Patterns of annual increment formation in otoliths of pomacentrids in the tropical western Atlantic: implications for population age-structure examination

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ABSTRACT: Only recently have managers and scientists begun to collect age and growth information necessary for effective management of tropical marine ichthyofaunal communities. The majority of studies that have taken place in the tropics have focused on the Pacific Ocean, primarily on Australia's Great Barrier Reef. In this study, otoliths were collected from 2 pomacentrids at 5 locations in the tropical western Atlantic, and examined for their ability to provide information on age. The collection sites for these 2 species, *Stegastes planifrons* and *S. partitus*, represent different ranges of annual temperature variation. Otoliths were examined for the presence of clear and interpretable increments as well as timing of increment formation. Annual increment quality varied between species and between regions, with the trend being decreasing clarity with decreasing temperature range. However, interpretable increments were discovered in areas with as little as a 3°C annual water temperature fluctuation. Marginal increment analysis of *S. planifrons* otoliths revealed that increments formed on the otoliths were deposited once a year during the spring or early summer, suggesting that pomacentrids in the tropical western Atlantic may be aged using the same techniques as in other tropical regions and temperate environments. Counts of annual increments revealed that *S. planifrons* was significantly longer-lived than predicted by other methods. Information on age and growth collected for reef fishes in studies such as this should provide managers with the life-history information needed to assess population stability and production. This information will be more difficult to obtain in low-latitude regions of the tropical western Atlantic.

KEY WORDS: Pomacentridae · *Stegastes planifrons* · *Stegastes partitus* · Longevity · Growth · Otolith · Validation · Reef fish

INTRODUCTION

Studies on the age and growth of marine fishes provide essential information for ecosystem management. From these basic life-history parameters, estimates of size and timing of recruitment, rate of growth, year-class strength, time of spawning, longevity, mortality, and production are derived. These data enable assessment of population stability or exploitability (Brothers 1979, Smith 1992) as well as efficiency of management strategies such as implementation of marine reserves (Trexler & Travis 2000).

Despite the importance of fish populations in supporting economies and providing sustenance to human populations in most tropical countries, estimates of these parameters are available for only a few species (Ehrlich 1975, Longhurst & Pauly 1987, Russ 1991). This is, in part, a reflection of early studies which showed that otolith increment deposition in the tropics could be subannual in nature (De Bont 1967, Pannella 1971, 1974, Miranda 1981, Casselman 1987). Additionally, increment clarity was found to be highly variable in quality between species, populations within a species, and individuals within a population (Fowler

1995). These complications are attributed to the limited change in temperature, productivity and lengthy reproductive cycles in the tropics (De Bont 1967, Pannella 1974, Thompson & Munro 1978, Sale 1980, Manooch 1987, Polunin et al. 1996).

In spite of the difficulties, successful ageing efforts have been conducted, particularly with commercially important species such as serranids and lutjanids (Johnson 1983, Mason & Manooch 1985, Manooch 1987, Ferreira & Russ 1995, Newman et al. 1996, see review by Fowler 1995). More recent studies have seen effort shift toward acquiring knowledge on selected non-commercial species in an endeavor to take a whole-ecosystem approach to population management. This information is essential for understanding ecosystem dynamics and significantly improving estimates of production (Russ 1991, Choat & Axe 1996). These efforts, while critical first steps, are usually limited to 1 location. (Ralston 1976, Hill & Radtke 1988, Fowler 1990, Fowler & Doherty 1992, Lou 1992, Choat & Axe 1996, Choat et al. 1996, Hart & Russ 1996, Meekan et al. 1999, 2001, Schwamborn & Ferreira 2002). Extrapolation of age structures and longevities across populations can result in significantly inaccurate values (Meekan et al. 2001); however, cross-population comparisons conducted by Meekan et al. (2001) in the eastern Pacific and by Fowler (1995) on the Great Barrier Reef are exceptions. Comparable studies have yet to be carried out in the tropical western Atlantic.

The goals of the present study were to (1) examine otoliths in 2 pomacentrid species (*Stegastes planifrons* and *S. partitus*) collected from the tropical western Atlantic for the appearance of annual increments (defined as the combination of a hyaline and an opaque zone) in their otoliths; (2) compare otoliths for clarity and interpretability of annual increments between geographically separated populations with differences in annual temperature range; and (3) present information on the age structure and growth of these 2 species.

MATERIALS AND METHODS

Species. This investigation examined otoliths in 2 pomacentrid species common throughout the tropical western Atlantic, *Stegastes planifrons* (threespot damselfish) and *S. partitus* (bicolor damselfish). The life cycles of both species include a dispersive planktonic larval stage and a relatively sedentary adult stage. This bipartite life history is shared by virtually all tropical reef fishes. The family Pomacentridae represents one of the numerically dominant tropical reef-fish taxa, and members of this family have a significant influence on the surrounding ecosystem. In particular, members of the genus *Stegastes* exhibit a high degree of territoriality, altering the presence of algal and invertebrate species including corals in their territories, and defend their territories from fish species many times their size (Myrberg & Thresher 1974, Thresher 1976, Wellington 1982).

