



Non-lethal aging of tropical catch-and-release sport fishery species

Ronald Baker^{a,b,c,*}, Michael Bradley^{a,b}, Stefano Freddi^b, Katya Abrantes^{a,b}, Adam Barnett^b, Marcus Sheaves^{a,b}

^a TropWATER, James Cook University, Townsville, Queensland, Australia

^b Marine Biology and Aquaculture Unit, College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

^c University of South Alabama, Dauphin Island Sea Lab, Dauphin Island, Alabama, USA

ARTICLE INFO

Handled by B. Morales-Nin

Keywords:

Lutjanus goldiei

Lutjanus fuscescens

Fisheries management

Recruitment

ABSTRACT

Non-lethal methods for deriving age estimates from species of conservation significance or those supporting catch-and-release sport fisheries can assist in their sustainable management. In this study we tested if dorsal spines provide equivalent age estimates to otoliths for two species of large tropical snappers (*Lutjanus goldiei* and *L. fuscescens*, Lutjanidae) that support a catch-and-release sport fishery in remote parts of Papua New Guinea. Comparison of putative age estimates from sections taken at the base, mid and tip of the dorsal spine revealed that the base sections provided the most similar ages to otoliths, while mid and tip sections underestimated otolith age, especially for older individuals. Dorsal spine base-sections provided equivalent age estimates to otoliths for both species across the full range of ages examined (up to 17 for *L. goldiei*, and 14 for *L. fuscescens*). Like other lutjanids, these species show a wide range in length-at-age. This means that small fish are not necessarily young fish, and recruitment could potentially fail for more than a decade before anglers or guides notice a lack of smaller fish in their captures, by which time the opportunity to identify and reverse the cause of recruitment failure may have passed. Dorsal spines provide an effective and minimally-harmful means of monitoring population age structure to ensure ongoing recruitment to the fishery, and offer the opportunity for engagement of anglers, guides, and community members in the sustainable management of this fishery.

1. Introduction

Information on the age distribution of a fished population is critical for many aspects of fishery management (Beverton and Holt, 1957). Fish otoliths provide robust age estimates for many species (Campana, 2001), but collecting them is a lethal procedure. For species of conservation concern, or those supporting catch-and-release sport fisheries, non-lethal approaches for aging can help to balance the conflicting needs of acquiring accurate biological data to monitor population recovery or sustainability, and the protection of vulnerable stocks (Metcalfe and Swearer, 2005; Murie et al., 2009).

Otoliths are widely used to age fish (Secor et al., 1995; Campana and Thorrold, 2001), however other structures such as scales, fin rays, and spines have a long history in fish aging studies (Jackson, 2007). Two key advantages of otoliths over other structures for aging fish are that otoliths grow continuously throughout a fish's life, and they are not subject to resorption that can modify the formation or persistence of increments (Campana and Neilson, 1985; Campana and Thorrold, 2001). Scales or spines may under-estimate the age of fish, especially older individuals (Barbour and Einarsson, 1987; Braaten et al., 1999),

due to the resorption of tissue during periods of low growth (Campana and Thorrold, 2001), or the crowding of annuli in the outer margins of the structure (Chilton and Beamish, 1982). Scales are subject to replacement during the life of a fish, which can also lead to the under-estimation of fish age (Ilies et al., 2014). Spines and fin rays may also be subject to occlusion, whereby calcified material in the centre of the structure is gradually replaced by vascular tissue, leading to the loss of inner growth increments (Drew et al., 2006). However, despite these potential issues, spines and scales can be sampled non-lethally (Hobbs et al., 2014; Ilies et al., 2014), and they have been shown to provide accurate age estimates for fish from a variety of environments (Cass and Beamish, 1983; Drew et al., 2006; Ilies et al., 2014). Among tropical species, Hobbs et al. (2014) found dorsal spines to provide reliable age estimates for the grouper *Plectropomus leopardus*. Similarly, *Lutjanus argentimaculatus* dorsal spines provide accurate estimates of age, while scales from the same fish are less reliable (Freddi et al. unpubl. data).

The objective of the present study was to determine if it is possible to obtain non-lethal age estimates for two large tropical snappers, the Papuan black bass *Lutjanus goldiei* (Macleay, 1882), and the spot-tail snapper *Lutjanus fuscescens* (Valenciennes, 1830). Virtually nothing is

* Corresponding author at: Dauphin Island Sea Lab, 101 Bienville Blvd, Dauphin Island, Alabama, 36528, USA.
E-mail address: Ronald.baker@jcu.edu.au (R. Baker).

