

Age, growth and mortality of white grunt (*Haemulon plumierii*) from the central coast of Brazil

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SUMMARY: White grunt (*Haemulon plumierii*) otoliths were collected from 1997 to 1999 off the central coast of Brazil. Analysis of the edges of otolith sections suggests that one translucent and one opaque zone are formed once a year. Observed size and age class ranges for *H. plumierii* were 218–378 mm total length (TL) and 2–28 years, respectively. The von Bertalanffy growth models estimated were significantly different between sexes. The growth models for females, males and all fish were $L_t = 298.0[1 - e^{-0.59(t-0.08)}]$, $L_t = 331.8[1 - e^{-0.35(t+1.08)}]$ and $L_t = 312.2[1 - e^{-0.48(t+0.32)}]$, respectively. Growth is fast during the first 4 years of life, when the average fish size is already in excess of 80% of the asymptotic size. The maximum age observed in this study is greater than those previously reported for *H. plumierii*. The natural mortality rate (M) estimate based on the oldest observed fish was 0.15 year⁻¹, while total mortality (Z) from the age-based catch curve was 0.21 year⁻¹ (95% confidence interval: 0.18–0.24 year⁻¹). These estimates show that the stock was under low to moderate levels of exploitation in the late 1990s.

Keywords: *Haemulon plumierii*, age, growth, mortality, reef, handlining, tropical fishery.

RESUMEN: EDAD, CRECIMIENTO Y MORTALIDAD DEL BOQUI COLORADO (*HAEMULON PLUMIERII*) EN LA COSTA CENTRAL DE BRASIL. – Otolitos sagita del boqui colorado (*Haemulon plumierii*) fueron recolectados entre 1997 y 1999 en la costa central de Brasil. El análisis de los incrementos marginales de secciones de los otolitos reveló que una zona translúcida y una zona opaca se forman anualmente. Los rangos de tallas y clases de edades observados fueron 218–378 mm de largo total (TL) y 2–28 años respectivamente. Los modelos de crecimiento de von Bertalanffy estimados fueron significativamente diferentes entre los sexos. Los modelos de crecimiento para hembras, machos y total para la población fueron $L_t = 298.0[1 - e^{-0.59(t-0.08)}]$, $L_t = 331.8[1 - e^{-0.35(t+1.08)}]$ y $L_t = 312.2[1 - e^{-0.48(t+0.32)}]$ respectivamente. El crecimiento es rápido durante los primeros cuatro años de vida, cuando la talla media ya representa más del 80% de la talla asintótica. La edad máxima observada en este estudio es mayor a la reportada previamente para *H. plumierii*. La tasa de mortalidad natural estimada (M) en base el ejemplar mayor fue de 0.15 años⁻¹, mientras que la mortalidad total (Z) de la curva de captura de edades fue de 0.21 años⁻¹ (95% intervalo de confianza: 0.18–0.24 años⁻¹). Estas estimativas muestran que el stock estaba sometido a un nivel de explotación bajo a moderado a fines de los años 1990.

Palabras llave: *Haemulon plumierii*, edad, crecimiento, mortalidad, arrecifes, pesquerías de línea, pesca tropical.

INTRODUCTION

White grunt, *Haemulon plumierii*, is a reef-associated species that attains maximum total lengths (TL) in excess of 500 mm (Froese and Pauly, 2006). It occurs from Chesapeake Bay in the USA (39°N) to the Brazilian southeast and central coasts (23°S) at depths of 3 to 40 m (Froese and Pauly, 2006; Potts

and Manooch, 2001). It is not a valuable species in Brazil and is caught mainly as a by-catch in the handline fishery that targets more valuable species such as *Cephalopholis fulva*, *Ocyurus crysurus* and *Rhomboplites aurorubens*.

There is no information on the population dynamics of *H. plumierii* from the central coast of Brazil. Previous studies based on otolith readings

for this species were carried out in different regions of the coast of the United States (Manooch, 1976; Padgett, 1997; Potts and Manooch, 2001; Murie and Parkyn, 2005) and Puerto Rico (Sadovy *et al.*, 1989). Murie and Parkyn (2005) reported significant growth differences for *H. plumierii* from regions that are not too far apart and suggested that the growth of this species may be modulated on a relatively small-scale or regional level. In this paper, we used sectioned sagittal otoliths collected off the central coast of Brazil in order to estimate growth parameters, population age and sex structure, and mortality rates for *H. plumierii*. The objective of our study was to complete a comprehensive study describing aspects of *H. plumierii* population dynamics in the southern Atlantic.

