# Age structure and growth of the dusky damselfish, *Stegastes fuscus*, from Tamandaré reefs, Pernambuco, Brazil

Silvia H.L. Schwamborn & Beatrice P. Ferreira

Departamento de Oceanografia, Universidade Federal de Pernambuco, Av. Arquitetura, s/n, Cidade

Universitária, 50.740-550, Recife, Pernambuco, Brazil (e-mail: slima@npd.ufpe.br)

Received 3 May 2000 Accepted 2 May 2001

Key words: Pomacentridae, age, growth, validation experiments, coral reefs

## **Synopsis**

Age structure and growth of *Stegastes fuscus* were investigated during the present study. Individuals were collected monthly by divers using nets and spears in the reefs off Tamandaré, Pernambuco, Brazil. Otoliths were removed from 346 individuals and sectioned transversally to determine individual age. Otolith sections showed a clear pattern of opaque and translucent bands. Opaque bands were counted and initially attributed to the age of individual fish. To determine the periodicity of band formation, a validation experiment was performed, in which individuals (n = 8) were injected with tetracycline ( $50 \text{ mg kg}^{-1}$ ) and kept in the laboratory for periods of three months to one year. Results of the validation experiment showed that one opaque band is deposited per year. The age of individuals collected from January to December 1995 ranged between 0 and 15 years. Analysis of margins of monthly collected individuals suggested that opaque bands are deposited during the dry season, between September and March. Readings of tetracycline-marked otoliths corroborated these results. The length-at-age curve yielded a growth constant (K) of  $0.19 \text{ y}^{-1}$ . The high variability of the length-at-age data indicated high variability in individual growth. Length-frequency data were also used to obtain growth parameters. The growth constant, as determined with these data was  $0.6 \text{ y}^{-1}$  and differed markedly from K values determined from length-at-age data. It was concluded that length-frequency data are not suitable to determine growth of this species. The present study showed that otoliths are a reliable structure for aging *S. fuscus*, which showed to be a relatively long-lived and slow-growing tropical reef species.

### Introduction

Pomacentrid fishes have strong influence on the recruitment and growth of corals (Lobel 1980, Horn 1989, Sebens 1994), invertebrates (Vine 1974, Mahoney 1981, Ferreira et al. 1998), algae (Brawley & Adey 1977, Mahoney 1981, Glynn 1990, Ferreira et al. 1998) and of other herbivorous fishes (see review in Jones 1991, Watson et al. 1996).

While ecological studies are numerous for pomacentrid fishes, information on secondary population characteristics such as age structure, growth and longevity are relatively scarce (Fowler 1990, Jones 1991). Considering the ecological importance of pomacentrids, information on age and growth of these fishes would

allow important inferences on the dynamics of their well defended territories through time for the reef community.

It is only recently that much effort has been invested in age determination of tropical reef fishes through the analysis of hard structures (Fowler 1990, Ferrel et al. 1992, Lou 1992, Bullock et al. 1992, Francis et al. 1992, Ferreira & Russ 1992, 1994, Doherty & Fowler 1994, Fowler & Short 1998). These studies have challenged the general belief that tropical fishes do not deposit true annual rings in their otoliths. Despite of that, data on age structure for reef fish populations are still scarce.

Brazilian reef fish fauna has been recently reviewed (Moura et al. 1999) and it is notable for the great

abundance of pomacentrids (Rodrigues 1994, Ferreira et al. 1996, Rosa & Moura 1997, Ferreira et al. 1998). Among pomacentrids, several species are endemic of Brazil (e.g. *Stegastes fuscus*, *S. sanctipauli* and *S. rocasensis*) (Emery 1972, Greenfield & Woods 1974, Lubbock & Edward 1981). In contrast to *S. sanctipauli* and *S. rocasensis* which are endemic of Brazilian offshore islands (Lubbock & Edward 1981), *S. fuscus* is restricted to Brazilian coastal reef formations (Maida & Ferreira 1997), where it is widely distributed (Moura et al. 1999).

S. fuscus is by far the most abundant fish species in the shallow waters of the Tamandaré reef complex, northeast Brazil (Ferreira et al. 1996). Territories defended by this species are largely distributed at reef crests and seem to be among the most productive and competitive areas of Tamandaré reefs due to the intense and active territorial behavior promoted by this species against a great variety of herbivorous fishes (Ferreira & Maida 1996). A recent study showed that S. fuscus territories in southeast Brazil have strong effects on the diversity and biomass of the epilithic algal community (EAC), which in turn provides shelter and food to a rich mesoinvertebrate fauna (Ferreira et al. 1998).

Despite of the ecological importance of *S. fuscus* for Brazilian reefs, little is known about its ecology and no information on its population biology is currently available. This study presents detailed information on age and growth of *S. fuscus* population at the Tamandaré reef complex, which comprises the first step toward an evaluation of the causes and consequences of their dominance at Tamandaré reefs and elsewhere in Brazil.

# Material and methods

S. fuscus Cuvier, 1830, were sampled from January to December 1995 at Tamandaré reefs, Pernambuco State, Brazil (Figure 1). Coral reef formations are arranged in lines which run parallel to the coastline and resemble fringing reefs (Maida & Ferreira 1997). The area has a tropical climate with a dry season (October–March) of air temperatures around 30°C, and a rainy season (May–September) of temperatures around 26°C (Maida & Ferreira 1997).