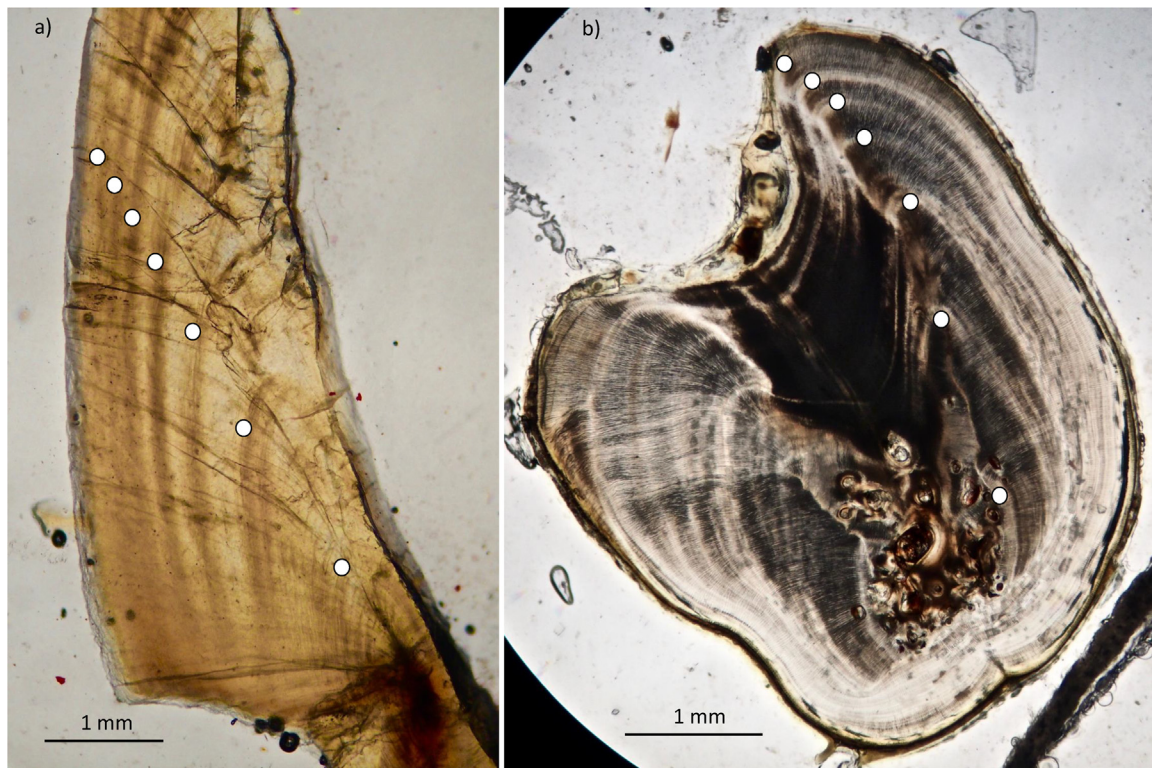


Fig. 1. Images of sections of a) otolith, and b) base of second dorsal spine of a 640 mm TL *Lutjanus goldiei*, with 7 annuli visible in each structure as indicated by white dots. The first increment in the spine section is almost obscured by occlusion and vascular tissue. Note that most age readings required manipulation of focus, magnification, field of view, and light intensity to identify annuli.

known of the biology or ecology of these species (Sheaves et al., 2016; Froese and Pauly, 2017). They grow to large sizes (> 20 kg) and form the basis of a wilderness-style catch-and-release sport fishery in remote parts of Papua New Guinea (Wood et al., 2013). The fishery has the potential to provide significant environmental and economic benefits to remote communities if it is managed sustainably (Barnett et al., 2016). A key element of management is to monitor the age structure of the fished populations. Our specific aim was to determine if dorsal spine sections provide equivalent age estimates to otoliths for these two species.

2. Materials and methods

2.1. Sample collection and preparation

Samples were taken from fish retained to provide a range of biological samples as part of a larger project examining the fishery ecology of *L. goldiei* and *L. fuscescens*. A total of 73 *L. goldiei*, and 78 *L. fuscescens* were sampled for this aging study on multiple dry-season (Apr–Nov) trips between May 2013 and April 2017. Fish were collected from the Pandi-Open Bay region (4°50'S, 151°30'E) of West New Britain, Papua New Guinea (PNG). Fish were measured (total length (TL) to nearest mm). Both sagittal otoliths were removed, rinsed, and blotted dry, and one randomly selected for aging. The second dorsal spine was removed from a subsample of *L. goldiei* (n = 46) and *L. fuscescens* (n = 30), by clipping with wire-cutters at the point of insertion. Other structures were considered for aging these fish. However, in a separate study scales were found to be unreliable for the close relative *L. argentimaculatus* and an initial small sample of *L. goldiei* (Freddi et al. unpubl. data), and spines have proven more reliable than fin rays in some species (Brusher and Schull, 2009), so these other structures were not considered further in the present study. To satisfy biosecurity requirements for importing samples from PNG to Australia, all samples were dried at 60 °C for 48 h before transport.

Otoliths were sectioned transversely through the core by either grinding and polishing on a Gemmasta Faceting Machine (Model GF4) using 1500 and 3000 grit grinding discs (small otoliths) or embedding in epoxy resin and cutting with a Buehler Isomet low speed saw (larger otoliths) before mounting and polishing the sawn sections as per small otoliths. Dorsal spines were embedded in epoxy resin, sectioned with the saw, and polished with 3000 grit grinding disks. All sections were regularly examined during polishing. Polishing ceased once growth increments were clearly visible rather than polishing to a consistent thickness, and final sections were all less than ca. 1 mm thick. Increments tended to be more visible in thicker sections of spines than of otoliths.

