

Age estimation and growth pattern of the grouper *Cephalopholis taeniops* (Epinephelidae) off the Cape Verde Archipelago, north-west Africa

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The grouper Cephalopholis taeniops is a carnivorous fish of the Cape Verde coastal marine ecosystem. Nothing is known regarding the age and growth of this epinephelid. In this study, the age and growth of C. taeniops was investigated by annual growth increment counts from 2804 specimens (7–51 cm total length) collected between January 2005 and December 2011. Whole otoliths underestimated the age indicated in sections by approximately 70%; therefore, sectioned otoliths were used in this study. A year's growth was represented by one opaque and one translucent ring. There was no apparent time lag from the start of the increase in the seawater temperature and the beginning of the formation of the opaque ring. The formation of the translucent rings coincided with a decrease in surface seawater temperature. Cephalopholis taeniops is a slow-growing and long-lived species, with ages of up to 20 years recorded. The seasonalized von Bertalanffy growth function was the best fitted among the four models tested, with an Akaike weight higher than 0.99. Growth was described by the seasonalized von Bertalanffy growth function as follows: $L_{\infty} = 54.26$ cm, $k = 0.135$ year⁻¹, $t_0 = -0.853$ year, $C = 0.439$ and $t_s = 0.667$.

Keywords: Epinephelidae, *Cephalopholis taeniops*, otoliths, age, growth, seasonalized von Bertalanffy growth function, Cape Verde Islands, Eastern Central Atlantic

Submitted 4 November 2013; accepted 1 September 2014; first published online 9 October 2014

INTRODUCTION

Groupers are of great importance in the marine ecosystems of all of the subtropical and tropical seas, and they play a basic role in the food chain because they are often one of the largest carnivores of the ecosystems in which they reside (Grandcourt *et al.*, 2009; Erisman *et al.*, 2010; Craig *et al.*, 2011). They are important to both commercial and recreational fisheries worldwide (Heemstra & Randall, 1999). As with other predatory fishes, grouper populations have been depleted by overfishing, the destruction of both juvenile and adult habitats, ineffective management plans for their fisheries or the lack of any management policies at all (Sadovy *et al.*, 2013). Grouper ecology is well-known in general, but detailed information on biological characteristics is scarce for many species.

The grouper *Cephalopholis taeniops* (Valenciennes, 1828) is a demersal species found in shallow tropical rocky reefs and sandy bottoms up to 200 m depth in the eastern Atlantic from the western Sahara to Angola, including Cape Verde and São Tomé and Príncipe islands (Rocha *et al.*, 2008; Craig *et al.*, 2011). It is a large-sized carnivorous species (Tariche, 2002; Brito *et al.*, 2011).

Cephalopholis taeniops is an important component of the Cape Verdean fisheries (Tariche, 2002). It is caught throughout the year and all over the archipelago by artisanal fishermen, mainly with handlines, and it is sold fresh in local markets. Artisanal fishermen have historically used the same size S-hook (7–9) for catching this species. The sustainable level of catches was estimated at 99 tons (Tariche, 2002); however, catches of this species increased from 50 to 375 tons during the period from 1986–2002. This high level of exploitation has produced a decrease in its abundance and size, and specimens are a lower proportion of the total abundance and biomass of the fishery (Tariche, 2002).

For this species, Siau (1994) described its sexual development and population structure in Senegal, Tariche (2002) studied aspects of the life history in the Cape Verde archipelago, Pereira *et al.* (2012) determined length–weight relationships in the Cape Verde islands, and Lino *et al.* (2011) researched its movement patterns on artificial reefs in the Cape Verde region. No information on age, growth or longevity exists, and it has been listed by the IUCN as a Data Deficient status (Rocha *et al.*, 2008). Understanding factors related to age, growth and longevity are particularly important for the management and conservation of groupers (Sadovy, 1997). Therefore, acquiring data on variables such as age composition, growth rate and lifespan are necessary to determine the vulnerability of each species to exploitation or create even the simplest management regulations (Young *et al.*, 2006).

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The lack of biological data on *C. taeniops* is particularly worrying because the correct management of biological resources should be grounded in the most complete information possible about the ecology of the species involved. For this reason, the goal of this paper is to estimate the age composition, longevity and growth rate of the population of *C. taeniops* from the Cape Verde Islands by means of otolith studies and applying indirect age validation methods to support the accuracy of the age estimates. These results may contribute to a better understanding of the ecology of this poorly understood species, and can be used to implement management rules.

MATERIALS AND METHODS

Sample collection

A total of 2804 individuals of *C. taeniops* from the islands of São Vicente and Santa Luzia (Cape Verde Islands, north-west Africa) (Figure 1) were sampled between January 2005 and December 2011. Of these, 2788 fish were caught by the local artisanal fleet with handlines at depths of 5–180 m. The remaining 16 individuals were collected with hand nets at depths of 2–5 m in a sampling which aimed to capture small fish during a fishing survey around these islands in April 2010 (cruise Cabo Verde 2010-04, Project PROACTIVA).