Individuals were collected monthly by divers using a purse seine and small spears. Sea urchin was used as bait to attract specimens out of their territories. Once attracted, the purse seine was placed between the individuals and the reef. The specimens were then caught with hand nets. A total of 346 individuals were

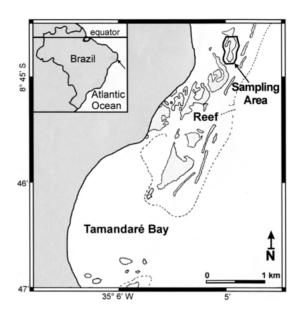


Figure 1. Map of Tamandaré reefs, showing the site where S. fuscus individuals were collected.

collected, measured, weighted to the nearest 0.1 g and dissected for removal of otoliths.

Sagittae pairs were washed in distilled water and stored dry. To increase the contrast between opaque and translucent bands, all sagittae were burned lightly on a hot plate at  $180^{\circ}$ C for up to 2 min (Christensen 1964). Whole otoliths were placed in a dark vial filled with immersion oil and read under reflected light with a dissecting microscope ( $16 \times$  magnification). Opaque bands in whole otoliths were counted over the distal surface from the nucleus to the dorsal side. Prior to sectioning, a subsample of 88 sagittae pairs was weighted to the nearest  $0.1 \, \mathrm{mg}$ .

Thin otolith sections were produced gluing the sagitta to a glass slide with a thermoplastic cement (Crystal Bond™ 509 adhesive) and grinding down (600–1000 grade sandpaper) its anterior and posterior regions to the nucleus plane (Ferreira & Russ 1994). To reduce scratches due to grinding process, sagittal ground planes were then polished down with aluminum micropolish (0.3 µm). Sectioned otoliths were examined under a dissecting microscope using reflected light and dark background, and under a compound microscope with transmitted light. Opaque bands in sectioned otoliths were counted from the nucleus to the proximal surface of the sagittae along the ventral margin of the sulcus acusticus. Terminology for otolith readings is used as defined by Wilson et al. (1987). To determine the period of band formation, the edge of the

otolith section was classified in opaque and translucent (Mace et al. 1990) and the frequency of occurrence of each band determined by month.

To assess the precision of readings, two readers counted opaque bands in both whole and sectioned otoliths without knowledge of fish size. A second reader tested the precision of the first reader for a subsample of 89 otolith sections (37%). The results were used to calculate the index of average percent error (IAPE) between readers (Beamish & Fournier 1981). If readings differed in more than 10% for a given otolith section, readings were repeated. An otolith was only considered unreadable and excluded from the analysis when the differences between readings did not improve after this procedure.

Accuracy of otolith readings was determined by validation experiments with tetracycline. Individuals were injected with tetracycline and kept in the laboratory for periods between three months and one year. Depending on fish size, two methods of tetracycline labeling were used. Fish larger than 7 cm standard length (SL) were injected in the celomic cavity with a dosage of 50 mg of tetracycline kg<sup>-1</sup> fish (Beamish & McFarlane 1987) at a concentration of 50 mg of tetracycline ml<sup>-1</sup> of sterile saline solution. For fishes between 6 and 7 cm SL, tetracycline was reduced to the concentration of 25 mg ml<sup>-1</sup> of sterile saline solution in order to obtain a measurable volume. Individuals smaller than 6 cm SL were marked by immersing fish in a solution of tetracycline and seawater. The concentration used in the immersion experiment was 300 mg l<sup>-1</sup> (Lou & Moltschaniwsky) 1992) and fish were kept in this solution for 12 h. Otoliths treated with tetracycline were sectioned in the same way as unlabeled otoliths and examined under a compound microscope with an ultraviolet light source to locate the fluorescent mark. The number of bands between the fluorescent mark and the edge was determined by examining the otolith section under an external fibre-optic light source together with the ultraviolet light of the compound microscope (Ferreira & Russ 1992).

A student t-test was used to compare the weight of left and right sagittae ( $\alpha=0.05$ ). Von Bertalanffy growth curve was fitted to length-at-age data using standard non-linear optimization methods in the SYSTAT (Wilkinson 1989). Residual plots were used to check the assumption of normality (Zar 1996). Growth parameters  $L_{\infty}$  (asymptotic length) and K (growth parameter) were also estimated by using length-frequency analysis. The ELEFAN software (Pauly & David 1981) incorporated into the FISAT

package (Gayanilo et al. 1996) was used for this purpose. Values of K and  $L_{\infty}$  were provided when the best fit is attained through an automatic search routine.

The relations between otolith weight, fish size and age were examined by simple linear regression analysis (Zar 1996). Multiple linear regression models were also used to evaluate the power of age determination predictions based on otolith weight and fish size (Boehlert 1983). All variables used in the multiple linear regression were log-transformed by  $\log(x+1)$  to conform to assumptions of linearity, normality and homogeneous variance (Zar 1996).

#### Results

Sagittae displayed the largest size among the three otolith pairs found in S. fuscus. Sagittae showed an oval shape, and were laterally compressed, presenting an heterosucoid sulcus acusticus and a rounded post-rostrum (Figure 2). A clear alternating pattern of opaque and translucent bands was observed in whole and sectioned otoliths. Opaque bands appeared white in whole otoliths under reflected light and dark in sectioned otoliths under a transmitted light. The burning process increased otolith opacity, thus improving the contrast between opaque and translucent bands. However, counting opaque bands in whole otoliths was difficult due to: (1) overlap of bands at the margin of the largest otoliths, (2) difficult visualization of bands around the nucleus and (3) constant discrepancy in the counts among different otolith regions. Because of these difficulties, the age of S. fuscus was estimated based only on sectioned otoliths. The thickness of the produced sections ranged between 0.5 and 1 mm. Deciding where to start the counts in sectioned otoliths was often difficult due to the opaqueness of the nucleus region. The indication of the first opaque band was the presence of a complete and clear translucent band just after the nucleus region.