Study sites. We chose 5 sites to investigate how clarity and interpretability of annual otolith increments were affected by variations in annual temperature range (Fig. 1, Table 1). We made 3 collections each at both the Flower Garden Banks and Florida Keys, and 1 each at the other 3 locations. Individual *Stegastas planifrons* collected from the Flower Garden Banks and Florida Keys were also used to investigate the timing of increment deposition. Both age-structure and growth patterns were then compared across populations. While the Belize collection was initially planned for comparison of age and growth parameters, the small number of clear and interpretable annual increments on otoliths at this site limited their utility. This was also the case with *S. partitus* otoliths collected from both the Flower Garden Banks and Belize.

All specimens were collected using a hand-held microspear. Standard length of the freshly caught fishes was measured to the nearest millimeter, and sex was determined on a subset of mature individuals. The sagittae produced the most easily interpreted annual increment structure. As a result, this was the
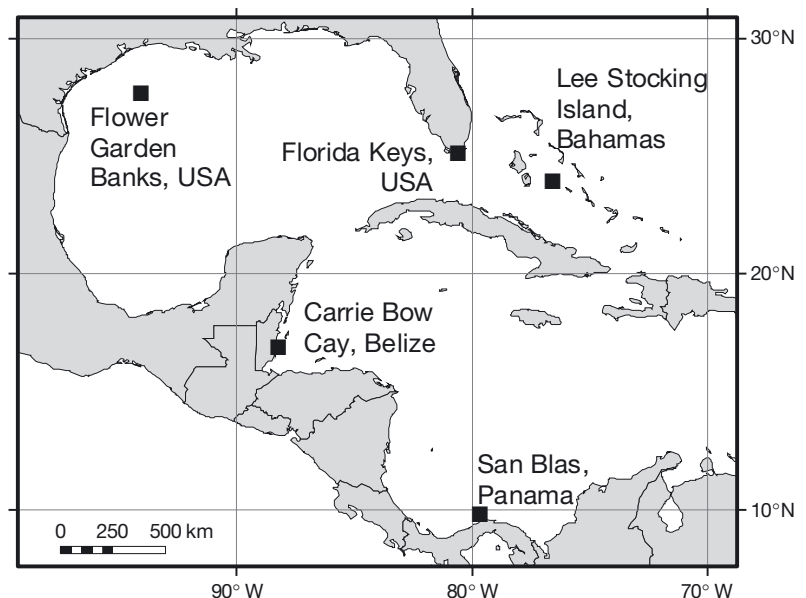

Fig. 1. Tropical western Atlantic. Study sites are marked by squares, and represent a range of annual temperature variations

Table 1. *Stegastes planifrons* and *S. partitus.* Location, date and annual temperature range of individuals collected throughout the tropical western Atlantic. Panama otoliths were collected by L. Gutierrez for a separate study and donated for comparison purposes. Numbers in parentheses: % of interpretable otoliths in overall collections at given site; –: none collected

Location	Collection date	*S. planifrons* (n)	*S. partitus* (n)	T range (°C)
Flower Garden Banks (27°52′ N, 93°48′ W)	Jun 98 Feb 99 Aug 99	92 55 (98%) 53	100 (70%) – –	19–30 (www.nodc.noaa.gov/BUOY/ buoy.html/)
Florida Keys (25°07′ N, (80°17′ W, 24°59′ N, 80°25′ W)	Jan 99 May 99 Aug 99	49 50 (99%) 102	– – –	21–31 (www.nodc.noaa.gov/BUOY/ buoy.html/)
Lee Stocking Island, Bahamas (23°47′ N, 76°07′ W)	May 99	20 (100%)	–	22–31 (www.ima-cpacc.gov.tt/ bahamas.htm/)
Carrie Bow Cay, Belize (16°47′ N, 88°05′ W)	Jul 98	101 (60%)	102	25–28 (www.mnh.si.edu/biodiversity/ ccre.htm/)
Punta de San Blas, Panama (9°30′ N, 79°00′ W)	Dec 93 Jun 94	15 (40%)	102 –	27–30 (D′Croz & Robertson 1997)

otolith used in all subsequent analyses. Otoliths were cleaned and placed in a drying oven for 12 h prior to examination. A dissecting microscope using transmitted light and 25× magnification was used to obtain information on otolith length (rostrum to postrostrum) and width (dorsal to ventral edge). Measurements were recorded to the nearest tenth of a millimeter using an ocular micrometer. The weight of each otolith was recorded to the nearest microgram. Although annual increments on whole otoliths were visible, those on the periphery of the otolith were difficult to distinguish in older individuals. By the time an individual had reached 4 to 5 yr, the primary axis of otolith growth had shifted and the increments had become narrower and closer together. As a consequence, it was necessary to cut a thin transverse section of approximately 0.3 mm in thickness through the otolith core. This section was used to measure otolith radius (focus to ventral side of sulcus) and count annual increments. (For a more complete description of otolith preparation methods see Secor et al. 1991 and Caldow 2000). All statistical analyses were done using SAS (1989) statistical software.

Validation of annual increment formation. To verify the timing of increment deposition, 3 conditions must be met (see Fowler 1990). First, a series of interpretable increments must be present; second, the increments must be formed on a regular timescale; and third, the otolith must grow continuously throughout the life of the fish. A visual inspection of the transverse sections revealed that the otoliths possessed interpretable increments. This was later quantified during the comparison of otolith clarity and interpretability.

