



Age and growth of southwestern Atlantic wreckfish *Polyprion americanus*

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Abstract

Southwestern Atlantic wreckfish *Polyprion americanus* (27°56'S and 34°52'S) were aged using transverse thin sections of the sagittae otoliths of 390 individuals (44–155 cm TL, total length). The index of average percentage error for independent readings of two readers was 3%, and 10% of the sections were considered illegible. Marginal state assessment of the whole otolith's margin ($n = 406$) showed that one opaque band (annulus) is laid down each spring–summer. Supposed daily ring counts confirmed what was thought to be the first annual band. Maximum observed age was 76 years for males and 62 years for females. The von Bertalanffy growth model was significantly different ($P < 0.01$) between males ($L_{\infty} = 109.5$ cm, $K = 0.084$ per year and $t_0 = -4.69$ years) and females ($L = 129.5$ cm, $K = 0.0534$ per year and $t_0 = -6.80$ years). The absence of wreckfish below 44 cm TL in the samples and younger than 1.5 years means that this is the minimum size and age of recruitment to the bottom.

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1. Introduction

Wreckfish, *Polyprion americanus* (Bloch and Schneider, 1801), of the family Polyprionidae (Eschmeyer, 1990), is a large demersal fish that inhabits continental and oceanic islands slopes of temperate and subtropical waters at both sides of the Atlantic Ocean, at the Mid-Atlantic Ridge, the Mediterranean, southern Indian Ocean and southern Pacific (Heemstra, 1986; Roberts, 1989, 1996; Sedberry et al., 1999). Recent studies using mtDNA and microsatellite, differentiated northern and southern wreckfish stocks, and

allelic variation at microsatellite loci differentiated wreckfish from two southern hemisphere locations, Brazil and the south Pacific (Ball et al., 2000).

Along southwestern Atlantic *P. americanus* occurs from 23°S, near Rio de Janeiro, Brazil, to 46°S, Argentina (Cousseau and Perrota, 1998; Peres, 2000). A wreckfish fishery with handlines from small boats off southern Brazil is recorded since 1973 (Santos and Rahn, 1978; Barcellos et al., 1991). In the nineties, the fishery changed to vertical longlines and then to steel wire longlines. The number of vessels increased from around 10 in the 1970s, to more than 35 in 1997. Although fishing power grew with gear development and expansion of fishing area, estimated annual landings decreased from 2772 (1989) to 1080 t (1995). Capture (kg) per hook, per days at sea, dropped from 0.72

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(1989) to 0.48 (1997–1998). This suggests that this stock may be endangered and needs to be managed (Peres, 2000).

Age estimates from band counts on aging structures and validation of the periodicity of their deposition are basic requirements to obtain growth rates, ages at maturity and recruitment, longevity and natural mortality rates. These are essential data for proper management of southwestern Atlantic wreckfish.

Band patterns on otoliths sections of *Polyprion* species have been considered unreliable (Paul, 1992) or difficult to count (Francis et al., 1999). *P. oxygeneios* (New Zealand hapuku) may attain more than 60 years of age (Francis et al., 1999) and *P. americanus* (southeastern USA wreckfish) up to 39 years (Vaughan et al., 2000), but there are no age estimates for *P. americanus* stocks in the southern hemisphere.

Here, the otolith transverse sections were chosen for age determination. The development of a method to prepare and read otoliths sections and find the periodicity of band formation, made it possible to determine longevity and growth models for male and female southwestern Atlantic wreckfish *P. americanus*.

2. Material and methods

2.1. Sampling

Biological samples were obtained from commercial landings (1990–1995) with different fishing gears and

from research surveys with bottom trawl (1986–1987) and longline (1996–1997) (Table 1). The study area was the continental shelf and slope off southern Brazil (27°56'S and 34°52'S), in water depths from 70 to 500 m.

In research cruise samples, fish total weight (TW in kg) and total length (TL in cm) were recorded. Length was measured between the end of the inferior jawbone and the end of the tail in natural position. Sex was determined by external examination of the gonads and both otoliths were stored dry for aging.

Wreckfishes from commercial landings are sold ice cooled and ungutted. As each fish may attain large body size and high prices, sampling procedures required fast and non-damaging techniques. Fish were measured from the posterior border of the eye orbit to the fork of the caudal fin (EF in cm) and converted to TL by the relationship $TL = -0.724 + 119.5EF$ (Peres and Haimovici, 1998). Sex was determined by extracting a small sample of the gonad with a surgical curette through the gonopore and the left otolith was obtained through the opercular openings and stored dry.

2.2. Readings on the otoliths

Whole otoliths of 406 wreckfish of both sexes (44–155.5 cm TL), immersed in 70% ethanol for 24 h, were examined with incident light over a black background. Thin transverse sections through the focus were obtained from otoliths embedded in a polyester resin with a single high concentration diamond wheel

Table 1

Sampling period, fishing gear, fishing area, TL (mm) and number (*n*) of fish examined for age and growth study of southwestern Atlantic wreckfish

Period	Gear/type ^a	Fishing area		TL (cm)	<i>n</i>
		Latitude	Water depth (m)		
1986/1987	BT/res	31°50'–34°52'S	120–450	57–115.5	43
1990	FT/com	33°55'S	70–90	44–51	22
1994	VL/com	30°45'–34°04'S	250–400	64–150.5	24
1994	BG/com	33°25'–33°43'S	220–320	44–132.5	27
1995	VL/com	28°40'–34°49'S	280–460	62–155.5	83
1995	L/com	30°05'–32°13'S	400–420	54–140.5	114
1995	BG/com	33°30'–33°50'S	90–320	44–130	31
1996/1997	BL/res	27°56'–34°29'S	130–500	49–123	62
Total		27°56'–34°52'S	70–500	44–155.5	406

^a BT: bottom trawl; BG: bottom gillnet; BL: bottom longline; FT: fish traps; VL: vertical line and hook; L: longline; res: research cruise; com: commercial.