Each fish was measured to the nearest mm for total length (TL) and weighed to the nearest g for total mass (TW). Sagittal otoliths were removed, cleaned and stored dry for later age determinations.

Otoliths interpretation

A subsample of 173 specimens from 13 to 51 cm TL was studied to determine the most adequate age reading method, either between whole otoliths or on 1 mm otolith sections. The subsample was compared using an age bias plot and a paired *t*-test analysis, and the five section-based age categories 1–4, 5–8, 9–12, 13–16 and 17+ years were estimated (Campana *et al.*, 1995; Campana, 2001). Otoliths were sectioned by their frontal plane following that of the fish (Wright *et al.*, 2002) and prepared according to McCurdy *et al.* (2002).

A binocular magnifying glass was used ($\times 10$) to conduct the readings. Whole otoliths were read on the concave part on the upper side (distal face) using reflected light. Otolith sections were read using reflected light. Prior to these readings, different liquids, which included seawater, ethanol and glycerol, were used in some otoliths to enhance the appearance of growth rings. Burning and staining techniques were also applied to enhance the appearance of growth rings (McCurdy *et al.*, 2002). There were no differences in the readings with different techniques for the enhancement of the growth rings; therefore, seawater was adopted as the standard protocol.

Finally, *annuli* were counted on otolith sections following the transverse axis. All sections were aged twice by two readers without prior information on length or time of capture. When counts did not agree, a third reading was performed, and the two concurring readings were accepted as the age of the fish. When the three counts differed, the otolith was

rejected from further analysis. In this comparison, readings were conducted in a random order (Dwyer *et al.*, 2003). Data obtained from each of the readings were recorded in independent files, following Morales-Nin & Panfili (2002a).

The marginal increment (distance from the inner margin of the outermost translucent ring and the periphery of each otolith, MI) was measured on otolith sections with an ocular micrometre (Figure 2). Measurements were always made along the longest axis of the otolith.

Data analysis

The bias and precision of *annuli* counts were compared between readers, using paired *t*-tests and age bias plots (Campana *et al.*, 1995; Campana, 2001). For each paired comparison, a coefficient of variation (CV) was also used to measure precision, together with a paired *t*-test to compare differences statistically (Chang, 1982; Dwyer *et al.*, 2003).

To validate the periodicity in the increment formation at each age class, a marginal increment analysis was performed (Panfili & Morales-Nin, 2002). Owing to the wide range of ages encountered, marginal increments were estimated by ages combined in four age groups representing, at least, young, moderate and old individuals (Campana, 2001).

Temperature data, obtained from the Marinemet Project (www.afrimet.org/marinemet/), were used to relate the formation of translucent and opaque rings in the otoliths to the sea surface temperature. Temperature data were also recorded from 0 to 200 m in depth around the islands by a sensor for temperature, pressure and conductivity (XR-420-CTD, Richard Branker Research Ltd), to corroborate changes in temperature with depth.

To assign the age class (number of calendar years after the birth date) to which a fish belonged the number of annual rings was counted, and information on the date of capture, the nature of the margin of the otolith, the main period of a seasonal increment formation and the birth date were taken into account (Morales-Nin & Panfili, 2002b). The 1st of July was considered as the birth date, corresponding to the mid-point of the spawning period. The difference between the date of capture and the birth date helped to estimate the annual fraction elapsed since the last birth date, and the annual fraction is added to the number of complete translucent rings to avoid any potential bias in growth estimates due to the differences in sampling data (Gordoa & Moli, 1997).

Growth models

Length-at-age was described using the von Bertalanffy growth function, the seasonalized von Bertalanffy growth function, the Schnute growth model and the Gompertz growth model (Pitcher & Macdonald, 1973; Ricker, 1975; Schnute, 1981). A non-linear method of Levenberg–Mardquart's algorithm was used to estimate the growth parameters. The selection of the best growth model was based on the Akaike information criterion (AIC), which can be expressed as follows: $AIC = n \ln((R_{SS}/n)^2) + 2j$, where R_{SS} is the residual sum of squares, n is the number of observations and j is the total number of estimated regression parameters (Shono, 2000). For model comparisons, the ΔAIC and the Akaike weights (w_i) were calculated. The model with the smallest AIC value was selected as the best model (A_b). The ΔAIC is the difference