It was then necessary to determine if differences in growth might translate into differences in either clarity or interpretability between left and right otoliths. A random sample consisting of 1 otolith from each individual in the first collection at the Flower Garden Banks was analyzed for differences in otolith length, width, radius, weight, and annual increment count between left and right otoliths using Hotelling′s *t*-squared test. The left otolith was sectioned and analyzed in all ensuing collections.

Marginal increment analysis was employed to examine the periodicity of increment formation. In this analysis, the distance from the outside edge of the opaque zone to the perimeter of the otolith is measured. An examination of multiple collections of otoliths acquired at different times of the year will reveal an increase in this distance until a new opaque zone is accreted. With this method there is no risk of either negatively affecting growth or causing mortality, both of which are associated with handling and injection stresses imposed by using biomarkers such as tetracycline (Brothers 1979, Manooch 1987, Hoedt 1992). This consideration was of particular concern at the deep Flower Garden Banks site, since individual fish would become stressed traveling from depth to the surface, with a significantly long interval at the surface imposed by diving restrictions.

High-resolution otolith images were produced on a black-and-white monitor using an Ikegami CCD video camera, standard PC computer, and a Leitz Dialux 20 microscope. The marginal increments, as well as the distance from the focus to each increment were measured at 100× magnification using Optimas imaging software. In order to standardize across all age groups and collection sites with differing otolith growth rates, marginal increment width was taken as a percentage of the full increment width (determined by averaging

the increment size over older individuals) for a given age group at each site (see Campana 1984). The mean value for each collection was then examined across collection periods to determine when the increment was formed. The similarity in timing of increment deposition between sites was evaluated by a Student's *t*-test on the mean proportion of increments formed at each site during the respective August collections. Each site was also analyzed separately. The relationship between marginal increment width and increment number was log-transformed to produce a linear relationship. Increment width and month of collection were then analyzed using ANCOVA.

To meet the third criterion, otoliths were examined for continual growth by analyzing the relationship between otolith length, width, radius, and weight on standard length.

Comparison of clarity and interpretability. All otoliths were subsequently examined for interpretability, defined as the percent of otoliths with annual increments that could be counted for a given species at a given location under 50× magnification. Increments were counted upon complete formation of an opaque zone. This information was compared against differences in annual temperature range to determine the correlation between the two. Interpretability as the sole measure of increment clarity failed to capture differences between sample locations apparent to the reader. As such, in addition to interpretability, subjective comments are provided to describe the relative clarity of increments on interpretable otoliths between sites.

Age and growth. Once the annual nature of increment deposition was validated, age was determined by counting the number of opaque zones from the focus to the ventral apex. Counting began at the first opaque zone after the larval period. The second author examined a percentage of the otoliths to aid in differentiating what would be considered an annual increment in cases where the opaque zone might just be forming at the otolith margin. An otolith with 1 opaque zone followed by a translucent region was said to be 1+ yr old. All otoliths were aged twice with at least 2 wk between counts. No reference was made to the length of the fish being aged during counting. If there was disagreement, up to 2 additional counts were made to clear up each discrepancy. If the otolith did not have countable rings, it was omitted from the ageing analyses and tallied for the comparison of interpretability. To obtain an estimate of precision, a paired-comparison *t*-test was performed on the first 2 counts of the Florida Keys data set. This enabled a determination of whether a significant difference occurred from a paired difference of 0 (Campana et al. 1995). In addition, an estimate of ageing precision was provided by the coefficient of variation averaged over all the otoliths (Chang 1982).

Using equal numbers of individuals for each collection, the relationship between otolith radius and fish length was then used to produce back-calculated size-at-age data. From these data, von Bertalanffy growth parameters were calculated using FISHPARM fisheries software.

The von Bertalanffy equation $l_t = L_\infty(1 - e^{-K(t - t_0)})$ commonly provides the best fit to length-at-age data in fish populations. The coefficient K takes into account the rate of catabolism of the organism and thus determines the rate at which the asymptotic length, L_∞, is approached. The equation is designed to calculate length (l) at a particular age (t).

RESULTS

Validation of annual increment formation

Examination of otolith length, width, radius, weight, and annual increment count showed no significant difference between left and right otoliths using Hotelling's *t*-squared test ($F = 0.4099$, df = 81, p = 0.84, n = 87). Consequently, the 2 otoliths were assumed to be identical in growth and interpretability.

Examination of the pooled Flower Garden Banks and Florida Keys marginal increment data is consistent with only 1 increment being formed annually (Fig. 2). The February 1999 collection had the highest mean proportion of marginal increment formed (0.78), whereas June 1998 and May 1999 had much lower means (0.32 and 0.36, respectively). Within individuals, the timing of annual increment deposition varied greatly. Some were in the process of accreting the opaque region in February while others still had not completed formation by August.

