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Short communication

Geographic influences on and the accuracy and precision of age estimates for the red bass, *Lutjanus bohar* (Forsskal 1775): A large tropical reef fish

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Abstract

The red bass is a large tropical reef fish (Lutjanidae, tropical snappers) that is harvested to varying extents throughout a widespread Indo-Pacific distribution. The aims of this study were to investigate the accuracy and precision of age estimates from transverse sections of sagittal otoliths and to assess effects on these of the geographic area of collection and otolith preparation method. Two independent validation studies suggested an approximately annual formation of annuli in otoliths, predominantly for otoliths with 4–10 annuli but also for one otolith with 29 annuli. Otolith sections produced exceptionally high annulus counts: up to 56 annuli for samples from the Great Barrier Reef (GBR), Australia; and up to 55 annuli from the Seychelles, indicating a high longevity for this species. The precision of otolith readings from the GBR (index of average percent error, IAPE = 3.21 ± 0.26 S.E.) was within commonly accepted bounds for age estimation (IAPE up to 5%) but precision of readings from the Seychelles was significantly lower (IAPE = 9.18 ± 0.47 S.E.) and outside of this "acceptable" range. Age-based biological parameters for red bass from the Seychelles should thus be applied with greater caution than those for red bass from the GBR. If basic demographic properties are assumed relatively constant across the wide geographic range sampled, however, results from the GBR could be used as more reliable preliminary data for precautionary management strategies in the Seychelles and elsewhere.

Keywords: Otolith; Age estimation; Validation; Tropical reef fish; *Lutjanus bohar*

1. Introduction

The two-spot red snapper or red bass, *Lutjanus bohar*, (Forsskal 1775) is a large tropical reef fish that has a widespread distribution throughout the Indo-West Pacific, occurring from the Marquesas and Line Islands to East Africa, and from Australia northward to the Ryuku Islands (Allen, 1985). In some areas, such as the Seychelles Republic, red bass is one of the main species caught by local fishers for consumption. In 2000, for instance, the annual catch of red bass by the Seychelles Whaler Handline Fishery peaked at 127.5 tonnes, ranking fifth out of all reef fish harvested in that year (2875 tonnes). The catch of red bass declined to 44.9 tonnes in 2003, out of 2441 tonnes of total reef fish caught (Government of Seychelles, 2004). In other areas red bass has a reputation for causing ciguatera poisoning and is not harvested for consumption. For instance, on the Great Barrier Reef (GBR), Australia, red bass have been avoided historically by most fishers because of its reputed toxicity (Gillespie et al., 1986) and it has recently (from 9 November 2003) been made a No-Take species on the GBR because of its association with ciguatera poisoning.

A preliminary study by Marriott (2002) of red bass populations on the GBR identified that this species was potentially long-lived and slow-growing. The harvest of red bass by commercial fisheries is cause for concern, therefore, because populations of long-lived, slow-growing species are less likely to

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produce sustainable harvest yields (Adams, 1980; Kirkwood et al., 1993) and are most likely to be heavily impacted by fishing (Parent and Schriml, 1995; Jennings et al., 1998; Musick, 1999). Previous studies of red bass population biology done in the Seychelles (Wheeler, 1953), East Africa (Talbot, 1960), New Caledonia (Loubens, 1980) and Papua New Guinea (Wright et al., 1986), however, have reported very different maximum age estimates (3–38 years). The reason(s) for these differences remain unresolved, but given the wide range in maximum age estimated and the different age estimation methods used (length frequency, scales, otolith sections, modal progression of length frequency, respectively), it is likely that the choice of age estimation method was largely responsible. The use of inaccurate age data for stock assessment and fisheries management can result in either the undercapitalisation of a fishery or the overfishing of an exploited stock (Beamish and McFarlane, 1983). It is therefore vital that differences in reported age estimates for the red bass be resolved in order to make more confident stock assessments for its management.