Otolith sections of all individuals treated with tetracycline (Table 1) displayed a clear fluorescent mark, when observed under UV light (Figure 3). Fish kept in captivity for a whole year showed one group of opaque and translucent bands, meaning that only one opaque band was deposited per year. The individual injected in March 1995 accidentally died in January 1996 (Table 1, Figure 4), with 289 days of life presented one narrow opaque band at the edge indicating that only one opaque band would be deposited in next two months. Opaque bands deposited in otoliths of all individuals

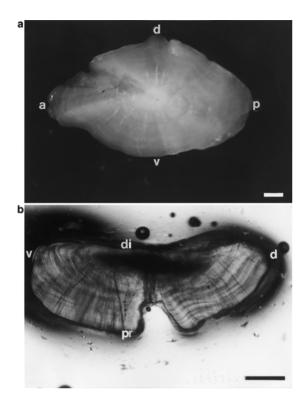


Figure 2. Whole and sectioned otolith of a 9 and a 10 year old S. fuscus, showing a dense central opaque region and a subsequent alternating sequence of opaque and translucent bands (a = anterior, p = posterior, d = dorsal, v = ventral, di = distal, pr = proximal. Scale bar =  $500 \,\mu m$ ).

Table 1. Summary of age validation experiments in aquaria for S. fuscus. L = fork length at the beginning of the experiment; <math>E = end of experiment; D = experiment duration.

L (cm)	Immersion (date)	Injection (date)	E (date)	D (days)	Age (years)
4.0	25.3.1995		8.1.1996	289	2
6.9	25.3.1995	29.7.1995	9.3.1996	350	5
7.6		21.7.1995	9.3.1996	354	5
8.2		16.8.1995	15.8.1996	365	7
7.4		28.7.1995	1.8.1996	370	7
5.0	25.3.1995		24.7.1995	121	3
3.8	25.3.1995		24.7.1995	121	3

kept in captivity were identical in appearance to those observed in otoliths of monthly collected fish. Individuals treated with tetracycline in March showed a fluorescent mark at the opaque band, whereas those injected in July and August (rainy season) presented the fluorescent mark at the translucent band. All fish treated with tetracycline and that died in March and

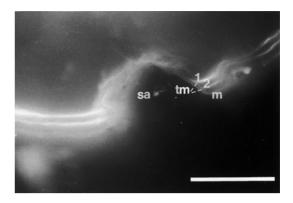


Figure 3. Photomicrograph of a sagitta from a S. fuscus individual marked twice with tetracycline 125 days apart (tm = tetracycline mark, m = margin, sa = sulcus acusticus. Scale bar =  $500 \,\mu m$ ).

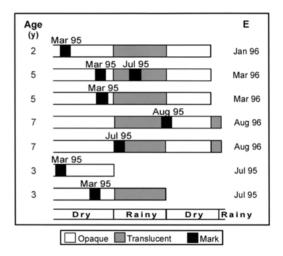


Figure 4. Diagrammatic representation of sectioned otoliths showing the relative position of the fluorescent mark in seven  $S.\ fuscus$  individuals treated with tetracycline. Bars represent the alternating pattern of opaque and translucent bands in sectioned otolith. Dates above bars indicate the time of the tetracycline treatment. A = age (years), E = end of experiment, rainy = rainy season, dry = dry season.

January 1996 had an opaque otolith margin in opposite to those that died in July and August 1996, which presented a translucent margin. The position of the fluorescent mark and the type of margin by the time of death shows that the opaque band was deposited between January and March (dry season). Average growth rate in the aquaria was  $1.1 \pm 0.8 \, \mathrm{cm} \, \mathrm{y}^{-1}$ .

The analysis of otolith margins showed that the proportion of individuals with an opaque otolith margin was highest during the dry season (September–April). During this period, less than 30% of otoliths presented

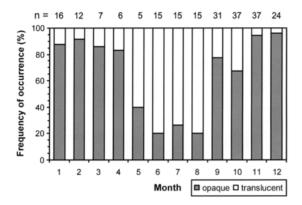


Figure 5. Percentage of opaque and translucent otolith margins observed in *S. fuscus* individuals collected by month.

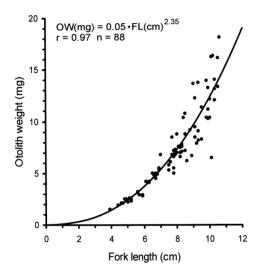


Figure 6. Relation between otolith weight and fork length for S. fuscus. FL = fork length (cm), OW = otolith weight (mg).

translucent bands in their margins (Figure 5). During the rainy season (May–August) otoliths with translucent bands in their margins accounted for more than 60%.

There was no significant difference between the weight of the left and right otolith (n = 170, p = 0.94). Otolith weight increased exponentially with fish length and the equation was in the form OW = 0.05  $FL^{2.35}(r = 0.97, n = 88)$ , where OW is otolith weight (in mg) and FL is the fork length in cm (Figure 6). The relationship between age (A, in years) and otolith weight was linear and described by the equation  $OW = 0.24 + 1.08 \, A$  (r = 0.88, n = 85) (Figure 7).