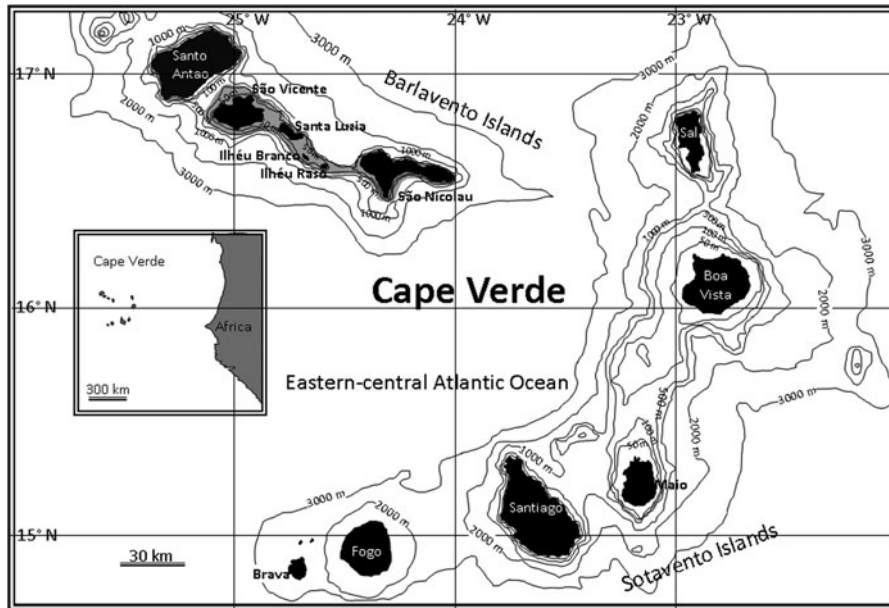


Fig. 1. Location of the sampling site in the Cape Verde Islands.

between the best model (A_b) and all other models (i), expressed as: $\Delta AIC_i = AIC_i - A_b$, and represents the probability of choosing the correct model from the group of models used. The w_i is calculated for each model as: $w_i = \exp(-\Delta AIC_i / 2) / \sum_{i=1}^r \exp(-\Delta AIC_i / 2)$.

RESULTS

Otolith ageing

Growth zones, presumed to be *annuli*, were observed easily for the first 1 to 7 years in both whole and sectioned otoliths

(Figure 2); subsequent *annuli* were more difficult to observe, especially in whole otoliths. Values of the matched pair t -test revealed that there were significant differences between the ages as determined by whole otoliths or sections across the 9–12, 13–16 and 17–20 section-based age groups (t -test, $t > 2.84 > t_{0.05, > 20} = 1.96$, $P < 0.01$). Age bias plots of ages estimated from whole otoliths compared with ages estimated from otolith sections revealed that readers 1 and 2 tended to underestimate ages of the whole otolith in older fish ($CV > 14.3\%$; $P < 0.01$) (Figure 3). Beginning at age 12, ages estimated from whole otoliths tended to be much lower than those estimated from otolith sections. In the oldest fish, whole otoliths underestimated the age indicated in

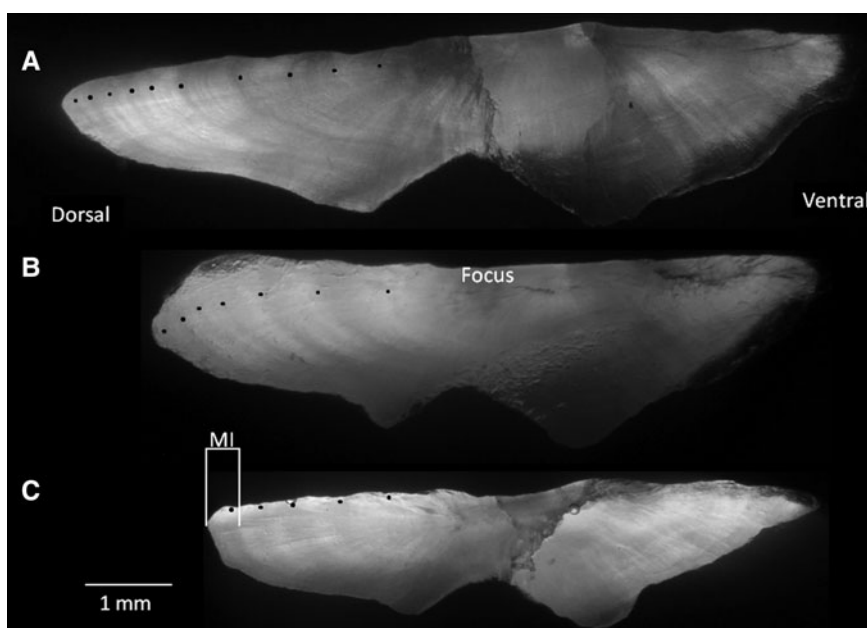


Fig. 2. Sectioned sagittal otoliths of *Cephalopholis taeniops* off the Cape Verde Islands. 10-year-old specimen (42.1 cm TL) (A); 7-year-old specimen (35.8 cm TL) (B); and 5-year-old specimen (29.7 cm TL) (C). MI is the marginal increment measured.



Fig. 3. Age bias plot for readers 1 (A) and 2 (B) ageing whole and sectioned otoliths of *Cephalopholis taeniops* off the Cape Verde Islands. Each error bar represents the SD. The 1:1 equivalence (solid line) is also indicated. The numbers indicate the sample size at each age.

sections by approximately 70%; therefore, the age was estimated from otolith sections.

Data analysis

The lowest values of the mean monthly marginal increments were recorded in February, with an increasing trend observed throughout the year (Figure 4). Irrespective of the number of translucent rings in the otolith sections, one mode was observed during a 12-month period. Therefore, it was assumed that each translucent ring represents an *annulus*, with a year's growth represented by an opaque and its adjacent translucent ring. One growth increment consisting of one opaque and one translucent ring was formed on an annual basis, with the opaque ring being deposited mainly between May and October (Figure 4). The cross-correlation between the monthly mean temperature and the opaque margin frequency (Spearman's $\rho > 0.996$, $P < 0.01$) showed that there was no apparent time lag from the start of the increase in seawater temperature and the beginning of the formation of the opaque ring. The formation of the translucent ring coincided with the decrease in the surface seawater temperature. The same pattern of variation in sea temperature was recorded with depth (Figure 5).