2.2. General aging procedure

All aging was completed by one person, with each structure aged three times with a minimum of 7 days between readings, and blind, i.e. with no knowledge of the identity of the fish or the previous age estimates. The median of the three age estimates was used as the final estimate. If the three age estimates spanned more than 3 years (i.e. $age_{max} - age_{min} > 2$; n = 8 of 151 otoliths and 22 of 112 spine sections), a fourth reading was conducted following the protocols above, and the median of the three estimates within a 3-year span was used as the final estimate. If after a 4th reading ages still did not converge to provide three estimates within a 3-year span (n = 1 otolith, 2 spine mid-sections and 2 spine base sections), the structure was excluded from further analyses. Many studies discard otoliths or other structures when consistent age estimates cannot be derived from the initial planned readings. However, because of the limited opportunities to collect samples of these species of conservation significance from remote locations, we chose to conduct a 4th reading and acknowledge the potential uncertainty around those age estimates (Pidcock et al., 2015b). The mean coefficient of variation (CV) was calculated to assess the relative precision of age estimates from each structure (Campana,

2001), and where a 4th reading was undertaken, all four values were included in calculations.

2.3. Aging otoliths

Putative age estimates were derived by counting apparent annuli in sectioned otoliths. Annuli were represented by paired translucent and opaque bands, and were counted at the sharply defined outer edge of the opaque zone (Fig. 1a). Although the periodicity and timing of formation of annuli has not been validated for *L. goldiei* or *L. fuscescens* (but see Section 2.5), annuli have been verified as the dominant visible increments for many other lutjanids (Cappo et al., 2000; Pidcocke et al., 2015a). The putative otolith age estimates derived for the present study were obtained from a larger set of samples including sectioned otoliths from twelve species of *Lutjanus* (authors unpubl. data), of which at least seven have been validated as forming annuli (Sheaves, 1995; Cappo et al., 2000). We therefore assumed the growth increments with similar appearance visible in non-validated species to represent annuli (Choat et al., 2009; Pidcocke et al., 2015a). The final age estimates derived from otoliths were used to construct length-at-(putative) age relationships for the two species.

2.4. Aging dorsal spines

A subsample of dorsal spines from 9 *L. goldiei* and 9 *L. fuscescens* were examined to identify increments in dorsal spine sections corresponding to annuli, if present, and to determine where longitudinally along the dorsal spine provides the most reliable age estimates. Each spine was sectioned in three positions: the base, being ~5 mm above the insertion point where the spine was clipped from the fish; the tip, being ~10 mm from the distal tip of the spine; and a mid-section half way between the base and tip sections. Spines ranged between 30 and 60 mm in length. As for aging of otoliths, annuli in spines were defined as paired opaque and translucent bands, and counted at the outer boundary of the opaque band (Fig. 1b).

Brusher and Schull (2009) found that the timing of deposition of increment boundaries in spines and otoliths can be offset by several months in juvenile goliath grouper *Epinephelus itajara*, and used this information together with knowledge of the timing of a short spawning season (i.e. consistent birthdate among individuals) to convert annuli counts into biological age classes to facilitate more direct comparisons between structures. However as noted above, the periodicity and timing of increment formation in our species has yet to be validated, and typical of other tropical snappers (Thresher, 1984) our species are reproductively active for > 6 months of the year (authors unpubl. data). Therefore a fixed birthdate cannot be assigned to these species, and our comparisons are based on raw counts of annuli in each structure. If the timing of deposition of the increment boundaries we counted does vary between structures, then age comparisons from fish collected in the intervening period would weaken any relationship in the age estimates between the two structures.

Preliminary examination of the subsample of spine sections

indicated that base sections provided the most similar age estimates to otoliths if the dominant increment structures were assumed to be annuli. Therefore, initial age-training was undertaken using spine base sections from three fish of known otolith age (Campana, 2001). This process allowed the reader to confidently identify increment structures within the dorsal spine sections corresponding to annuli, if present, i.e. regular prominent increments approximately corresponding in number to the otolith age were assumed to be annuli. The subsample of dorsal spine sections were then aged blind as per otoliths, three times with at least 7 days between readings, and training using the same three base sections was repeated prior to each reading. Complete aging of the subsample of spine sections from the three regions of the dorsal spine confirmed that base sections provided the most similar age estimates to otoliths (see Section 3.3). The training dorsal spine sections were randomised through the full sample set and aged as per all other sections so that they could be included as part of the full data set.

