizoprionodon* genus: *Rhizoprionodon taylori* (Ogilby 1915) in Australia (Simpfendorfer, 1993), the Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson 1836) in the Gulf of Mexico (Branstetter, 1987*b*; Carlson & Baremore, 2003) and in the south-eastern U.S.A. (Loefer & Sedberry, 2003). This annual growth band deposition is often seen in other species having a seasonal reproductive cycle similar to *R. acutus* (Capapé *et al.*, 2006; Ba *et al.*, 2013*a*). Despite this result, further validation of the annual periodicity of the ring pattern observed in *R. acutus* could also be added through techniques such as chemical marking, bomb carbon dating or tag–recapture studies.

RHIZOPRIONODON ACUTUS GROWTH

Multiple growth functions are often calculated and compared in order to characterize adequately the growth of a given species (Cailliet *et al.*, 2006; Katsanevakis, 2006; Diouf *et al.*, 2009). The three growth models used in this study (VBGF, GGF1 and
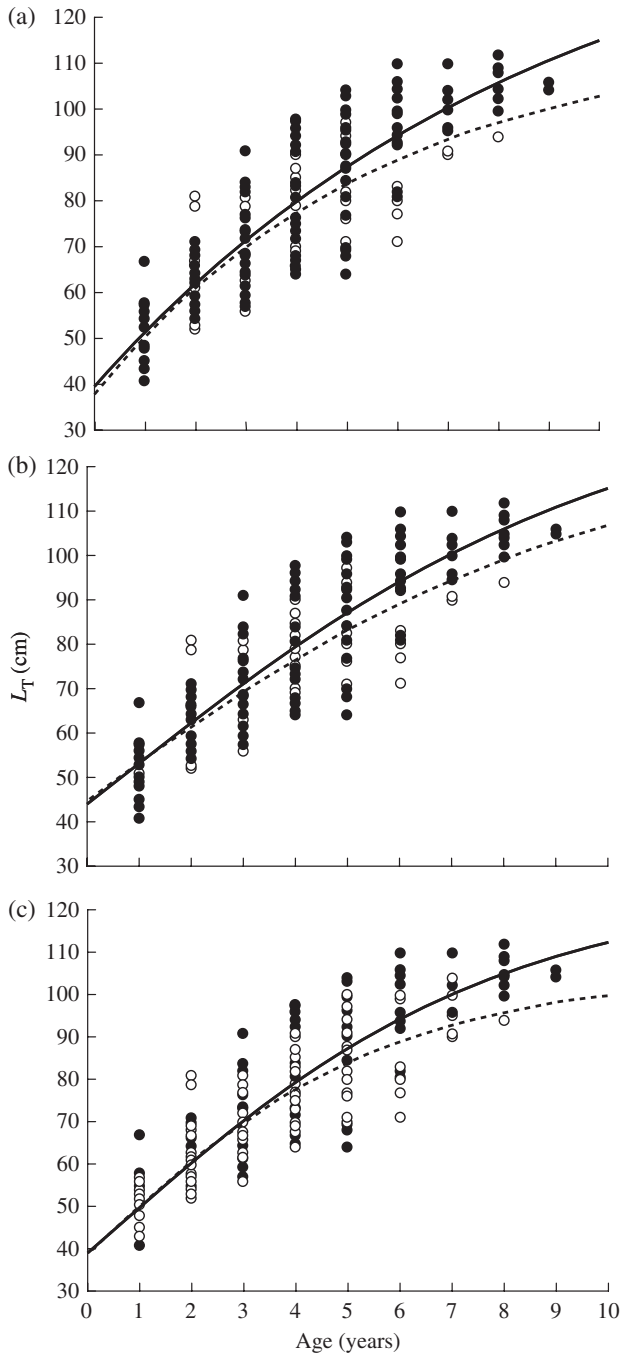
FIG. 6. Growth model curves (a) von Bertalanffy growth function (VBGF), (b) GGF1 and (c) GGF2 of females (●——; $n = 267$) and males (○----; $n = 156$ from observed total length (L_T)-at-age data for *Rhizoprion-odon acutus* in West African waters (see Table I).
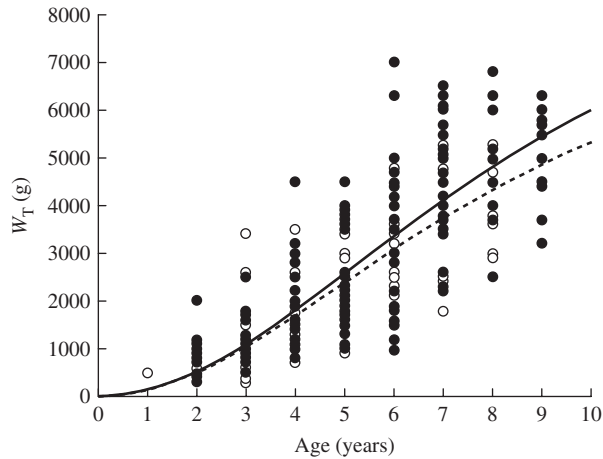
FIG. 7. von Bertalanffy growth modelling in mass of females ($\bullet$ ——; $n = 267$) and males ($\circ$ - - - -; $n = 156$)
Rhizoprionodon acutus in West African waters (see Table I).

