



Received: March 1, 2014 Accepted: June 1, 2014 doi: 10.1111/jai.12633

# J. Appl. Ichthyol. 31 (2015), 57–64 © 2014 Blackwell Verlag GmbH ISSN 0175–8659

# Age, growth and mortality of *Lutjanus alexandrei* in estuarine and coastal waters of the tropical south-western Atlantic

By A. Aschenbrenner and B. P. Ferreira

Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, PE, Brazil

## Summary

Otolith-based methods were used to determine life history traits of the endemic Brazilian snapper (Lutjanus alexandrei) in estuarine and coastal environments in the south-western Atlantic. Fishes were caught as juveniles inside mangrovebordered estuaries by traditional corral fisheries whereas adults were captured at sea using motorboats with trap and gill nets. Fish were sampled during landings and 331 otolith pairs were extracted from L. alexandrei. Inshore mangroves comprised individuals of 0-4 years (mean: 2 years), while individuals in deeper reef environments were older (range: 3-22; mean: 8 years), indicating an ontogenetic shift at approximately age 3 or 4. Edge analysis was used to validate the annual deposition in the otoliths, suggesting that opaque growth rings were formed between April and September. Age-at-length data were used to predict L. alexandrei growth rates using the von Bertalanffy growth model from where the parameters were calculated:  $L_{\infty} = 31$  cm,  $t_0 = -1.26$ ,  $r^2 = 0.97$ . Mortality rates were estimated for coastal habitats, with Z = 0.22 and S = 0.78 year<sup>-1</sup>, based on ages 7-17. Additionally, evidence of ontogenetic migration is provided by age and size structure.

# Introduction

Commonly called 'Baúna' by the fishermen, the Brazilian snapper (*Lutjanus alexandrei*) is endemic to the Southern Hemisphere. Formerly misidentified as grey snapper *Lutjaus griseus*, the species was recently described correctly by Moura and Lindeman (2007). *Lutjanus alexandrei* is only recorded for the tropical portion of the southwestern Atlantic continental shelf, and has a narrower latitudinal range than its western Atlantic congeners. Brazilian snapper habitats include coral reefs, rocky shores, coastal lagoons with brackish water, mangroves, and other shallow waters. Recorded depths range from intertidal (early stages only) to at least 60 m (authors pers. obs.).

Despite the reproductive biology recently described for *L. alexandrei* (Fernandes et al., 2012), other life history information (e.g. age, growth and feeding) are still lacking for this species. This hinders our ability to assess their population status and develop appropriate management plans, thus emphasizing the importance of biological and ecological studies on this endemic species. In this context, age, growth, and mortality data represent basic life history information

essential to understand the population dynamics of this species (Manooch, 1987; Lai et al., 1996; Campana, 2001). Furthermore, spatial distribution of size-classes of a fish species may reveal movement from one habitat to another with ontogeny (Cocheret de la Morinière et al., 2003) that has important implications for spatially-based management (Moura et al., 2011).

In response to these needs, otolith-based techniques were used to examine the age structure of *L. alexandrei* in both early life (estuarine) and adult (coastal) habitats, whereby the timing of the ontogenetic shift between the two habitats was also investigated. Age information was combined with length data to provide the first growth estimates for *L. alexandrei* in both early life and adult habitats. Finally, the age and abundance information was used to predict mortality rates, which together with growth and longevity parameters are important input for stock assessment models.

## Materials and methods

Sampling was conducted at one estuarine area and adjacent coastal areas along the tropical portion of the south-western Atlantic coast (7°44′S, 34°49′W–9°05′S, 35°15′W). The region is characterized by Atlantic rain forests, mangroves, sandbanks, estuaries, seagrass beds and coral reefs (Ferreira et al., 2004) that form an interconnected highly productive system supporting important artisanal fisheries (Ferreira and Maida, 2006). Specimens of *L. alexandrei* were obtained through fish landings in two localities on the coast of Pernambuco State (Itamaracá and Barra de Sirinhaém) and one location on the coast of Alagoas State (Japaratinga) (Fig. 1a). Individuals inhabiting mangroves were sampled at the Formoso River estuarine complex (Fig. 1b). Both estuarine and coastal areas were sampled between May 2010 and July 2012.

A total sample of 371 *L. alexandrei* was collected; the fish were weighed and measured individually. In coastal areas most samples were obtained during landings from gillnet fisheries operating over the continental shelf at depths between 30–60 m. In order to increase samplings for growth estimates, specimens were also obtained from trap fishery landings operating at the same depths as the gillnet fisheries. No individuals were recorded from hook and line fisheries. In the estuary all individuals were obtained from corral fisheries, operating at depths 0–2 m, over estuary margins and parallel to mangrove tree roots.