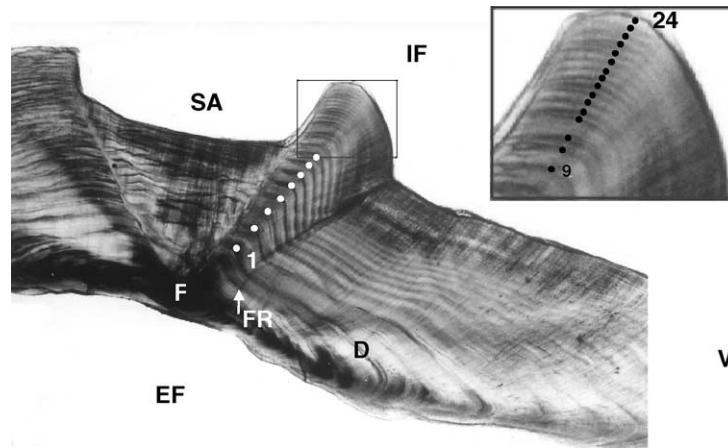


Fig. 1. Transverse otolith section, 0.18 mm thick, observed with transmitted light (32 \times). Otolith from a female wreckfish (127 cm TL) captured in October 1995 off southern Brazil. Counted opaque annual bands (white or black circles), sulcus acusticus (SA), internal face (IF), external face (EF), ventral margin (V), focus (F), first opaque band (1), first discontinuity (D), false ring (FR).

with a Burhler-Isomet low-speed saw. Band patterns were clearer in sections of 0.20–0.25 mm thick for the smaller fish (TL < 75 cm) and 0.15–0.20 mm thick, for larger ones. Sections with more than 30–40 bands were ground further on 1000-grade sandpaper until 0.11–0.15 mm thick. All sections were mounted on glass slides with xylol base mounting media (ENTELAN Merck).

Undamaged otolith sections ($n = 390$) were examined with transmitted light under a compound microscope (40–100 \times). Opaque bands were counted from the focus to the outer edge of the sulcus (Fig. 1). Thinner sections (0.11–0.15 mm thick), usually from older fish, were also examined with incident light under a dissecting microscope with low magnification to confirm the band patterns on the central area near the focus. After several preliminary readings, final individual blind counts were made independently by two readers. If band counts differed, both readers examined the section together and if no agreement could be reached the otolith was rejected.

Counts between successive readings of the same reader and between the two readers varied due to (1) high number of bands, (2) splitting of opaque bands in some portions of the section, or (3) very irregularly spaced bands. Initial agreement between independent readers was 30.5% and disagreement by only one band was 26.5%. Following a common reading and discussion 89.5% of the otoliths were considered readable.

For 3.6% of them, agreement was not possible and the other 6.9% were considered unreadable by one or both readers. The index of average percentage error (IAPE, Beamish and Fournier, 1981), was calculated as

$$\text{IAPE} = \frac{1}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right]$$

where N is the number of fish aged, R the number of times each is aged, X_{ij} the i th age determination of the j th fish and X_j the average age calculated for the j th fish. The IAPE between independent counts ($n = 2$) was 2.91%.

Narrow opaque bands, assumed to be daily rings (Campana, 1992), were examined on the otoliths sections of four wreckfish (45–90.5 cm TL, 2–22 years old). The sections were hand ground until 0.04–0.09 mm thick and mounted on glass slides with mounting media. They were counted from the focus to the first discontinuity (Fig. 1), along the external face, on a compound microscopy (400–1000 \times). This discontinuity was similar to the ultra structures in the otoliths of the eel *Anguilla anguilla* (Lecomte-Finiger, 1992). Differences of maximum and minimum counts for three readings of each section by the same reader did not exceed 9.9% (Table 2).

The terminology used to otolith description was adapted from Wilson et al. (1987) and Moralis-Nin (1992) (Table 3).

Table 2
Number of narrow opaque bands, considered daily, on wreckfish otolith sections^a

TL (cm)	Age	Sex	FC	FD(1)	FD(2)	FD(3)	FD(mean)	%
49	3	Female	137	373	356	362	363.7	4.78
90.5	22	Male	155	387	372	384	381	4.03
54	3	Male	141	393	382	386	387	2.88
45	2	Unknown	–	400	364	368	377.3	9.89

^a For each section, length, age and sex of the fish, number of daily bands from the focus to the end of the central opaque area (FC), number of daily bands from the focus to the first discontinuity (FD) for three counts (first, second and third), the mean number of daily bands and the percent difference (%) between the minimum and maximum number counted on each section.

2.3. Validation

The periodicity of band depositions was assessed by monthly proportions of opaque margins in sectioned and whole otoliths. The posterior end of the whole otoliths was chosen for younger fish and the edge of the rostrum for older ones (Fig. 2).

2.4. Growth

Length at age data was fitted with non-linear iterative procedure (Gauss–Newton) to the von Bertalanffy growth model (von Bertalanffy, 1938), VBGM: $L_t = L_\infty(1 - e^{-K(t-t_0)})$, where L_t is the length (cm)

at age t (years), L_∞ the asymptotic length (cm), K the growth coefficient (per year) and t_0 the theoretical age at zero length (years). Growth curves between sexes were compared with a likelihood ratio test (Kimura, 1980; Cerrato, 1990), for immature (TL < 75 cm), adults (TL > 75 cm) and for all wreckfish together.

Length–weight regression for sexes combined ($n = 207$, 44–145.5 cm TL, 1.2–53 kg TW, $r^2 = 0.98$) was $W = (6.29 \times 10^{-6})L^{3.21}$ (Peres and Haimovici, 1998). Weight at age was calculated using this relationships and estimated length at age.