GGF2) fitted the data well for growth in length and mass. The Gompertz model with
an estimated size at birth (GGF2), however, was the best model with no uncertainty as
indicated by AIC_c values (Table I). Even if the von Bertalanffy model is most often used
to describe fish growth, an increasing number of elasmobranch studies indicated that
the Gompertz model might better describe their growth (Mollet *et al.*, 2002; Wintner
et al., 2002; Cailliet *et al.*, 2006; Katsanevakis, 2006). The Gompertz model is then
commonly used as growth function for Chondrichthyans (Mollet *et al.*, 2002; Braccini
et al., 2007) and is then particularly relevant for comparisons. Cailliet *et al.* (2006)
recommended using the size at birth in the growth models instead of t_0, because it
can be biologically meaningful. The L_0 values calculated in this study for both sexes
were biologically reasonable compared with the published data on size at birth for this
species in this area (Capapé *et al.*, 2006; Ba *et al.*, 2013a). The ratio of L_b and estimated
L_0 with values <1 for both sexes indicated no severely biased growth estimates as it
was shown for other shark species (Pardo *et al.*, 2013).

Based on the growth rate values, *R. acutus* have a relatively slow growth rate along the
Senegalese coast. Other studies of *Rhizoprionodon* spp. have estimated a wide range
of K values, from 0·17 to 1·34 for males and 0·16 to 1·01 for females (Table II). Com-
parison of *R. acutus* growth rates from this study with others suggested that *R. acutus*
is a comparatively slow or intermediate growing species. Growth rates also vary exten-
sively within species depending on local water temperature and productivity (Barker
et al., 2005). The K values of the GGF2 estimated in this study were different from
those estimated in Australia for *R. acutus* and from other species of the genus (Harry
et al., 2010). Geographic variation is a possible factor which could account for growth
differences between areas as it was documented for other shark species, *Sphyrna tiburo*
(L. 1758) (Lombardi-Carlson *et al.*, 2003) and *Carcharhinus limbatus* (Müller & Henle
1839) (Carlson & Sulikowski, 2006). Growth curves change in response to environ-
mental conditions and fishing pressure. *Rhizoprionodon acutus* in West Africa with a
slower growth rate, size and age of maturity higher in comparison with the population
in Australia (Harry *et al.*, 2010) and all other species of the genus, is likely to become

TABLE II. Growth parameters of *Rhizoprionodon* species reported in the literature