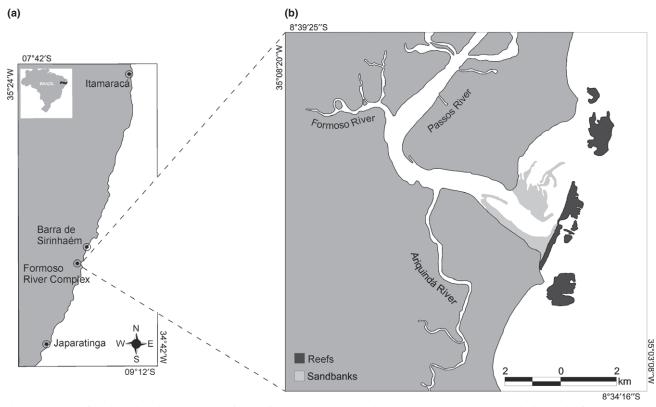


Fig. 1. (a) Map of study region showing general fish landings along the coast where *L. alexandrei* were collected; (b) detail of Formoso River mangrove complex

Length and weight data from each fish were recorded to the nearest mm (total, fork and standard length, TL, FL and SL, respectively) and weighed to the nearest 0.1 g [total weight (TW)]. The relationship between total length (TL) and total weight (TW) LWRs for L. alexandrei was determined by the equation  $\log W = \log a + b \log TL$ , where W is the weight of the fish in grams, TL is the total length in centimeters; and a and b are the intercept and the slope of the regression line, respectively. LWRs were also performed separately for estuarine juveniles and sub-adults, as well as adults collected in the coastal areas to assess possible differences in development phases between habitats. The 95% confidence limits (CL) of b were calculated to estimate differences between individuals collected in estuarine and coastal areas (Zar, 1999).

The logarithmic presentation not only linearizes the relationship but also corrects for the increase in variation with length (Froese, 2006). Only extreme outliers attributed to data error were omitted from analyses. In addition, regressions among size variables total (TL), fork (FL) and standard (SL) length are provided.

Sagittal otolith pairs were obtained from 341 individuals. Otoliths were then cleaned, dried, labeled and stored in plastic vials. All undamaged, whole otoliths were weighed to the nearest 0.0001 g. The left otolith of each individual was embedded in transparent polyester resin and allowed to harden for 24 h. Transverse sections (0.5 mm) that included the core were cut using a Isomet low-speed saw (Buehler).

Thin sections were hand polished using 400-1200 grit wetdry sandpaper until annuli were clearly defined; the sections were then mounted on histological slides using Entelan and cover slips. Age was assigned according to annuli formation, defined as the area consisting of one opaque zone and one translucent zone (Ferreira and Russ, 1994). The counting of otolith rings in sectioned otoliths was performed using a stereomicroscope with reflected light at 40× magnification on a black background. Under reflected light, the opaque marks had an intense milky white appearance, while the translucent marks had a darkened tone. Otolith images were captured using the IMAGE PRO PLUS V. 4.5 computer program (SPSS Inc., 1999). Otolith readings were performed on the ventral side along the same transect from the nucleus to the outer edge parallel to the sulcus acusticus, as indicated with dots in Fig. 2. Each otolith section was read three times without the prior knowledge of fish length or other data and the age estimates recorded as the average of the three readings. A subsample of n = 100 otolith sections was randomly selected and evaluated by a second reader to confirm readings. The precision between readings was estimated using the Average Percent Error (APE) (Beamish and Fournier, 1981).

Marginal zone or edge analysis was used to validate the annual deposition of the opaque zone in the *L. alexandrei* otoliths. Growth zones on the proximal margin of the otolith were recorded as either translucent or opaque (Beckman and Wilson, 1995; Panfili and Morales-Nin, 2002) for age classes 2–12 years. Frequency of the opaque margin per month was

then plotted to determine the period of opaque zone deposition. Edge analysis was based on the assumption that the relative frequency of edge zones follows a yearly sinusoidal cycle when plotted against time (Campana, 2001).

Growth parameters were estimated by fitting lengths-at age-to the von Bertalanffy growth equation:  $L_t = L_{\infty}[1 - e^{k(t-t_0)}]$ , where  $L_t$  is the TL at age t,  $L_{\infty}$  the theoretical asymptotic length, k the body growth coefficient and  $t_0$  the theoretical age when fish length is equal to 0.

Estimates of the instantaneous rate of total mortality (Z) were obtained using the age based catch-curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class ( $N_t$ ) was plotted against their corresponding age (t), and Z was estimated from the descending slope b. Estimates of the survival rate (S) were then calculated by  $S = e^{-Z}$  (Robson and Chapman, 1961).

