

# Growth and longevity in acanthurid fishes; an analysis of otolith increments

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**ABSTRACT:** Increments in the sagittal otoliths from 10 species of acanthurid fishes from eastern Australian coral reefs were used to estimate age. The species included representatives of 5 genera: *Acanthurus lineatus*, *A. olivaceus*, *Ctenochaetus striatus*, *Zebrasoma scopas*, *Naso brevirostris*, *N. hexacanthus*, *N. tuberosus*, *N. unicornis*, *N. vlamingii*, and *Prionurus maculatus*. Systematic increments consisting of alternating opaque and translucent bands were observed in the sectioned sagittae of all 10 species. Regression of numbers of increments on sagittal weights revealed consistent linear relationships between these variables in all species examined indicating continuous growth in sagittal thickness over the life span. For *A. lineatus*, *A. olivaceus*, *C. striatus* and *Z. scopas* recapture of specimens injected with tetracycline confirmed an annual pattern in increment formation with an opaque band being formed in early austral summer. Size at age plots revealed consistent growth patterns and life spans. All species examined had life spans of 30 to 45 yr in which rapid initial growth over 3 to 4 yr was followed by extended periods of asymptotic growth. In these species up to 80% of linear growth was accomplished in the initial 15% of the life span. Analysis of otoliths from the 5 species of *Naso* and *P. maculatus*, while not validated, revealed similar increment distributions within the sagitta, similar relationships between increment number and otolith weight, and similar size at age plots. Acanthurid fishes from eastern Australia appear to have consistent patterns of growth and longevity despite marked differences in asymptotic size, diet and mode of life.

**KEY WORDS:** Acanthurid fishes · Growth · Longevity · Otolith increments · Validation

## INTRODUCTION

Fishes of the family Acanthuridae are abundant and defining members of coral reef fish faunas (Russ 1984a,b, Choat & Bellwood 1991, Williams 1991). Although usually classified as herbivores, these fishes exhibit a variety of feeding patterns including detritus feeding, macroalgal browsing and selective feeding on large gelatinous zooplankton (Jones 1968, Winterbottom & McLennan 1993, Clements & Choat 1995). Five genera, *Naso*, *Zebrasoma*, *Paracanthurus*, *Acanthurus* and *Ctenochaetus*, are present on Indo-Pacific reefs with species of *Acanthurus* and *Ctenochaetus* being dominant members of some faunas (Choat & Bellwood 1985, Williams 1991, McClanahan 1994). A sixth genus, *Prionurus*, appears to be restricted to subtropical reef habitats (Choat 1991).

The phylogenetic relationships and feeding patterns amongst these genera have been analysed by Winterbottom & McLennan (1993). There are a wide range of dietary patterns exhibited with macroscopic algal browsing being the plesiomorphic condition. The basal species within *Naso* and *Acanthurus* appear to be herbivorous with carnivory a derived condition. Species within the Acanthuridae also display a wide range of maximum sizes ranging from 180 mm standard length (SL) in members of the genus *Ctenochaetus* to 860 mm SL in some species of *Naso* (Randall et al. 1990).

The purpose of this study was to examine size at age, growth rates and life spans in a suite of Indo-Pacific acanthurid species. The availability of a phylogenetic classification provides an appropriate framework for the comparison of growth rates and longevity across a range of feeding types, size ranges and taxonomic identities in this ecologically diverse group of coral reef fishes.

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The increasing documentation of the annual nature of sagittal increments (Manooch & Drennon 1987, Fowler 1990, 1995, Ferreira & Russ 1992, 1994, Lou 1992, Doherty & Fowler 1994) provides a basis for estimating growth rates and life spans in coral reef fishes in general and acanthurids in particular (Hart & Russ in press). Our study provides further support for the identity of annual sagittal increments in members of the acanthurid genera *Acanthurus*, *Ctenochaetus* and *Zebrasoma* and for their use as demographic tools.

Estimates of age structure and growth rates of tropical demersal fishes are biased toward particular taxa, particularly lutjanids, haemulids, sparids and serranids (Buesa 1987, Fowler 1995). These large carnivores are relatively easy to sample for tagging purposes, and, as traditional targets for coral reef fisheries (Alcala & Russ 1990), are likely to provide good returns to recapture schemes (Munro & Williams 1985). However, they represent only a limited range of the taxa that make up reef fish assemblages. Emphasis on these groups will produce a selective picture of growth and life history patterns in coral reef fishes.

Other taxa such as acanthurids, scarids, siganids and labrids are both highly characteristic of coral reefs and increasingly targeted in localized reef-based fisheries (Russ 1991, DeMartini 1993, Wright 1993). Information on their demography is relatively limited, partly due to the difficulty in sampling and establishing mark-recapture programs, especially in the larger and more active members of the Acanthuridae and Scaridae. Consequently, for many large and previously abundant groups of reef fishes we lack even rudimentary information on growth rates and life spans.

This problem is illustrated by members of the genus *Naso*. Nasiid acanthurids are difficult to sample and collect, especially in an unharmed state suitable for tagging. Although they may be locally abundant and important in some coral reef fisheries, there is little chance that they will be included in conventional fisheries programs.

An opportunity to sample numbers of *Naso* species was provided by a related study on acanthurid feeding and digestion (Clements & Choat 1995). This provided substantial numbers of *Naso* distributed amongst 5 species for the analysis of sagittal increments. These data are presented for comparative purposes. As we have not unambiguously established the annual nature of these increments, estimates of growth and longevity in *Naso* are presented as hypotheses for further examination.

## MATERIAL AND METHODS

**Study species and localities.** Four acanthurid species, *Acanthurus olivaceus*, *Acanthurus lineatus*, *Zebrasoma*

*scopas* and *Ctenochaetus striatus* were used for estimates of growth and longevity based on validated sagittal annuli. These species covered a range of feeding types (Jones 1968, Robertson et al. 1979, Robertson & Gaines 1986, Clements & Choat 1995) including sand and sediment grazing (*A. olivaceus*), algal grazing (*A. lineatus*), algal browsing (*Z. scopas*) and detrital feeding (*C. striatus*). The majority of individuals of these species were collected from reefs surrounding Lizard Island (14°40' S, 145°28' E) with a small number being collected from adjacent mid-shelf reefs.

In addition, 5 species of the genus *Naso* (*N. brevirostris*, *N. hexacanthus*, *N. tuberosus*, *N. unicornis* and *N. vlamingii*) with a dietary range spanning algal browsing, planktivory and coprophagy (Robertson 1982, Clements & Choat 1995) were examined for patterns of sagittal increments. Most specimens of *Naso* spp. were collected on fronts and passes of the Outer Barrier Reefs (Hicks, Day & No Name Reefs) 15 to 25 km northeast of Lizard Island (general collection data are shown in Table 1). Most acanthurids were collected by spearing or by 1.5 × 30 m drive nets on reef crests and slopes. Small individuals were collected using fine-mesh (5 mm) drive nets.