A Student's *t*-test revealed that a significantly smaller proportion of the annual increment had formed in the August Florida Keys collection than in the
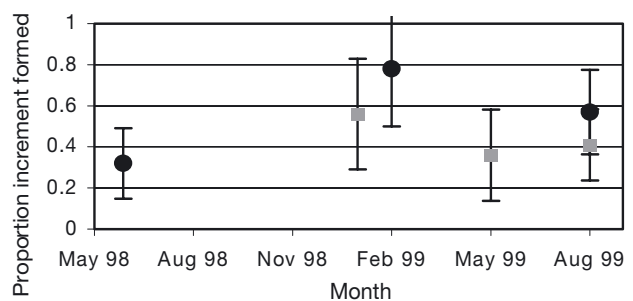

Fig. 2. *Stegastes planifrons*. Mean proportion of marginal increment at Flower Garden Banks (●) and Florida Keys (■). Dips around June 1998 and May 1999 suggest that increments are formed sometime in spring to early summer. Error bars represent 1 SD from mean

Flower Garden Banks collection during the same period (t = 5.0614, df = 148, p < 0.0001, n = 150). Since populations were not synchronized with respect to the timing of annual increment formation, each population was analyzed separately using ANCOVA. The dependent and independent variables were increment width and month of collection, respectively, while age functioned as the covariate. Increment width and age were transformed to their natural logs. The tests were significant at both the Flower Garden Banks (F = 39.1, df = 2, p < 0.0001, n = 194) and the Florida Keys (F = 10.7, df = 2, p < 0.0001, n = 197) indicating that marginal increment width was significantly related to month. The least-squares difference between the May and August collections at the Florida Keys was not significant, however (p = 0.09).

Otolith length and width both showed a positive linear relationship with standard length at each location (Figs. 3 & 4). Otolith radius and weight, however, continued to increase at a relatively constant rate, even when the standard length began to plateau at approximately 70 cm (Figs. 3 & 4).

Comparison of clarity and interpretability

As expected, the otoliths of both *Stegastes planifrons* and *S. partitus* had greater overall morphological similarity to other species in the genus *Stegastes* (see photos in M. Meekan et al. 1999, author's pers. obs.) than to other pomacentrids (see photos in Fowler 1990, 1995, Fowler & Doherty 1992). Prior to the embedding procedure, the otolith appeared nearly opaque; however, with the addition of immersion oil or the embedding Spurr, otolith clarity was greatly enhanced. The distance between annual increments decreased as they approached the periphery. As a result of the curvature in the otolith and the proximity of the outermost increments to each other, the pattern became less distinguishable toward the edge.

Once sectioned, the interpretability of the outermost annual increments increased. The opaque zones proximal to the center of the otolith were broader and more
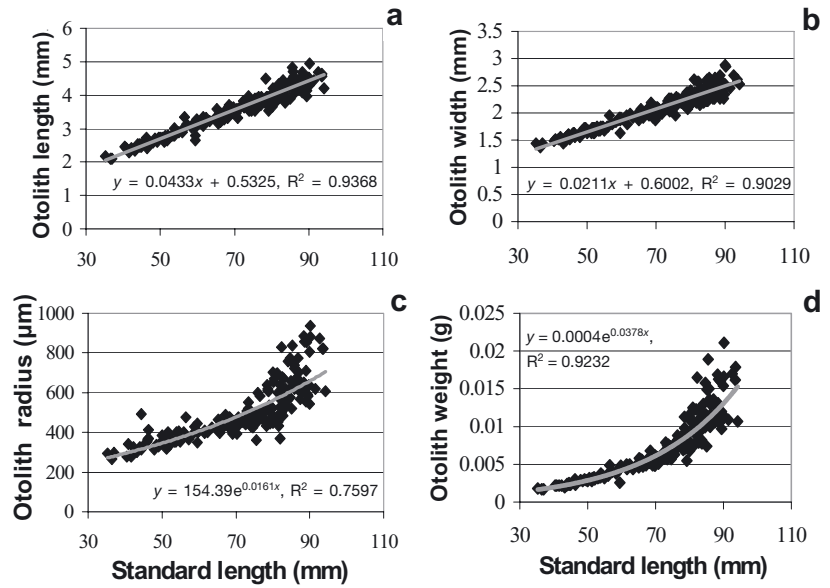

Fig. 3. *Stegastes planifrons.* Individual regressions of otolith length, width, radius and weight on standard length of *S. planifrons* from Flower Garden Banks
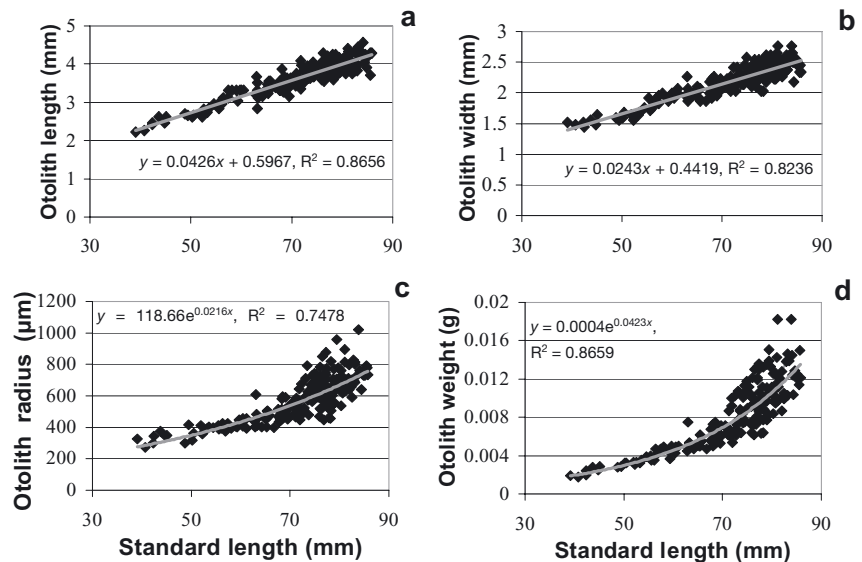

Fig. 4. *Stegastes planifrons.* Individual regressions of otolith length, width, radius and weight on standard length of *S. planifrons* from Florida Keys

diffuse than the distal zones, making their interpretation comparatively more difficult. As later increments accreted, however, they became narrower in incremental width and less diffuse, resulting in a better-defined structure. Initially, the increments are produced at a faster rate of growth along the dorsal–ventral axis, but around the fourth increment the majority of growth takes place in the direction of the sulcus.