Differences between otolith weights were tested using paired *t*-test. Because age data between estuarine and coastal habitats did not show a normal distribution or homoscedasticity, differences in the mean values were evaluated using the non-parametric Mann–Whitney *U*-test (Sokal and Rohlf,

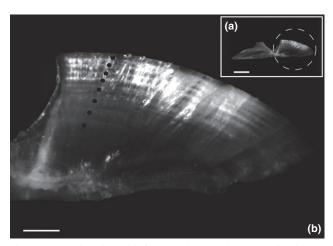


Fig. 2. (a) Sectioned otolith from nucleus to the outer edge of otolith margin; Scale bar = 1 mm. (b) Detailed sectioned otolith showing alternating pattern of opaque and translucent zones of an 8-year-old  $L.\ alexandrei.$  Scale bar = 0.3 mm

1995). The differences in average TL between estuarine and coastal habitats were examined using a *t*-test and corroborated by the Kolmogorov–Smirnov nonparametric test (Sokal and Rohlf, 1995).

### Results

### Size structure

Total length (TL) of fish sampled in the estuary ranged from 6 to 22 cm, and average size was 15.4 cm (n = 166); for coastal areas the size range TL was 20.7–33.1 cm, and average size 27.3 cm (n = 205) (Fig. 3). Detailed information on length per location is given in Table 1. Mean sizes (TL) were significantly different for estuarine and coastal areas (t-test, P < 0.05).

The estimated parameters of the length-weight relationships (LWRs) (Fig. 4a) and size-size regressions for L. alexandrei are given in Table 2. All LWRs were significant for this species (P < 0.01). Values of b found for L. alexandrei, show that the Brazilian snapper tends to grow slightly faster in length than in weight, for an allometric negative growth (Table 2).

Comparison of b values for juveniles and sub-adults were significantly different from the adult population (P < 0.05). Adult individuals collected in coastal areas displayed values slightly smaller when compared to individuals collected in estuarine areas (Table 2), the inflection point being observed at about 20 cm (Fig. 4b).

## Otolith microstructure

Average percent error (APE) among three readings was 5.4% performed by a primary reader, and 9.7% between two readers representing good reproducibility between readings. All otolith cross-sections were considered legible, and opaque rings were distinct and easily counted (Fig. 2).

Edge type analysis was performed on n = 257 otoliths, as 43 were considered unreadable and therefore excluded. The monthly proportion of otoliths with opaque margins was highest (>50%) from April to September (autumn-winter) (Fig. 5), while translucent margins reached higher proportions (>50%) from October to March (spring-summer).

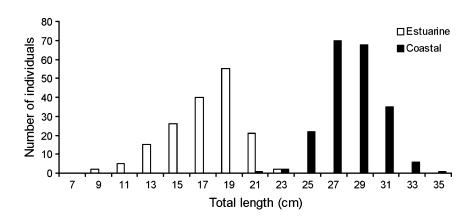


Fig. 3. Size distribution of total length of L. alexandrei for estuarine and coastal areas, May 2010 to July 2012 (n = 371)

## Age structure

Predicted ages of L. alexandrei ranged from 0 to 4 (mean = 2) for individuals from estuarine habitats (n = 143), with 2 years being the dominant age class in the estuary (46.5%) (Fig. 6). Age increased significantly for L. alexandrei collected in coastal areas, ranging from 3 to 22 years (n = 188). The ascending wing of the catch curve on coastal habitats occurred at age 7, suggesting that L. alexandrei are fully recruited to deeper coastal areas at this age. Mean age of L. alexandrei for coastal habitats was 8 years. Age distributions obtained for individuals sampled in estuarine and coastal areas were significantly different (Mann–Whitney U-test P < 0.05).

### Growth and age-at-length data

Age-at-length data fitted to the von Bertalanffy (VB) model showed an initial rapid growth pattern for L. alexandrei during the first years of life. Similar to other lutjanids, a noticeable slowing down occurred at approximately age 4, when the species reached an average 72% of its asymptotic length. Using the VB model, length-specific growth coefficient (k) for L. alexandrei was estimated to be 0.24  $\pm$  0.01 SE, with  $L_{\infty}$  estimated to be 31 cm  $\pm$  0.2 SE, (Fig. 7). Age-at-length data revealed that L. alexandrei presents an initial rapid growth

Table 1 Summary size collection for *L. alexandrei* in total length (TL), May 2010 to June 2012

	Size mean (cm)	Range (cm)	n
Estuarine	15.4	6.0–22.0	166
Coastal	27.3	20.7–33.1	205

phase, with individuals reaching more than 50% of their asymptotic length by age 2 (Table 3).

## Mortality

Estimates of total mortality (Z) for coastal individuals derived from catch curves and sampled with gillnets in hard bottom areas were  $Z = 0.22 \text{ year}^{-1}$  and  $S = 0.78 \text{ year}^{-1}$ , with  $r^2 = 0.83$ , n = 168 (Fig. 8).