Out of 2804 otoliths examined, only 239 (8.52%) were discarded because they were unreadable, broken or provided different age estimates across readings. In total 2565 individuals ranging from 7.4 to 51.1 cm TL were used to estimate age and growth. Both values of the coefficient of variation were low ($CV \text{ reader } 1 = 8.5\%$, $P = 0.974$; $CV \text{ reader } 2 = 9.1\%$, $P = 0.965$), indicating the reliability of the ageing procedure adopted and a reasonable level of consistency (or reproducibility) between readings.

Up to 20 growth rings, assumed to be *annuli*, were visible in the otolith sections (Table 1). The dominant age classes were 3- to 9-year-old fish; only 4.9% of fish were 10 years old or older (Figure 6 and Table 1). Over 30% of the growth was achieved in the first year of life. In the fourth year, fish

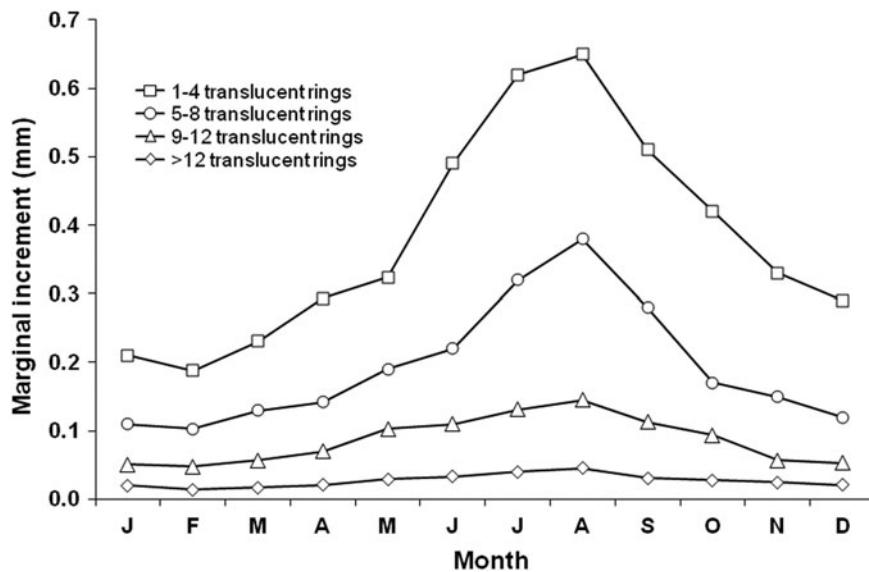


Fig. 4. Mean monthly marginal increments in otoliths of *Cephalopholis taeniops* off the Cape Verde Islands by age categories: individuals with 1-4 ($N = 501$), 5-8 ($N = 1812$), 9-12 ($N = 180$), and >12 translucent rings ($N = 62$).