Of the *Stegastes planifrons* otoliths collected from the Flower Garden Banks, 98% were interpretable compared with 99% at the Florida Keys; however, clarity was noticeably higher in otoliths collected from the Flower Garden Banks location. All the otoliths collected in the Bahamas were useable for deciphering age, although the increments were not as clear as those in either the Flower Garden Banks or Florida Keys. In Belize and Panama, 60 and 40% of the otoliths were interpretable, respectively. In these otoliths, increments appeared roughly equivalent in clarity between the 2 locations and were significantly less clear than at any of the other 3 sites (Table 1, Fig. 5).

The transition from translucent to opaque zones was less pronounced in otoliths of *Stegastes partitus* than in those of *S. planifrons*. Of the *S. partitus* otoliths collected, 20 were sectioned and analyzed for interpretability and clarity from each location, the Flower Garden Banks and Belize. Thin sections revealed a very limited increase in increment clarity from whole otoliths. In the Flower Garden Banks, 70% of *S. partitus*' otoliths were aged, while only 20% of *S. partitus*' otoliths from Belize were readable. The 20% aged otoliths from Belize did, however, show annual increments that were roughly equivalent in clarity with those collected from the Flower Garden Banks (Table 1, Fig. 5). Although ageing of these fish was attempted, no marginal increment analysis was performed due to the difficulty of visualizing increments and the large numbers of individuals that would be required as a result.

Age and growth

The first 2 annual increment counts at the Florida Keys were statistically different using a paired comparisons *t*-test ($t = 2.4$, df = 196, p = 0.02, n = 197); however, this proved to be a directional error as the reader became more familiar with the increment pattern. The coefficient of variation averaged over all otoliths was 0.05. Of the paired counts of annual increments in the otoliths, 3% differed by 2 annual increments or more, and the third count of increments resolved virtually every discrepancy.

Individuals in the 0+ age group were underestimated in the population age structure because the collection method was unable to capture recruits or juveniles <35 mm. Thus, information on this age group is not presented here. Individuals of the 1+ age group were susceptible to collection via the microspear sampling method, although it must be noted that their numbers appear low at the Flower Garden Banks in relation to the 2+ and 3+ age groups, and it is likely that this was also due to bias inherent in the collection method.

Due to variability in timing of annual increment deposition and time of sampling, the age of each individual was adjusted based on whether an increment had recently accreted on the otolith. In this manner, the collections could be combined and the population age structures compared. Over two-thirds of the data were contained in the first 4 age groups and over 90% in the ninth age group at the Flower Garden Banks (Fig. 6). The age–frequency plot for the Florida Keys
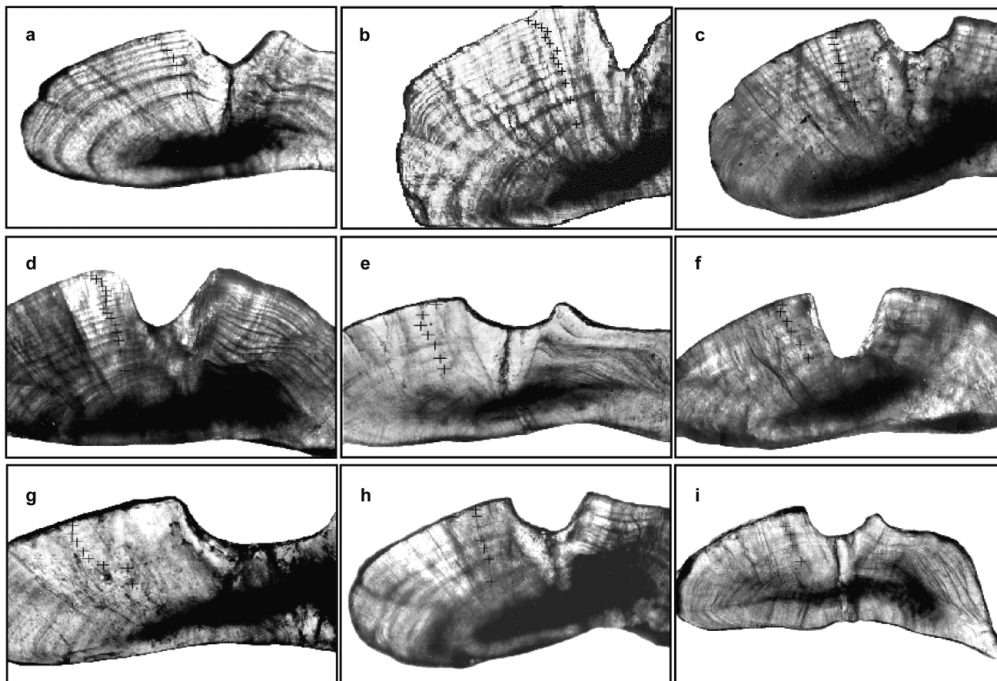