All remaining dorsal spines were sectioned at the base and aged as per the process described above. Occlusion and vascularisation was observed in the core of dorsal spine sections of around half the fish. When the area of occlusion was visually estimated to be larger than the typical diameter of the inner one or two annuli in non-occluded base sections, $n = 1$ or 2 was added to the count of visible increments to derive the age estimate for that spine section. This approach proved effective for our study where one individual aged all structures. However, for the application of dorsal spines for monitoring the age structure of these populations, we recommend that a set of reference spines are measured to more objectively estimate if the area of occlusion in any individual spine is larger than measured diameters of typical inner growth increments on non-occluded spines (Tserpes and Tsimenides, 1995). Because of the wide range in size at age (see 3.2 below), we recommend measuring the diameter of growth increments as a proportion of spine diameter rather than as absolute measurements.

2.5. Marginal increment analysis

Marginal increment analysis was undertaken in an effort to validate the periodicity of formation of the increments counted during aging. We analysed all otoliths and dorsal spine base-sections that were successfully aged. The width of the partially formed marginal increment was measured as a proportion of the previous complete increment in each structure.

3. Results

3.1. Precision of age estimates for individual structures

The majority of otolith and spine sections examined provided consistent age estimates from the first three readings, i.e. estimates within a 3-year range (Table 1). A fourth reading was required for eight of the 151 otolith sections, and for all but 1 otolith this provided three estimates within a 3-year span. The otolith from a 659 mm *L. goldiei*

Table 1

Number of age-readings required to derive final age estimate, and coefficient of variation (CV) of age estimates, from otoliths and dorsal spines of *Lutjanus goldiei* and *L. fuscescens*. n = number of structures analysed; 3rd - number of structures and % of total (in parentheses) for which age estimates were within a 3 year span after 3 readings; 4th - number (and percentage) of structures requiring 4th reading to derive age estimate; no age - number (and percentage) of structures for which four readings did not yield three age estimates within a 3-year span.

	<i>Lutjanus goldiei</i>					<i>Lutjanus fuscescens</i>				
	n	3rd	4th	no age	CV	n	3rd	4th	no age	CV
Otolith	73	68 (93)	4 (5)	1 (1)	9.0	78	75 (96)	3 (4)	0 (0)	8.3
Spine - Base	46	39 (85)	5 (11)	2 (4)	8.2	30	22 (73)	8 (27)	0 (0)	7.4
Spine - Mid	9	6 (67)	2 (22)	1 (11)	10.4	9	6 (67)	2 (22)	1 (11)	11.5
Spine - Tip	9	8 (89)	1 (11)	0 (0)	19.3	9	9 (100)	0 (0)	0 (0)	12.7

provided age estimates of 13, 9, 13, and 9. No dorsal spine was collected from this fish, and it was excluded from further analyses. Estimates from spine sections were more variable than those from otoliths (Table 1), with 1 of 18 spine-tips, 6 of 18 spine-mid sections, and 15 of 76 spine-base sections requiring a 4th reading. After the 4th reading, age estimates from 2 spine mid-sections (1 of each species) and 2 spine base-sections (both from *L. goldiei*) failed to converge, and these were excluded from further analyses (Table 1). The excluded spine-base sections were from a 620 mm *L. goldiei* with an otolith age of 15 and spine ages of 15, 12, 7, and 13, and a 437 mm *L. goldiei* with an otolith age of 10 and spine ages of 7, 6, 9, and 10. The coefficient of variation in age estimates was lowest for the spine bases and highest for the spine tips for each species (Table 1). Spine bases and otoliths provided similarly precise estimates of age for each species (coefficient of variation (CV) range 7.4–9.0). CV values indicate similar precision in our age readings to other published studies (Campana, 2001), but it should be noted our CV values are from a single reader, they do not reflect precision among multiple readers.

3.2. Otolith age – fish length relationships

Based on our putative otolith age estimates, both *L. goldiei* and *L. fuscescens* show a wide range in length-at-age (Fig. 2). For example, *L. goldiei* around 450 mm in length ranged in age from 3 to 12 years. The largest *L. goldiei* examined was an 819 mm fish, estimated to be 11 years old, while the oldest individual was a 770 mm fish estimated to be 18 years old (Fig. 2a). Only two individual *L. goldiei* < 400 mm TL were captured, a 287 mm fish and a 360 mm fish, both estimated to be 4 years old. The oldest *L. fuscescens* sampled were two fish estimated at 14

years old, one 529 mm and the other 585 mm, while the largest fish was a 606 mm individual estimated at 9 years (Fig. 2b). The length-at-age plots indicate that our sample does not include the asymptote of the growth curve for either species, i.e. that our sample does not include the largest, oldest individuals of the populations.

3.3. Position of dorsal spine section

For both *L. goldiei* and *L. fuscescens*, the base section of the dorsal spine provided the most similar counts of annuli to the otolith (Fig. 3). The base, mid and tip sections from dorsal spines provided similar age estimates to otoliths for the youngest fish of each species, but the mid and tip sections increasingly underestimate otolith age for older fish. Based on these findings, all remaining fish were aged using sections from the base of the dorsal spine.