A small number of acanthurids including members of the genus *Naso* and *Prionurus maculatus* were collected from Middleton Reef (29°28' S, 159°7' E) the southern most true coral reef. The sampled individuals represented acanthurids subject to stronger environmental signals than those on northern reefs and the sagittae were retained for comparison with Lizard Island material.

**Tagging and otolith processing.** The main tagging program was carried out at Lizard Island in November 1991 and February 1992, although a small number of acanthurids were tagged at Lizard Island in 1989. In addition, a supplementary tagging program for *Naso brevirostris* was carried out at Hicks Reef in November 1993. Fish were collected for tagging by the use of 1.5 × 30 m drive nets (50 mm mesh) measured to the nearest mm for standard length (SL) and fork length (FL) and tagged immediately on site. Individually numbered T-bar anchor tags were inserted between the dorsal pterygiophores. Each fish was injected in the visceral cavity with a solution of oxytetracycline and saline with a dosage of 50 mg kg<sup>-1</sup> body weight of fish (McFarlane & Beamish 1987) with the dosage converted to length of fish based on length-weight relationships (see Table 2). Recaptures were made by spearing at tagging sites after periods at liberty ranging from 11.5 to 48 mo.

It was not possible to obtain tagging records for 0+ fish. To check the position of the first annulus, newly settled fish were maintained in an outdoor aquarium system for periods of greater than 365 d. Fish of known

size and estimated age at capture were examined for annulus formation after periods of 12 to 24 mo.

On capture, fish were placed on ice and processed in the laboratory on the same day. Length (SL and FL) measurements to the nearest mm and total weight to the nearest gram were made by measuring board and an electronic balance. For each individual, gutted weight and weight of the alimentary tract, liver and gonad were also obtained. Both sagittae and lapillae were removed, cleaned in distilled water and stored dry after washing with ethanol.

Only sagittae were used for aging purposes. One of each pair was weighed to 0.1 mg. This was embedded in epoxy resin, sectioned transversely at 300 to 500  $\mu\text{m}$  through the core using a low speed Buehler isomet saw and ground using 600, 800 and 1200 grit abrasive paper. Otolith sections were mounted on a glass slide with thermoplastic glue (Crystallbond) and polished using 0.3 micron alpha alumina powder and a polishing cloth.

Sectioned otoliths were examined under both high power and dissecting microscopes using transmitted light. Each otolith was examined and read independently at 3 different times at a minimum of 3 wk apart for incremental bands representing annuli. Counts of increments were taken at the positions shown in Fig. 1.

Precision of age estimates was then calculated using the Index Average Percent Error of Beamish & Fournier (1981). For species of the genus *Naso* counts were made on samples which included small individuals (<4 increments) and larger individuals with >4 increments. Accuracy of sagittal readings was assessed using the position of tetracycline bands in the otolith relative to the positions of opaque increment structures and the sagittal margin.

Validated length at age plots were fitted to a regression model. Regressions of the form  $\log y = \log a + b \log x$  gave the best fit to the data. The main purpose of this study was to describe the observed patterns. No attempt has been made at this stage to fit growth models with particular assumptions to the data. For species of *Naso* the x-axis was identified only as sagittal increments (number of bands). The relationship between otolith weight and annulus number was examined by least-squares regression analysis with sagittal weight as the independent variable.

The numbers, size ranges, tagging and recapture data for each of the 10 species sampled for this study are provided in Table 1.

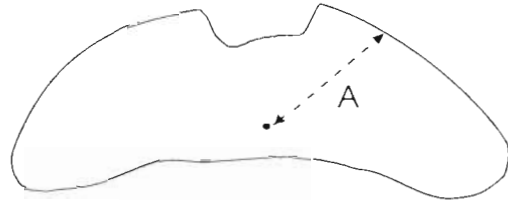


Fig. 1. Sagittal otolith in sectional view. Line A identifies the track along which counts of increments were made.

## RESULTS

### Length-weight relationships

Length-weight relationships in the 10 species examined displayed predictable values ( $b$  ranged from 2.50 to 3.06) when the equation  $W = aL^b$ , where  $L$  was standard length, was fitted (Table 2). The  $r^2$  values ranged from 0.963 to 0.999.

### Otoliths and validation

When viewed in transverse section, sagittae of *Acanthurus lineatus*, *A. olivaceus*, *Zebrasoma scopas* and *Ctenochaetus striatus* showed well defined systematic increments or banding patterns with opaque bands alternating with translucent bands (Fig. 2). Compared with other reef fishes such as scarids (Lou 1992) and serranids (Ferreira & Russ 1994), opaque bands were more numerous and tightly spaced, especially near the outer margins of the sagitta. Although some difficulty was encountered in identifying structures near the margins, total counts of opaque bands could be made in all species examined. The difficulties in obtaining consistent preparations and measurements at the margin made attempts to monitor mar-

Table 1. Number and size ranges of 10 species of acanthurid collected for otolith processing and tagging program

Species	No. fish	Size range (mm)	No. tagged	Size range (mm)	Total no. of recaptures	No. otoliths with tetracycline band
<i>Acanthurus lineatus</i>	94	76–206	45	169–195	6	4
<i>A. olivaceus</i>	177	26–248	21	147–242	4	3
<i>Ctenochaetus striatus</i>	176	28–197	143	115–186	27	22
<i>Zebrasoma scopas</i>	70	24–157	47	91–144	18	10
<i>Naso brevirostris</i>	173	47–330	186	117–340	2	0
<i>N. hexacanthus</i>	61	57–534	0	–	–	–
<i>N. tuberosus</i>	85	28–457	1	216	0	0
<i>N. unicornis</i>	56	50–457	0	–	–	–
<i>N. vlamingii</i>	92	53–387	6	153–190	0	0
<i>Prionurus maculatus</i>	16	252–566	0	–	–	–

Table 2. Length-weight relationships of 10 species of acanthurid fishes used in this study. For each species estimates of the parameters  $a$  and  $b$  for the relationship  $W = aL^b$ , coefficient of determination ( $r^2$ ), and the sample size ( $n$ ) are provided. Length is standard length (mm)

Species	$a \times 10^{-5}$	$b$	$r^2$	$n$	Size range (mm)
<i>Acanthurus lineatus</i>	22.19	2.691	0.963	94	76–206
<i>A. olivaceus</i>	3.385	3.055	0.998	177	26–248
<i>Ctenochaetus striatus</i>	3.517	3.066	0.993	176	28–197
<i>Zebrasoma scopas</i>	6.302	2.948	0.994	70	24–157
<i>Naso brevirostris</i>	10.88	2.743	0.994	173	47–330
<i>N. hexacanthus</i>	5.94	2.854	0.998	61	57–534
<i>N. tuberosus</i>	9.064	2.806	0.999	85	28–457
<i>N. unicornis</i>	8.495	2.843	0.997	56	50–457
<i>N. vlamingii</i>	7.533	2.843	0.993	92	53–387
<i>Prionurus maculatus</i>	62.0	2.504	0.989	15	207–447

ginal increment patterns (Manooch & Drennon 1987, Lou 1992) unreliable.