Otolith weight was well described as a function of age and fish size, as indicated by the results of the

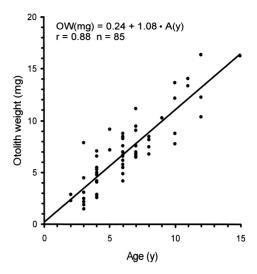


Figure 7. Relation between otolith weight and age for S. fuscus. OW = otolith weight (mg), A = age (years).

Table 2. Statistics and associated coefficients of multiple regression analysis of fork length, otolith weight, and age of *S. fuscus*. Model I – dependent variable = otolith weight (g); model II – dependent variable = age (years), SE = standard error, p = probability of error.

	Coefficient	SE	p	Partial r <sup>2</sup>
Model I				
Intercept	-0.0059	0.0001	< 0.001	
Age	0.0007	0.00008	< 0.001	0.7494
Fork length	0.0011	0.00015	< 0.001	0.1161
Multiple	$r^2 = 0.85$			
regression				
Model II				
Intercept	2.74	1.13	0.02	
Otolith weight	734.32	85.41	< 0.001	0.7394
Fork length	-0.23	0.20	0.26	0.0012
Multiple	$r^2 = 0.74$			
regression				

multiple regression analysis (Table 2). The amount of variance explained by age and fish size in the model I was 74% and 1.2%, respectively. Otolith weight was a good predictor of age, as indicated by the partial regression coefficients in the model II. In this case, otolith weight accounted alone for 74% of the variability in age of *S. fuscus*, while the amount of variance explained by length showed no significance.

The relationship between fork length (FL) and standard length (SL) was linear and described by the equation FL = 0.28 + 1.12 SL, (n = 280, r = 0.98).

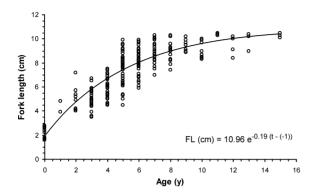


Figure 8. Von Bertalanffy growth curve fitted to length-at-age data of all age classes of *S. fuscus*. FL = fork length (cm).

Length-weight relationship was described by the equation  $w = 0.02 \, \text{FL}^{3.12}$  (n = 320, r = 0.99).

Age determined for 230 individuals ranged between 0 and 15 years. The percentage of otolith sections considered unreadable and thus not included in the age determination analysis was 16.7% out of the total produced and analyzed (n = 276). The average percent error between readers was very low with only 9%. The growth curve obtained by age-at-length data was well described by a von Bertalanffy growth, with  $L_{\infty}=10.96\,\mathrm{cm},~K=0.19\,\mathrm{y}^{-1}$  and  $t_0=-1$  as the best set of parameters (Figure 8). The large variability of length at age shows a high variability in individual growth.

Growth parameters  $L_{\infty}$  and K were also calculated from length-frequency data, although there was no clear pattern of modal progression. The best fit was obtained at  $L_{\infty}=12.7$  and K=0.6 ( $r_n=0.22$ ).

# Discussion

The clarity of the observed patterns and the annual periodicity of the bands in otoliths of *S. fuscus* corroborate the viability of the use of these structures for tropical fishes, as observed for the damselfishes *P. moluccensis* and *P. wardi* in Australia (Fowler & Doherty 1992), as well as for other tropical species (Longhurst & Pauly 1987, Fowler 1990, Ferrel et al. 1992, Lou 1992, Bullock et al. 1992, Fowler & Doherty 1992, Francis et al. 1992, Ferreira & Russ 1992, 1994). Changes in relative size and shape of the otoliths during fish growth may change the appearance and the periodicity of the formation of bands, probably making a validation necessary for every age class (Beamish & McFarlane 1987). In our validation experiments, we

used individuals that were two, five, and seven years old, thus covering several age classes. Since no differences in the pattern of bands were found between age classes, an annual periodicity was also assumed for age classes that were not validated. The same criterion has been used for other species (Paul 1992, Anderson et al. 1992), as age validation is difficult to obtain for all age classes, especially for older individuals (Paul 1992).

Studies on otolith microstructure have shown that opaque and translucent bands are composed by sequences of micro-increments (Casselman 1983, Campana & Neilson 1985, Victor & Brothers 1982). The differences in shape and width of these microincrements in the two types of bands make them optically distinct when analyzed under low magnification (Gauldie 1988, Victor & Brothers 1982). Otoliths of fishes held in captivity may exhibit a microincrement pattern that differs from the one observed in nature (Campana 1984, Siegfried & Weinstein 1989, Hendricks & Torsello 1994). These differences refer to micro-increment appearance and width (Siegfried & Weinstein 1989). Comparison of micro-increment patterns of wild-caught and aquarium-held fishes under low magnification did not reveal any differences in the general appearance of bands for S. fuscus, suggesting that laboratory conditions did not change microincrement pattern to be perceptible at this level. Also, individual growth in the aquaria was in the same range as would be expected in the field, based on our length-at-age analysis.