Species	L_∞ (cm)	K (year^{-1})	n	Authors	Region (or oceanic basin)
Rhizoprionodon acutus	126·5 (M)/139·5 (F)	0·18 (M)/0.17 (F)	156 (M)/267 (F)	This study	Senegalese coast
R. acutus	82·1 (M)/86·1 (F)	0·94 (M)/0·63 (F)	127 (M)/38 (F)	Harry *et al.* (2010)	North-eastern coast of Australia
Rhizoprionodon lalandii	78·1	0·3	84	Lessa *et al.* (2009)	Northern coast of Brazil
Rhizoprionodon porosus	112·9	0·17	134	Lessa *et al.* (2009)	
Rhizoprionodon terraenovae	92·5	0·45	215	Parsons (1985)	North central Gulf of Mexico
R. terraenovae	108	0·36	20	Branstetter (1987*a*)	Laboratory aquaria
R. terraenovae	94	0·85 (M)/0·63 (F)	304	Carlson & Baremore (2003)	Gulf of Mexico
R. terraenovae	98·3 (M)/98·8 (F)	0·50 (M)/0·49 (F)	116 (M)/123 (F)	Loefer & Sedberry (2003)	South-eastern U.S.A.
Rhizoprionodon taylori	65·2 (M)/73·2 (F)	1·34 (M)/1·01 (F)	52 (M)/85 (F)	Simpfendorfer (1993)	North Queensland, Australia

M, males; F, females.

heavily exploited and more sensitive to overexploitation. Carlson & Baremore (2003) have shown a decrease in the size at maturity and an opposite trend in the growth rate of *R. terraenovae*. In this study, both parameters have shown a downward trend for *R. acutus*. For Carlson & Baremore (2003), the increase in growth rate of *R. terraenovae* resulted from a decrease in the competition in the Gulf of Mexico with an increase of food availability; this does not appear to be the case in this study for *R. acutus*. *Rhizoprionodon acutus*, similar to the lemon shark *Negaprion brevirostris* (Poey 1868), might be an exception to slow-growing species, which are found in subtropical and tropical waters (Simpfendorfer *et al.*, 2002). According to those authors, carcharhinid species with slower growth rates spend some or all of their time in temperate waters, whereas those with faster growth rates are more often found in tropical waters. According to Branstetter (1990), slow-growing and coastal species, such as *R. acutus*, protect their nurseries as it is the case for other sharks along the Senegalese coast (Capapé *et al.*, 2006). Length-selective fishing mortality could explain the observed differences in growth curves (Walker *et al.*, 1998). The decrease of growth rates could result in an artificial selection by the fishing gears (Moulton *et al.*, 1992). Many data have highlighted and reinforced the understanding that species with slower growth rates and later ages of maturity, such as *R. acutus*, are more susceptible to possible extinction risks (Cortés, 2000; García *et al.*, 2008). Consequently, management measures must be implemented for this species.

The older females observed in this study were 9 years ($L_T = 106$ cm) and the older males were 8 years ($L_T = 104$ cm). In Australia, maximum ages were younger for females (8·1 years) and for males (4·5 years) (Harry *et al.*, 2010), the individual sizes being smaller in this area. Asymptotic lengths predicted by the GGF2 were higher than the observed maximum lengths for both sexes; this pattern could result from the lack of large specimens in the landings. The 1–3 year-old fish, due to either sampling effects or fishing pressure, dominated the age structure (Fig. 5).

The data on growth in mass of *R. acutus* are the first available and will be very useful for management of this species. The results of this study suggest that *R. acutus* tended towards W_∞ but grew very little in mass at older ages. According to this study, growth gain of females was greater than that of males, confirming the sexual dimorphism for this species (Capapé *et al.*, 2006; Ba *et al.*, 2013a). The variation of asymptotic mass between males and females might be related to the sex-specific preferences in the food-searching sites. As females have larger stomach, this may influence the mass of the animals (Ba *et al.*, 2013b). This feature could also be explained by the need for females to reach a larger size to support embryos because of their viviparity (Walmsley-Hart *et al.*, 1999; Ba *et al.*, 2013a).

CONSEQUENCES FOR *R. ACUTUS* EXPLOITATION

The results of this study, and particularly the slow estimated growth rate, provide evidence of variable growth rate of this species over its distribution area (Walker *et al.*, 1998). Stevens *et al.* (2000) reported a possible change in the growth of sharks and batoids resulting in selective fishing mortality. Length-selective fishing mortality with the effect of altering the length–frequency composition of sharks in particular age classes of the wild population could explain the differences in the growth rates of *R. acutus* between locations (Moulton *et al.*, 1992). As observed by Walker *et al.* (1998), small sharks swim through gillnets but become progressively more vulnerable