### Discussion

To our knowledge, this is the first study reporting information on growth, mortality and length-weigh relationship of L. alexandrei in northeast Brazil. Values of b differ between life stages, revealing two growth stanzas (Fulton, 1904): a juvenile/sub-adult estuarine/mangrove phase and an adult marine/reef phase. Growth stanzas are expected for different life stages, and higher values of b are usually expected for smaller individuals and lower values for larger ones (Stergiou and Fourtouni, 1991). Estimates of separate length-weight relationships for different development phases or growth stanzas are particularly important as these not only can indicate shifts in diet as expected in ontogenetic shifts in habitat, but also because the resulting parameters will be more useful if within the size range to which the relationship will later be applied (Froese, 2006). The b values reported here for L. alexandrei life phases as well as pooled samples fall within the normal expected range for b values for fish of 2.5-3.5 (Froese, 2006) and yet agreed with the values found in the literature for Lutjanus congeners in the south and north Atlantic that presented a b range of 2.6–3.3 (Frota et al., 2004; Froese and Pauly, 2013).

Maximum recorded size for L alexandrei was (TL = 3 3.1 cm), which suggests that L alexandrei might be the

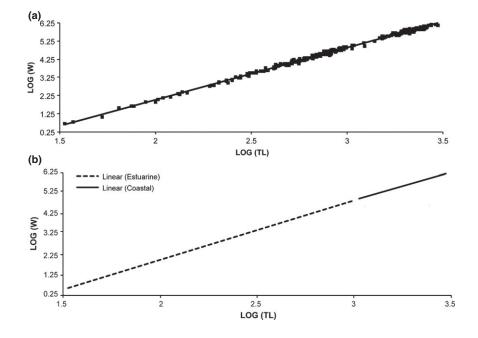


Fig. 4. (a) Logarithmic length—weight relationship  $\log W = \log a + b \log TL r^2 = 0.99$  for overall *L. alexandrei* population of n = 288. (b) LWRs showing two growth stanzas for estuarine size range (6 to 20 cm)  $n = 171 r^2 = 0.99$  and coastal individuals size range (20 to 33 cm)  $n = 117 r^2 = 0.94$ 

■ Translucent

smallest Atlantic lutjanid, well below the maximum of 45.3 cm SL recorded for *L. synagris* (Cervigón, 1993; Freitas et al., 2011) as well as for northern Atlantic lutjanus congeners (Allen, 1985; Froese and Pauly, 2013).

Results from edge-type analyses suggest the annual otolith ring formation for *L. alexandrei*, and formation of the opaque ring between autumn–winter; this period is corroborated by several authors who also found annual ring formations for others lutjanid congeners (Newman et al., 1996, 2000; Claro et al., 1999; Cappo et al., 2000; Luckhurst et al., 2000; Burton, 2001, 2002).

Size and age distributions of *L. alexandrei* were significantly different between estuarine and coastal areas. Size and

depth trends have been registered for other lutjanid species in the Southern Atlantic, e.g. for *L. jocu* (Moura et al., 2011), and a positive relationships between depth and size was also observed for five species of snappers, *L. jocu*, *L. analis*, *L. synagris*, *O. chrysurus* and *L. vivanus* (Frédou and Ferreira, 2005). However, the present study is the first record of a marked and distinct size and age habitat shift.

The most frequent age class in the estuary was 2 years, probably as younger fish are not yet fully recruited to corral fisheries. Little overlap was observed for age-classes 3 and 4, suggesting that the species might leave the nursery areas at this age, performing a fast transition. In addition, the low frequency of age 4 individuals in the estuary and their simul-

Table 2 Overall *L. alexandrei* LWR log  $W = \log a + b \log TL$  parameters for whole population; n = 288, estuarine individuals n = 171, coastal individuals n = 117 and size regressions (Y = a + bX) among total (TL), fork (FL) and standard (SL) length n = 288

Habitat	Variables	Size range TL (cm)	a	b	95% CL of <i>b</i>	$r^2$
Pooled	W-TL	6–33	0.022082	2.8994	2.870-2.929	0.99
Estuarine	W-TL	6–20	0.021595	2.9144	2.885-2.944	0.99
Coastal	W-TL	20-33	0.039113	2.7224	2.597-2.848	0.94
Pooled	TL-FL	6–33	-0.0617	1.0732	1.062-1.084	0.99
Pooled	TL-SL	6–33	-0.2629	1.2831	1.274-1.292	0.99
Pooled	FL-TL	6–33	0.2047	0.9245	0.915-0.934	0.99
Pooled	FL-SL	6–33	-0.0121	1.1846	1.168-1.201	0.98
Pooled	SL-TL	6–33	0.2674	0.7762	0.771 - 0.782	0.99
Pooled	SL-FL	6–33	0.2414	0.8319	0.820-0.844	0.98