Independent counts of bands were used to estimate precision, expressed as the average percent error (Beamish & Fournier 1981). For *Acanthurus lineatus*, *A. olivaceus*, *Ctenochaetus striatus* and *Zebrasoma scopas* precision of counts varied from 5.3 to 5.9% (Table 3). As the number of increments within each

otolith was relatively large, these results suggest an acceptable level of precision in counts of sagittae made independently at different times. For species of the genus *Naso*, precision was relatively low when sagittae with less than 4 increments were counted (Table 3). This indicates that the position and clarity of the initial increments in this genus are variable and special care should be taken in determining their position.

The relationship between number of opaque bands (expressed as age) and sagittal weight was examined by fitting least-squares regressions to the data (Fig. 3). For all species there was

a significant positive relationship between fish age and otolith weight, although the form of the relationship varied amongst the species. Our interpretation is that otoliths show continuous linear or curvi-linear growth increase in weight over the life span of the fish.

A total of 263 individuals of the 4 species were tagged. The great majority of these were adult fishes (Table 1). Fifty-five tagged fish were recovered after

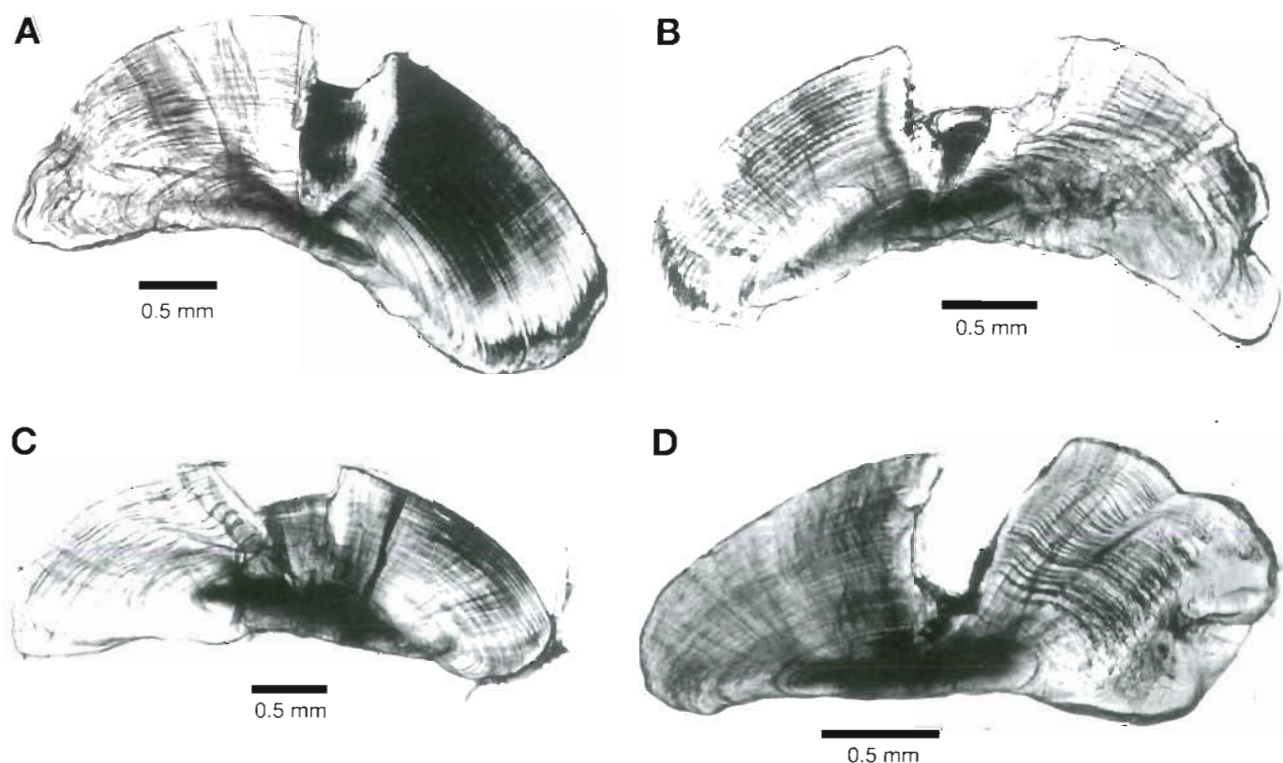


Fig. 2. Sectioned sagittae of acanthurids showing increments. SL: standard length. (A) *Acanthurus lineatus*: 193 mm SL, North Reef Lizard Island; (B) *A. olivaceus*: 186 mm SL, North Reef Lizard Island; (C) *Ctenochaetus striatus*: 141 mm SL, North Reef Lizard Island; (D) *Zebrasoma scopas*: 134 mm SL, Osprey Island Lizard Island

Table 3. Average percentage errors calculated from 3 independent readings of each otolith in 9 species of acanthurid. For the 5 species of *Naso*, otolith counts were partitioned into samples in which all individuals were counted

Species	n	Percentage error
<i>Acanthurus lineatus</i>	78	5.5
<i>A. olivaceus</i>	58	5.3
<i>Ctenochaetus striatus</i>	100	6.7
<i>Zebrasoma scopas</i>	31	5.9
<i>Naso brevirostris</i>	109	14.6
<i>Naso brevirostris</i> <sup>a</sup>	37	5.6
<i>N. hexacanthus</i>	51	8.4
<i>N. hexacanthus</i> <sup>a</sup>	32	4.6
<i>N. tuberosus</i>	45	7.0
<i>N. tuberosus</i> <sup>a</sup>	40	6.1
<i>N. unicornis</i>	44	15.8
<i>N. unicornis</i> <sup>a</sup>	16	5.1
<i>N. vlamingii</i>	74	7.2
<i>N. vlamingii</i> <sup>a</sup>	29	8.1

<sup>a</sup>Samples in which only individuals with >3 bands were counted

a period of greater than 11 mo. The distribution of individuals amongst the 4 study species and the percentage return rates from tagging was *Acanthurus olivaceus*: 4, 19%; *A. lineatus*: 6, 13.3%; *Zebrasoma scopas*: 18, 38.2%; and *Ctenochaetus striatus*: 27, 18.8%. The mean percentage return rate for the whole tagging pool was 21.5%, which reflects the sedentary nature of the species selected. *A. lineatus*, which has