Ages were assigned based on annuli counts, assuming 1 September as the theoretical birthday,

Table 3
Terminology used to otolith description of southwestern Atlantic wreckfish, adapted from Wilson et al. (1987) and Moralis-Nin (1992)

Annulus (opaque band)	A concentric mark on any ageing structure that allows interpretation of growth in terms of age. In whole and sectioned wreckfish otolith, concentric and continuous opaque bands with a discontinuity, white under incident light and dark with transmitted light were counted as annual bands
Central area	In the wreckfish otolith it is an area between the focus and the first translucent annual band (associated with a depression on the external face). It is predominantly opaque. In whole otolith, it can be large and diffuse, or composed by one to three opaque areas, considered false rings. On the sections, it was the most difficult portion to interpret the growth band pattern
Discontinuity	This was the main criterion used to identify the first annual band on wreckfish otolith sections. It is a concentric and continuous structure like “thin crack” when viewed under a compound microscope (50–100×) in otolith sections of less than 0.15–0.17 mm thick. It is found, usually, between the end of the translucent band and the beginning of the opaque one
Daily ring	On wreckfish otolith sections (0.04–0.09 mm thick), narrow concentric and continuous opaque bands, with smooth transition in width and contrast were counted as “daily” bands
Area, region, zone, mark	Auxiliary terms used to describe the ageing structures, with no relation with a temporary scale
False ring	Any opaque area similar to an annual band but interrupted or without a “discontinuity” (if in the central area of the section)
Focus	Real or hypothetical origin of the whole or sectioned otolith, used as a reference to begin counts or measurements of growth bands. On wreckfish otolith the focus is opaque. Under incident light and dark bottom, the focus appears as a small brilliant white circle in the central area of the lateral face (concave). In the sections, under transmitted light, it is a dark circular area in the central area, near to the margin of the lateral face

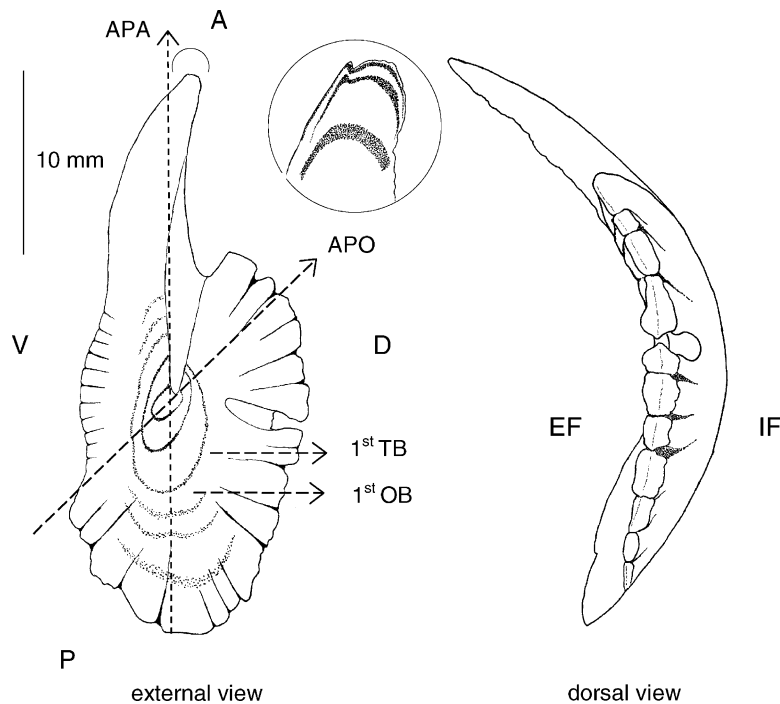


Fig. 2. View of the left otolith from a female wreckfish, 145.5 cm TL and 51 years old, captured in November 1994 off southern Brazil. Otolith external face observed with reflected light over a dark background. Ventral margin (V), dorsal (D), posterior (P), anterior (A), first translucent band (first TB), first opaque band (first OB), antero-posterior axis (APA), original antero-posterior axis (APO). Magnified opaque otolith rostrum's edge (10×). Otolith dorsal view showing the otolith curvature, external face (EF), and internal face (IF).

considering the spawning season in the region (Peres, 2000).

3. Results

3.1. Otolith structure

In wreckfish, the sagittae otoliths are elongated, laterally compressed, curved and very fragile (Fig. 2). Their surfaces are irregular, with many mounts and crenellations. The external face of the otolith is concave with grooves and ridges radially disposed. With age, the rostrum becomes conspicuous and curved, the sulcus acusticus gets deeper and the irregularities on the surface get strongly marked. The antero-posterior axis rotates during otolith growth and for older fish it may be up to 30° or 40°. Due to this rotation, transverse sections through the focus changed planes with ages.

3.2. Band patterns on sectioned and whole otoliths

Viewed with transmitted light, otolith sections have a dark central area (opaque) around the focus and a dark line that radiates along the external face surface (Figs. 1 and 3a). Translucent bands were wider than the opaque ones near the focus but this width difference progressively diminished from the focus to the border. For the same otolith, width of the translucent bands increased with thinner sections.