3.4. Dorsal spine age vs. Otolith age

Sections from the base of the dorsal spine provided similar annuli counts to otoliths for both species (Fig. 4). Dorsal-spine ages tended to deviate more from otolith ages for *L. fuscescens* than for *L. goldiei*, yet the oldest individuals of both species had similar age estimates from both structures. The greatest deviation between structures for *L. goldiei* was an individual estimated at 12 years from the otolith and 9 from the dorsal spine (Fig. 4a). For *L. fuscescens*, the greatest deviations were for two individuals where the dorsal spine estimate was 3 years older than the otolith age, and one individual where the dorsal spine age was 3 years lower than the otolith age (Fig. 4b). Despite some variation between structures, dorsal spine ages could clearly distinguish fish

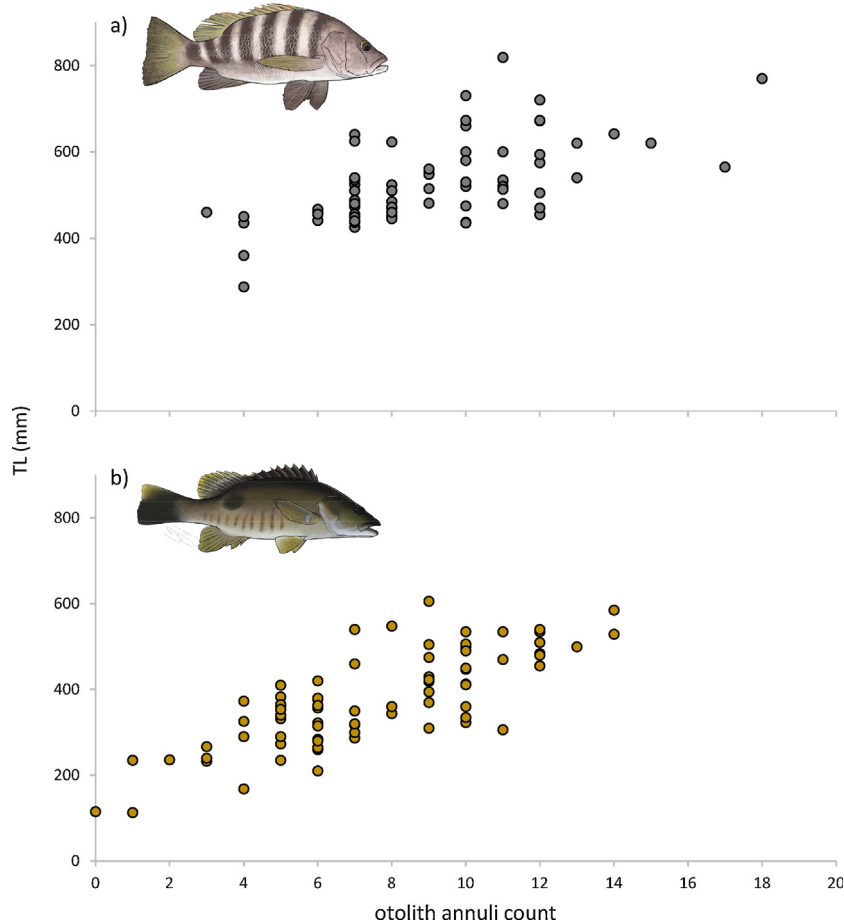


Fig. 2. Length-at-age plots for a) *L. goldiei* (n = 72), b) *L. fuscescens* (n = 78) from the Pandi-Open Bay region of West New Britain, Papua New Guinea, based on counts of presumed annuli in sectioned sagittal otoliths. TL = total length.