Fig. 5. *Stegastes planifrons* otoliths collected from Flower Garden Banks aged at (a) 7+ yr and (b) 13+ yr, from Florida Keys at (c) 11+ yr and (d) 15+ yr, from the Bahamas at (e) 7+ yr, from Panama at (f) 6+ yr, and from Belize at (g) 8+ yr. *S. partitus* otoliths collected from Flower Garden Banks aged at (h) 7+ yr, and from Belize at (i) 5+ yr
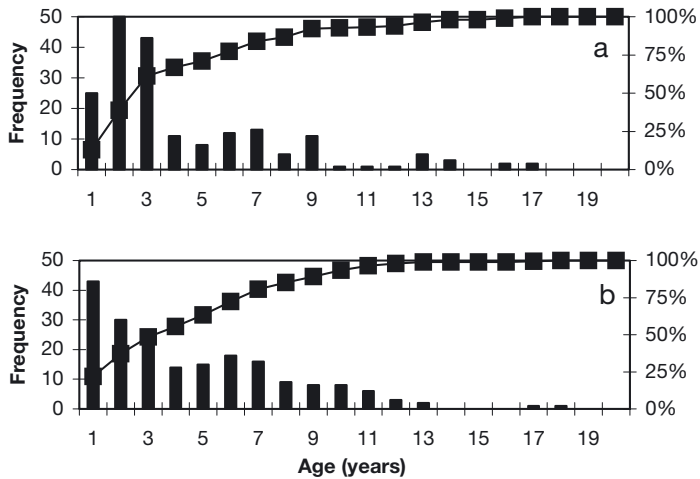
Fig. 6. *Stegastes planifrons.* Age–frequency distributions of fish from (a) Flower Garden Banks (n = 194) and (b) Florida Keys (n = 197); (■) cumulative frequency

reveals a more evenly spread distribution across age. There were more individuals in the lower age classes, but a second rise in abundance level occurred around the 6+ and 7+ yr old fishes. This pattern was observed to a lesser extent in the Flower Garden Banks, which had an additional peak around the 9+ age group. Individuals from the Florida Keys tended to live longer,

with two-thirds of the individuals present in the first 6 age classes. As the increment pattern of *Stegastes partitus* appeared nearly identical to that of *S. planifrons*, they were aged in the same manner. The oldest individuals of each species comprised a 19+ yr old *S. planifrons* from the Florida Keys population and a 7+ yr old *S. partitus* from the Flower Garden Banks (Table 2).

Von Bertalanffy growth-at-age parameters for *Stegastes planifrons*, obtained from back-calculated size-at-age data, revealed increased growth in the Flower Garden Banks compared to the Florida Keys (Table 2). Most of the growth of individual fish occurred in the first few years (Fig. 7). By Age 4, individuals from both locations had grown to nearly 75 % of their maximum length, as predicted by L_∞. *S. planifrons* is one of the largest and *S. partitus* one of the smallest members of the genus *Stegastes* from the tropical western Atlantic. The smallest individuals found with mature gonads were a 63.2 mm male and 65.3 mm female at the Florida Keys, and a 69.5 mm male and 61.6 mm female at the Flower Garden Banks.

DISCUSSION

This study suggests that the pomacentrids *Stegastes planifrons* and *S. partitus* in the tropical western

Table 2. *Stegastes* spp. Estimated maximum longevity and von Bertalanffy growth parameters K and t_0. am: actual measurement included when no von Bertalanffy estimates provided; fl: fork length; FGB: Flower Garden Banks; FK: Florida Keys; –: no data

| Location	Maximum Longevity (yr)	Length (yr⁻¹)	K (yr)	t_0 (yr⁻¹)	r^2	Source
S. planifrons						
FGB	17+	96.59 ± 1.25	0.2261 ± 0.0138	−1.930 ± 0.185	0.93	Present study
FK	19+	87.45 ± 1.32	0.1938 ± 0.0175	−3.996 ± 0.407	0.89	Present study
Bahamas	7+	81.0 am	–	–		Present study
Belize	12+	87.8 am	–	–		Present study
Panama	6+	–	–	–		Present study
S. partitus						
FGB	7+	70.0 am	–	–		Present study
Belize	5+	67.1 am	–	–		Present study
Bahamas	5+	–	–	–		M. Hixon (pers. comm.)
S. fuscus						
Brazil	15+	109.6 fl	0.19	−1		Schwamborn & Ferreira (2002)
S. leucostictus						
Puerto Rico	<3	67.75	2.2995	−0.239		McGehee (1995)
S. partius						
Puerto Rico	<3	84.98	1.752	−0.199		McGehee (1995)
S. planifrons						
Puerto Rico	3+	85.35	1.095	−0.290		McGehee (1995)
S. variabilis						
Puerto Rico	3+	95.78	1.46	−1.77		McGehee (1995)
S. planifrons						
Jamaica	4+	96 am	–	–		Williams (1978)
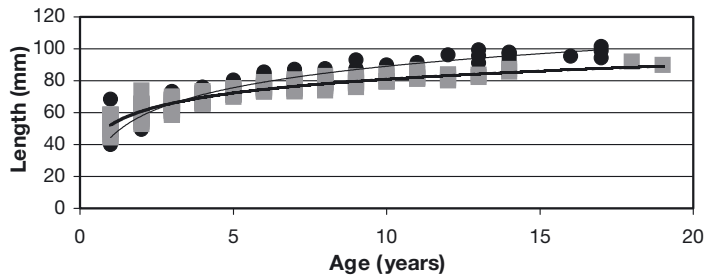
Fig. 7. *Stegastes planifrons.* Length-at-age plot for fish of ≥1+ yr, showing greater size-at-age for Flower Garden Banks (●; n = 194) vs Florida Keys (■; n = 197). Data were best fit with a von Bertalanffy growth curve (see Table 2 for parameters)