On the sections thinner than 0.15 mm, it was possible to observe a structure like a “thin crack”, the discontinuity, between the end of the first translucent band and the beginning of the first opaque band. Thin transverse otolith sections (0.04–0.09 mm) showed pairs of opaque and translucent narrow bands (Fig. 3b). The mean number of these bands, considered daily rings, from the focus to the first discontinuity was 377.3, almost 1 year (Table 2). Thus, for wreckfish, the discontinuity and the end of the first

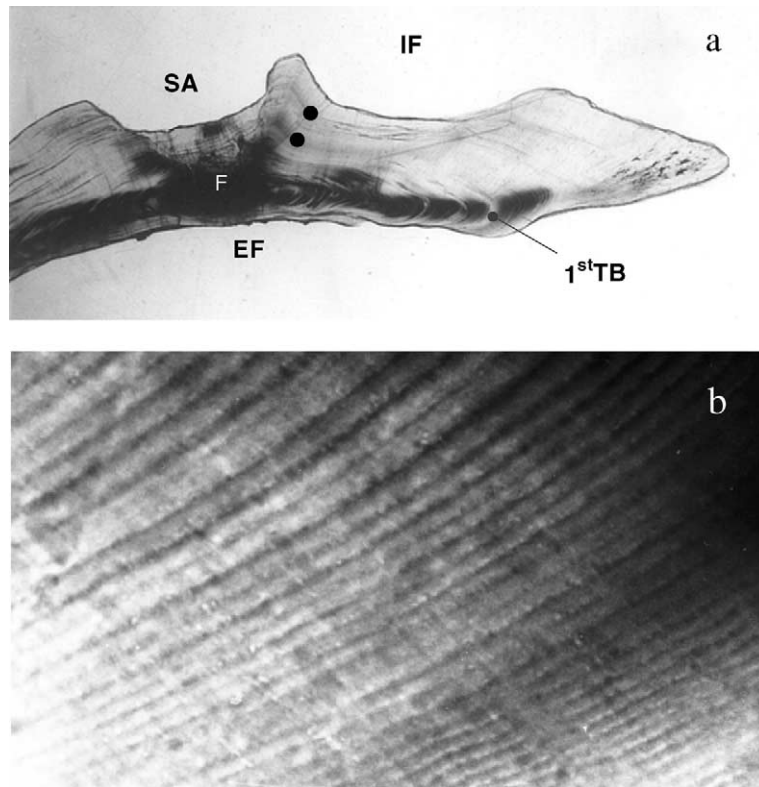


Fig. 3. Transverse otolith section (0.04 mm thick) of a 54 cm TL wreckfish, captured in September 1994 off southern Brazil. (a) Observed with transmitted light (32 \times). Annual opaque bands (black circles), sulcus acusticus (SA), internal face (IF), external face (EF), first translucent band (first TB), focus (F). (b) Observed in higher magnification (1000 \times) showing general aspect of the narrow opaque bands, considered daily rings, in the opaque otolith central area, adjacent to the external face near to the first annual translucent band.

crest on the external surface of the otolith were both used as criteria to detect the first annual band. One to three translucent narrow translucent rings were frequently observed before the first annual band, and were considered false (Fig. 3a).

The following continuous opaque bands were considered annual and counted on the dorsal margin of the sulcus (Fig. 1). Some were very irregularly spaced and this was considered the main cause of low precision of preliminary readings. Although they were frequent, for each section their number was never more than 1–5. Counting every band, independent of their spacing resulted in lower IAPE.

The border type was inconsistently classified between successive readings for 62.2% of the 390 otolith sections. Sometimes, even sequential sections of the

same otolith had different classifications. This was due to either extremely thin opaque bands at the border or misinterpretation of the border type caused by optical distortions.

Examined with incident light over a black background, the central area of whole otoliths is brilliant white and may show one to three false rings. The first translucent band is always associated with a depression. The central area is surrounded by a clear and distinct opaque band, the first annual band (Fig. 2). The following 6–12 bands could be easily observed in the posterior and dorsal region of the otoliths and the others along the rostrum. The border type, opaque or translucent, was consistently classified between two independent readings of the same reader for 80.3% of the 406 otoliths.

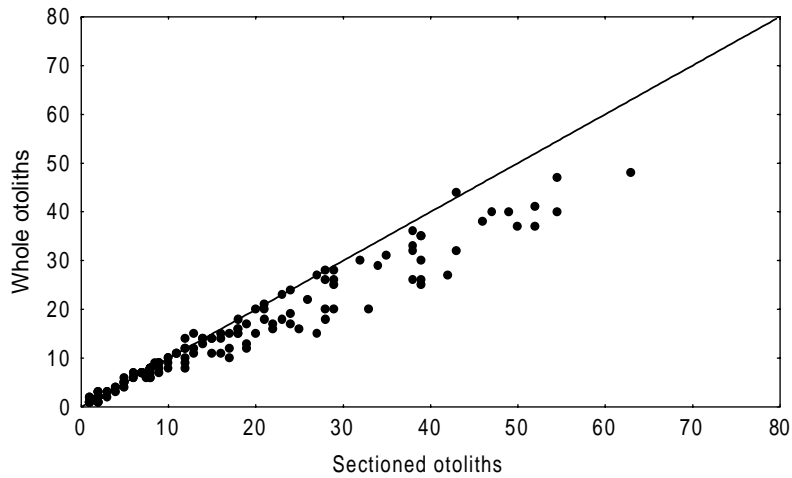


Fig. 4. Number of opaque bands counted on whole and sectioned otoliths of southwestern Atlantic wreckfish. It also shows the bisection line.

Age determinations were similar for sectioned and whole otoliths, although the number of opaque bands on otolith sections was progressively higher for older fishes (Fig. 4). This indicates that the best age estimates are on sectioned otoliths. Co-linearity between readings on whole and sectioned otoliths means that the band patterns are the same and the used criteria for band counts are consistent.