Both methods, labeling with tetracycline and analysis of marginal increments, showed that opaque bands in otoliths of S. fuscus were deposited during the dry season (September-March), when water temperature reaches a maximum. The dry season was also the period of deposition of opaque bands in otoliths of the Australian damselfishes Pomacentrus moluccensis (Fowler 1990) and P. wardi (Fowler & Doherty 1992). Experimental evidence has shown that the deposition of otolith increments is related to somatic growth, the opaque bands being deposited during periods of faster growth (Molony & Choat 1990, Mugiya & Oka 1990, Sogard 1991). However, an independence of otolith formation and somatic growth has also been suggested (Casselman 1990). Several authors have emphasized that the relation between somatic growth and the formation of otolith bands is far more complex than a linear causal relationship (Secor & Dean 1989, Wright et al. 1990, Casselman 1990). The impact of environmental factors and endogenous rhythms on

otolith growth has also been discussed (Campana & Neilson 1985, Radtke & Shafer 1992, Sepulveda 1994, Linkowski 1996). It has been suggested that for tropical fishes, variation in temperature may trigger seasonal changes in otolith growth independently from changes in somatic growth (Fowler & Doherty 1992, Ferreira & Russ 1992). Although seasonal changes in somatic growth and endogenous cycles may play a role in the deposition of alternating bands, the variation in water temperature seems to be the variable that best explains the pattern in otolith band formation for *S. fuscus* in the present study.

According to Fowler & Doherty (1992), continuous otolith growth, even when somatic growth is asymptotic, is one of the main conditions for these structures to be adequate for age determination. Continuous otolith growth is especially important for age determination of long-living species (Sparre et al. 1989, Pawson 1990). The good linear correlation of otolith weight and age found for *S. fuscus* indicates continuous otolith growth, thus sustaining the suitability of these structures for age determination in this species. The appropriateness of otoliths for age determination was also evidenced by a low average between-reader error. This was probably due to the clear pattern of opaque and translucent bands visible in our sections.

A high degree of subjectivity persists in all visual methods of age determination (Boehlert 1983), which are also very costly and time-consuming (Longhurst & Pauly 1987). An alternative method, that avoids this subjectivity, is the use of otolith size and weight for age determination (Pawson 1990, Ferreira & Russ 1994, Worthington et al. 1995). In spite of the close relationship between age and otolith weight for S. fuscus, the high variability of otolith weight-at-age hampered the use of this variable for an accurate prediction of age. Similar results were observed for P. moluccensis and P. wardi (Worthington et al. 1995), where the overlap in the range of otolith weights for fish from adjacent ageclasses resulted in incorrectly aged individuals. When otolith weight does not lead to a complete separation of age classes, it should be avoided as the only age determination method (Pawson 1990).

Our results on age and growth, based on the reading of otolith sections, evidenced that S. fuscus reaches medium longevity and shows slow growth. According to Buesa (1987), demersal tropical fishes with less than 50 cm length will grow fast in the first years, being able to attain 84–99% of their  $L_{\infty}$  when they are between two and six years old. In contrast, demersal species with an  $L_{\infty}$  of more than 50 cm would reach only

about 63% of their  $L_{\infty}$  after eight years. The growth of *S. fuscus* was within the growth pattern expected for a species smaller than 50 cm. Similar growth has been observed for *P. moluccensis* in Australia (Fowler 1990). In spite of this fast growth in the first years of life, a value of K of  $0.19 \, y^{-1}$  as calculated from length-atage data, indicates that the growth of *S. fuscus* is slow, when compared with previous studies on pomacentrid growth, where values of K between 0.3 and  $4.0 \, y^{-1}$  have been found (Fowler 1990, Arias-González et al. 1993).

In contrast to length-at-age data, length-frequency data of S. fuscus were difficult to interpret due to the lack of a clear progression of modes (Pauly & David 1981). A similar situation has been described for length–frequency data of S. nigricans (Arias-González 1993). For tropical species with long periods of partial spawning, methods based on length data are particularly inadequate (Gjosaeter et al. 1984), since modes are generally obscure (Morales-Nin & Ralston 1990) or the observed modes are an inadequate representation of the modes in the population (see review in Hilborn & Walters 1992). Further, poorly definable modes may lead to the overestimation of K (Basson et al. 1988). This would be a possible explanation for the difference in K obtained from length-frequency and length-at-age data for S. fuscus.

A number of studies have shown that the adjustment of mean length or length increments to the von Bertalanffy growth curve does not give successful results, because it does not take into account the individual variability in growth (Moreau 1987). The mathematical expression for growth should explain, in average, the growth in length for one given population. However, when mean lengths are used, mean growth estimated for the population can be underestimated. According to Stamatopoulos & Caddy (1989) and Moreau (1987), when a method recognizes the individual variability of the growth, it allows the possibility of estimating the growth parameters for groups of the population and also investigates the factors affecting the growth of these groups. The high variability of length-at-age found in S. fuscus indicates that length, as a substitute of age, could give spurious information about the growth of this species. Thus, besides the mathematical constraints of using length instead of age, the consequence would be a poor understanding of the processes involved in the maintenance of the S. fuscus population in the ecosystem.

Longevity of tropical fish species has been controversial (Fowler 1990, Fowler & Doherty 1992,

Clarke 1970, Robertson et al. 1993, Robertson & Brothers 1997). Our age data based on sectioned otoliths suggest that the population of S. fuscus at the Tamandaré reefs is one of the most long-living damselfish populations recorded so far, with a maximum age of 15 years. Similar results were obtained through analysis of otoliths and scales for the Pacific damselfishes P. moluccensis and P. wardi, with maximum ages of 10 and 12 years, respectively (Fowler 1990, Fowler & Doherty 1992) and for Hypsypops rubicunda, with a maximum age of 12-13 years (Clarke 1970). For the Japanese damselfish Stegastes altus, where data on age were obtained by in situ observation of tagged individuals, maximum age was found to be 15 years (Kohda 1996). In contrast, the available information on age of damselfishes from the Caribbean has given longevity as low as 1-2 years, from data obtained through otolith analysis and mortality rates for six Stegastes species (Robertson & Brothers unpublished data) and 2-4 years estimated from data on survivorship of settlers of four Stegastes species (McGhee 1995). Differences in methodologies applied (e.g. use of juvenile mortality instead of age data) might have led to underestimation of the longevity for the Caribbean Stegastes.