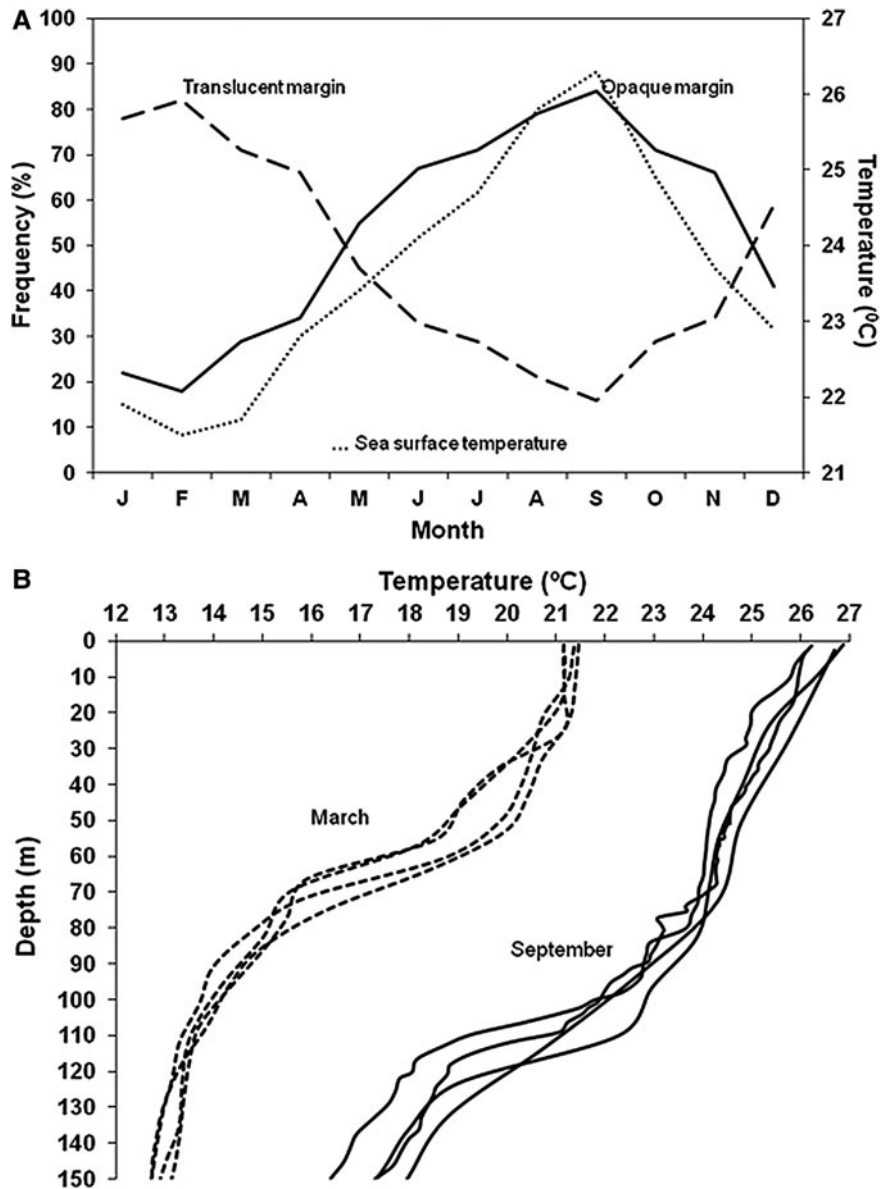


Fig. 5. Mean monthly percentage of otoliths with opaque and translucent margins in *Cephalopholis taeniops* off the Cape Verde Islands, and the mean monthly variation of the sea surface temperature (A). Variation of the sea temperature between 0 and 150 m of depth in Cape Verde waters during the months of March and September 2011 (B).

attained a size that was approximately half of the maximum length observed.

Growth models

The four growth models used gave good fits to the length-at-age data (Table 2). The seasonalized von Bertalanffy growth function was the best of the growth models fitted, with an Akaike weight (w_i) higher than 0.99 (Table 2); the other models gave very low values of w_i , indicating that they do not fit the length-at-age data well. Therefore, the seasonalized von Bertalanffy growth function was used to represent growth (Figure 6). The computed value of 0.167 for the winter point of the seasonalized von Bertalanffy growth function indicated that the lowest growth rate occurs at about 4 months before the birth date, indicating that growth is reduced in late winter.

DISCUSSION

Age estimation in epinephelids is often complicated because of the narrow fit between the growth rings towards the margins of the otolith, especially in older specimens (Manickchand-Heileman & Phillip, 2000). Sometimes, age estimation is difficult due to the thickness of the otoliths, making it necessary to obtain otolith sections instead. In the case of *C. taeniops*, the narrowness between the growth rings produces an underestimation of age in older fish making it necessary to read otolith sections. In all studies performed on species of the genus *Cephalopholis* it has been necessary to create otolith sections to age the fish (Chan & Sadovy, 2002; Araújo & Martins, 2009).

The values of the coefficient of variation obtained in this study suggest that the levels of precision are in line with the reference values, as indicated by Campana (2001).

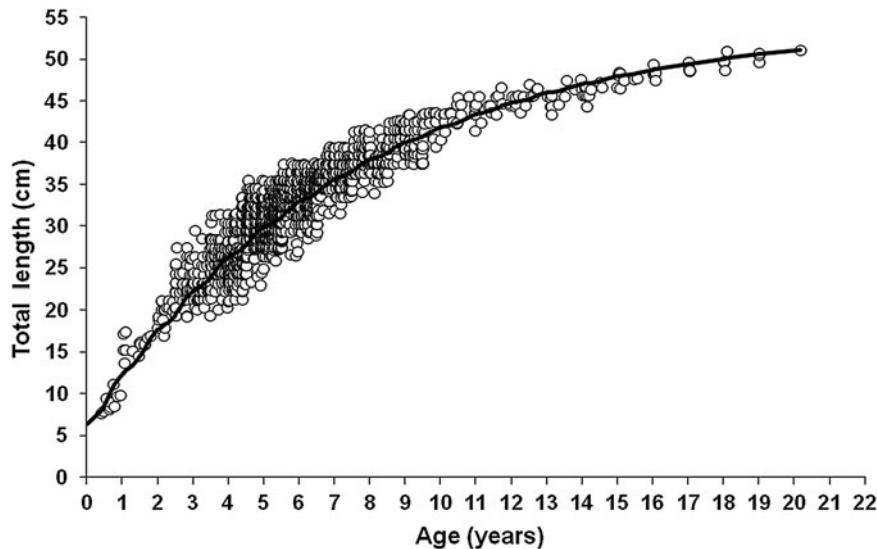


Fig. 6. Seasonalized von Bertalanffy growth curve for *Cephalopholis taeniops* off the Cape Verde Islands.