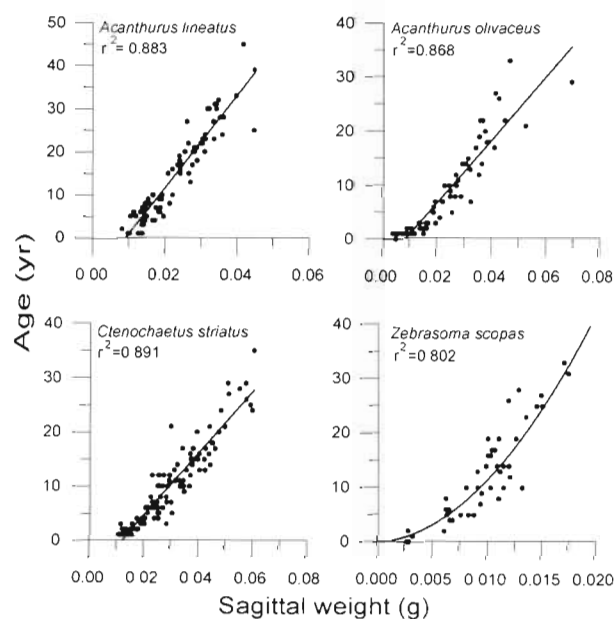


Fig. 3. Least-squares regressions of sagittal increments (age) on sagittal weight. *Acanthurus lineatus*:  $y = -10.07 + 1077.79x$ ,  $n = 80$ ; *A. olivaceus*:  $y = -5.12 + 580.88x$ ,  $n = 57$ ; *Ctenochaetus striatus*:  $y = -7.03 + 571.01x$ ,  $n = 120$ ; *Zebrasoma scopas*:  $\log y = 11.11 + 1.89 \log x$ ,  $n = 43$

deciduous scales, appeared to suffer the greatest post-tagging mortality. The mean time at liberty in months for each species was *A. olivaceus*, 11.7; *A. lineatus*, 14.3; *Z. scopas*, 16.4; and *C. striatus*, 11.6. A number of *Z. scopas* were collected after periods of 21 to 36 mo at liberty. This species was more sedentary and appeared to retain tags longer than other acanthurids.

Some individuals of *Ctenochaetus striatus* and *Acanthurus lineatus* were recovered with only the tag base present. As these sedentary species were tagged over a single month-long period, time at liberty could be established. Fifty-four of the tagged individuals were recaptured within 25 m of the original tagging site. The exception was a single *A. olivaceus* recovered 350 m from the tagging site. Not all recovered individuals showed a resolvable tetracycline band under fluorescent light. In 5 *C. striatus*, 8 *Z. scopas*, 2 *A. lineatus*, and 1 *A. olivaceus* the band was either too faint or absent. The remaining recaptures all showed clear tetracycline bands (Fig. 4).

The majority of returns showing successful tetracycline injections had been tagged in November. Representatives of the 4 species showed clear tetracycline bands directly associated with an opaque band (Fig. 5). In each case the opaque band was followed by a larger translucent band. Our interpretation is that opaque bands are laid down in early summer, a view that is consistent with the sagittal patterns seen in other reef fishes (Fowler 1990, 1995, Ferreira & Russ 1994). Fishes tagged in November 1991 and collected in November 1992 showed a tetracycline band associated with an opaque band and a translucent zone extending to the sagittal margin (Fig. 5). Over the 11.5 mo period between tagging and recapture a single opaque and translucent band was present. There was some difficulty in determining the status of bands at the outer margin of the sagitta.

A number of tagged fish were collected after being at liberty for periods greater than 12 mo. A small individual of *Ctenochaetus striatus* tagged in February 1992 showed a tetracycline mark at the outer edge of an opaque band. This individual was collected in November 1993 and showed a single opaque and 2 translucent bands. This was a small individual that had shown a relatively large growth increment. A further individual of *C. striatus* tagged in November 1991 and collected in October 1992 showed a single translucent band. However, this individual had been previously tetracycline-injected in November 1989 during a pilot study program. The October 1992 record was the second recapture. For the period November 1989 to November 1991, 2 translucent and 2 opaque bands were recorded. For the period November 1989 to October 1992, there were 2 opaque and 3 translucent bands (Fig. 5). An individual of *Z. scopas* tagged in November



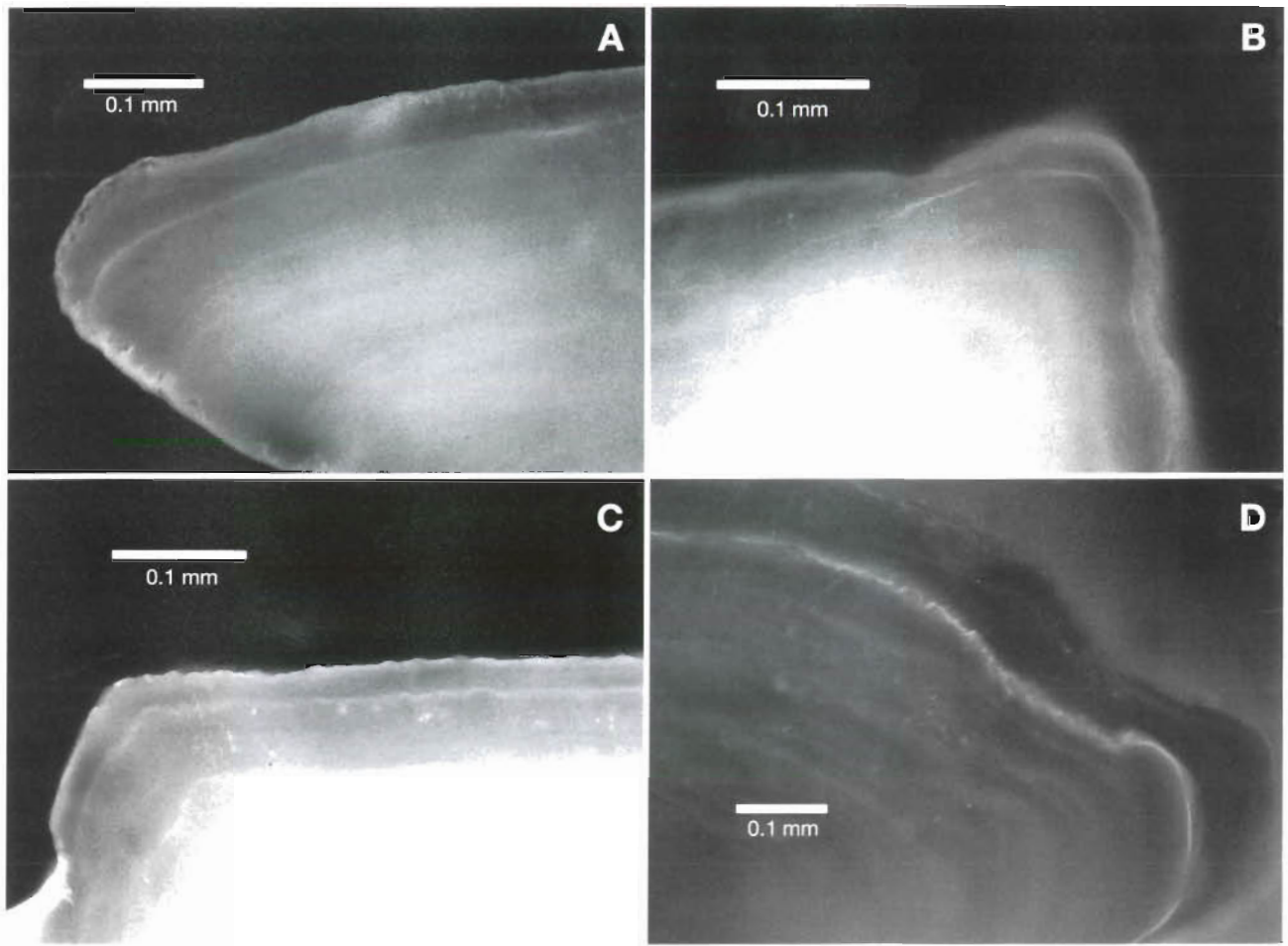
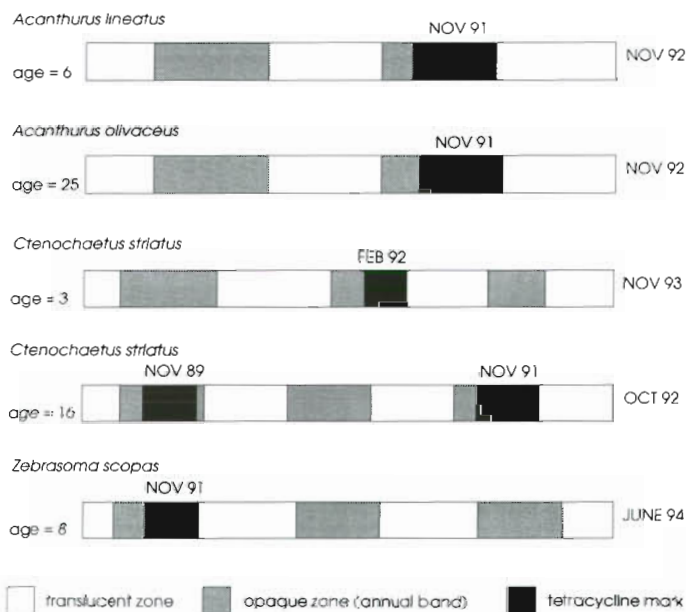