Atlantic produce 1 increment per year on their otoliths, making the otolith a useful structure in ageing these species. Additional studies are necessary, however, to determine if these findings can be replicated across other genera in the family Pomacentridae, or across families. As reported by Fowler (1995), clarity and interpretability of these annual increments can differ between species, between separate populations within a species, and between individuals within a population. Data from the present study indicates that while ageing is possible in the tropical western Atlantic, it becomes more difficult as sea-surface temperature variation decreases (Table 1). Furthermore, this study demonstrates that small tropical reef fishes have the potential to be quite long-lived; hence, any negative impact on reef-fish densities may have long-term implications for population structure.

Validation of annual increment formation

All 3 criteria proposed by Fowler (1990) for annual increment validation were met. Otoliths collected from both the Flower Garden Banks and Florida Keys showed clear, discernable increments. These increments, examined across all age groups, were similar in appearance to validated annual increments of other members of the genus *Stegastes*, and measurements of the marginal increments also supported the conclusion that they are annual. The highest mean values for proportion of increment formed were in the January/ February time period and the lowest during May/June, indicating that deposition of the opaque portion of the increment took place in spring time, coincident with low water temperatures at both sites. This observation is concordant with the findings of other studies in both Florida and the Gulf of Mexico (Johnson 1983, Barger 1985, Mason & Manooch 1985) and many other locations (Fowler 1995). It must be noted that in the present study, variability in timing of opaque zone accretion

did exist between individuals within a population and between populations. The difference during the August collection between the 2 sites indicates that increments may form at an earlier date at the Flower Garden Banks location. Since seasonal highs and lows at these 2 sites occurred at similar times, this again suggests that causal factors other than temperature are also important in increment formation. Lastly, the relationships between both otolith weight and radius and standard length demonstrate that throughout the life of the fishes, even during periods when little increase in body size occurs, the otolith continues growing. For this reason, the otolith is unlikely to lack any annual increments due to halted growth or resorption, a problem frequently encountered with fish scales (Campana & Neilson 1985).

Comparison of clarity and interpretability

In general, *Stegastes planifrons* otoliths had the most pronounced annual increments where the temperature range was greatest. Of the otoliths collected from the Flower Garden Banks, which had an 11°C temperature range, 98% were considered interpretable. This is only a loose correlation, however, and other factors such as local production or differences in length and timing of reproductive season may have been contributing factors. Differences in increment clarity between sites with similar temperature ranges, such as Belize and Panama, as well as the Florida Keys and Bahamas, support the latter conclusion. The 2 southernmost sites, Belize and Panama, did however have discrete highs and lows. The Belize population contained the greatest number of interpretable otoliths and had the lowest annual temperature range. This observation is consistent with that of Fowler (1995), who recorded the same phenomenon on the Great Barrier Reef.

While an age-structure examination of pomacentrids in Belize and the Caribbean side of Panama would be a lengthy and difficult task, it is interesting to note that a 3°C temperature range appears to be sufficient for annual increment deposition. Previously, Longhurst & Pauly (1987) noted that a 4 to 5°C temperature range was necessary for increment formation. Although increments in *Stegastes planifrons* and *S. partitus* otoliths were not validated to be annual at these additional locations, their appearance was very similar to those produced in the northern locations, as well as to those of *Stegastes* collected from the eastern Pacific (authors' pers. obs.). Furthermore, tetracycline-validated annual increments have been recorded from *S. fuscus* in Belizean waters, where annual temperature varies by only 2°C (S. H. L. Schwamborn pers. comm.). This provides further evidence that a 4 to 5°C temperature

range is not necessary for increments to form and that temperature may not be the only factor affecting otolith-increment formation.

Otoliths collected from *Stegastes partitus* also displayed decreased interpretability at the site with the lowest annual temperature range. Individuals collected from the Flower Garden Banks had substantially higher numbers of interpretable otoliths than individuals collected from Belize; however, legible otoliths from Belize were similar in clarity to those collected from the Flower Garden Banks. This is probably due to differences in the quality of sample preparation and the low number of individuals examined.

Stegastes partitus collected from both locations had a greater proportion of individuals with uninterpretable otoliths than did *S. planifrons*. Since the initial otolith annual increments laid down were less well defined than later ones, this observation could, in part, have been due to the younger age of *S. partitus* individuals. A comparison of individuals with identical ages from each species, however, suggests that the observed differences were real. Such a difference found between species at the same location led Fowler & Doherty (1992) to suggest that genetic factors are involved in effecting deposition, while differences in a species' otoliths between sites suggest that environmental factors play an important role.