However, the differences in longevity observed for damselfish populations in the Pacific, Caribbean and Brazil could also be related to different structuring processes, such as competition for territories and predation, which might have had different impacts on these populations. Predation is one of the major processes causing mortality of reef-associated fishes (Caley 1993, Hixon 1991, Hixon & Beets 1993) and is known to regulate the size of populations in reef communities (see review in Beukers & Jones 1997). The diversity of damselfishes found in Caribbean areas is higher in comparison to that encountered in Brazil (Sebens 1994). At Tamandaré reefs, S. fuscus is clearly the dominant species, where it coexists with only one other species of the same genus, S. variabilis (Ferreira et al. 1996). In addition, intensive artisanal fishery at Tamandaré reefs might have changed the community structure by removing species with important roles (e.g. natural predators of S. fuscus) (Ferreira et al. 1996). The described situation suggests that the population of S. fuscus is presently under low levels of competition and predation, which in turn could be an explanation for the relatively long life span of this species at Tamandaré

Regardless of its causes, the high longevity found here, associated with the high abundance suggests that the dusky damselfish plays an important role in the reef community at Tamandaré reefs. Ferreira et al. (1998) used cage exclusion experiments to evaluate how *S. fuscus* affected the benthic community structure in its territories in southeastern Brazil and found that diversity and biomass of the epilithic algal community was higher inside *S. fuscus* territories, showing a more abundant and diverse mesoinvertebrate fauna. Thus, if high longevity indicates a certain stability of the population, it is expected that the persistence and dominance of *S. fuscus* territories at Tamandaré reefs have strong effects on the diversity of the reef community.

# Acknowledgements

Many thanks to the staff of Centro de Pesquisa e Extensão Pesqueira do Nordeste, in Tamandaré, for providing facilities and local support. We would like to thank C.M. de Queiroz, L.T. Montenegro, J.F. da Silva and S.N. Leitão for all laboratory support and to J.P. de Barros for his valuable assistance with the validation experiments. Thanks also to M. Maida, M. da Silva and A. Teixeira for the help in the field. Thanks to R. Schwamborn for his comments and suggestions in the elaboration of the manuscript. This work is part of a master thesis by the senior author, from the Universidade Federal de Pernambuco. The financial support for this work was provided by grants of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

## References cited

Anderson, J.R., A.K. Morison & D.J. Ray. 1992. Validation of the use of thin-sectioned otoliths for determining the age and growth of golden perch, *Macquaria ambigua* (Perciformes: Percichthyidae), in the lower Murray-Darling basin, Australia. Aust. J. Mar. Fresh. Res. 43: 1103–1128.

Arias-Gonzales, J.E., R. Galzin & F. Torres, Jr. 1993. Growth and mortality of *Ctenochaetus striatus*, *Stegastes nigricans* and *Sargocentron microstoma* in Tiahura Reef, Moorea Island, French Polynesia. NAGA 16: 32–35.

Basson, M., A.A. Rosenberg & J.R. Beddington. 1988. The accuracy and reliability of two new methods for estimating growth parameters from length-frequency data. J. Cons. Perm. int. Explor. Mer. 44: 277–285.

Beamish, R.J. & D.A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38: 982–983.

Beamish, R.J. & G.A. McFarlane. 1987. The forgotten requirement for age validation in fisheries biology. Trans. Amer. Fish. Soc. 112: 735–743.

- Beukers, J.S. & G.P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114: 50–59.
- Boehlert, G.W. 1983. Using objective criteria and multiple regression models for age determination in fishes. U.S. Fish. Bull. 83: 103–117.
- Brawley, S.H. & W.H. Adey. 1977. Territorial behavior of three-spot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Env. Biol. Fish. 2: 45–51.
- Buesa, R.J. 1987. Growth rate of tropical demersal fishes. Mar. Ecol. Prog. Ser. 36: 191–199.
- Bullock, L.H., M.D. Murphy, M.F. Godcharles & M.E. Mitchell. 1992. Age, growth and reproduction of jewfish *Epinephelus ita-jara* in the eastern Gulf of Mexico. U.S. Fish. Bull. 90: 243–249.
- Caley, M.J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar. Biol. 117: 33–43.
- Campana, S.E. & J.D. Neilson. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014–1032.
- Campana, S.E. 1984. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder *Platichthys stel-latus*. Can. J. Zool. 62: 1507–1512.
- Carr, M.H. & M.A. Hixon. 1995. Predation effects on early postsettlement survivorship of coral-reef fishes. Mar. Ecol. Prog. Ser. 124: 31–42.
- Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures: techniques and tools. NOOAA Tech. Rep. NMFS 8: 1–17.
- Casselman, J.M. 1990. Growth and relative size of calcified structures of fish. Trans. Amer. Fish. Soc. 119: 673–688.
- Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Cons. Perm. Int. Explor. Mer. 29: 73–81.
- Clarke, T.A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monog. 40: 189–212.
- Doherty, P. & A. Fowler. 1994. Demographic consequences of variable recruitment to coral reef populations: a congeneric comparison of two damselfishes. Bull. Mar. Sci. 54: 297–313.
- Emery, A.R. 1972. A new species of damselfish (Pisces: Pomacentridae) from eastern of Southern America. Copeia 1972: 330–335.
- Ferreira, B.P. & G. Russ. 1992. Age, growth and mortality of the coral trout *Plectropomus maculatus*, (Pisces: Serranidae) from the Central Great Barrier Reef, Australia. Aust. J. Mar. Fresh. Res. 43: 1301–1312.
- Ferreira, B.P. & G. Russ. 1994. Age validation and estimation of growth rate of the coral trout *Plectropomus leopardus* (Lacepède 1802) from Lizard Island, Northern Great Barrier Reef. U.S. Fish. Bull. 92: 46–57.
- Ferreira, C.E.L., J.E.A. Gonçalves, R. Coutinho & A.C. Peret. 1998. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. J. Exp. Mar. Biol. Ecol. 229: 241–264.
- Ferreira, B.P., M. Maida & A.E.T. Souza. 1996. Levantamento inicial das comunidades de peixes recifais da Região de Tamandaré-PE. Boletim Técnico do CEPENE 3: 211–230.
- Ferrel, D.J., G.W. Herry, J.D. Bell & N. Quartararo. 1992. Validation of annual marks in the otoliths of young snapper, *Pagrus auratus* (Sparidae). Aust. J. Mar. Fresh. Res. 43: 1051–1056.