Fig. 4. Sectioned sagittae of acanthurids recovered after successful tetracycline treatment. (A) *Acanthurus lineatus*: 179 mm SL, North Reef Lizard Island; (B) *A. olivaceus*: 201 mm SL, North Reef Lizard Island; (C) *Ctenochaetus striatus*: 177 mm SL, Granite Bluffs, double injected; (D) *Zebrasoma scopas*: 136 mm SL, North Reef Lizard Island



1991 and recaptured June 1994 showed 2 opaque and 3 translucent bands (Fig. 5).

As an additional check on validations, we grew newly settled acanthurids in an outdoor aquarium system for periods greater than 12 mo. These included 1 *Acanthurus olivaceus* and 2 *A. nigricauda*, a species which is common at the same locality as the study species. All showed clear annuli which were consistent with the ages of the individuals (Fig. 6).

Fig. 5. Diagrammatic sequence of opaque and translucent increments in the sagittae of 5 acanthurids recovered after tetracycline treatments. Diagrams show relative positions of tetracycline bands, increments and otolith margin. Dates represent time of tagging (top of each bar) and time of collection (end of each bar). Age is an estimate at time of tagging. The fourth example (*Ctenochaetus striatus*) was double-tagged

### Size at age

Size at age data plotted for each species revealed consistent and highly characteristic patterns (Fig. 7). These showed rapid growth for the first 3 to 4 yr of life in all 4 species. Beyond 4 yr, growth declined sharply, resulting in an extended period over which little change in size occurred. Equations of the general form  $\log y = \log a + b \log x$  adequately described the relationship between age and size (Fig. 7) accounting in general for more than 50% of the variation in the size/age relationship. Counts of annuli suggested that each of the study species was relatively long-lived. The maximum number of annuli recorded ranged from 32 to 35 in *Acanthurus olivaceus*, *Ctenochaetus striatus* and *Zebrasoma scopas* and up to 46 in *A. lineatus*. Size is a poor predictor of age in these fishes.

In all species there was evidence of very rapid initial growth especially during the first 2 yr of life. It proved impossible to tag and follow such young individuals in the field. As a check we maintained 1 of the study species, *A. olivaceus*, in an outdoor aquarium for a period of 16 mo. The 30 mm SL newly recruited individual grew to 139 mm SL in 16 mo, which was consistent with the length at age plot for this species. The sectioned sagitta displayed 1 annulus (Fig. 6).

The relationship between size at age was variable, especially in *Ctenochaetus striatus*. Some of the vari-

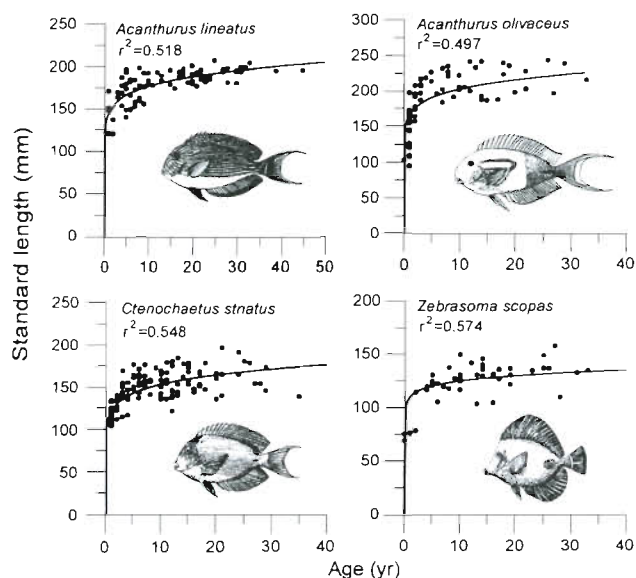


Fig. 7. Size at age relationships for 4 species of acanthurid for which validation of sagittal increments was obtained. The equation  $y = ax^b$  was fitted to each data set

ability was explained by partitioning size at age plots by locality. Most individuals of this species were collected at Lizard Island from adjacent habitats, North Reef and Granite Bluffs (Choat & Bellwood 1985). Collections from North Reef showed a more variable distribution of ages with size and a lower asymptotic size than those from Granite Bluffs.

Specimens from Granite Bluffs had a faster growth rate and achieved a greater size than those from North Reef (Fig. 8A). Comparison of the log-transformed data identified significantly different slopes for the fitted regression lines (General Linear Models Procedure;  $p = 0.0041$ ).