to capture as they grow. The gillnets, the main fishing gear used along the Senegalese coast to capture *R. acutus* (Ba *et al.*, 2013*a*), have the effect of culling a higher proportion of slower-growing sharks among the older population (Stevens *et al.*, 2000). Density-dependent factors could cause a change in the growth of a population due to exploitation. This effect could explain the size and age structure of *R. acutus* in this study (Svedäng & Hornborg, 2014). Reduction of the growth rate could also result from differences in fishing intensity, with greater exploitation rates causing smaller sizes (at maturity and maximum) through density-dependent compensation or simply artificial selection for smaller sizes (Olsen *et al.*, 2004). Ba *et al.* (2013*a*) observed a reduction in the size range of *R. acutus* in the study area as it has been shown in other species of the genus (Carlson & Baremore, 2003; Motta *et al.*, 2005). Therefore, precautionary measures should be taken into account for this overexploited species and special management actions should be undertaken to ensure its sustainability (Rose *et al.*, 2001).

A hypothesis of seasonal enrichment of the continental shelf followed by different predator species with an increase of interspecific and intraspecific competition could lead to the low growth rates of *R. acutus* (Walker *et al.*, 1998; Ba *et al.*, 2013*a*). This result is highlighted by the numerous proportion of individuals with empty stomachs throughout the year for this species (Ba *et al.*, 2013*b*). The decreasing food availability for *R. acutus* along the Senegalese coast could lead starving individuals to approach and be caught by baited fishing gear; this may have consequences on growth. An opposite trend was exhibited for its congener *R. terraenovae* in the Gulf of Mexico (Carlson & Baremore, 2003). Low growth coefficients for *R. acutus* reported in this study could provide indices of fisheries overexploitation and might lead to changes in its ecosystem status in this region (Shepherd & Myers, 2005). Musick (1999) noted that species with a K coefficient close to 0·1 are very vulnerable to overexploitation and the value in this study was not very far from 0·1. Even though differences in vertebral preparation samples and in band counting could produce variation in the growth rates, this study showed a low growth rate for *R. acutus* in relation to other *Rhizoprionodon* species, especially tropical species (Carlson & Baremore, 2003). Notwithstanding these previous hypotheses to explain low growth rate, it is difficult to evaluate the relative effects of all the potential causes of growth rate reduction.

Age at maturity is also a critical variable for demographic modelling of elasmobranch populations, and therefore for fisheries management. The size at the first sexual maturity was 92·5 cm L_T for females and 82 cm L_T for males along the Senegalese coast (Ba *et al.*, 2013*a*). These values correspond to individuals of 5·8 and 4·8 years for females and males, not far from their maximum ages. Such information can have important effects on stock assessments and fishery models (Musick, 1999; Campana, 2001). Harry *et al.* (2010) estimated the age at first sexual maturity using the mean-adjusted age at first band at 1·6 years for females and 1·0 years for males. Surprisingly, these values are very far from the present data (5·8 and 4·8 years for females and males, respectively). For other *Rhizoprionodon* species, male and female *R. taylori* matured after only 1·0 years (Simpfendorfer, 1993), *Rhizoprionodon lalandii* at 3·3 years, *Rhizoprionodon porosus* at 2·6 years (Lessa *et al.*, 2009) and *R. terraenovae* at 2·6 years (Loefer & Sedberry, 2003). The previous estimations of age at maturity gave younger ages, and the evolution of this age, which is probably linked with overexploitation, should be checked carefully. Life-history traits, such as slow growth rates, mean that many sharks have a low resilience to fishing mortality, being more susceptible to overfishing

than most teleosts and invertebrate species (Musick *et al.*, 2000; Frisk *et al.*, 2001). In addition, *R. acutus* gathers in schools by sex and reproductive state (Ba *et al.*, 2013*a*), so that fishing may deplete large segments of particular age classes or sexes, including reproductively active segments (Heyman *et al.*, 2001). Management of the *R. acutus* fishery may need to incorporate this new data into fishing management practice, also taking into account differences between sexes.

Consequently, more efforts to increase the knowledge of the population biology of *R. acutus* should be made in order to ensure its sustainable management. This study provides the first detailed estimates of age and growth for *R. acutus* in West African waters, and should be used in further stock evaluations in this region.

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