- Fowler, A.J. 1990. Validation of annual growth increments in the otoliths of a small tropical coral reef fish. Mar. Ecol. Prog. Ser. 64: 25–38.
- Fowler, A.J. & P.J Doherty. 1992. Validation of annual growth increments in the otoliths of two species of damselfish from southern Great Barrier Reef. Aust. J. Mar. Fresh. Res. 43: 1057–1068.
- Fowler, A.J. & D.A. Short. 1998. Validation of age determination from otoliths of the king george *Sillaginoides punctata* (Perciformes). Mar. Biol. 130: 577–587.
- Francis, R.I.C.C., L.J. Paul & K.P. Mulligan. 1992. Aging of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. Aust. J. Mar. Fresh. Res. 43: 1069–1089.
- Gauldie, R.W. 1988. Similarities in fine structure of annual and non-annual check rings in the otolith of the New Zealand snapper (*Chrysophrys auratus*). New Zealand J. Mar. Fresh. Res. 22: 273–278.
- Gayanilo F.C., P. Sparre & D. Pauly. 1996. The FAO-ICLARM stock assessment tools (FISAT) user's guide. FAO Computerized Information Series (Fisheries) 8: 1–126.
- Gjsoaeter, J., P. Dayaratne, O.A. Bergstad, H. Gjsoaeter, M.I. Sousa & I.M. Back. 1984. Aging tropical fish by growth rings in the otoliths. FAO Fish. Circ. 776: 1–54.
- Greenfield, D.W. & L.P. Woods. 1974. *Eupomacentrus diencaeus*Jordan and Rutter: a valid species of damselfish from western tropical Atlantic. Fieldiana 65: 9–19.
- Hendricks, M.L. & D.L. Torsello. 1994. Use of otolith microstructure to distinguish wild from hatchery-reared American shad in the Susquehanna River. N. Amer. J. Fish. Manage. 14: 151–161.
- Hilborn, R. & C.F. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, London. 570 pp.
- Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. pp. 465–507. *In*: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs, Academic Press, San Diego.
- Hixon, M.A. & J.P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63: 77–101.
- Horn, M.H. 1989. Biology of marine herbivorous fishes. Oceanog. Mar. Biol. Annu. Rev. 27: 167–272.
- Jones, G.P. 1991 Post-recruitment processes in ecology of coral reef fish populations: a multifactorial perspective. pp. 294–328.
   In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs, Academic Press, San Diego.
- Kerr, L.R., K.L. Lang & P.S. Lobel. 1997. PCB contamination relative to age for a Pacific damselfish, *Abudefduf sordidus* (Pomacentridae). Biol. Bull. 193: 270–281.
- Kohda, M.A. 1996. A damselfish living for more than 15 years: a longevity record for small reef fishes. Ichthyol. Res. 43: 459–462.
- Linkowski, T.B. 1996. Lunar rhythms of vertical migrations coded in otolith microstructure of North Atlantic lanternfishes, genus *Hygophum* (Myctophidae). Mar. Biol. 124: 495–508.
- Lobel, P.S. 1980. Herbivore by damselfihes and their role in coral reef community ecology. Bull. Mar. Sci. 30: 273–289.
- Longhurst, A.R.O. & D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego. 407 pp.
- Lou, D.C. 1992. Validation of annual growth bands in the otolith of tropical parrotfish (*Scarus schlegeli* Bleeker). J. Fish Biol. 41: 775–790.