These differences were also reflected in the plot of sagittal weight and age (Fig. 8B). In the older age classes the faster growing individuals from Granite Bluffs showed heavier sagitta for a given age. Comparison of the regression lines in Fig. 8B identified significant differences between the slopes (General Linear Models Procedure;  $p < 0.0001$ ). Local differences in growth rate and otolith/somatic relationships may be a consistent feature of this detritus feeding acanthurid.

### Otolith increments in the genus *Naso*

Sectioned sagittae from 5 species, *Naso brevirostris*, *N. hexacanthus*, *N. tuberosus*,

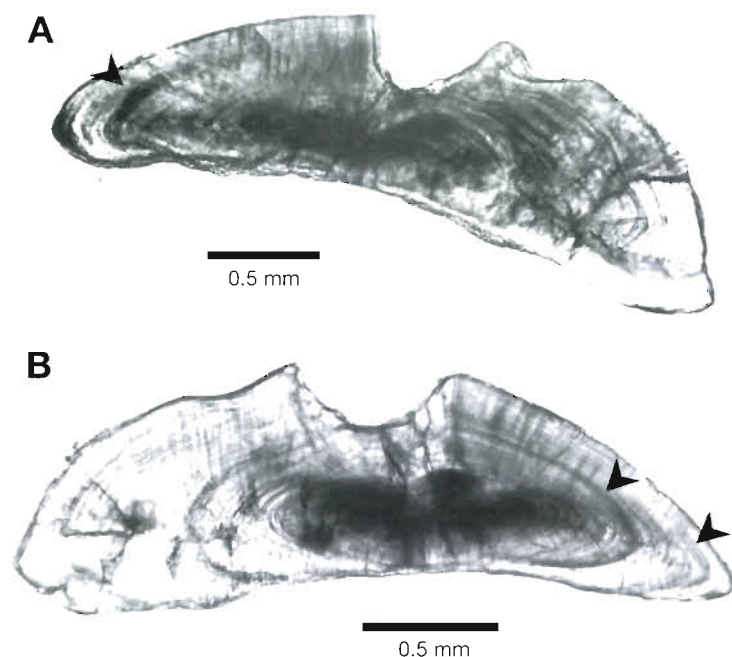


Fig. 6. Sectioned sagittae of 2 species of acanthurid maintained in an outdoor aquarium for periods greater than 12 mo. (A) *Acanthurus olivaceus*: 16 mo; (B) *A. nigricauda*: 27 mo. Arrows show positions of annuli

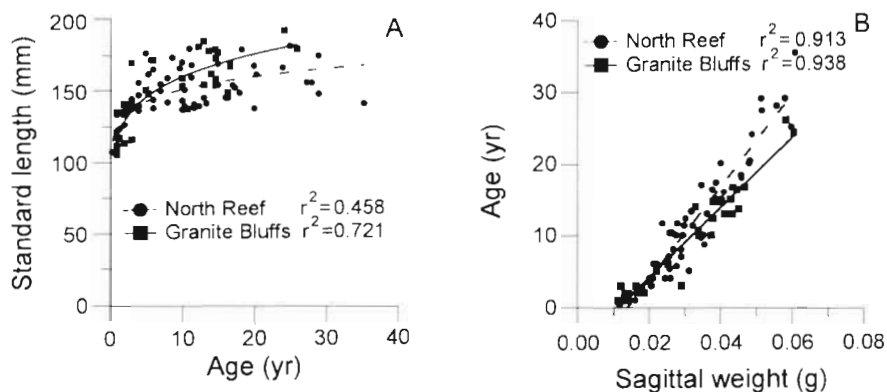


Fig. 8. (A) Locality-specific size at age relationships for *Ctenochaetus striatus* from North Reef (dashed line) and Granite Bluffs (solid line) Lizard Island. (B) Locality-specific age/sagittal weight relationships for *C. striatus* from the same localities