MATERIALS AND METHODS

Samples of *H. plumierii* were collected from 1997 to 1999 along the Brazilian central coast (12–22°S). In October and November 1997, a few samples were obtained from bottom longline research surveys conducted on the continental shelf margin and on the submarine banks. The bulk of the samples were collected on a monthly basis from 1998 to 1999 from commercial handline fishery landings in the city of Vitória. For each sample total length (TL mm), total weight (TW g) and sex information were recorded. Sagittal otoliths were extracted, dried and stored in labelled paper envelopes.

Undamaged otoliths were weighed (OW) to the nearest 0.1 mg. The otoliths were then embedded in epoxy resin. Two dorso-ventral sections of 0.3 mm were taken around the core using a Buehler-Isomet low-speed saw and mounted on dark glass slides with synthetic Canada Balsam. The sections were viewed under reflected light with a dissecting microscope at 30–40 magnifications. Two growth zones were visible (Fig. 1): an opaque white zone and a translucent zone that was dark and slightly narrower than the opaque one under reflected light. The otolith core was composed mainly of opaque material and was followed by a narrow translucent zone. The first two opaque zones after the core were broader but slightly diffuse, and darker and less conspicuous than the following ones. The authors counted the numbers of translucent zones, starting from the first conspicuous zone that followed the core. Readings that did not agree were re-inspected. Samples for which an

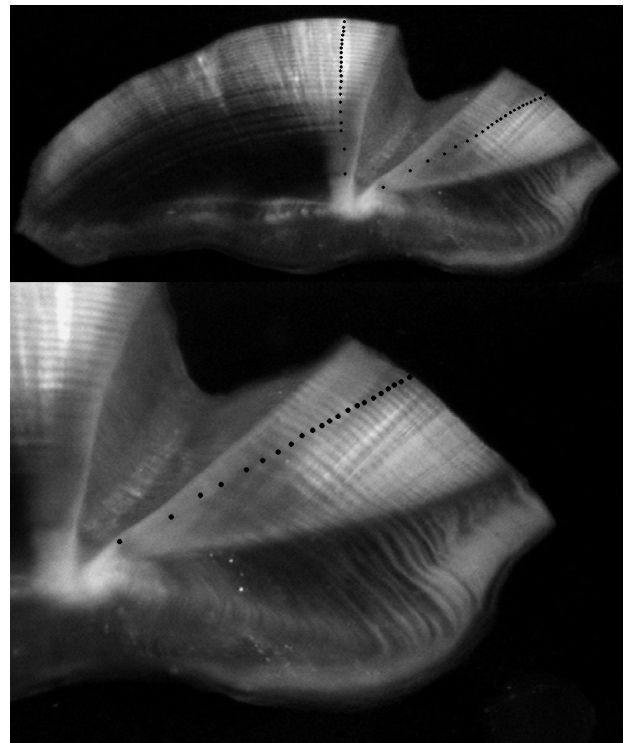


FIG. 1. – Views of an otolith transverse section (0.3 mm thick) observed with reflected light. Left otolith from a female *H. plumierii* that was 360 mm total length and 22 years old, caught in July 1998 off the central coast of Brazil.

agreement could not be reached were excluded from the data set. The age at which the first translucent zone is formed was calculated as the time between the mean birth date, estimated as the main spawning peak that occurs in May (unpublished data), and the peak of formation of translucent zones. Subsequently, the age was calculated as the age at formation of the first zone plus the number of translucent zones outside the first and the time between the formation of the last zone and capture.

The periodicity of growth zone formation was assessed by means of median marginal increment analyses and analyses of the variation of the proportion of otoliths with translucent and opaque zones at the structure margin. The marginal increment was estimated as: $MI = (R - R_n) / (R_n - R_{n-1})$, where R is the total radius, R_n the last zone radius and R_{n-1} the penultimate zone radius. Measurements were taken along the ventral margin of the *sulcus acousticus* (Fig. 1). Average ages of males and females were tested for differences with the Student's t-Test ($\alpha = 0.05$) (Zar, 1996).