3.3. Validation

Periodicity of band depositions was validated by monthly proportions of opaque margins of whole otoliths (Fig. 5, Table 4). For adult wreckfish ($n = 290$, 75–155.5 cm TL) almost 100% of the legible borders were opaque from November to February and less than 5% from April to June. Despite the smaller

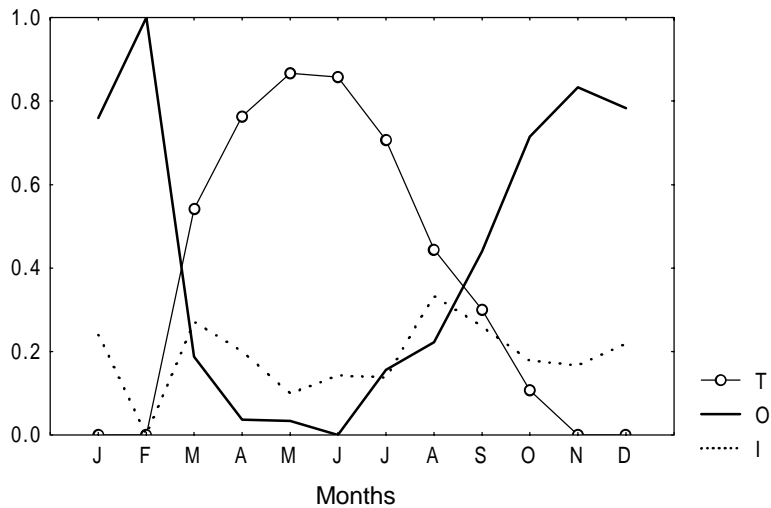


Fig. 5. Monthly proportion of border type, translucent (T), opaque (O) and illegible (I) observed in whole otoliths ($n = 406$) of southwestern Atlantic wreckfish.

Table 4
Number of opaque margins (O), translucent (T) and illegible (I) observed per month, on whole wreckfish otoliths^a

Month	Immature			Adults A			Adults B			%			n
	T	O	I	T	O	I	T	O	I	T	O	I	
January	–	–	–	–	5	3	–	14	3	–	76.0	24.0	25
February	–	1	–	–	–	–	–	–	–	–	100.0	–	1
March	14	4	6	8	3	2	4	2	5	54.2	18.8	27.1	48
April	16	2	–	23	–	10	3	–	1	76.4	3.6	20.0	55
May	–	–	1	14	–	2	12	1	–	86.7	3.3	10.0	30
June	1	–	–	4	–	–	1	–	1	85.7	–	14.3	7
July	17	1	3	31	14	8	29	2	4	70.6	15.6	13.8	109
August	4	3	2	1	–	–	3	1	4	44.4	22.2	33.3	18
September	5	12	2	6	7	4	4	3	7	30.0	44.0	26.0	50
October	–	4	–	1	7	3	2	9	2	10.7	71.4	17.9	28
November	–	6	–	–	–	–	–	4	2	–	83.3	16.7	12
December	–	10	2	–	1	1	–	7	2	–	78.3	21.7	23
Total	57	43	16	88	37	33	58	43	31			19.7	406

^a Immature wreckfish (TL < 75 cm), adults A (75 cm < TL < 100 cm) and adults B (TL > 100 cm). Percentage of translucent, opaque and illegible margins within total number of examined otoliths per month (n).

sample size, the same pattern was observed for immature fish (45–75 cm TL, $n = 116$). It is concluded that, annually, one opaque band is laid down from late winter to summer. Higher proportions of illegible margins (non-coincident or doubtful) occurred during transitional months, when fishes are beginning to deposit opaque (August–September) or translucent (March) material on the otoliths (Fig. 5, Table 4).

3.4. Growth

As growth differences were not observed between sexes for immature fish (Table 5), 22 unsexed wreckfish (44–55 cm TL, 1–3 years old) were included in the VBGM for males, females and gathered sexes. Growth was significantly different between sexes, of adults and of all wreckfish together (Table 5). So, growth

Table 5
Maximum likelihood comparison for the VBGM parameters between sexes of southwestern Atlantic wreckfish^a

H_0	Equal L	Equal K	Equal t_0	All equal
Immature (TL < 75 cm) ($n = 53$)				
Observed F	0.4182	0.2131	0.2359	0.4461
Fixed F (0.05)	4.05	4.05	4.05	2.8
Probability	0.4932	0.6243	0.6064	0.685
	Accepted	Accepted	Accepted	Accepted
Adults (TL > 75 cm) ($n = 265$)				
Observed F	9.33	4.43	2.02	22.12
Fixed F (0.05)	3.88	3.88	3.88	2.64
Probability	0.0022	0.03409	0.1509	<0.00001
	Rejected	Rejected	Accepted	Rejected
All ($n = 328$)				
Observed F	131.88	9.04	2.44	22.25
Fixed F (0.05)	3.87	3.87	3.87	2.63
Probability	<0.00001	0.0026	0.1156	<0.00001
	Rejected	Rejected	Accepted	Rejected

^a The curves were adjusted and compared for immature fish (TL < 75 cm), adult (TL > 75 cm) and all together. The observed F , fixed F ($P = 0.05$), the probability that the null hypothesis (H_0) is accepted or rejected.