Sagittal otoliths of *C. taeniops* grow proportionally through the life of the fish, and display a regular and interpretable pattern of growth marks, which can be used to assess the age of an individual. One opaque ring and one translucent ring are formed in the otolith each year, allowing the assignation of age with relative ease. This pattern has been observed in all studies carried out on *Cephalopholis* species (Craig *et al.*, 1999; Potts & Manooch, 1999; Chan & Sadovy, 2002; Araújo & Martins, 2006, 2009; Trott, 2006). Evidence indicates that almost all tropical epinephelids (and all *Cephalopholis* species studied) lay down increments annually (Craig *et al.*, 1999; Potts & Manooch, 1999; Chan & Sadovy, 2002; Araújo & Martins, 2006, 2009; Bustos *et al.*, 2009; Choat *et al.*, 2009), including species in which annual periodicity has been confirmed by bomb radiocarbon analysis or OTC marks (Mosse, 2003; Trott, 2006).

The pattern of ring formation at the same time in both juveniles and adults suggests that the regulating mechanism cannot be related solely to somatic growth or to reproductive activity. Wright *et al.* (2002) indicated that ring formation is an independent physiological process, more directly responsive to environmental variations. In this sense, the translucent and opaque rings are deposited on the otoliths of this grouper in winter and summer months, respectively. The opaque ring is formed when temperature reaches high levels (sea surface, 26–27°C; 100 m depth, 22.5°C), whereas the translucent ring is formed when the temperature is lower (sea surface, 21.5°C; 100 m depth, 14°C) (Figure 5). Manickchand-Heileman & Phillip (2000) indicated that a seasonal difference of 2–6°C is sufficient to cause the formation of these growth rings in *Epinephelus flavolimbatus* and *Mycteroperca interstitialis*. This pattern of opaque ring formation is characterized by being broad-ranging in time and taking place in the summer months, coincident with the pattern described by Chan & Sadovy (2002) for *Cephalopholis boenack* and Araújo & Martins (2006) for *Cephalopholis fulva*.

Data available suggest that the increase in water temperature causes the formation of the opaque rings. The same close link between water temperature and the formation of opaque rings has been found for *Mycteroperca fusca* from

the Canary Islands (Bustos *et al.*, 2009). Furthermore, Beckman & Wilson (1995) found that the period of formation of opaque rings essentially coincided with the summer months for most species distributed over lower latitudes. Moe (1969) noted that cycles of growth may be related to physiological changes linked to temperature, feeding regimes and reproductive cycles in *Epinephelus morio* from the eastern Gulf of Mexico. In this study, the formation of the opaque ring occurs during the reproduction period (unpublished data), as has been found in other species of the genus, such as *C. boenack* (Chan & Sadovy, 2002) and *C. fulva* (Araújo & Martins, 2006). Taking into account that reproductive processes represent an energy cost for animals and, consequently, a decrease or even the stop of somatic growth, it was expected that the formation of the opaque rings would be affected by these processes. However, this has not been observed for *C. taeniops* in the studied area, suggesting that reproductive cycles do not affect the formation of the opaque rings.

The oldest fish found in this study was 20 years old. The maximum age observed was similar to what was found for *Cephalopholis hemistiktos* in Jamaica where specimens of up to 26 years were found (Mathews & Samuel, 1987), *C. fulva* in Brazil (25 years) (Araújo & Martins, 2006, 2009) and *Cephalopholis panamensis* in Mexico (14 years) (Craig *et al.*, 1999). However, the maximum age observed differs substantially from what was described for *C. boenack* in Hong Kong (11 years) (Chan & Sadovy, 2002), *C. fulva* in the USA and Bermuda (13 and 28 years) (Potts & Manooch, 1999; Trott, 2006), *Cephalopholis spiloparaea* (7 years), *Cephalopholis urodeta* (10 years), *Cephalopholis leopardus* (4 years), *Cephalopholis sexmaculata* (8 years) and *Cephalopholis argus* (5 years) in Papua New Guinea (Fry *et al.*, 2006). The differences found among populations of the same species or species of the same genus, especially in island populations, may be attributed to differences in environmental conditions or in the method used (length frequency analysis or otolith readings), or attributed to differences in levels of exploitation. Populations under high levels of exploitation show changes in growth and in their reproductive patterns (Gulland, 1983), and the depletion of the oldest age class causes an

Table 1. Age-length key for *Cephalopholis taeniops* off the Cape Verde Islands. X is the mean total length, N is the number of fish by age class, and SD is the standard deviation. Length classes are in 1 cm intervals.