■ Opaque % Type of margins Month

Fig. 5. Monthly frequency of opaque and translucent margins of sectioned otoliths, *L. alexandrei*, May 2010 to July 2012 (n = 257)

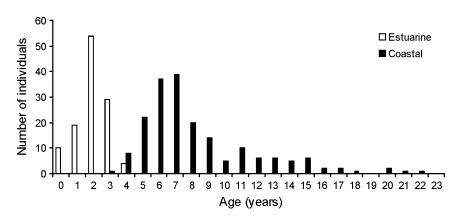


Fig. 6. Age distributions among estuarine (n = 143) and coastal areas (n = 188), *L. alexandrei*, sampled May 2010 to July 2012

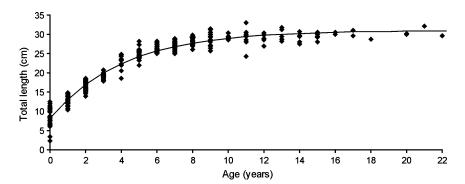


Fig. 7. The von Bertalanffy growth curve for L. alexandrein = 331

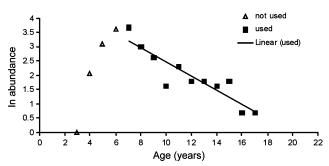


Fig. 8. Coastal area estimates of total mortality Z for L. alexandrei collected by gillnets n=168

Table 3 Age-at-length (TL) and cumulative percentage by year up to 10 years for *L. alexandrei* 

Age (years)	Length (cm)	Cumulative length by year (cm)	
0	8.3	8.3	27.0
1	13.1	4.8	42.4
2	17.0	3.9	54.9
3	20.0	3.0	64.7
4	22.4	2.4	72.4
5	24.2	1.9	78.4
6	25.7	1.5	83.1
7	26.8	1.1	86.8
8	27.7	0.9	89.7
9	28.5	0.7	92.0
10	29.0	0.6	93.8

taneous occurrence in the marine area suggest that individuals around this age are moving out of the estuary and are in the process of spending a year or two in shallower costal areas before moving out to the deeper fishing area.

The use of nursery inshore habitats especially for small juvenile fish is an ecological strategy, as such habitats provide maximum food availability and minimize the incidence of predation while providing shelter. As fish grow, a shift in habitat from estuarine to coastal or mudflat habitats may be a response to changes in diet, foraging efficiency, vulnerability to predators, and biological factors such as reproduction (Laegdsgaard and Johnson, 2001).

Ontogenetic migration for snappers is well known (Nagelkerken et al., 2000; Sheaves and Molony, 2001; Nagelkerken and van der Velde, 2002; Cocheret de la Morinière et al., 2003, 2004; Mumby et al., 2004; Faunce and Serafy, 2007; Jones et al., 2010; Moura et al., 2011). Lindeman et al. (1998) noted two basic types of habitat selection for snappers: the juveniles of some species are usually found in shallow estuaries, while adults inhabit bays, estuaries, and reef environments of shelf waters. Migrations towards deeper areas might be related to: (i) diet shift, such as is recorded for *Lutjanus griseus* (Starck, 1970) and *L. apodus* (Rooker, 1995); and (ii) sexual maturation and/or reproduction (Gerking, 1994; Sierra et al., 2001; Kimirei et al., 2013). Fernandes et al. (2012) estimated the size of first sexual maturity for *L. alexandrei* to be 17 cm SL; this value is approximately 21.5 cm TL (conversion TL-SL based on Table 2 length–length relationship), which is very close to the largest specimen recorded in the mangrove area with 22 cm TL.

Length-at-age growth of von Bertalanffy model for L. al-exandrei showed an initial rapid growth pattern and slowing down as individual length increases. The growth coefficient and  $L_{\infty}$  observed for L. alexandrei matches that of most reef fishes, displaying a fast initial growth and decreasing as the length-at-age population increases (Choat and Robertson, 2002). Values of k found for L. alexandrei in the growth equation agreed with values found the in literature for the lutjanidae family k range (0.1–0.35) (Manooch, 1987), although  $L_{\infty} = 30$  cm found this species to be the smallest by comparison with the lutjanidae family (Manooch, 1987).

Observed longevity for *L. alexandrei* was 22 years; most congeners of lutjanidae that reach larger sizes and also experience ontogenetic migration show better longevity: *L. griseus* 24 years (Burton, 2001), *L. analis* 29 years (Burton, 2002), and *L. jocu* 25 years (Rezende and Ferreira, 2004). However, this pattern was not observed for *L. synagris* 19 years (Luckhurst et al., 2000), *L. griseus* in southern Florida 15 years (Burton, 2001), *O. chrysurus* southern Florida 14 years (Johnson, 1983), and *O. chrysurus* northeastern Brazil 19 years (Araújo et al., 2002), possibly related to fishing pressure. Fisheries have an important impact on longevity: usually when fishing pressure is high, longevity and size tend to diminish among fish populations, especially for target species (Ricker, 1975).