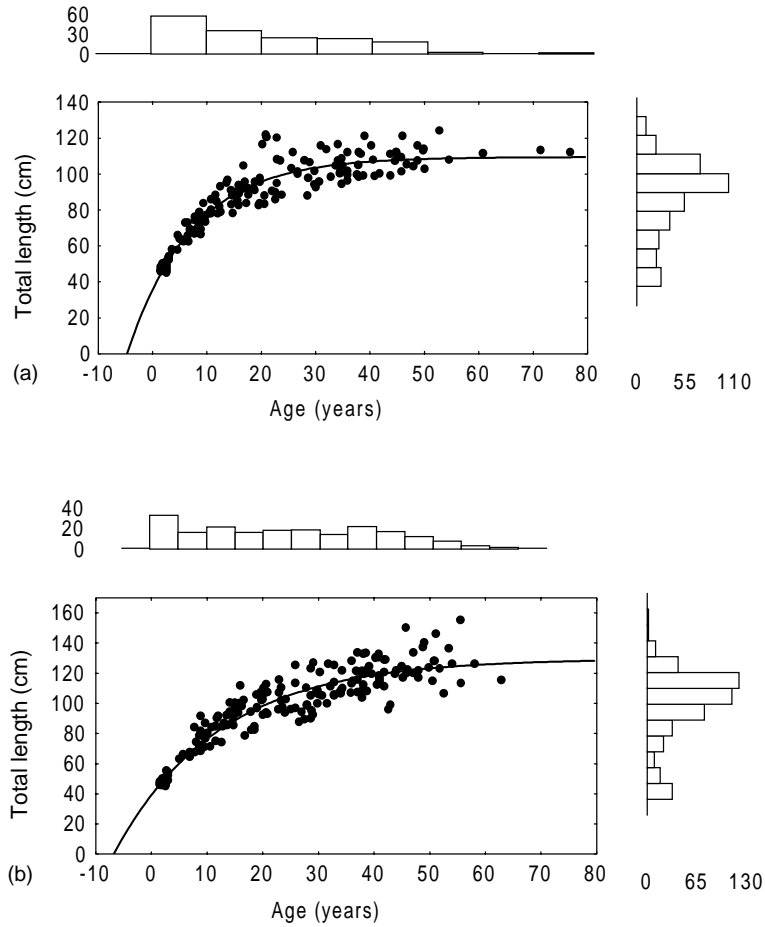


Fig. 6. Age at length data and fitted VBGM for southwestern Atlantic wreckfish. Frequency distributions of ages and lengths are shown at respective axes. (a) Males ($n = 141$) and unsexed fish smaller than 55 cm TL ($n = 22$). (b) Females ($n = 174$) and unsexed smaller than 55 cm TL ($n = 22$). See text for parameter values.

rates between sexes become different after sexual maturation. Females attain larger sizes than males of the same ages (Fig. 6). Ages varied from 1 to 76 years old for males ($n = 141$, 47–126 cm TL), 1–62 years for females ($n = 174$, 45.5–155.5 cm TL) and the fitted VBGM were

$$Lt_{\text{males}} = 109.5(1 - e^{-0.084(t+4.69)})$$

$$(n = 163, \text{S.E.} = 6.886, r^2 = 0.90)$$

$$Lt_{\text{females}} = 129.5(1 - e^{-0.053(t+6.80)})$$

$$(n = 196, \text{S.E.} = 9.129, r^2 = 0.88)$$

$$Lt_{\text{both sexes}} = 121(1 - e^{-0.063(t+6.30)})$$

$$(n = 337, \text{S.E.} = 9.207, r^2 = 0.85)$$

Growth equations in weight were

$$Wt_{\text{males}} = 21.8(1 - e^{-0.084(t+4.69)})^{3.21}$$

$$Wt_{\text{females}} = 37.5(1 - e^{-0.053(t+6.80)})^{3.21}$$

4. Discussion

The difficulties to get consistent reading criteria leading to low counting precision were described for

New Zealand hapuku, *P. oxygeneios* (Francis et al., 1999). USA wreckfish, *P. americanus* have been considered one of the most difficult fish species to age (Potts, 2000). Aging southwestern Atlantic wreckfish, *P. americanus*, was possible by counting the opaque bands (annulus) in transverse sections of the sagittae otoliths. It was shown that one opaque band is deposited each spring–summer. The number of bands increased with body size and spacing between them decreased gradually from the focus to the margins, confirming their adequacy for age and growth studies (Brennan and Cailliet, 1989; Casselman, 1990).

Here, when wreckfish otoliths were sectioned at usual thickness (0.3–0.5 mm), band patterns were unreliable. The lack of sharpness of the growth bands observed in several age and growth studies of *Polyprion* species is probably caused by the irregularities on the otolith surface. Narrow deposition layers on these irregular surfaces and sectioned in different planes (in part, caused by the torsion of the antero-posterior axis) may produce “ghosts” of adjacent bands, making it difficult to delineate the limits of each band, and therefore, count them. This is why thinner sections (0.11–0.15 mm) resulted in clearer band patterns, specially for older fish where annual bands are narrower spaced and the irregularities on the otolith surface are strongly marked.

Besides thinner sections, aging was much improved by clear definition of the criteria used to identify the first annual band, because the otolith central area may show one to three false rings. These criteria included the observation of growth features on the surface of whole and sectioned otolith (the ridge, associated with the central area, and the groove, associated with the first translucent annual band) and the presence of a “discontinuity”. Ridges on the otolith surface have been used as an auxiliary criterion to define annual rings of *Seriola dumerili* (Thompson et al., 1999) and *Istiophorus platypterus* (Prince et al., 1986).

Daily rings of other fish species (Stevenson and Campana, 1992) are very similar to the narrow opaque bands counted on wreckfish otolith microstructure (400–1000 \times). Wreckfish spawning season in the study area is from late July to early October (Peres, 2000) and coincides with the beginning of the deposition of the opaque material on the otolith. The mean

number of these bands from the focus to the end of the otolith central area (the opaque portion before the assumed first annual band) was 144. This is about the number of days of the opaque deposition period observed for older wreckfish. The mean number of narrow bands, from the focus to the first annual opaque band (discontinuity) was 377, almost the number of days in 1-year period. These results together indicate that (1) the narrow bands might be considered daily marks; (2) the criteria used to identify the first annual band are adequate; (3) the deposition of opaque material during the first year follows the observed pattern for older fish. Even with circumstantial evidence that the narrow bands are daily growth marks, we emphasized the need for a further validation of wreckfish daily rings.

The difficulty to assess marginal state in otolith sections was also observed for New Zealand hapuku (Francis et al., 1999). The monthly proportion of opaque margins in whole otoliths permitted us to validate the periodicity of band deposition on southwestern Atlantic wreckfish otoliths. Except for very young fish, the clearer margin pattern was at the edge of the otolith rostrum, presumably because it has a high rate of deposition (the fastest growth axis) and its surface is more regular than the rest of the otolith. This method might be applied to other species with irregular otolith surfaces and unreliable margins on otolith sections, such as the Serranidae species, to which *Polyprion* has traditionally been aligned.