The relationships between TW and TL, TL and R, age and OW were best described by the linearised (log-transformed) form of the power function

($y = ax^b$). Analysis of covariance was used to determine whether there were significant differences between the slopes of male and female models ($\alpha = 0.05$) (Zar, 1996).

The von Bertalanffy growth model was fitted to the observed lengths-at-age. The model is described by the equation $L_t = L_\infty[1 - e^{-K(t-t_0)}]$, where L_t is the length at time t (years), L_∞ is the theoretical mean maximum length (mm), K is a constant expressing the curvature of the growth function, and t_0 is the theoretical time at which L is 0 (Ricker, 1975). Models for males, females and both sexes were estimated using the Gauss-Newton algorithm of the non-linear least-squares estimation module of the R software (R Development Core Team, 2006). Likelihood ratio tests (Kimura, 1980; Cerrato, 1990) were used to test for differences between male and female models ($\alpha = 0.05$).

The total mortality rate estimate, Z , was obtained by using the age-based catch curve as the slope of a linear regression of natural log-transformed observed numbers at age (Ricker, 1975). The natural mortality rate was estimated using the model of Hoenig (1983), $\ln[M] = 1.46 - 1.01 \ln[t_{\max}]$, where t_{\max} is the maximum observed age (years). Fishing mortality and exploitation rates were then estimated as $F = Z - M$ and $E = F/Z$, respectively (Ricker, 1975).

RESULTS

A total of 627 specimens of *H. plumierii* (Fig. 2) ranging from 218 to 378 mm TL were sampled. There were 329 females (230–370 mm TL), 289 males (218–378 mm TL) and 9 specimens that could not have their sexes identified (290–318 mm TL). The size frequencies of males and females were markedly different. Females dominated size classes lower than 310 mm (mean = 295.4 ± 2.4 mm; $\alpha = 0.05$), whereas males were more abundant than females in the upper size classes (mean = 318 ± 3.1 mm; $\alpha = 0.05$). The length-weight relationship was not significantly different between sexes ($p > 0.05$) and was described by the equation $TW = 2 \times 10^{-5} TL^{2.978}$ ($r^2 = 0.887$; $n = 624$, $p < 0.01$).

Counts of translucent zones were obtained from 518 (83.8%) of the 618 otolith sections that we were able to examine. As the bulk of the samples was represented by relatively old fish, it was fairly difficult to observe and measure the accretion of newly formed material at the margin of the otoliths section.

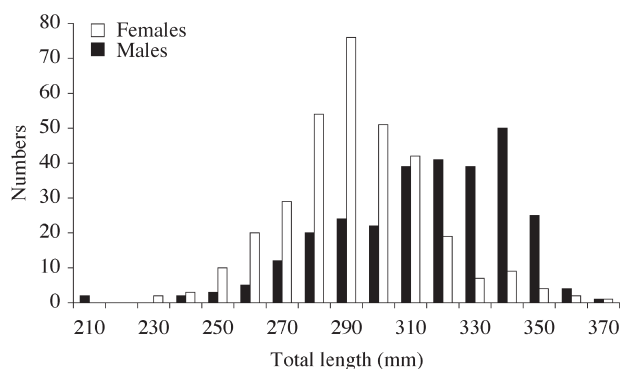


FIG. 2. – Length frequency distribution (10 mm length classes) of male and female *H. plumierii* sampled for age determination between 1997 and 1999 along the central coast of Brazil.