Many studies of tropical reef fish have demonstrated that fish age can be estimated reliably from the transverse sections of sagittal otoliths (Fowler, 1995; Choat and Robertson, 2002). Some recent studies, however, have reported a reduced contrast between opaque and translucent zones on the otoliths of tropical reef fish sampled from lower latitudes (Fowler and Doherty, 1992; Choat et al., 2003; Smith and Deguara, 2003), indicating that the accuracy and/or precision of this method might be compromised by geographic differences in otolith readability. Even if a reduced contrast between opaque and translucent zones does not cause inaccurate or biased (Kimura and Lyons, 1991) age readings, it is likely to result in more frequent random ageing errors (imprecision). It is important to acknowledge that imprecise age readings could also have important management implications. For instance, apart from smoothing differences in the year class strength of age distributions (Kimura and Lyons, 1991), random ageing errors also have been demonstrated to bias estimates of mortality from the average age method (Powers, 1983), catch-curve analysis (Barlow, 1984) and optimum fishing mortality from yield per recruit analysis (Lai and Gunderson, 1987).

We aim, firstly, to establish the accuracy of red bass otoliths as chronometers recording age and the precision of age estimates made from transverse sections of red bass otoliths in order to determine the validity of this method for application to research on red bass population biology. We looked at samples collected from the Seychelles (3–10°S) to provide basic demographic information for the management of harvested stocks there and from the GBR (14–18°S) to determine the reliability of recent biological findings by Marriott (2002). Secondly, we compared and contrasted the accuracy and precision of results from these different areas to explore potential geographic effects, whilst controlling for otolith preparation method, age reader and age estimation method and to shed light on the large differences in maximum age of red bass estimated previously.

2. Methods

Biological samples and associated field data were collected from the northern and central sections of the Great Barrier Reef (GBR; 14°30′S, 145°20′E to 18°50′S, 147°40′E) and the Seychelles Republic (3°50′S, 50°10′E to 10°10′S, 57°10′E). Red bass were collected by line fishing, from depths of 5 to 35 m on the GBR and from 5 to 65 m in the Seychelles. Red bass were collected from the GBR through two sampling programs: (1) research catch surveys of the CRC Reef “Effects of Line Fishing” Experiment (detailed sampling methods in Mapstone et al., 2004; October 1995 to November 2001, $n = 1059$) and (2) monthly samples from the landed catches of commercial reef line fishers (July 2001 to June 2002, $n = 216$). In the Seychelles, red bass were sampled monthly by the Seychelles Fishing Authority from landed catches of the artisanal line fishing fleet (March 2000 to August 2002, $n = 836$).

Sagittal otoliths were transversely sectioned in random order using a standard procedure (Ferreira and Russ, 1994). Otolith sections were then further processed to improve the contrast between opaque and translucent zones using one of four methods: acid etching; hand-polishing; mechanical-polishing; or acid etching followed by mechanical-polishing. Acid etching was done by placing one or two drops of 15% hydrochloric acid solution onto sections for approximately 60 s. Sections were viewed at 40× magnification with transmitted light, and if increments were not clearly discernable, this process was repeated. Hand-polishing involved rubbing hand-held otoliths against 1200-grade wet and dry emery paper on a flat surface under tap water. Mechanical polishing was done using a Kemet (300 series) variable speed lapping machine fitted with a disc of 1200-grade wet and dry emery paper and supplied with running tap water.

Fish age, in years, was then estimated by enumerating opaque increments along the ventral sulcus of otolith sections, from the primordium to the proximal surface margin, when viewed with transmitted light under low (40×) to medium (100×) power magnification (Fig. 1). Opaque increments were categorised as pseudoannuli and excluded from age readings if their position or optical density relative to other opaque increments in the otolith was interpreted to be irregular by the age reader (R.J.M.). Two or more opaque increments were grouped and interpreted as a single annulus when they were interpreted to be confluent (Crabtree et al., 1995).

Otoliths were stained with oxytetracycline (OTC) as a means of validating the accuracy of age readings (Beamish and McFarlane, 1983). Two red bass received intraperitoneal injections of OTC at a dosage of $50\,\mathrm{mg\,kg^{-1}}$ body weight shortly after capture and were kept in a large aquarium facility at James Cook University under natural photo-period for approximately 17 months, from November 1999 to April 2001. These fish were fed a varied diet of pilchards, squid, and small reef fish *ad libitum*. They were euthanized in 2001 to identify the position of OTC staining, subsequent otolith