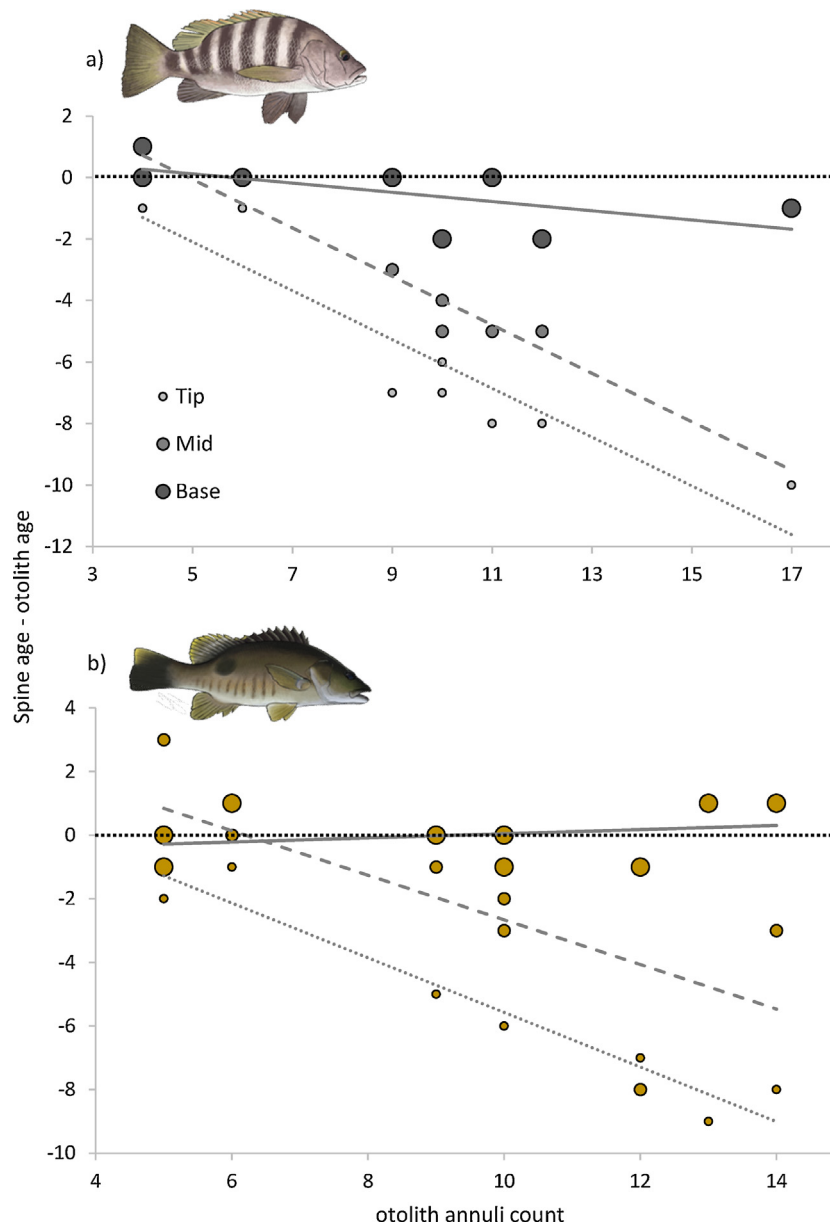


Fig. 3. Deviation of annuli counts from different regions of the dorsal spine from those obtained from otoliths for a) *Lutjanus goldiei* and b) *L. fuscescens*. Symbol size reflects position of dorsal spine section: large symbol, solid line – base of spine; medium symbol, dashed line – middle of spine; small symbol, dotted line – tip of spine. Horizontal dotted line at 0 on y-axis indicates agreement between dorsal spine and otolith age estimates.

estimated from otoliths to be > 10 years from those < 5 years (Fig. 4), which for both species could be individuals of similar size (Fig. 2).

3.5. Marginal increment analysis (MIA)

The lack of a sufficient sample size for rigorous MIA means that our MIA results should be treated cautiously (Campana, 2001). The otoliths of both species and the dorsal spines of *L. fuscescens* showed similar trends suggestive of annual formation of increments counted as annuli during aging (Supplementary Fig. 1). The widths of the marginal increments in the dorsal spines of *L. goldiei* were more variable.

4. Discussion

There was strong agreement between the putative age estimates from sectioned sagittal otoliths and sections from the base of the second dorsal spine. This indicates that, at least for fish within the age ranges

examined here, a dorsal spine will provide a similar age estimate as the otolith for *L. goldiei* and *L. fuscescens*. Sections from the base of the dorsal spine provided reliable age estimates, while those from the middle or tip of the spine underestimated age. Therefore it is important that the spine is clipped from the fish at the point of insertion to allow a section to be taken from as close to the base as possible.

A key aspect of the sport fishery based on these species is that anglers travel to remote locations to experience fishing in wilderness areas (Barnett et al., 2016). However, despite its remote location, the region is under increasing pressure from large-scale logging, plantation agriculture and other pressures that have the potential to impact on habitat quality and connectivity for the completion of these species' lifecycles (Sheaves et al., 2016). As such, a key management issue is to monitor the age structure of fish in this fishery, to allow early detection of any impacts that threaten the sustainability of populations (Metcalf and Swearer, 2005).

