

Age-based life history of humpback red snapper, *Lutjanus gibbus*, in New Caledonia

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Abstract

This paper examines the life history of humpback red snapper *Lutjanus gibbus*, an important fishery species for coastal communities across the Indo-Pacific, in southern New Caledonia, where the species is lightly exploited. A total of 243 *L. gibbus* were sampled between January 2013 and December 2016 from occasional harvests of commercial fishers. Examination of sectioned otoliths revealed that opaque increment formation occurred annually between November and March, coinciding with the species' spawning season. Estimates of maximum age were similar between sexes, with observed ages of 38 and 36 years for females and males, respectively, extending the reported longevity of this species by at least 11 years. Growth differed significantly between sexes, with males reaching greater length at age and greater asymptotic length than females (38.88 v. 31.46 cm fork length (L_F)). Total mortality for all samples was estimated as 0.13 and was slightly higher for males (0.16) than females (0.11). Estimates of natural and fishing mortality were low and slightly higher for males than females. Male *L. gibbus* were found to mature at slightly greater lengths and younger ages than females, with the length and age at which 50% of individuals attained maturity estimated to be 25.8 cm L_F and 3.9 years of age for females and 26.8 cm L_F and 3.4 years of age for males. The results provide key baseline information from which to assess the effect of fishing on the species for populations in New Caledonia and adjacent locations and, when viewed with those of other studies, highlight the importance of understanding spatial patterns in demography of harvested fish species across gradients of exploitation and environmental influences.

KEY WORDS

age, demography, growth, Lutjanidae, mortality, reproduction

1 | INTRODUCTION

Tropical snappers (Lutjanidae) are a common and widespread component of shallow and deep-water fisheries in tropical and subtropical waters worldwide. Their significance to commercial, artisanal and subsistence harvests is demonstrated by the numerous studies that have focused on their biology and ecology, with particular emphasis placed on describing age-based and reproductive

biology (Luers *et al.*, 2018; Newman *et al.*, 1996; Shimose & Nanami, 2014), as well as movement patterns, habitat use and population connectivity (Grober-Dunsmore *et al.*, 2007; Hitt *et al.*, 2011; Kennington *et al.*, 2017). As a group, lutjanids are unequivocally considered gonochoristic, whereby individuals are either female or male from earliest development and no sex change occurs throughout the life span. Harvested lutjanids are known to have moderate to high life spans, ranging from 10 to 55 years or more, with

longevity positivity related to body size (Heupal *et al.*, 2010; Marriott *et al.*, 2007).

Of the 60+ species of Lutjanidae that occur in the Indo-West Pacific region, one of the most heavily harvested is the humpback red snapper *Lutjanus gibbus* (Forsskål, 1775). *Lutjanus gibbus* is harvested by a variety of fishing gears, though most commonly by hook and line, spears and nets, and forms an important component of coastal fisheries in the Indo-Pacific. In Funafuti, in the Pacific Island nation of Tuvalu, Moore *et al.* (2014) observed the species to constitute 36% of handline–bottom fishing catches by abundance and 26% by mass, while in Pohnpei, in the Federated States of Micronesia, the species is the most commonly caught species among all gear types (Rhodes *et al.*, 2007).

In recognition of the species' importance to fisheries within the Indo-Pacific region, a number of recent studies have examined aspects of the biology of *L. gibbus*. However, discrepancies exist among published studies. In southern Japan, at c. 24° N, Nanami *et al.* (2010) observed a maximum age of 24 years and significant sexual dimorphism in length at age, with males reaching a larger length at a given age than females. Taylor *et al.* (2018) found a similar pattern of sex-specific growth and report a maximum age of at least 27 years for the species in American Samoa at c. 14° S. In contrast, Heupal *et al.* (2010) observed a maximum age of 12 years and considerable overlap in lengths at a given age between females and males for populations on the Great Barrier Reef, Australia, between 14° S and 21° S, although these authors noted that the smallest and largest (and thus presumably the oldest) size classes were poorly represented in catches in their study. Holloway *et al.* (2015) observed a maximum age of only 9 years within a marine protected area in northern Sulawesi, Indonesia, at approximately 1° N. Notwithstanding possible sampling biases, such differences likely reflect differences in environmental conditions, in particular water temperature and fishing pressure experienced between locations (Barnett *et al.*, 2017; Munch & Salinas, 2009).