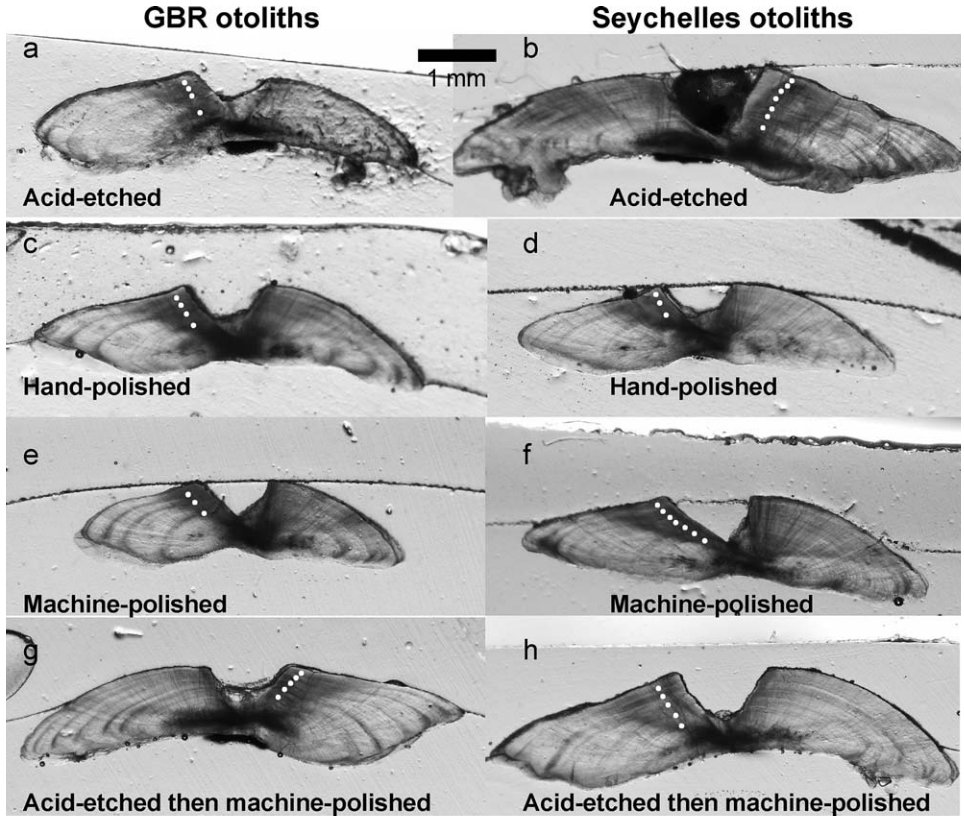

Fig. 1. Transverse sections from each area prepared by each method. Areas (2) indicated on top of panel; section preparation methods (4) labelled for each otolith. White dots indicate positions of annuli along reading axis. Otoliths were dissected from red bass that were: (a) 305 mm; (b) 561 mm; (c) 296 mm; (d) 313 mm; (e) 231 mm; (f) 381 mm; (g) 385 mm; (h) 412 mm fork length.

growth and any deposited opaque increment(s) on otolith sections. Seasonal patterns in daily water temperatures in the aquarium during the experiment were similar to those on Myrmidon reef (18°16′S, 147°23′E), which was close to the sites where these fish were sampled (Fig. 2).

The relative distance from the marginal increment to the margin of some otolith sections was quantified on a monthly basis to obtain further evidence of the periodicity of opaque increment deposition in both areas (GBR: $n = 96$; Seychelles: $n = 106$). "Nominal" age estimates were assigned to each otolith from the first set of age readings. Widths of marginal increments and penultimate increments were then measured along the ventral sulcus of otolith sections viewed with transmitted light, but it was difficult to confidently discern opaque margins because of shadow effects (Gauldie, 1988) and narrow increment widths. In a revised approach, therefore, otolith sections were viewed with reflected light against a black background and increment widths were measured at the ventral edge of otolith sections, along the axis from the primordium to the ventral tip. Opaque margins were judged to be more easily discerned and widths of full increment cycles were larger and so measurement errors were likely to be reduced (Cappo et al., 2000) using this method. Electronic images of otolith sections were captured using the "Seqsnap" computer program (Version 1.0; Imaging Technology Inc.). The widths of the penultimate cycle and marginal increments (Fig. 3) were measured using "Image Tool for Windows" software (Version 3.00; UTHSCSA). The MIR was calculated as the width of the marginal increment divided by the width of the penultimate cycle (Fowler and Short, 1998).