Processes controlling otolith growth are still not completely explained. Some authors believe that opaque or translucent band formation is linked with external factors as water temperature, photo period or food availability. Others, associate the type of band deposition with endogenous events as reproduction, migration or physiological stress. Fishes inhabiting temperate waters usually deposit fast growing—opaque bands—in summer months and slow growing—translucent bands—in winter (Pannela, 1980; Chilton and Beamish, 1982). Secor and Dean (1989) observed that when otolith growth is fast, the deposition is opaque, lightweight and contains more protein. During slower growing period, the deposition is translucent, heavier than the opaque one and has less protein and more calcium. Wright (1991) showed that the otolith growth of *Salmo salar* is related to a high metabolic rate and not to fish body growth.

For New Zealand hapuku, austral winter–spring is the time of opaque band formation (Francis et al., 1999), about the same period observed for south-western Atlantic wreckfish, late winter to summer. In the study area (1) water temperatures in the summer (below 80 m) are 3 °C higher than in winter (18.5–15.5 °C) (Bakun and Parrish, 1991); (2) due to slope upwellings in winter–spring (Garcia, 1997), ocean productivity and food availability are higher (Ciotti et al., 1995); (3) in winter–spring, adult wreckfish does a northern migration to spawn and has a higher food uptake (Peres, 2000). These events may all be related to higher metabolic rates of southwestern Atlantic wreckfish.

Body sizes of USA wreckfish captured with line and hook were 75–146 cm TL (Sedberry et al., 1999). New Zealand hapuku captured with bottom trawl were 41–147 cm TL, but most fish were less than 85 cm (Francis et al., 1999). The size range of aged southwestern Atlantic wreckfish (44–155.5 mm TL), captured with several fishing gears was about the same as in other studies. Despite having just a few large fish, the maximum observed age for hapuku was 63 years, not far from the maximum ages observed for southwestern Atlantic wreckfish (62 years for females and 76 years for males). Maximum age for USA wreckfish stock was 39 years (Vaughan et al., 2000), about half of the other studies. Here, counting all continuous opaque bands, even some which could be false rings (very irregularly spaced), might have generated some overestimated readings. But this cannot explain the observed differences because the number of these bands was never more than one to five for each otolith section.

The K values obtained here (0.053 females, 0.084 males) were similar to those of hapuku, 0.061–0.079 gathered sexes (Francis et al., 1999) and USA wreckfish, 0.073 also for sexes together. The t_0 values of the VBGM obtained for all *Polyprion* species were strongly negative: –6.80 and –4.69 years for southwestern Atlantic wreckfish; –12.48 and –16.56 years for USA wreckfish (Vaughan et al., 2000); –4.06 to –5.75 for New Zealand hapuku (Francis et al., 1999). This might indicate that VBGM does not fit the data for small fish or may be due to the absence of small fishes in the samples.

Juveniles of *Polyprion* species are pelagic, live associated with floating objects and capturing them is ex-

tremely difficult (Roberts, 1996; Sedberry et al., 1996; Francis et al., 1999). Francis et al. (1999) estimated for New Zealand hapuku a pelagic phase of 3–4 years (about 50 cm TL). From a sample of 7654 southwestern Atlantic wreckfish, caught with different gears, no fish were smaller than 44 cm TL, only 5 were below 45 cm TL (0.07%) and 50 fishes were 45–50 cm TL (0.7%) (Peres, 2000). All sampled fish below 55 cm TL were aged. Wreckfish from 44 to 45 cm TL were 1.5–2.5 years old, so this is the size and age of the recruitment to the bottom in the study area.

Negative values of t_0 are frequent among species with rapid growth during the first year and reduced growth rates in the following years (Sadovy et al., 1992; Newman et al., 1996; Craig et al., 1997). There are no data on the 1-year-old wreckfish in the study area, but the results indicate that their lengths should be around 35 or 40 cm. The growth rate of southwestern Atlantic wreckfish in its pelagic phase must be faster than the observed after the settlement to the bottom. Fit two VBGM, one for the pelagic and one for demersal phase, could be a solution (Vooren, 1977; Craig et al., 1997). However, there are no catches of wreckfish juveniles (<1.5 years) off southern Brazil. So, we consider that the fitted VBGM describes body growth with age, for male and female, for the size range recruited to the bottom and commercially exploited.