The presence of small fish in the fishery does not confirm successful

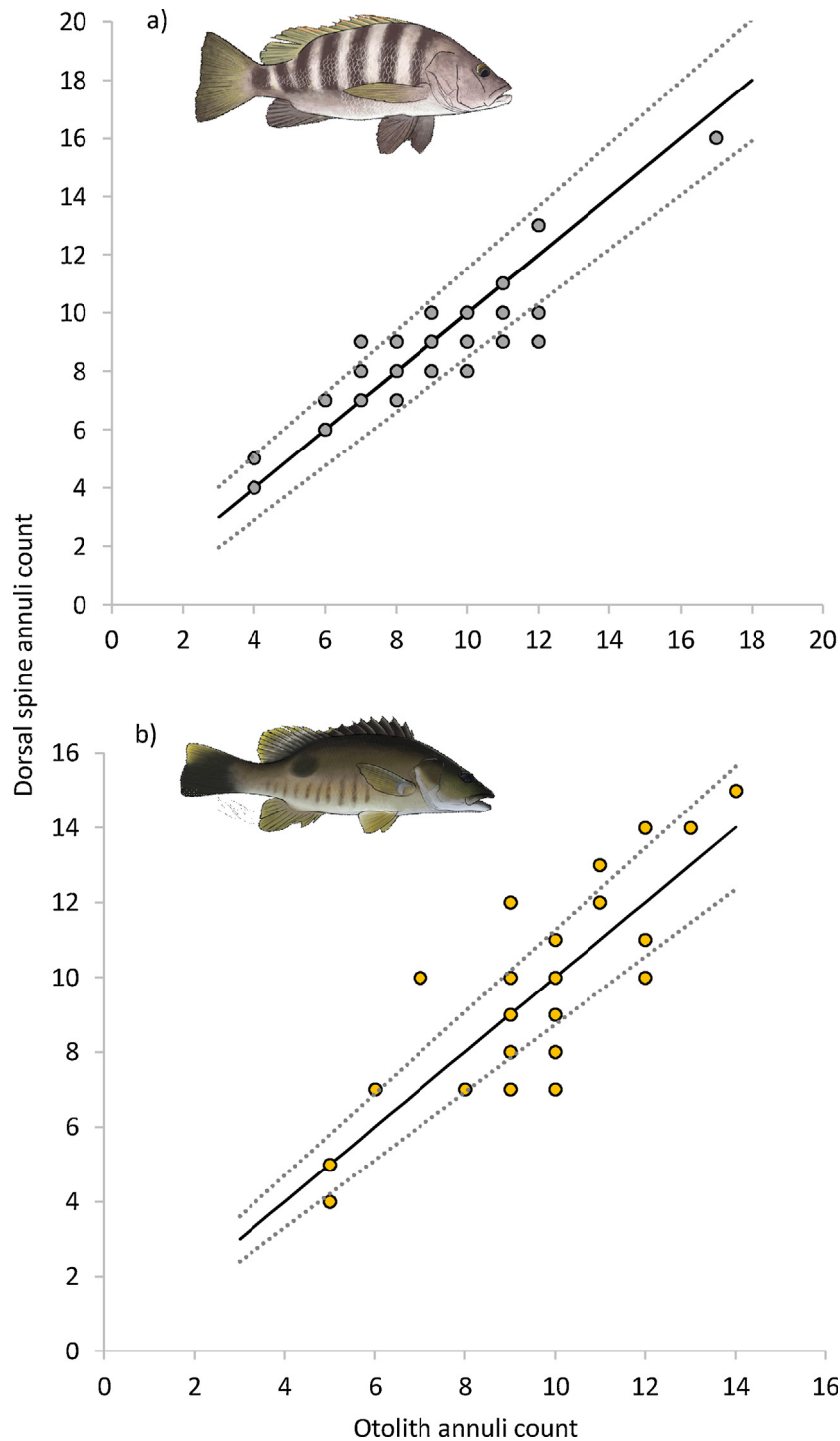


Fig. 4. Comparison of otolith and dorsal spine base-section age estimates for a) *Lutjanus goldiei* (n = 44), and b) *L. fuscescens* (n = 30). 95% confidence intervals around 1:1 lines are based on variation in individual readings of otoliths used to derive age estimates for full sample presented in Fig. 2.

recruitment of young fish to the fished population. As with other lutjanids, these species have a wide range in size-at-age (e.g. Sheaves, 1995; Heupel et al., 2010; Cappo et al., 2013). For example, the smallest *L. goldiei* typically captured in the sport fishery are around 450 mm TL (Fig. 2a), and among our samples age estimates for these fish ranged from 3 to 12 years. This means that small fish are not necessarily young fish, and recruitment could potentially fail for more than a decade before anglers or guides notice a lack of smaller fish in their captures, by which time the opportunity to identify and reverse the cause of recruitment failure may have passed. Our data indicates

that while dorsal spines do not precisely match the age estimates of otoliths, they do provide similar ages, and they can certainly distinguish young (i.e. < 5) from old (> 10) individuals. Therefore, aging using dorsal spines provides simple and effective means of monitoring recruitment to the fishery while minimising impacts on populations that support a catch-and-release fishery.

Given that the objectives of this study were to determine if the target species of a catch-and-release sportfishery can be successfully aged using non-lethal means, it is essential to address two key issues; 1) the periodicity and timing of deposition of the increments visible in the

sectioned otoliths and dorsal spines of these species need to be validated, and 2) we need to confirm that removal of a dorsal spine from these fish is non-lethal. Choat et al. (2009) advocate that while age validation should be undertaken whenever practical, the real logistical challenges for achieving this in many situations should not preclude otherwise important work on the demography of fishes in remote areas.

Marginal increment analysis, although widely employed, is often an unreliable method for validating increment periodicity (Campana, 2001; Pidcocke et al., 2015a). Our specimens were collected within a limited period of each year (Apr–Nov), and with limited sample sizes across multiple age-classes we were unable to apply this method with the level of rigour suggested by Campana (2001). Since it was beyond the scope of the present study to apply more rigorous methods for validating the periodicity of increment formation, we attempted MIA, and temporal trends in the marginal increment widths measured in the otoliths of both species and the dorsal spines of *L. fuscescens* were suggestive of annual formation. However, until more rigorous validation is undertaken these results should be treated with caution.