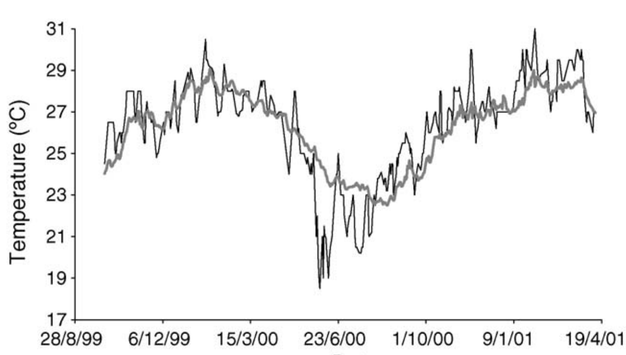

Fig. 2. Oceanic vs. aquarium facility temperature readings recorded during the OTC experiment. Oceanic daily water temperature readings (grey) from Myrmidon reef (18°16′S, 147°23′E), close to sites of sample collection, were recorded at noon (12:00 h; Steinberg and Burrage, 2001). Aquarium facility (MARFU, James Cook University) daily water temperature readings (black) were recorded in the morning (07:30 to 12:00 h).

Means of MIRs were then calculated for each sample month and geographic area. Only otolith sections with nominal age estimates ranging from 4 to 10 years and those for

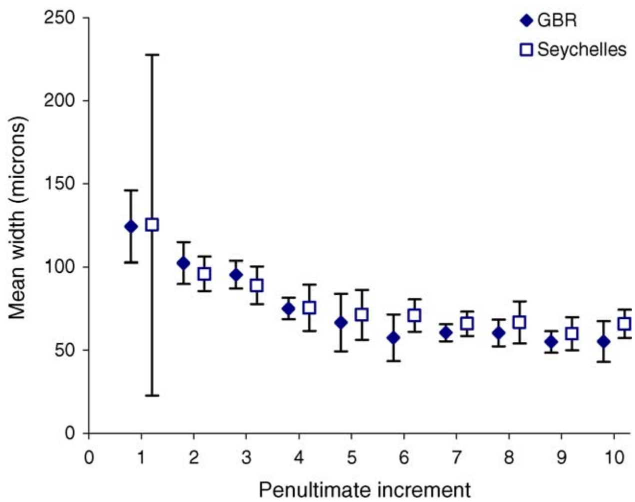

Fig. 3. Penultimate increment widths with nominal age. Measurement done along the ventral sulcus whilst viewing otolith sections with transmitted light at 100× magnification. Error bars are 95% confidence intervals.

which the position of the marginal increment relative to the otolith margin could be confidently discerned were measured. Successive opaque increments after the tenth annulus were not measured because they became obscured by "increment crowding" when viewed with reflected light. Sections with nominal age estimates of less than 4 years were excluded because penultimate and marginal increments decreased markedly in width (Fig. 3), which would likely bias mean MIRs downwards and thus underestimate the formation period.

Random sub-sampling of otoliths collected prior to November 2001 from the GBR ($n = 320$ from 1097 otoliths read) and prior to June 2001 from the Seychelles ($n = 402$ from 645 otoliths read) was done for a second, independent set of age readings. Up to five otolith sections, if available, were randomly selected from each nominal age group for each geographic area and method. Average percent error (APE; Beamish and Fournier, 1981) and coefficient of variation (CV; Chang, 1982) were then calculated as average indices of ageing precision. APE scores were negatively skewed (skewness = +2.28 ± 0.09) and heteroscedastic ($F_{7,714} = 13.3$; $p = 0.0001$), so the non-parametric Kruskal–Wallis test followed by post hoc Dunn's multiple comparison tests (Zar, 1999) were used to compare ageing precision (APE) among groups.