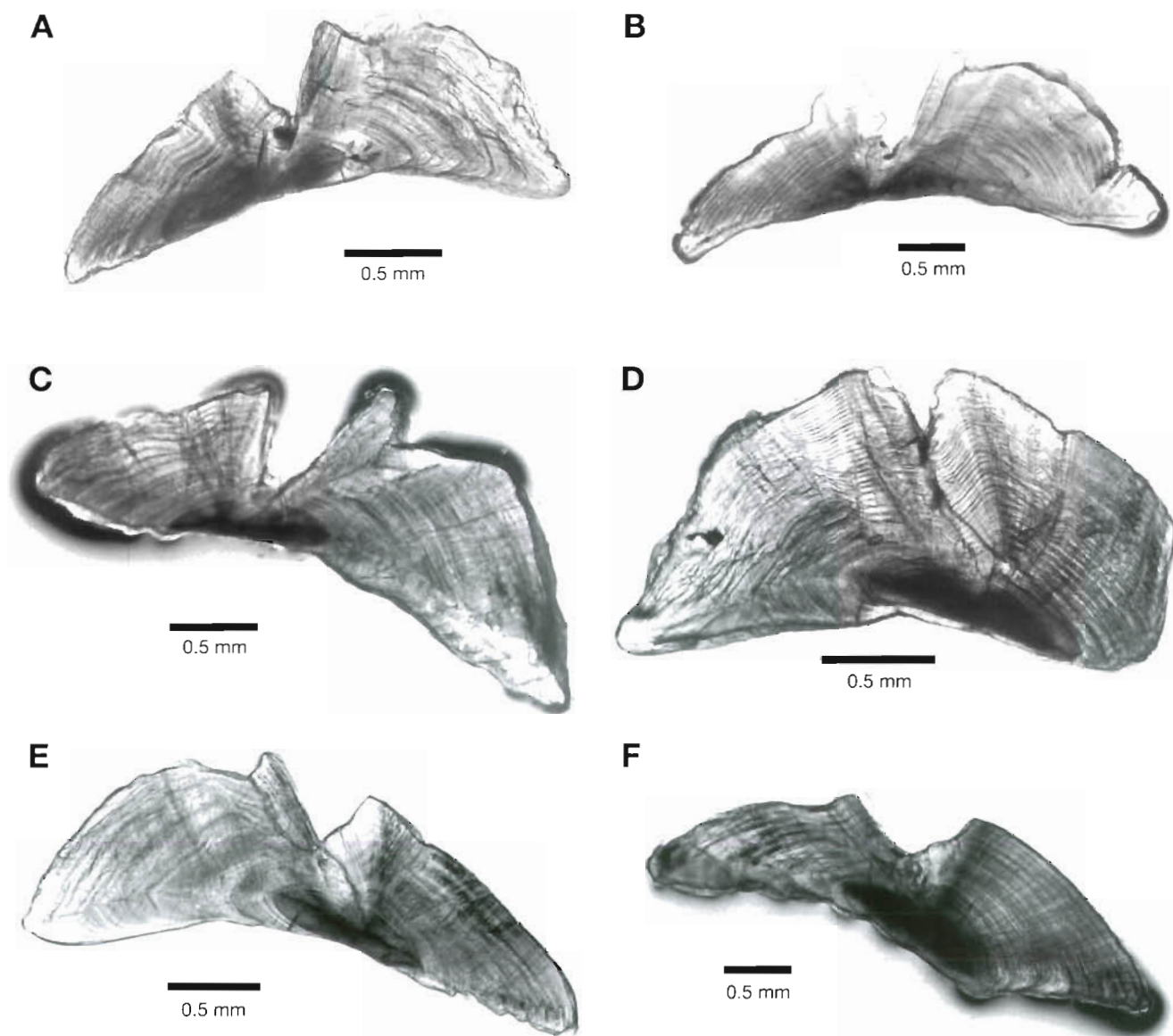


Fig. 9. Sectioned sagittae for 5 *Naso* species and *Prionurus maculatus* showing sagittal increments. (A) *N. brevirostris*: 312 mm SL; Hicks Reef; (B) *N. hexacanthus*: 454 mm SL, Hicks Reef; (C) *N. tuberosus*: 444 mm SL, Day Reef; (D) *N. unicornis*: 364 mm SL, Middleton Reef; (E) *N. vlamingii*: 295 mm SL, No Name Reef; (F) *P. maculatus*: 348 mm SL, Middleton Reef



*N. unicornis* and *N. vlamingii*, were found to display clear patterns of annuli alternating with translucent zones (Fig. 9). Despite a major tagging effort it was not possible to validate the annual nature of these increments. A total of 121 *N. brevirostris* were tagged and injected on reefs at Lizard Island in February 1992 and a further 57 on Hicks Reef (outer Barrier Reef) in November 1993. Only 2 returns were obtained and none displayed a detectable tetracycline mark in the otolith. There is some possibility that members of this genus do not take up tetracycline at the dosages used.

Sagittal weight showed a strong positive relationship with the number of increments in all species (Fig. 10). This was similar to that seen in species of *Acanthurus*, *Ctenochaetus* and *Zebrasoma*. The relationship between fish length and number of sagittal increments generated patterns similar to the size at age data for *Acanthurus*, *Ctenochaetus* and *Zebrasoma*. However,

for *Naso brevirostris*, *N. hexacanthus*, *N. unicornis* and *N. vlamingii* the approach to an asymptotic length was more gradual without the abrupt transition between 2 growth phases. Length continued to increase with increment number. A similar pattern was seen in a small sample of *Prionurus maculatus* collected from Middleton Reef. In *N. tuberosus* the pattern was closer to that seen in the other genera with an abrupt attainment of symptotic growth. Regression equations were fitted to the data. The best fit for *N. urevirostris*, *N. unicornis* and *P. maculatus* was obtained from power curves. For *N. hexacanthus*, *N. tuberosus* and *N. vlamingii* exponential plots gave the best results (Fig. 11). The number of increments suggests that members of the genus *Naso* attain the same maximum ages as the other acanthurids, in excess of 40 yr for the planktivores *N. hexacanthus* and *N. vlamingii* and in excess of 20 yr for *N. unicornis*, *N. tuberosus* and *N. brevirostris*.

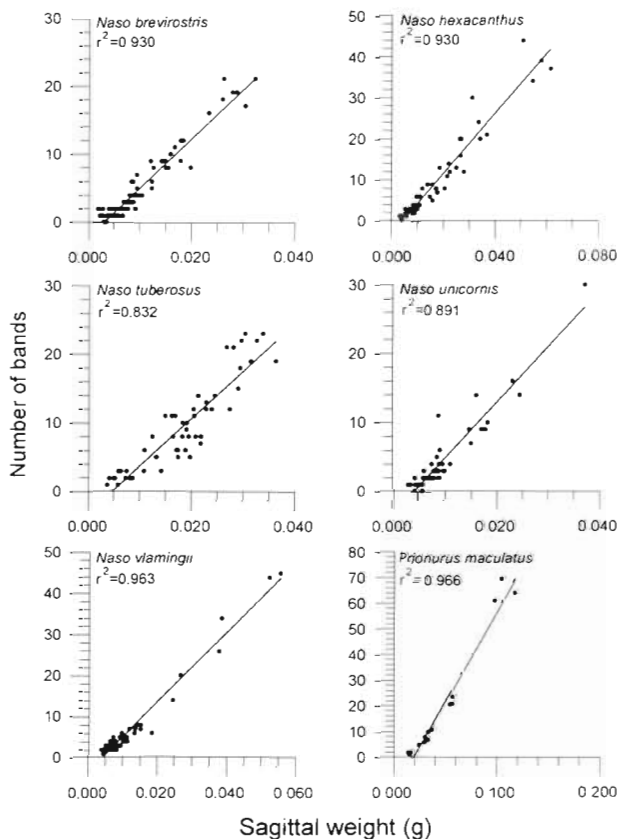


Fig. 10. Least-squares regressions of sagittal increments (number of bands) on sagittal weights for 5 species of *Naso* and *Prionurus maculatus*. (A) *N. brevirostris*:  $y = -2.18 + 711.09x$ ,  $n = 112$ ; (B) *N. hexacanthus*:  $y = -2.77 + 721.73x$ ,  $n = 50$ ; (C) *N. tuberosus*:  $y = -3.23 + 686.10x$ ,  $n = 55$ ; (D) *N. unicornis*:  $y = -3.43 + 805.14x$ ,  $n = 45$ ; (E) *N. vlamingii*:  $y = -3.50 + 838.78x$ ,  $n = 74$ ; (F) *P. maculatus*:  $y = -14.65 + 705.99x$ ,  $n = 16$