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References

- Bakun, A., Parrish, R.H., 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy *Engraulis anchoita* of the southwestern Atlantic. *ICES J. Mar. Sci.* 48, 343–361.
- Ball, A., Sedberry, G., Zatcoff, M., Chapman, R., Carlin, J., 2000. Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers. *Mar. Biol.* 137 (5/6), 1077–1090.
- Barcellos, L., Peres, M., Wahrlich, R., Barison, M., 1991. *Optimização bioeconômica dos recursos pesqueiros marinhos do Rio Grande do Sul*. Editora da FURG, Rio Grande, 58 pp.
- Beamish, R., Fournier, D., 1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38, 982–983.
- Brennan, J., Cailliet, G., 1989. Comparative age-determination techniques for white sturgeon in California. *Trans. Am. Fish. Soc.* 118, 296–310.
- Campana, S., 1992. Measurement and interpretation of the microstructure of fish otoliths. In: Stevenson, D., Campana, S. (Eds.), *Otolith Microstructure Examination and Analysis*. Canadian Special Publication of Fisheries and Aquatic Sciences 117, pp. 59–71.
- Casselman, J., 1990. Grow and relative size of calcified structures of fish. *Trans. Am. Fish. Soc.* 119, 673–688.
- Cerrato, R.M., 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47, 1416–1426.
- Chilton, D., Beamish, R., 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60.
- Ciotti, A., Odebrecht, C., Fillmann, G., Möller, O., 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. *Cont. Shelf Res.* 15 (14), 1737–1756.
- Cousseau, M., Perrota, R., 1998. *Peces marinos de Argentina: biología, distribución, pesca*. INIDEP, Mar del Plata, Argentina.
- Craig, P., Choat, J., Maxe, L., Saucerman, S., 1997. Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa. *Fish. Bull. US* 95, 680–693.
- Eschmeyer, W., 1990. *Catalog of the Genera of Recent Fishes*. California Academy of Sciences, San Francisco.
- Francis, M., Mulligan, K., Davies, N., Beentjes, M., 1999. Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*. *Fish. Bull. US* 97, 227–242.
- García, C., 1997. Physical oceanography. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), *Subtropical Convergence Environments: The Coast and Sea in the Southwestern Atlantic*. Springer, Berlin.
- Heemstra, P., 1986. Family No. 165: Polyprionidae. In: Smith, M.M., Heemstra, P. (Eds.), *Smith's Sea Fishes*, 6th ed. Springer, Berlin.
- Kimura, D.K., 1980. Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull. US* 77 (4), 765–776.
- Lecomte-Finiger, R., 1992. The crystalline ultrastructure of otoliths of the eel (*A. anguilla* L. 1758). *J. Fish Biol.* 40, 181–190.
- Moralis-Nin, B., 1992. Determination of growth in bony fishes from otolith microstructure. *FAO Fisheries Technical Paper*, vol. 322. FAO, Rome, 51 pp.
- Newman, S., William, D., Russ, G., 1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetti* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. *Aust. J. Mar. Freshwater Res.* 47, 575–584.
- Pannela, G., 1980. Growth patterns in fish sagittae. In: Rhoads, D.C., Lutz, R.A. (Eds.), *Skeletal Growth of Aquatic Organisms*. Plenum Press, New York, pp. 519–560.
- Paul, L., 1992. Age and growth studies of New Zealand marine fishes, 1921–1990: a review and bibliography. *Aust. J. Mar. Freshwater Res.* 43, 983–1013.
- Peres, M., 2000. *Dinâmica populacional e pesca do cherne-poveiro Polyprion americanus (Bloch e Schneider, 1801) (Teleostei: Polyprionidae) no sul do Brasil*. Ph.D. Thesis. Fundação Universidade Federal do Rio Grande, Rio Grande, Brazil, 151 pp.
- Peres, M., Haimovici, M., 1998. A pesca dirigida ao cherne-poveiro, *Polyprion americanus* (Polyprionidae, Teleostei) no sul do Brasil. *Atlântica*, Rio Grande 20, 141–161.
- Potts, J., 2000. Personal communication. Center for Coastal Fisheries and Habitat Research—NOAA, Road Beaufort, NC, USA.
- Prince, E., Lee, D., Wilson, C., Dean, J., 1986. Longevity and age validation of tag-recaptured Atlantic sailfish, *Istiophorus platypterus*. *Fish. Bull. US* 84, 493–502.
- Roberts, C., 1989. Reproductive mode in the percomorph fish genus *Polyprion* Oken. *J. Fish Biol.* 34, 1–9.
- Roberts, C., 1996. Hapuku and bass: the mystery of the missing juveniles. *Seafood NZ* 4 (1), 17–21.
- Sadovy, Y., Figuerola, M., Román, A., 1992. Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St. Thomas. *Fish. Bull. US* 90, 516–528.
- Santos, A., Rahn, E., 1978. Sumário das explorações com espinhel de fundo ao longo da costa do Rio Grande do Sul. *Relatório Síntese* 4, SUDEPE/PDP, Brasília, Brazil, 41 pp.
- Secor, D., Dean, J., 1989. Somatic growth effects on the otolith—fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 46, 113–121.
- Sedberry, G., Carlin, J., Chapman, R., Eleb, B., 1996. Population structure in the pan-oceanic wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae) as indicated by mt-DNA variation. *J. Fish Biol.* A 49, 318–329.
- Sedberry, G., Andrade, C., Carlin, J., Chapman, R., Luckhurst, B., Manooch III, C., Menezes, G., Thomsen, B., Ulrich, G., 1999. Wreckfish *Polyprion americanus* in the North Atlantic: fisheries, biology and management of a widely distributed and long-lived fish. *Am. Fish. Soc. Symp.* 23, 27–50.
- Stevenson, D., Campana, S. (Eds.), 1992. *Otolith Microstructure Examination and Analysis*. Canadian Special Publication of Fisheries and Aquatic Sciences 117, Ottawa, 126 pp.
- Thompson, B., Beasley, M., Wilson, C., 1999. Age distribution and growth of greater amberjack, *Seriola dumerilli*, from north-central Gulf of Mexico. *Fish. Bull.* 97, 362–371.

- Vaughan, D., Manooch III, C., Potts, J., 2000. Assessment of the wreckfish fishery on the Blake Plateau. In: Proceedings of the Charleston Bump Symposium, Charleston, SC.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 10 (2), 181–213.
- Vooren, C., 1977. Growth and mortality of Tarakihi (Pisces: Cheiloactylidae) in lightly exploited populations. NZ J. Mar. Freshwater Res. 11 (1), 1–22.
- Wilson, C., Beamish, R., Brothers, E., Carlander, K., Casselman, J., Dean, J., Jearld, A., Prince, E., Wild, A., 1987. Glossary. In: Summerfelt, R.C., Hall, G.E. (Eds.), Age and Growth of Fish. Iowa State University Press, pp. 527–530.
- Wright, P., 1991. The influence of metabolic rate on otolith increment width in Atlantic salmon parr (*Salmo salar* L.). J. Fish Biol. 38, 929–933.