Total mortality Z in reef areas was 0.22 year<sup>-1</sup>, a rate that can be considered low if compared to other congeners species, e.g. L. griseus southern Florida Z = 0.95 and northern

Florida Z = 0.34 (Burton, 2001), L. analis Florida Z = 0.49and (Burton, 2002) and L. synagris Gulf of Mexico Z range 0.375-0.5767 (Johnson et al., 1995). Lower mortality rates may be related to the fact that L. alexandrei is not the main target of any fisheries, and, as opposed to most lutjanids, is not caught by hook-and-line, which is the main snapperdirected fishery (Rezende et al., 2003; Frédou et al., 2006). Considering that L. alexandrei is not recorded in official statistical landings (IBAMA, 2006, 2007), and according to information from sample landings is not the target species for traps or gillnets, we believe this Z value might be important for future comparisons as a reference value, especially if fishing pressure somehow increases on this species. The recent development of trap fisheries targeting reef species for export markets (Marques and Ferreira, 2010), may mean increased pressure on these populations, since both the lane and Brazilian snappers are commonly caught by this fishery (Margues and Ferreira, 2010). In the absence of controls of fishery landings, population parameters are important reference points for impact evaluation.

The results presented here fill an important niche in biological aspects of this still poorly studied endemic Brazilian snapper. Ontogenetic migration evidence enhances the importance of including essential habitat assessment in fishery management strategies and habitat and ecosystem connectivity in the planning and design of marine reserves.

# Acknowledgements

We are grateful to Dr. Jay Rooker for all valuable suggestions and comments on the manuscript, as well as Simone Marques for helping with the figures and layout. We thank Universidade Federal de Pernambuco – UFPE and Centro de Pesquisa e Gestão de Recursos Pesqueiros do Litoral Nordeste – CEPENE/ICMBIO for use of their laboratory and facilities. We also acknowledge Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES for financial support (as a grant to A. Aschenbrenner).

# References

- Allen, G. R., 1985: Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO, Rome, 208 pp.
- Araújo, N. J.; Martins, A. S.; da Costa, K. G., 2002: Idade e Crescimento da Cioba, *Ocyurus Chrysurus* da Costa Central do Brasil. Rev. Bras. Oceanor. 50, 47–57.
- Beamish, R. J.; Fournier, D. A., 1981: A method for comparing the precision of a set of age determinations. Can. J. Fish Aquat. Sci. 38, 982–983.
- Beckman, D. W.; Wilson, C. A., 1995: Seasonal timing of opaque zone formation in fish otoliths. In: Recent developments in fish otolith research. D. H. Secor, J. M. Dean and S. E. Campana (Eds). University of South Carolina Press, Columbia, pp. 545– 565
- Beverton, R. J. H.; Holt, S. J., 1957: On the dynamics of exploited fish populations. Fishery Investigations Series II. Ministry of Agriculture, Fisheries and Food, London. 533 pp.
- Burton, M. L., 2001: Age, growth, and mortality of gray snapper, Lutjanus griseus, from the east coast of Florida. Fish. Bull. 99, 254-265