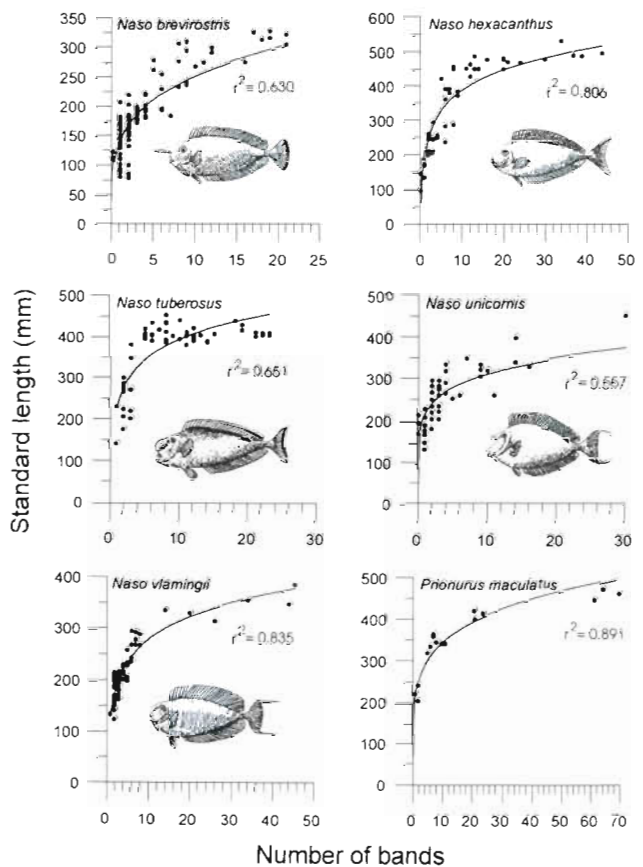


Fig. 11. Relationship between size (SL) and sagittal increments (number of bands) for 5 species of *Naso* and for *Prionurus maculatus*. For *N. brevirostris* ( $n = 112$ ), *N. unicornis* ( $n = 45$ ) and *P. maculatus* ( $n = 16$ ) data are fitted to the equation  $y = ax^b$ . For *N. hexacanthus* ( $n = 50$ ), *N. tuberosus* ( $n = 55$ ) and *N. vlamingii* ( $n = 74$ ) data are fitted to  $y = ae^{bx}$

## DISCUSSION

This study supports the conclusion of Fowler (1995) that many species of coral reef fishes show clearly defined macroscopic increments in transverse sections of their otoliths, and that when validated the periodicity of increments is annual. These increments are finding increasing use as demographic tools in the study of reef fishes (Doherty & Fowler 1994, Ferreira & Russ 1994, Worthington et al. 1995). Our study increases the taxonomic and ecological range of coral reef species for which demographic information may be derived from otolith structure.

A major conclusion from the analysis of acanthurid otoliths was that most species were long-lived, with rapid initial growth which resulted in an asymptotic size being achieved early in life. This pattern is confirmed by independent work on the acanthurid *Acanthurus nigrofusus* (Hart & Russ in press). Consequently, many age classes will accumulate within a relatively narrow size range. In these circumstances the analysis of size frequencies will be of little value as a demographic tool. Similar conclusions have been generated by the study of otoliths of coral-reef associated lutjanids (Newman et al. in press).

The use of otolith increments to estimate growth rates and age structure in tropical reef fishes has encountered 2 types of problems. Firstly the deposition of macroscopic increments may be irregular or may not occur at all (Longhurst & Pauly 1987). Fowler (1995) suggested that at least for Great Barrier Reef species this will not be a major problem. In some circumstances consistent and discernable increments may occur but the schedule of deposition may not be annual. For example, Milton et al. (1995) argued that increments observed in the sectioned sagittae of some tropical lutjanids may be deposited from 1.6 to 2.4 times per year. However, it is unclear what type of environmental signals would drive such an increment pattern. This conclusion was based on radiometric techniques.

Examples of radiometric analysis of otoliths in other species of fish have shown that estimates of age from sectioned otoliths and from radiometry are consistent. To date the examples have been from long-lived temperate water fishes (Smith et al. 1995, Stewart et al. 1995). Radiometric assays of long-lived tropical species such as *Ctenochaetus striatus* for which validation of annuli is available would be informative. Assays of *Naso* otoliths would also be useful, as it has proved difficult to validate increment formation in this apparently long-lived group. Analysis of the patterns of growth in different otolith dimensions may also provide an insight into life spans and growth in body size. The results of McFarlane & Beamish (1995) sug-

gested that estimates of growth in otolith thickness would be particularly useful in this context.

In the 4 species in which annual increment formation was validated we were able to estimate the seasonal pattern of deposition of opaque and translucent bands. The deposition of a single opaque band occurred in the early summer which is consistent with most other coral reef fishes (Fowler 1990, 1995, Ferreira & Russ 1994). Although acanthurids may show a strong annual cycle of reproductive events (Robertson 1983, Fishelson et al. 1987), the deposition of annual rings prior to sexual maturity indicates that this is not the primary stimulus for annulus formation. Acanthurids do show annual cycles of fat deposition and condition (Montgomery & Galzin 1993), indicating that systematic changes in metabolic activity occur within the year in the tropics.

Acanthurids constitute a coherent phylogenetic grouping (Winterbottom 1993, Winterbottom & McLennan 1993) with *Naso* the sister group to all other acanthurid genera and *Ctenochaetus* the most derived member of the generic assemblage. Within this assemblage there is evidence of considerable differentiation with respect to diet and feeding behaviours (Randall 1956, Winterbottom & McLennan 1993, Clements & Choat 1993) and in the sizes attained among species (Smith 1966, Jones 1968, Randall et al. 1990). Our findings suggest that despite these differences there is an underlying unity in growth patterns and life spans.

The 10 species examined were all characterised by rapid growth during the first 3 to 5 yr of life. Approximately 80% of linear growth was accomplished within the initial 15% of the life span. This pattern was apparent in very small sedentary species, *Ctenochaetus striatus* and *Zebrasoma scopas* and suggested in large pelagic planktivores such as *Naso hexacanthus*. Although there is relatively little information available on acanthurid growth, Randall's studies on *Acanthurus triostegus* (Randall 1961) confirm our findings of very rapid initial growth.

The highly partitioned nature of age-specific growth in acanthurids has implications for demographic monitoring. Recruits would grow through the smaller size stages very rapidly and merge with the adult population. Monitoring to detect recruitment pulses would need to be designed so that inputs could be identified before this occurred. For adult populations identification of previous recruitment pulses would require analysis of otolith characteristics. The linear relationship between otolith weight and age provides a basis for this (Fletcher 1991), provided the relationship is properly calibrated (Worthington et al. 1995).

The unexpected finding of this study was the distribution of ages in acanthurids. Our estimated longevity suggests that natural mortality rates will be low. Much of the demographic information available to date is

biased to particular taxa which may be relatively short-lived (Buesa 1987). This will have important implications for the management of fisheries which include acanthurids and other long-lived species (Russ 1991, DeMartini 1993, Wright 1993). Analysis of otolith structures will have an increasingly important role in the management of reef-based fisheries.

**Acknowledgements.** The study was supported by an ARC grant to J.H.C. A tagging pilot study was supported by an ARC grant to J.H.C. and G. R. Russ. Facilities and logistic support were provided by the Lizard Island Research Station and the Australian Museum. Laboratory work and access to aquarium facilities were supported by the James Cook University internal grant system. Assistance with the tagging and sampling program was provided by B. Kerrigan, C. Clements, V. Gleeson, E. Hutchinson, A. Ayling and D. Lou. This work benefited from discussions with G. Russ, D. Bellwood, P. Craig, C. Clements, A. Hart, J. Higgs and D. Williams. N. Moltschanivskyj provided assistance and advice with data analysis. Original drawings were done by Lucy Smith.

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*This article was presented by G. F. Humphrey (Senior Editorial Advisor), Sydney, Australia*

*Manuscript first received: June 19, 1995*

*Revised version accepted: November 16, 1995*