- Lou, D.C. & N.A. Moltschaniwskyj. 1992. Daily increments in juvenile tropical parrotfishes and surgeonfishes. Aust. J. Mar. Freshwater Res. 43: 973–981.
- Lubbock, R. & A. Edward. 1981. The fishes of Saint Paul's Rock. J. Fish Biol. 18: 135–157.
- Mace, P.M., J.M. Fenaughty, R.P. Coburn & T.J. Doonan. 1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the North Chatham Rise, New Zealand J. Mar. Fresh. Res. 24: 105–119.
- Mahoney, B.M. 1981. An examination of interespecific territoriality in the dusky damselfish, *Eupomacentrus dorsopunicans* Poey. Bull. Mar. Sci. 31: 141–146.
- Maida, M. & B.P. Ferreira. 1997. Coral reefs of Brazil: an overview. Proc. 8th Int. Coral Reef Sym. 1: 263–274.
- McGehee, M.A. 1995. Juvenile settlement, survivorship and *in situ* growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. Env. Biol. Fish. 44: 393–401.
- Molony, B.W. & J.H. Choat. 1990. Otolith increment widths and somatic growth rate: the presence of a time lag. J. Fish Biol. 37: 541–551.
- Morales-Nin, B. & S. Ralston. 1990. Age and growth of *Lutjanus kasmira* (Forskal) in Hawaiian waters. J. Fish Biol. 36: 191–203.
- Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. pp. 81–113. *In*: R.C. Summerfelt & E.H. Gordon (ed.) The Age and Growth of Fish, Iowa State University Press, Ames.
- Moura, R.L. de, J.L. Gasparini & I. Sazima. 1999. New records and range extentions of reef fishes in the Western South Atlantic, with comments on reef fish distribution along the Brazilian coast. Rev. Bras. Zool. 16: 513–530.
- Mugiya, Y. & H. Oka. 1990. Biochemical relationship between otolith and somatic growth in the rainbow trout *Oncorhynchus mykiss*: consequence of starvation, resumed feeding, and diel variations. U.S. Fish. Bull. 89: 239–245.
- Paul, L.J. 1992. Age and growth studies of New Zealand marine fishes, 1921–90: a review and bibliography. Aust. J. Mar. Freshwater Res. 43: 879–912.
- Pauly, D. & N. David. 1981. ELEFAN 1, a BASIC program for the objective extraction of growth parameters from length frequency data. Meeresforsch. Rep. Mar. Res. 28: 205–211.
- Pawson, M.G. 1990. Using otolith weight to age fish. J. Fish Biol. 36: 521–531.
- Radtke, R.L. & D.J. Shaffer. 1992. Environmental sensitivity of fish otolith microchemistry. Aust. J. Mar. Fresh Res. 43: 935–951.
- Rodrigues, M.C.M. 1994. Efeito do territorialismo de *Stegastes rocasensis* (Pisces: Pomacentridae) sobre a comunidade de algas e fauna associada na Reserva Biológica do Atol das Rocas, Brasília. M.Sc. Thesis, University of Brasilia, Distrito Federal. 53 pp.
- Rosa, R.S. & R.L. Moura. 1997. Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve off Northeastern Brazil. Proc. 8th Int. Coral Reef Sym. 1: 983–986

- Schmitt, R.J. & S.J. Holbrook. 1996. Local-scale patterns of larval settlement in planktivorous damselfish do they predict recruitment? Mar. Freshwater Res. 47: 449–463.
- Sebens, K.P. 1994. Biodiversity of coral reefs: what are we losing and why? Amer. Zool. 34: 115–133.
- Secor, D.H. & J.M. Dean. 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.
- Sepulveda, A. 1994. Daily growth increments in the otoliths of European smelt *Osmerus eperlanus* larvae. Mar. Ecol. Prog. Ser. 108: 33–42.
- Siegfried II, R.C. & M.P. Weinstein. 1989. Validation of daily increment deposition in the otoliths of spot (*Leiostomus* xanthurus). Estuaries 12: 180–185.
- Sogard, S.M. 1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. Can. J. Fish. Aquat. Sci. 48: 1862–1871.
- Sparre, P., E. Ursin & S.C. Venema. 1989. Introduction to tropical fish stock assessment. Part 1 Manual. FAO Fisheries Technical Paper 306.1: 57–123.
- Stamatopoulos, C. & J.F. Caddy. 1989. Estimation of von Bertalanffy growth parameters: a versatile linear regression approach. J. Cons. Int. Explor. Mer. 45: 200–208.
- Steele, M.A., G.E. Forrester & G.R. Almany. 1998. Influences of predators and conspecifics on recruitment of a tropical and a temperate reef fish. Mar. Ecol. Prog. Ser. 172: 115–125.
- Victor, B.C. & E.B. Brothers. 1982. Age and growth of the fallfish Semotilus corporalis with daily otolith increments as a method of annulus verification. Can. J. Zool. 60: 2543–2550.
- Vine, P.J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coralreef ecology. Mar. Biol. 24: 131–136.
- Watson, M., D. Righton, T. Austin & R. Ormond. 1996. The effects of fishing on coral reef fish abundance and diversity. J. Mar. Biol. Ass. U.K. 76: 229–233.
- Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT Inc., Evanston.
- Wilson, C.D., K.B. Brothers, J.M. Casselman, C.L. Smith & A. Wild. 1987. Glossary. pp. 207–208. *In*: R.C. Summerfelt & G.E. Hall (ed.) The Age and Growth of Fish, Iowa State University Press, Ames.
- Worthington, D.G., P.J. Doherty & A.J. Fowler. 1995. Variation in the relationship between otolith weight and age: implications for the estimation of age of two tropical damselfish (*Pomacentrus moluccensis* and *P. wardi*). Can. J. Fish. Aquat. Sci. 52: 233–242.
- Wright, P.J., N.B. Metcalfe & J.E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr. J. Fish Biol. 36: 241–249.
- Zar, J.H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River. 662 pp.