Size (cm)	Age group (years)																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
7	1		3																				
8	4																						
9	4																						
10																							
11	1																						
12																							
13		1																					
14		1																					
15		3																					
16		2	3																				
17		2	5																				
18			4																				
19			8	5																			
20			9	4	2																		
21			3	15	5																		
22			1	33	16																		
23				24	29	1																	
24				11	58	1																	
25				9	64	3																	
26				8	74	14	1																
27				3	38	58	2																
28				2	23	97	1																
29				1	16	134	17																
30					11	139	17																
31					8	137	55																
32						136	78	6															
33						73	101	15															
34						33	90	35	2														
35						13	96	61	7														
36							48	79	21														
37							13	57	38	13													
38								20	43	19													
39								10	38	24	1												
40									14	21	2												
41									8	20	2	1											
42										17	12	1											
43										2	14	6	2	1									
44											1	6	6	3	1								
45												3	6	6	6								
46													1	2	6	3							
47														1	2	4	2						

Continued

Table 1. Continued

Size (cm)	Age group (years)																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
48																					
49																					
50																					
51																					
X	9.04	15.70	18.96	23.21	25.94	30.72	33.71	36.20	38.37	40.17	42.75	44.08	45.01	45.45	46.21	47.50	48.31	49.02	49.78	50.35	51.10
N	10	9	33	115	344	839	519	283	171	116	32	17	15	13	15	10	8	7	5	3	1
SD	1.06	1.19	1.60	2.03	2.19	2.09	2.01	1.55	1.54	1.65	1.10	1.10	0.87	0.99	0.84	0.71	0.58	0.48	0.81	0.57	

Table 2. Growth parameter values and model selection criterion for *Cephalopholis taeniops* off the Cape Verde Islands. L_{∞} is the asymptotic length, k is the growth coefficient, t_0 is the theoretical age at zero length, C is the amplitude of the fluctuation in seasonal growth, t_s is the addition of the point of the minimum growth +0.5, y_1 is the estimated mean length of the smallest age in the sample, y_2 is the estimated mean length of the largest age in the sample, and a and b are the model parameters. r^2 is the determination coefficient, AIC is the Akaike's Information Criterion, ΔAIC are the AIC differences between models, and w_i are the Akaike weights. SD is the standard deviation.

Model/parameter	Estimate (\pm SD)	r^2	AIC	ΔAIC	w_i
von Bertalanffy growth function					
L_{∞} (cm)	54.43 (0.69)	0.878	7984.04	354.36	<0.0001
k (year ⁻¹)	0.133 (0.008)				
t_0 (year)	-0.883 (0.134)				
Seasonalized von Bertalanffy growth function					
L_{∞} (cm)	54.26 (0.52)	0.886	7629.67	0	>0.9999
k (year ⁻¹)	0.135 (0.007)				
t_0 (year)	-0.853 (0.102)				
C	0.439 (0.019)				
t_s	0.667 (0.012)				
Gompertz growth model					
L_{∞} (cm)	52.15 (0.41)	0.874	8135.66	505.98	<0.0001
k (year ⁻¹)	0.147 (0.007)				
t_0 (year)	0.492 (0.073)				
Schnute growth model					
y_1 (cm)	8.05 (0.18)	0.876	8046.31	416.63	<0.0001
y_2 (cm)	51.10 (0.01)				
a	0.176 (0.018)				
b	0.7104 (0.297)				

underestimation of their longevity. Araújo & Martins (2009) noted the inadequacy of the length frequency study in these species. In general, the species of *Cephalopholis* have a characteristically long lifespan and grow slowly ($k = 0.11 - 0.19$ years⁻¹) (Mathews & Samuel, 1987; Craig et al., 1999; Potts & Manooch, 1999; Araújo & Martins, 2006, 2009; Trott, 2006). Age 0 to age 1 specimens have been largely unavailable in the sampling effort owing to minimum size limits applied to the fishery. They were only collected with hand nets at depths of 2–5 m in a sampling aimed at the capture of small fish during a fishing survey. The low number of individuals aged higher than 10 years in the sample population likely results from their removal from the population through both fishing and natural mortalities. Figure 7 shows the decrease of individuals higher than 42 cm (>10 years) in the catches around the Cape Verde Islands from 1996 to 2012.

The four growth models explain over 87% of the growth pattern, as shown by the determination coefficient for each curve. Although the use of the von Bertalanffy growth model has been criticized on various accounts (Booth, 1997) because of its use of parameters of scarce biological significance (Schnute, 1981) or the absence of parameters which consider seasonal variations in the growth rate (Pauly, 1980), this model has been chosen to describe patterns of growth in species of *Cephalopholis* (Craig et al., 1999; Potts & Manooch, 1999; Chan & Sadovy, 2002; Araújo & Martins, 2006, 2009; Trott, 2006; Choat et al., 2009). The VB function provides a simple model with a smaller number of parameters than other models, which nevertheless allows for a comparison among species and groups of species. However, the seasonalized von Bertalanffy growth function is the best model