3. Results

Although regularly-spaced opaque increments were visible on otolith sections from both areas, those from the Seychelles appeared faint relative to those from the GBR (Fig. 1). Hand-polishing and machine-polishing appeared to improve the readability of annuli on GBR otoliths (Fig. 1(a), (c), (e) and (g)) but this was not as apparent on Seychelles otoliths (Fig. 1(b), (d), (f) and (h)). Some damage from acid-etching

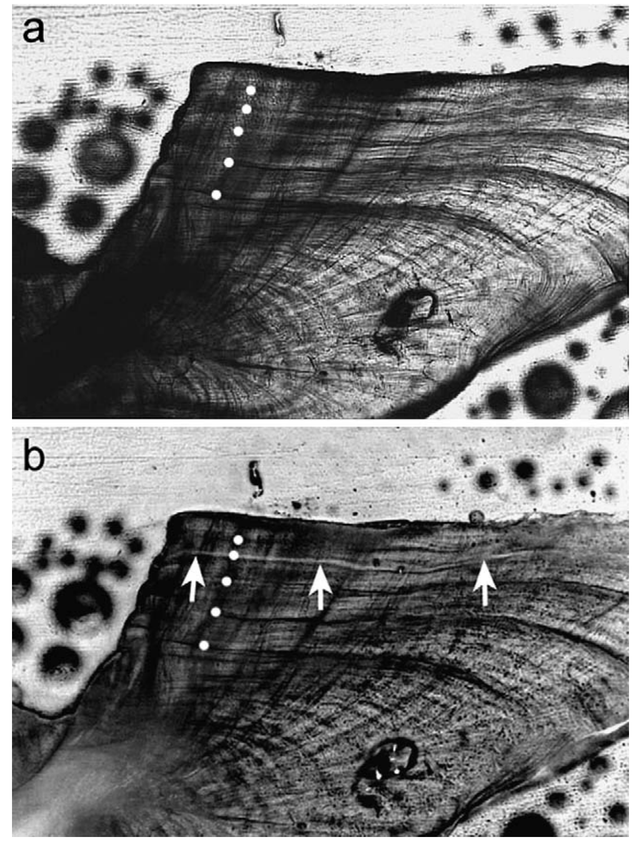

Fig. 4. Position of opaque increments (a) and oxytetracyline (OTC) band (b) of a 447 mm fork length red bass estimated to be nominally 5 years of age. This fish was sampled from Fork Reef (18°37′S, 147°34′E) on the GBR and injected with OTC on 30th October 1999 and then kept in a large aquarium until 5th April 2001.

of an otolith section for too long can also be seen in Fig. 1(a), which was an occasional disadvantage of this method.

The two fish subjected to OTC treatment were nominally aged as 5 (Fig. 4(a)) and 29 (Fig. 5) years when sacrificed. The

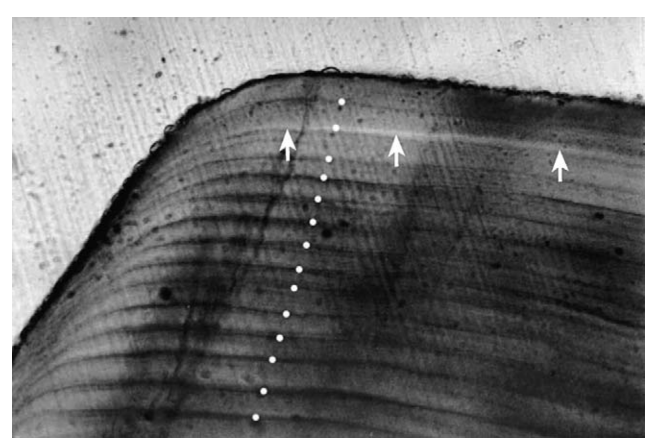

Fig. 5. Position of oxytetracyline (OTC) band on the otolith section of a 650 mm fork length red bass estimated to be nominally 29 years of age. This fish was sampled from Yankee Reef (18°34′S, 147°30′E) on the GBR on 4th November 1999, injected with OTC the next day, and then kept in a large aquarium until 9th April 2001.