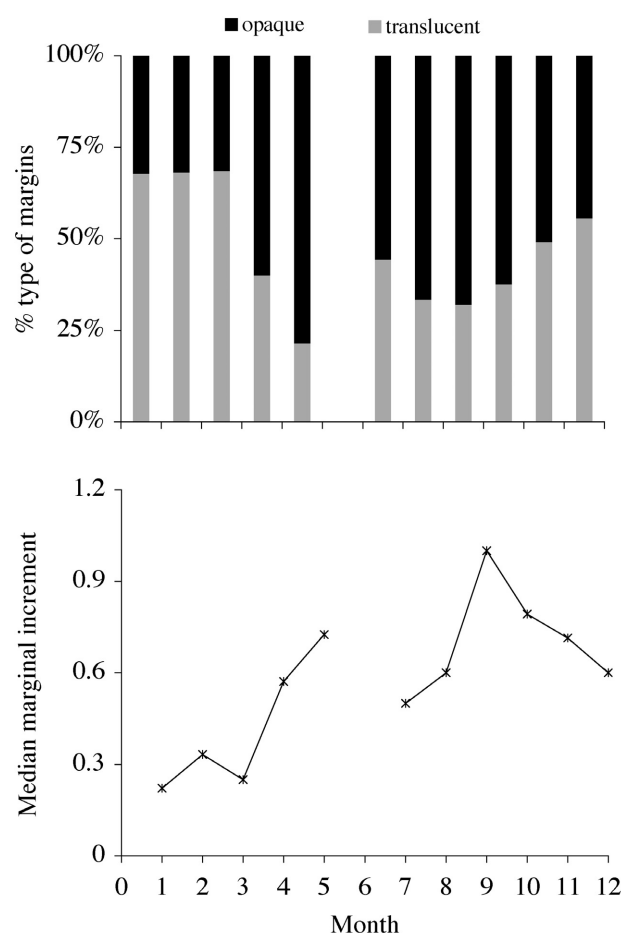


FIG. 3. – Monthly frequency of opaque and translucent margins and monthly median marginal-increment of sectioned otoliths of *H. plumierii* sampled between 1997 and 1999 along the central coast of Brazil.

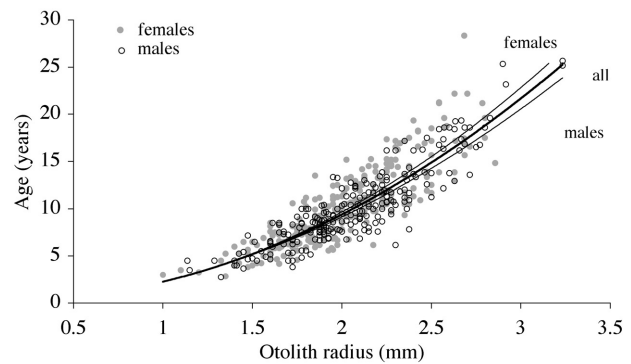
The proportion of otoliths with translucent margins was highest (>50%) from December to March (Fig. 3). Translucent margins were fairly frequent in all other months sampled, but the proportions were always less than 50%. The median marginal incre-

TABLE 1. – Average observed total lengths-at-age (TL) of *H. plumierii* collected off the central coast of Brazil between 1997 and 1999.

Age (yr+)	Females		Males		All fish	
	Average TL (mm)	n	Average TL (mm)	n	Average TL (mm)	n
2	270.0	1	260.0	1	265.0	2
3	239.8	4	265.3	3	252.5	8
4	271.5	11	281.1	17	277.3	29
5	290.9	21	290.7	12	290.8	33
6	293.2	33	318.5	23	303.6	56
7	290.9	25	316.3	34	305.7	61
8	292.6	18	319.8	27	308.9	45
9	299.9	25	320.3	24	309.9	49
10	292.6	24	323.0	25	307.6	50
11	296.5	31	323.7	15	305.3	46
12	299.0	15	330.1	14	314.0	29
13	300.0	15	338.3	15	319.2	30
14	301.5	11	340.0	1	304.7	12
15	305.7	7	352.0	1	311.5	8
16	290.9	8	325.1	10	309.9	18
17	295.9	8	304.5	4	298.8	12
18	293.6	5	342.3	7	322.0	12
19	287.8	4	333.3	3	307.3	7
21	301.7	3			301.7	3
22	332.5	2			332.5	2
23	322.0	1	362.0	1	342.0	2
25			337.3	3	337.3	3
28	294.0	1			294.0	1

ments also seemed to show an annual cycle, with the lowest values observed from January to March, when the proportions of translucent margins were at their highest level. These results suggested that there was a formation of one translucent zone and one opaque zone once a year. Observed age classes ranged from 2 to 28 years, with 54.1% of the fish falling between 7 to 12 years inclusive. Fish younger than 7 years and older than 12 years represented 24.7 and 21.2% of the fish sampled, respectively (Table 1). The average ages of males (9.9 years) and females (10.4 years) were not significantly different ($p = 0.18$). The average age for sexes combined was 10.1 years (95% confidence interval: 9.8–10.5 years).