Facilities were not available to house fish for long enough to oxytetracycline (OTC) mark and rear individuals for validation, and fish held in captivity may present abnormal otolith structures (Campana, 2001). Anecdotal accounts indicate very low tag-returns from black bass tagged elsewhere in PNG, and we anticipated difficulty in recovering any fish recaptured by local people outside the sport-fishery. In addition, externally tagging large numbers of OTC-marked fish that are targeted in a remote area wilderness-style fishery may diminish the experience of anglers who subsequently recapture tagged individuals, thereby impacting on the long-term viability of the industry in the study area (Arlinghaus et al., 2007). Therefore, we did not attempt to OTC mark and release fish, and we present putative age estimates from each structure assuming that the dominant visible increments are annuli (Choat et al., 2009; Pidcocke et al., 2015a).

It is likely that the increments counted in the two target species are annuli. All structures were aged blind amongst samples including otoliths from 12 species of *Lutjanus* (authors unpub. data), at least seven of which have previously been validated as forming annuli (Cappo et al., 2000). As a result of this approach, the increments counted as putative annuli in the two target species had the same appearance as the most prominent increments in validated species. Regardless of the structures used for aging, the ongoing management of this sportfishery will rely on the assumption that the dominant visible increments are annuli until these are validated as such, and we have demonstrated that sections of the dorsal spine will provide equivalent age estimates to those from otoliths.

Ideally, the removal of a dorsal spine would have minimal effect on survival or fitness for these fish. We found the central part of the dorsal spine of larger individuals of both species undergoes occlusion, i.e. the resorption of bone material and replacement with blood vessels (Drew et al., 2006). This may increase the potential for injury by removal of the dorsal spine, serve as a site for infection, or release body fluids that may attract predators (Dallas et al., 2010). However, the removal of a dorsal spine has proven to be non-lethal for a variety of species (e.g. Metcalf and Swearer, 2005; Hobbs et al., 2014), including some released back into the natural environment after spine removal (Brusher and Schull, 2009). In addition, these species show excellent survival from the surgical implantation of acoustic tags (authors unpubl. data). It therefore seems likely these fish would be resilient to dorsal spine removal. Further work using acoustic telemetry to investigate the impacts of catch-and-release on these species can identify any lethal or sub-lethal effects of spine removal.

Although the asymptote of the growth curve was not reached, meaning that the largest oldest individuals of the population were not sampled, gathering age-data from larger older individuals is not currently an important issue for the management of this fishery. Survival of large trophy fish after catch-and-release is certainly critical to the sustainability of the fishery, and we plan to address this through acoustic

telemetry studies. The key management issue requiring age data from these populations is monitoring recruitment of young fish into the fishery, rather than deriving any age-based parameters associated with the oldest fish in the populations. Moreover, we did not intend to kill the largest caught fish because those are particularly valuable to this catch-and-release fishery, and the few that were captured were used in the acoustic tagging study. Discussion with guides suggests that while we did not retain the largest fish during this study, the size range of our sample includes the great majority of fish captured in the sport fishery. As such, the utility of dorsal spines for aging larger older fish was unimportant to the objectives of this study, but based on evidence from other studies, it is likely that dorsal spines will underestimate the ages of fish older than sampled here.

Based on our findings, sections from the base of the dorsal spine will provide equivalent age estimates to otoliths for fish up to ca. 15 years old for two tropical snappers that support a sport fishery of considerable economic significance to remote communities. There is great potential for the sport-fishery itself to provide the local or national fisheries authority with samples of dorsal spines from each region in the fishery, since the removal and storage of these samples does not require any specialised training or facilities. Engaging anglers and members of the remote communities to participate in the management of this fishery helps to maximise the likelihood of positive outcomes for all stakeholders (Barnett et al., 2016).

Declaration of interest

None.

Contributors

RB conceived the study; all authors contributed to the design of the study; RB, KA, AB and MS collected the samples; SF conducted a literature review; MB and SF developed the aging protocols; MB sectioned and aged the samples and completed the MIA; RB analysed the data and wrote the paper with input from all authors. All authors have approved the final submission.

Acknowledgements

We thank Riccard and Nathalie Reimann of Baia Sport Fishing PNG and the people of Baia Village for their support of this work. Lina Pandihau (Papua New Guinea National Fisheries Authority) provided assistance with field work and logistical planning. Claudia Trave produced the images of *L. goldiei* and *L. fuscescens*. Field work was conducted with permission of, and in collaboration with, the PNG National Fisheries Authority, and in accordance with JCU Animal Ethics guidelines under JCU Ethics Permit A2308. This work was funded by the PNG National Fisheries Authority and the Australian Centre for International Agricultural Research under grant FIS-2013-015, and these agencies provided broad objectives and advice on research directions. RB was partially supported by a grant from the Tropical Landscapes Joint Venture between JCU and CSIRO.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2018.06.011>.

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