- Burton, M. L., 2002: Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. Fish. Res. **59**, 31–41.
- Campana, S. E., 2001: Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59, 197–242.
- Cappo, M.; Eden, P.; Newman, S. J.; Robertson, S., 2000: A new approach to tetracycline validation of the periodicity and timing of increment formation in the otoliths of 11 species of *Lutjanus* from the central great barrier reef. Fish. Bull. 98, 474–488.
- Cervigón, F., 1993: Los peces marinos de Venezuel, Vol. 2. Fundación Científica Los Roques, Caracas, 497 pp.
- Choat, J.; Robertson, D. Ř., 2002: Age-based studies. In: Coral reef fishes: dynamics and diversity in a complex ecosystem. P. Sale (Ed.). Academic Press, San Diego, pp. 57–80.
- Claro, R.; Sierra-Sierra, L. M.; García-Artega, J. P., 1999: Biologia del jocu, *Lutjanus jocu* (Bloch y Schneider, 1801) (Pisces: Lutjanidae) em las zonas NE y SW de la plataforma cubana, II. Alimentación, edad y crecimiento. Rev. Invest. Mar. 20, 30–38.
- Cocheret de la Morinière, E.; Pollux, B. J. A.; Nagelkerken, I.; van der Velde, H. G., 2003: Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations. Estuar. Coast. Shelf Sci. 57, 1079–1089.
- Cocheret de la Morinière, E.; Nagelkerken, I.; van der Meij, H.; van der Velde, G., 2004: What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? Mar. Biol. 144, 139–145.
- Faunce, C. H.; Serafy, E. J., 2007: Near shore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*heamulum sciurus*): environmental gradients and ontogenetic shifts. Bull. Mar. Sci. 80, 473–495.
- Fernandes, C. A. F.; Oliveira, P. G. V.; Travassos, P. E. P.; Hazin, F. V. H., 2012: Reproduction of the Brazilian snapper, *Lutjanus alexandrei* Moura & Lindeman, 2007 (Perciformes: Lutjanidae), off the northern coast of Pernambuco, Brazil. Neotrop. Ichthyol. 10, 587–592.
- Ferreira, B. P.; Maida, M., 2006: Monitoring Brazilian Coral Reefs: status and perspectives. Serie Biodiversidade, 18. MMA/SBF, Brazil.
- Ferreira, B. P.; Russ, G. R., 1994: Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacépède 1802) from Lizard Island, Northern Great Barrier Reef. Fish. Bull. 92, 46–57.
- Ferreira, B. P.; Messias, L. T.; Maida, M., 2004: The Environmental Municipal Councils as instruments for coastal integrated management: the *Área de Proteção Ambiental Costa de Corais (AL/PE)* experience. J. Coast. Res. **39**, 1003–1007.
- Frédou, T.; Ferreira, B. P., 2005: Bathymetric trends of Northeastern Brazilian snappers. Braz. Arch. Biol. Technol. 48, 787–800.
- Frédou, T.; Ferreira, B. P.; Letourneur, Y., 2006: A univariate and multivariate study of reef fisheries off northeastern Brazil. ICES J. Mar. Sci. 63, 883–896.
- Freitas, M. O.; Moura, R. L.; Francini-Filho, R. B.; Minte-Vera, C. V., 2011: Spawning patterns of commercially important reef fish (Lutjanidae and Serranidae) in the tropical western South Atlantic. Sci. Mar. 75, 135–146.
- Froese, R., 2006: Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J. Appl. Ichthyol. 22, 241–253.
- Froese, R.; Pauly, D., Eds, 2013: FishBase. World Wide Web electronic publication (Version 08.2013). Available at: http://www.fishbase.org (accessed on 15 July 2013).
- Frota, L. O.; Costa, P. A. S.; Braga, A. C., 2004: Length-weight relationships of marine fishes from the central Brazilian coast. NAGA Worldfish Center Q. 27, 20–26.
- Fulton, T. W., 1904: The rate of growth of fishes. Twenty-second annual report, part III. Fisheries Board of Scotland, Edinburgh, pp. 141–241.
- Gerking, S. D., 1994: Feeding ecology of fish. Academic Press, San

- IBAMA, 2006: Relatório Final do Projeto de Monitoramento da Atividade Pesqueira do Litoral do Brasil. Projeto ESTATPES-CA. Brazil.
- IBAMA, 2007: Estatística da Pesca: grandes regiões e unidades da federação. IBAMA, Brazil.
- Johnson, A. G., 1983: Age and growth of yellowtail snapper from South Florida. Trans. Am. Fish. Soc. 112, 173–177.
- Johnson, A. G.; Collins, L. A.; Dahl, J.; Baker, M. S., 1995: Age, growth, and mortality of lane snapper (*Lutjanus synagris*) from the northern Gulf of Mexico. In: Proceedings of the Annual Conference Association of Fish & Wild Agencies. Southeast Fisheries Science Center, Panama, pp. 178–186.
- Jones, D. L.; Walter, J. F.; Brooks, E. N.; Serafy, J. E., 2010: Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. Mar. Ecol. Prog. Ser. 401, 245–258.
- Kimirei, I. A.; Nagelkerken, I.; Trommelen, M.; Blankers, P.; Hoytema, N.; van Hoeijmakers, D.; Huijbers, C. M.; Mgaya, Y. D.; Rypel, A. L., 2013: What drives ontogenetic niche shifts of fishes in coral reef ecosystems? Ecosystems 16, 783–796.
- Laegdsgaard, P.; Johnson, C., 2001: Why do juvenile fish utilize mangrove habitats? J. Exp. Mar. Biol. Ecol. 257, 229–253.
- Lai, H. L.; Galucci, V. F.; Gunderson, D. R.; Donnelly, R. F., 1996:
  Age determination in fisheries: methods and applications to stock assessment. In: Stock assessment quantitative methods and applications for small-scale fisheries. V. F. Gallucci, S. B. Saila, D. J. Gustafson and B. J. Rothschild (Eds). Lewis Publishers, Florida, pp. 82–170.
- Lindeman, K. C.; Diaz, G. A.; Serafy, J. E.; Ault, J. S., 1998: A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. In: Proceedings the Gulf and Caribbean Fisheries Institute, pp. 385–416.
- Luckhurst, B. E.; Dean, M. J.; Reichert, M., 2000: Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. Mar. Ecol. Prog. Ser. 203, 255–261.
- Manooch, C. S. III, 1987: Age and growth of snappers and groupers. In: Tropical snappers and groupers: biology and fisheries management. J. J. Polovina and S. Ralston (Eds). Westview Press, Boulder, pp. 329–373.
- Marques, S.; Ferreira, B. P., 2010: Composição e características da pesca de armadilhas no litoral Norte de Pernambuco Brasil. Bol. Tec. Cient. CEPENE 18, 49–60.
- Moura, R. L.; Lindeman, K. C., 2007: A new species of snapper (Perciformes: Lutjanidae) from Brazil, with comments on distribution of *Lutjanus griseus* and *L. apodus*. Zootaxa **1422**, 31–43.
- Moura, R. L.; Francini, R. B.; Chaves, E. M.; Minte-Vera, C. V.; Lindeman, K. C., 2011: Use of riverine through reef habitat systems by dog snapper (*Lutjanus jocu*) in eastern Brazil. Estuar. Coast. Shelf Sci. **95**, 274–278.
- Mumby, P. J.; Edwards, A. J.; Arias-González, E. J.; Lindeman, K. C.; Blackwell, P. G.; Gall, A.; Gorczynska, M. I.; Harborne, A. R.; Pescod, C. L.; Renken, H.; Wabnitz, C. C. C.; Llewellyn, G., 2004: Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536.
- Nagelkerken, I.; van der Velde, G., 2002: Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherland Antilles)? Mar. Ecol. Prog. Ser. 245, 191–204.
- Nagelkerken, I.; van der Veldea, G.; Gorissena, M. W.; Meijera, G. J.; van't Hofc, T.; den Hartoga, C., 2000: Importance of man-