The parameters of the predictive models relating total length, otolith radius, otolith weight and age of

FIG. 4. – Relationship between sectioned otolith radius and age of *H. plumierii* sampled between 1997 and 1999 along the central coast of Brazil.

H. plumierii are presented in Table 2. Otolith radius showed a poor relationship with fish size: the models explained less than 30% of the observed variation. The covariance analysis showed that the slopes of male and female models were significantly different ($p < 0.05$). The poor relationship between these two variables shows that the growth in fish length is to some degree uncoupled with the growth of the otolith radius. This poor relationship could introduce bias in the estimation of the growth curve if back-calculation was to be used to estimate the size at the time of formation of each observed growth zone. On the other hand, otolith dimensions showed a very good relationship with the observed ages. Otolith radius was the best predictor of fish age. No significant difference was detected ($p = 0.25$) between male and female model slopes. The model for sex combined explained approximately 78% of the observed variation (Fig. 4). Otolith weight was not an good age predictor as otolith radius. Females and male model slopes were significantly different ($p < 0.01$), with females tending to have lighter otoliths than males of the same age (Fig. 5). The models explained about 71% (females) and 74% (males) of the observed variation.

TABLE 2. – Predictive models relating total length (TL), otolith radius (R), otolith weight (OW) and age of *H. plumierii* collected off the central coast of Brazil between 1997 and 1999.

Sex	Dependent variable	Independent variable	Model	r ²	n
Female	TL	R	$\log(TL) = 0.176 \log(R) + 2.414$	0.177	255
Male	TL	R	$\log(TL) = 0.255 \log(R) + 2.424$	0.282	224
All	TL	R	$\log(TL) = 0.225 \log(R) + 2.415$	0.204	483
Female	Age	R	$\log(Age) = 2.116 \log(R) + 0.348$	0.772	255
Male	Age	R	$\log(Age) = 1.999 \log(R) + 0.359$	0.783	224
All	Age	R	$\log(Age) = 2.057 \log(R) + 0.354$	0.776	483
Female	Age	OW	$\log(Age) = 1.486 \log(OW) - 2.701$	0.705	266
Male	Age	OW	$\log(Age) = 1.261 \log(OW) - 2.201$	0.741	232
All	Age	OW	$\log(Age) = 1.326 \log(OW) - 2.333$	0.687	503

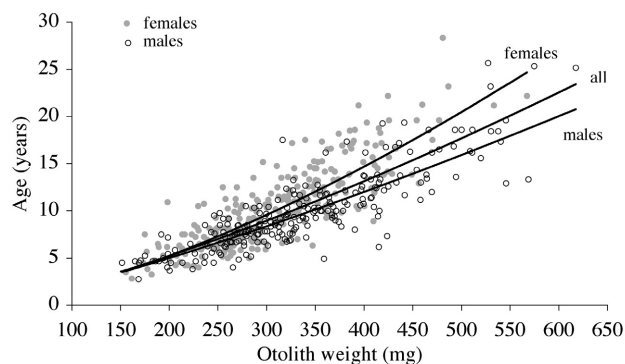


FIG. 5. – Relationship between otolith weight and age of *H. plumierii* sampled between 1997 and 1999 along the central coast of Brazil.

TABLE 3. – Growth parameters (\pm standard error; $\alpha = 0.05$) of the von Bertalanffy function estimated from observed lengths-at-age of *H. plumierii* collected off the central coast of Brazil between 1997 and 1999.

Parameter	All	Female	Male
L_{∞} (mm)	312.2 (1.79)	298.0 (1.71)	331.8 (3.24)
K (year ⁻¹)	0.48 (0.08)	0.59 (0.14)	0.35 (0.07)
t_0 (year)	-0.32 (0.75)	0.08 (0.89)	-1.08 (1.05)
r^2	0.16	0.14	0.3
Numbers	518	273	240

The von Bertalanffy growth curve was fitted to observed lengths-at-age for all fish, and separately for each sex (Fig. 6, Table 3). Growth of *H. plumierii* is fast up to the fourth year of life, when the fish length is in excess of 80% of the asymptotic size. Growth rate is much reduced afterwards, falling to less than 10% per year. Growth models of *H. plumierii* were significantly different between sexes ($p < 0.01$), with males having larger asymptotic sizes than females ($p < 0.01$). The estimated K and t_0 were not significantly different between sexes ($p > 0.05$).