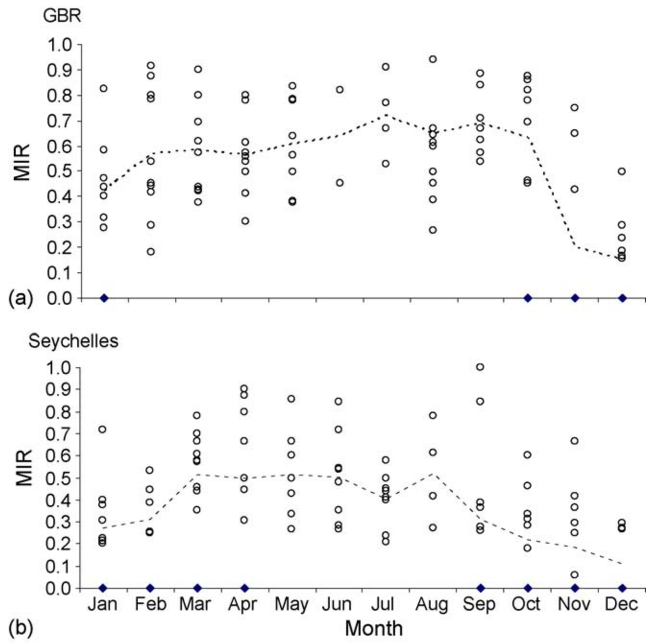

Fig. 6. Marginal increment analyses plots of marginal increment ratios (MIR) for otoliths collected from the (a) GBR and (b) Seychelles. Open circles are data from otoliths with a transparent margin; filled diamonds are from otoliths with an opaque margin; dashed lines are the mean MIR calculated per month.

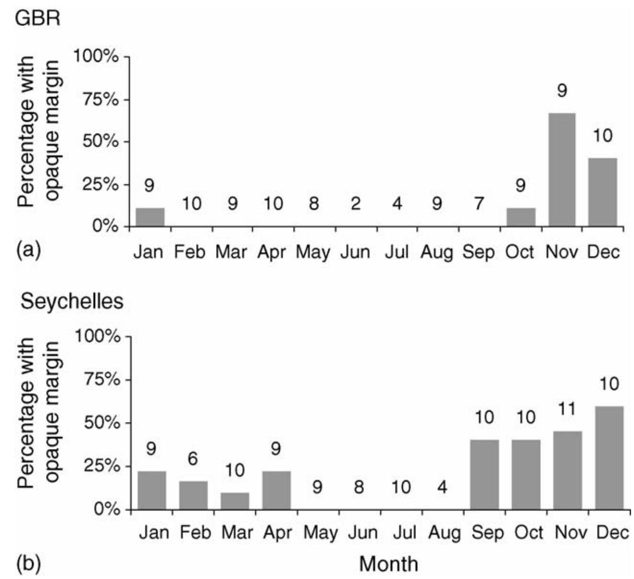

Fig. 7. Edge analysis of otoliths from the GBR and Seychelles. Numbers denote sample sizes.

OTC injections resulted in a fluorescent mark on otolith sections from both fish when viewed with transmitted ultra-violet light (Figs. 4(b) and 5). One complete opaque increment and a margin of additional otolith material was visible between the OTC mark and the proximal edge of otoliths from both fish, indicating an approximately annual deposition rate of opaque increments during the 17 month growth period. The OTC mark was also in approximately the same position as the penultimate opaque increment on both otoliths, indicating that the penultimate increments were formed at approximately the same time as the OTC injection in both fish (late October to early November, 1999). This timing concurs with that suggested by the marginal increment analysis of red bass otoliths from the GBR (Fig. 6(a)). Plots of mean MIR by month indicate annual cycles of opaque increment deposition in otoliths of nominally 4–10 year old fish from the GBR and Seychelles (Fig. 6(b)), although the distribution of MIR data from the Seychelles is scattered and less convincing than that from the GBR (Fig. 6). Annual minimum mean MIR (approximating the time of increment cycle completion) occurred in November and December for both areas, although this was less clearly defined for Seychelles' otoliths. An edge analysis revealed that opaque increments formed over a much longer period in the Seychelles (September to April) than on the GBR (October to January; Fig. 7).

Mean ranks of APE differed significantly among the eight treatment groups (2 geographic areas × 4 preparation methods; Kruskal–Wallis test; $\chi^2_7 = 133.956, p < 0.001$). Multiple comparisons revealed that geographic area significantly affected precision, since mean ranks of APE were significantly higher for all four Seychelles treatment groups (Seychelles IAPE = 9.18 ± 0.47 S.E.; Mean CV = 12.98 ± 0.67 S.E.) than for any of the GBR groups (GBR IAPE = 3.21 ± 0.26 S.E.; Mean CV = 4.53 ± 0.37 S.E.) (Table 1). No apparent differences in mean rank between methods within either geographic area were statistically significant. Further, the ordering of methods was not consistent between areas. It was thus inferred that the method of otolith

Table 1
Dunn's multiple comparison tests[a]