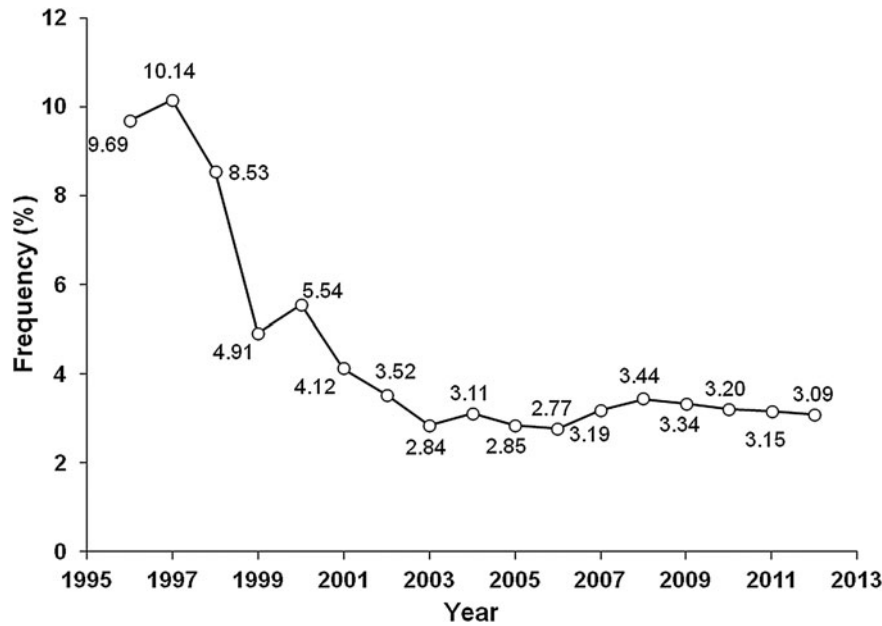


Fig. 7. Frequency of individuals of *Cephalopholis taeniops* longer than 42 cm (>10 years) caught around the Cape Verde Islands from 1996 to 2012.

describing the growth of *C. taeniops* in the Cape Verde Islands because a seasonal growth pattern exists there.

Cephalopholis taeniops found off the Cape Verde Islands is a slow-growing species ($k = 0.13 \text{ years}^{-1}$), as was found for *C. fulva* ($k = 0.14 \text{ years}^{-1}$) (Potts & Manooch, 1999; Araújo & Martins, 2006; Trott, 2006), *C. panamensis* ($k = 0.19 \text{ years}^{-1}$) (Craig *et al.*, 1999), *C. hemistiktos* ($k = 0.11 \text{ years}^{-1}$) (Mathews & Samuel, 1987) and *Cephalopholis cruentata* ($k = 0.12 \text{ years}^{-1}$) (Potts & Manooch, 1999). This slow growth pattern, common to all species of the genus *Cephalopholis*, is characteristic of a species that belongs to a high trophic level and has a moderate to long lifespan (Bullock & Murphy, 1994).

The t_0 value obtained in this study was negative, as was obtained in other studies conducted on this genus (Craig *et al.*, 1999; Potts & Manooch, 1999; Chan & Sadovy, 2002; Araújo & Martins, 2006, 2009; Trott, 2006; Choat *et al.*, 2009). Negative t_0 values are common in species that grow rapidly during the first year of life, and slowly later in life (Sadovy *et al.*, 1992; Craig *et al.*, 1997). Although there are scarce data on the 1-year-old *C. taeniops* in the study area, their mean lengths are approximately 15–16 cm TL (30% of the maximum size observed).

The growth of epinephelids tends to be faster in the first stages of life, and slows down considerably later (Bullock & Murphy, 1994; Manickchand-Heileman & Phillip, 2000; Araújo & Martins, 2006, 2009). *Cephalopholis boenak* has been shown to grow to reach 90 mm in length in its first 18 months of life in Hong Kong (Liu & Sadovy, 2005) and *C. panamensis* has been shown to grow 160 mm year^{-1} in its first few years of life in Mexico (Craig *et al.*, 1999) and in Brazil (Araújo & Martins, 2006, 2009), with a reduction in growth rate to 10–23 mm year^{-1} between 2 and 7 years of age (Araújo & Martins, 2006, 2009). For this reason, the seasonalized von Bertalanffy growth function does not properly describe the growth of the Epinephelidae species as far as the first few years of life are concerned.

Apart from the fact that the fishery tends to select the biggest groupers for economic reasons, the characteristics of

the growth and reproductive aspects (Siau, 1994) of *C. taeniops*, with a long lifespan, slow growth and late sexual maturation, make this species highly susceptible to overfishing (Sadovy *et al.*, 2013). To achieve the correct management and recovery of the populations, it is necessary to analyse and determine the characteristics of its habitat and its possible anthropogenic alteration (Erisman *et al.*, 2010), the distribution and the movement of the age groups and the existence of possible processes of aggregation during the spawning period, as in *C. boenak* in Hong Kong (Liu & Sadovy, 2005). It is also necessary to evaluate how fishing activity affects these aggregation processes, which causes vulnerability in other groupers (Sadovy, 1997; Chiappone *et al.*, 2000).

ACKNOWLEDGEMENTS

The authors are very grateful to two anonymous reviewers for their critical and useful comments on the manuscript which enabled the contents to be improved. This publication is contribution no. 1 of the Partnership between the INDP (Department of Fisheries Research, DIH) and the ULPGC (Department of Biology) for biological studies on *Cephalopholis taeniops* from the Cape Verde Islands, signed in January 2012. Most data come from the monitoring programme of the fishery for this target species, developed by the INDP. The remaining data corresponding to the smaller individuals were obtained during the cruise Cabo Verde 2010-04, in the frame of the Project PROACTIVA (Dirección General de Relaciones con África, Canary Islands Government).

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