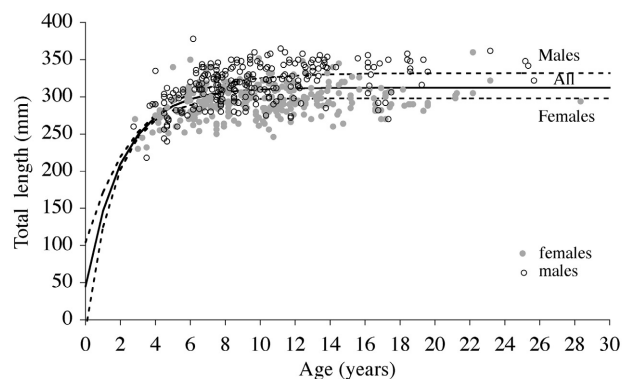


FIG. 6. – Von Bertalanffy growth curve of male and female *H. plumierii* sampled between 1997 and 1999 along the central coast of Brazil.

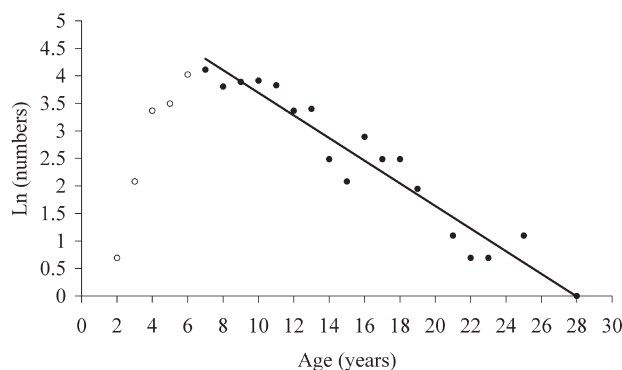


FIG. 7. – Age-based catch curve for *H. plumierii* sampled between 1997 and 1999 along the central coast of Brazil.

The maximum observed age of *H. plumierii* along the central coast of Brazil was 28 years old. This estimate was used in the model of Hoenig (1983), giving an M estimate of 0.15 year⁻¹. The age distribution of *H. plumierii* suggests that fish younger than 7 years old were not fully recruited to the fishing gear or under-sampled due to some unknown bias (Fig. 7). Total mortality rate (Z) estimated using ages ranging from 7 to 28 years was 0.21 year⁻¹ (95% confidence interval: 0.18-0.24, $r^2 = 0.928$; $p < 0.01$). Fishing mortality (F) was 0.06 year⁻¹. Exploitation rate ($E = F/Z$) was 0.28.

DISCUSSION

This study has shown that it is possible to age *H. plumierii* off the central coast of Brazil using otolith sections. Results of marginal-increment analysis and variation in the frequency of opaque and translucent zones on the margin of sectioned otoliths suggested that there was an annual periodicity in the deposition of the growth zones. We also observed that the mass and thickness of otoliths increased throughout the lifespan. These two criteria, periodicity of growth zone deposition and structure continued growth even when somatic growth is much reduced, are fundamental for the ageing methodology (Beamish and McFarlane, 1983).

Annual formation of growth zones has been observed for *H. plumierii* in studies that applied marginal increment analyses (Potts and Manooch, 2001) and a combination of that method with oxytetracycline injection (Murie and Parkyn, 2005). Translucent zones dominated summer months and opaque zones were more frequent during the rest of the year along the central coast of Brazil. These results differ from those of Potts and Manooch (2001) and Murie and