Treatment group	n	IAPE	Mean rank
(a) Statistics			
GBR-AM	56	2.24 (0.51)	226.20 (22.09)
GBR-AE	74	2.88 (0.44)	262.55 (19.71)
GBR-HP	98	3.22 (0.46)	269.25 (17.96)
GBR-MP	92	4.04 (0.60)	293.45 (19.20)
SC-MP	78	7.00 (0.73)	400.35 (22.75)
SC-AM	74	8.47 (1.00)	420.45 (23.12)
SC-HP	168	9.11 (0.71)	434.81 (14.98)
SC-AE	82	12.03 (1.34)	489.47 (19.90)

(b) Test result

	Most precise							Least precise
Geographic area	GBR	GBR	GBR	GBR	SC	SC	SC	SC
Method	AM	AE	HP	MP	MP	AM	HP	AE

[a] Treatment groups are combinations of geographic area: Great Barrier Reef (GBR), Seychelles (SC); and otolith section preparation method: acid-etched (AE), hand-polished (HP), machine-polished (MP), acid-etched followed with machine-polishing (AM). (a) Statistics: IAPE, index of average percent error. Numbers in parentheses are standard errors of the estimates. (b) Test result: non-parametric multiple comparisons (Dunn, 1964 in Zar, 1999) that account for tied rankings and unequal sample sizes among groups. Groups connected by bold lines were not significantly different at the 5% significance level, adjusted for experiment-wise error rate.

preparation did not consistently or significantly influence ageing precision.

4. Discussion

Evidence from all validation studies supported the accuracy of the red bass otoliths from the GBR and Seychelles as recorders of fish age. Although the majority of evidence was presented for otoliths with 4–10 annuli, evidence was also presented for an otolith with 29 annuli. This otolith was from a female that was much longer (601 mm fork length when first captured) than previous estimates of average length at maturity reported for this species (Wheeler, 1953; Talbot, 1960; Wright et al., 1986), indicating that its maturity was not likely to have affected the observed periodicity of opaque increment formation. The only other study to have done an OTC banding experiment for red bass was by Cappo et al. (2000), who inferred that opaque increment deposition might have been approximately annual (or longer). Cappo et al. (2000) made this prediction using a model of otolith growth that combined measurements of otolith increment widths and position of the OTC mark, although no opaque increment was observed between the OTC mark and margin of that otolith.

Although marginal increment analyses from both geographic areas indicated opaque increment deposition in November and December, the evidence was less definitive for otoliths from the Seychelles than for those from the GBR. Opaque increments were observed to form over a longer period in otoliths from the Seychelles than in otoliths from the GBR. Opaque increments may form over a longer period in the Seychelles because of reduced seasonal amplitude in climactic variations that may trigger opaque increment deposition. Alternatively, increased errors in the identification of marginal increments in otoliths from the Seychelles due to poorer readability could have resulted in more variability about mean monthly MIRs and a "smearing" of the annual mean MIR pattern.

Otoliths sampled from the lower-latitude Seychelles were more difficult to read because they formed opaque increments that were less distinct from interspaced transparent zones. This was consistent with observations made for other species in other studies (Fowler and Doherty, 1992; Choat et al., 2003; Smith and Deguara, 2003). The poorer readability of Seychelles otoliths resulted in age readings with a significantly lower precision than readings from the GBR. The aging precision of GBR samples was within levels frequently tolerated by many aging laboratories and reported in the literature (Campana, 2001) but was not for Seychelles samples. This means that the precision of age data collected from the Seychelles should be considered carefully when those age data are used for stock assessment. For instance, aging imprecision could be explicitly accounted for in age-structured stock assessment models (Fournier and Archibald, 1982; Richards et al., 1992) and uncertainties owing to associated biases in age-based population parameters (Powers, 1983; Barlow, 1984; Lai and Gunderson, 1987) could be appropriately acknowledged.

The results of this study therefore support the accuracy of age estimates from otolith sections of red bass collected from the GBR and lend support to the age-based biological parameters reported by Marriott (2002) for GBR populations. Age-based results from Seychelles samples, however, will be more uncertain. In light of the demonstrated high longevity and slow growth for this species from both areas, however, (Marriott, unpublished data) we urge managers to adopt precautionary approaches for the harvest of red bass because these characteristics suggest a high susceptibility to fishing impacts and potential population collapse through overexploitation.

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