- groves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar. Coast. Shelf Sci. **51**, 31–44.
- Newman, S. J.; Williams, D. Mc. B.; Russ, G. R., 1996: Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. Mar. Freshw. Res. 47, 575–584.
- Newman, S. J.; Cappo, M.; Williams, D. Mc. B., 2000: Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. Fish. Res. 48, 1–14.
- Panfili, J.; Morales-Nin, B., 2002: Validation and verification methods. B. Semi-direct validation. In: Manual of sclerochronology. J. Panfili, de Pontual H., H. Troadec, P. J. Wright (Eds). IFREMER-IRD, Brest, pp. 129–134.
- Rezende, S. M.; Ferreira, B. P., 2004: Age, growth and mortality of dog snapper *Lutjanus jocu* (Bloch & Schneider, 1801) in the northeast coast of Brazil. Braz. J. Oceanogr. 52, 107–121.
- Rezende, S. M.; Ferreira, B. P.; Fredou, T., 2003: A pesca de lutjanideos no nordeste do Brasil: Histórico das pescarias, características das espécies e relevância para o manejo. Bol. Tec. Cient. Cepene 11, 257–270.
- Ricker, W. E., 1975: Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 pp.
- Robson, D. S.; Chapman, D. G., 1961: Catch curves and mortality rates. Trans. Am. Fish. Soc. 90, 181–189.
- Rooker, J. R., 1995: Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. Bull. Mar. Sci. **56**, 881–894.
- Sheaves, M.; Molony, B., 2001: Coherent patterns of abundance and size of a tropical snapper in dynamic estuary systems. Wetl. Ecol. Manag. 9, 429–439.
- Sierra, L. M.; Claro, R.; Popova, O. A., 2001: Trophic biology of the marine fishes of Cuba. In: Ecology of the marine fishes of cuba. R. Claro, K. C. Lindeman and L. R. Parenti (Eds). Smithsonian Institution Press, Washington, DC, pp. 115–148.
- Sokal, R. R.; Rohlf, F. J., 1995: Biometry: the principles and practice of statistics in biological research, 3rd edn. W. H. Freeman, New York, 887 pp.
- SPSS Inc., 1999: SPSS Base 5.0 for Windows user's guide. SPSS, Chicago.
- Starck, W. A., 1970: Biology of the gray snapper *Lutjanus griseus* (Linnaeus), in Florida Keys. Stud. Trop. Oceanogr. 10, 1–150.
- Stergiou, K. I.; Fourtouni, H., 1991: Food habits, ontogenetic diet shift and selectivity in Zeus faber. J. Fish Biol. 39, 589–603.
- Zar, J. H., 1999: Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River, 931 pp.

Author's address: Alexandre Aschenbrenner, Programa de Pós-Graduação em Oceanografia, Universidade Federal de Pernambuco, Av. Arquitetura, s/n, Cidade Universitária, Recife, Pernambuco, CEP 50740-550, Brazil. E-mail: brenner.ale@gmail.com