Parkyn (2005), who observed opaque zones occurring in a shorter period, mainly during spring months of the northern hemisphere, while translucent margins dominated the remaining months. Those authors also reported that the formation of opaque zone is somewhat coincident with the spawning season in the different areas studied. The spawning season of *H. plumierii* along the central coast of Brazil (unpublished data) is protracted, lasting several months but with a peak in May, coinciding with the period of maximum occurrence of opaque rings at the margin of the otolith sections, similarly as reported above for other stocks. Morales-Nin and Panfili (2005) revisited the issue of seasonality and otolith growth in tropical environments. As they state, several studies have been carried out on age and growth of tropical species and have shown that seasonal patterns in otolith growth have been validated and that even slight changes in temperature, a few degrees in reef habitats, can induce different otolith growth patterns. The average monthly temperature in the region of the present study can vary as much as 3 degrees between summer and winter months and March is the hottest month (Nimer, 1989). Hence, it is also possible that changes in sea temperature are related to the deposition of growth zones in the otoliths of *H. plumierii* along the central coast of Brasil, with the translucent zone deposition occurring mainly in the period of higher temperatures. However, we do not have sufficient information to try to propose a definite causal relationship between any environmental or endogenous factors with the deposition of otolith growth zones, and further research should be done to clarify this issue.

Differently from Potts and Manooch (2001) and Murie and Parkyn (2005), we observed opaque zones that were slightly wider than the translucent ones. This feature was related mainly to the first two opaque growth zones, which looked broad and diffuse under reflected light. Allman *et al.* (2005) observed that *Lutjanus campechanus* commonly have a broad and diffuse first opaque zone, a feature that has also been reported for tropical lutjanids and other reef fishes (Fowler, 1995). This feature led Allman *et al.* (2005) to measure the distal edge of the first zone instead of the centre of the zone as they did for the other opaque zones. They also reported that translucent zones narrow as fish age. We observed many old individuals with translucent and opaque zones with similar widths (see Fig. 1). Differences in the interpretation of the otolith struc-

ture can also be partially related to the different ways of examining the sections, i.e. with either transmitted light or reflected light, and also to the thickness of the sections. Murie and Parkyn (2005) used transmitted light, which likely makes the opaque zone look a bit narrower than it is under reflected light.

The maximum estimated age (28 years) in this study is well above the estimates of Potts and Manooch (2001) and Murie and Parkyn (2005), who reported maximum ages of 15 and 18 years, respectively. Padgett (1997) observed a maximum age of 27 years but also observed that 95% of the samples were between age 1 and 8. This is quite different from the age structure along the central coast of Brazil, where old fish (>10 years) were relatively abundant. The continued growth of the otoliths of *H. plumierii* along the central coast of Brazil and the good relationship between age and otolith weight and between age and otolith thickness give additional evidence of the accuracy of the age estimation protocol used in this study. Therefore, we are confident about the age structure for the species in the area studied. The difference from the northern hemisphere could be related to either differences in fishing pressure or differences in the lifespan of the stocks of these areas.

Growth parameters for *H. plumierii* estimated in previous studies were considerably variable (Table 4). The reported ranges for K and L_{∞} estimates were 0.08 to 0.41 year⁻¹ and 291 to 640 mm, respectively (Manooch, 1976; Sadovy *et al.*, 1989; Padgett, 1997; Potts and Manooch, 2001; Murie and Parkyn, 2005), while in the present study K and L_{∞} estimates varied from 0.35 to 0.59 year⁻¹ and 298 to 332 mm, respectively. Growth parameter estimates can differ as a function of many factors, such as environmental conditions, genetic differences, differences in fishing pressure, methodology employed and bias caused by sampling and aging errors. Murie and Parkyn (2005) stated that growth parameters of *H. plumierii* estimated by Padgett (1997) could not be compared directly with their estimates and the estimates of Potts and Manooch (2001) because the first published study used mean back-calculated lengths-at-age based on back-calculating to all previous annuli, whereas the others used back-calculated lengths to only the most recently formed opaque zone. Similarly, the present results would not be directly comparable with the results of the previous works, since we did not use back-calculated lengths

TABLE 4. – Growth parameters of the von Bertalanffy function estimated for the southern United States and Caribbean stocks of *H. plumierii* (adapted from Murie and Parkyn, 2005).