Age and growth

While it is known that pomacentrids in the eastern Pacific can live up to 32 yr of age and specimens of >15 yr are frequently found, it was previously thought that longevity of pomacentrids in the tropical western Atlantic was between 1 and 2 yr (Robertson & Brothers 1996). Studies by Williams (1978), McGehee (1995), M. Hixon (pers. comm.) and Schwamborn & Ferreira (2002) along with the present study indicate that longevities in tropical western Atlantic pomacentrids are frequently much higher. The estimates from the first 2 studies, however, were not nearly as high as those in the present study (4+ yr for *Stegastes planifrons* and just under 3 yr for *S. partitus*). In these studies, the authors either monitored new recruits or employed length–frequency analysis to determine longevity. Monitoring new recruits does not account for older individuals already resident in the population, and necessarily examines only a limited number of individuals; length–frequency analysis is only capable of revealing age groups in the first few years due to the large amount of overlap in size classes (Gjosaeter et al. 1984) (Fig. 7). Clearly these methods are not sufficient to elucidate age structure and longevity in a population, since they are prone to underestimate age. The results of the latter 2 studies are comparable to our own. M. Hixon (pers. comm.) found, via tag and recapture, that *S. partitus* survived to 5+ yr, and Schwamborn & Ferreira (2002), used tetracycline given to captive individuals to determine that *S. fuscus* off Brazil had a 15+ yr longevity.

Longevities between populations in the present study also differed little. Population age structure in the Flower Garden Banks (Fig. 6) showed high levels of initial recruitment followed by a rapid decline in numbers and finally a low level of mortality consistent with the timing of the size-asymptote. Alternatively, instead of changing mortality rate, the age structure may be reflecting variability in recruitment. The Florida Keys population age structure (Fig. 6) showed similar trends to the Flower Garden Banks data, with the primary difference being a paucity of individuals in the earlier age classes, suggesting low recruitment in 1997 and 1998.

Individuals from both the Florida Keys' and Flower Garden Banks' populations showed rapid initial increases in size followed by a plateau in growth rate consistent with the findings of other authors (Buesa 1987, Hill & Radtke 1988, Fowler 1990, Fowler & Doherty 1992, Choat & Axe 1996, Choat et al. 1996, Kohda 1996, Meekan et al. 1999). This early asymptote in growth indicates selection for high allocation effort into the production of eggs or sperm as the fishes age. Tropical reef-fishes are known to undergo prolonged spawning periods (Brothers 1979) and produce millions of eggs in their lifetime. Since virtually all tropical reef fishes have some form of planktonic larval stage, they are subject to many biological and physical factors in the open ocean that result in high pre-recruitment mortality. For these reasons it is clearly adaptive to grow quickly and invest in reproduction as soon as possible. Beverton & Holt (1959) suggested that the tradeoff for increased growth rate is decreased longevity and decreased length. Pomacentrids tend to be quite small in relation to other herbivorous fishes but, as demonstrated, many species are long-lived. Additionally, as *Stegastes planifrons'* growth rate decreases, mortality declines also. This suggests that upon nearing their optimal size, individuals are more readily able to avoid predation.

Von Bertalanffy growth curves revealed a greater size at the same age for the Flower Garden Banks' population compared to the Florida Keys' population. Despite its depth, regional upwelling could be responsible for increased production at the Flower Garden Banks causing the increased size-at-age. Differences in competition or the presence of predators cannot be excluded as a factor in size distribution. Pitcher (1992) also demonstrated differences in growth between reefs, as well as in separate habitats, within a reef on the Great Barrier Reef.

The notion that all reef fishes have rapid growth and short lifespans has persisted over time (Pannella 1974, Williams 1978, Sale 1980, Gjosaeter et al. 1984, Robertson & Brothers 1996). Rapid growth and a short lifespan are characteristics of populations capable of recovering quickly from stress such as high fishing pressure. Evidence compiled from otolith studies such as this indicates that reef fishes frequently live for more than 10 yr and even up to 70 yr (e.g. Aldenhoven 1986, Manooch 1987, Choat & Axe 1996, Choat et al. 1996, Meekan et al. 2001). Populations of long-lived species such as these are less likely to recover as quickly (Longhurst & Pauly 1987). Furthermore, by underestimating age and consequently overestimating growth rates of populations, one would overestimate fish productivity within an ecosystem. This clearly has profound consequences for fishery and ecosystem management.

The demonstration that the age of small tropical fishes can be accurately determined by annual increments produced in their otoliths will allow managers to gain accurate estimates of productivity, as well as stability of their populations. The evidence provided here suggests that multiple factors are responsible for the formation of these annual increments. While these factors affect species to different degrees, increment clarity consistently decreased in both species examined in areas with decreased temperature variation. As coral reef fishes live longer than originally suspected and are more susceptible to overfishing than temperate species (Russ 1991, Bohnsack 1993), detailed knowledge of the life-history parameters provided by studies of age and growth become increasingly important. Increased attention, however, should be given to low-latitude regions of the tropical western Atlantic, where this type of information is more difficult to acquire.

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