Author	L_{∞} (mm)	K (year ⁻¹)	t_0 (year)	Sex	Area
Manooch (1976)	640	0.11	-1.01	All	Carolinas
Sadovy <i>et al.</i> (1989)	321	0.34	0.33	All	Puerto Rico
Padgett (1997) ¹	370	0.32	-0.36	Male	Carolinas to northeast Florida
Padgett (1997) ¹	334	0.35	-0.70	Female	Carolinas to northeast Florida
Padgett (1997) ²	514	0.11	-4.99	Male	Carolinas to northeast Florida
Padgett (1997) ²	353	0.29	-3.79	Female	Carolinas to northeast Florida
Potts and Manooch (2001)	591	0.08	-4.21	All	Carolinas
Potts and Manooch (2001)	327	0.19	-4.21	All	Southeast Florida
Murie and Parkyn (2005)	345	0.41	-0.85	Male	Florida Gulf coast (N-central)
Murie and Parkyn (2005)	317	0.35	-1.68	Female	Florida Gulf coast (N-central)
Murie and Parkyn (2005)	319	0.36	-1.89	Male	Central
Murie and Parkyn (2005)	295	0.30	-3.44	Female	Central

1: Estimates based on scientific survey data.

2: Estimates based on commercial fisheries data.

to estimate the growth parameters. In addition to these differences, Potts and Manooch (2001) weighted the equation using the inverse of sample size at each age to give more weight to rare old fish when estimating the growth parameters. This is partially responsible for the large differences observed between their results and ours. On the other hand, Murie and Parkyn (2005) suggested that the growth of *H. plumierii* might be modulated on a relatively small-scale or regional level. They observed significant differences between the data sets they analysed for the north-central and central coasts of the Florida Gulf and between their estimates and the results of Potts and Manooch (2001).

Despite the differences in the methodology applied and possible bias and environmental differences, some estimates of Murie and Parkyn (2005) and some estimates reported by Padgett (1997) were quite similar to some estimates we obtained (Table 4). Murie and Parkyn (2005) described the growth pattern of *H. plumierii* from the Gulf coast of Florida as being fast during their first 4 years, followed by slower growth after age 5-6, when a “growth plateau” is observed. This is quite similar to the growth of *H. plumierii* along the central coast of Brazil. In this region the species growth also falls quite rapidly after the first few years, but the growth de-acceleration is faster. As a result the growth coefficient (K) estimates for the stock along the central coast of Brazil were higher. Some other similarities are evidenced by the pattern of otolith radius and fish length relationship, particularly the results of Padgett (1997), who observed r^2 values as low as 0.18, as we did in this study.

Average length for ages 1 and 2 estimated in this study with the estimated von Bertalanffy model var-

ied from 125 to 172 mm and from 202 to 216 mm, respectively. Average back-calculated length for ages 1 and 2 reported in Potts and Manooch (2001) varied from 107 mm to 162 mm and from 197 to 218 mm, respectively, depending on the age class of the fish and the region from which the samples were taken. Therefore, although we found just a few fish younger than 3 years of age, the average lengths estimated with the estimated von Bertalanffy model seem to be a good approximation of the actual sizes for the young ages of the species.

Newman *et al.* (1996), Newman (2002) and Hart and Russ (1996) provided evidences that the application of Hoenig's equation (1983) gives similar estimates of M to those derived from age-based catch curves of unexploited stocks, and Newman (2002) suggested that the use of that method will provide at least an upper limit for the estimate of M. The estimate of M for the *H. plumierii* stock along the central coast of Brazil was 0.15 year⁻¹, while total mortality (Z) was 0.21 year⁻¹ (95% confidence interval: 0.18-0.24 year⁻¹). These estimates suggest that the stock was under low to moderate levels of exploitation in the late 1990s, and that the estimated lower limit of mortality from the catch curve could be used as an upper limit for M. Alternatively, it is possible that the longevity of *H. plumierii* is in excess of 30 years, so M calculated with the model of Hoenig (1983) would be overestimated.

The stock of *H. plumierii* in the late 1990s was under lower fishing pressure than other reef fish such as some Lutjanidae and Serranidae species that are the main target of the fishery. The depth range of *H. plumierii* is somewhat different to that of the target species. The species tends to be found in coastal and relatively shallow areas and is caught mainly in

the upper limit (30-40 m) of its depth range distribution. Considering the observed age selectivity pattern and the fact that small, immature young specimens are less frequent in deeper waters, the fishery might have had a low or moderate impact on this stock in the late 1990s.

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