Understanding the biology of exploited species is important for developing appropriate assessment approaches and developing effective harvest strategies and management plans. In the Pacific Islands and elsewhere, many fisheries agencies are moving towards, or contemplating moving towards, life history-based approaches to monitoring and assessment of their data-poor fisheries resources. For such assessments to be as accurate as possible, it is imperative to obtain regionally-relevant estimates of a species' biology in the absence, or near-absence, of fishing pressure. However, for *L. gibbus*, available estimates of demographic parameters to date have come from populations facing moderate to high levels of fishing pressure. For example, in American Samoa, the focal area of Taylor *et al.* (2018), *L. gibbus* forms the 12th most harvested species (of c. 300 species) by mass (Pacific Islands Fisheries Science Centre, 2018, cited in Taylor *et al.*, 2018).

This paper examines life history of *L. gibbus* from southern New Caledonia, where the species is subject to low fishing pressure relative to other locations across its range. Unlike elsewhere in the Pacific, *L. gibbus* is not actively targeted in New Caledonia and was only

occasionally harvested by commercial fishers during the study period for this paper (T. Tiburzio, Département de l'aquaculture et des pêches, pers. comm.; B. Moore, pers. obs.). Fisher and market-based collections were undertaken over a period of 4 years to provide detailed information on growth, life span, mortality, maturity and spawning seasonality.

2 | MATERIALS AND METHODS

2.1 | Study area, sample collection and gonad processing

All samples of *L. gibbus* used in this study ($n = 243$) originated from fishing trips in southern New Caledonia (Figure 1) between January 2013 and December 2016. Samples were collected from commercial fishers who typically used handline–bottom fishing gears, or from vendors at the central fish market in Nouméa, where the fisher, collection location, date of collection and fishing gear used was known. On each sampling day, vendors were visited soon after opening and all available fish were purchased for life-history analysis to avoid biasing of the size distribution due to buyer's preference. For each fish collected, the fork length (L_F ; to the nearest 0.1 cm) and mass (W_T ; to the nearest 1 g, if available) was measured and the sagittal otoliths were removed, cleaned and stored dry in plastic vials. Gonads were dissected, trimmed of extraneous fat and connective tissue, weighed (W_G ; to the nearest 0.1 g), sexed and staged macroscopically into stages adapted from Brown-Peterson *et al.* (2011): I, immature; II, developing; III, spawning capable; IV, running ripe (*i.e.*, actively spawning subphase); V, regressing; VI, regenerating. Gonads were then fixed in 10% buffered formalin for later histological processing. Owing to concerns over ciguatera fish poisoning, a number of fish ($n = 97$) were gutted at sea, resulting in damage to the gonads. While some of these individuals could still be reliably sexed and staged both macroscopically and histologically, individuals with damaged gonads were not used in assessments of the gonadosomatic index (I_{GS}).

2.2 | Age estimation

A single otolith from each fish was embedded in epoxy resin and sectioned transversely through the primordium, in a direction perpendicular to the sulcus acusticus, using a low speed saw with a diamond tipped blade. Otolith sections (up to three per individual) were cut thinly (0.3 mm) to improve increment clarity. Sections were mounted on glass slides with a cover slip using casting resin. Opaque increments on each otolith section were counted using a compound microscope using a combination of reflected and transmitted light. The opaque increments were counted primarily along an axis from the primordium to the otolith margin on the ventral rim of the sulcus acusticus, as this was typically the axis with the most well-defined increments. However, other axes were examined as a reference when opaque increments were unclear on the primary axis. All otolith sections were read by two experienced readers. One reader (reader 1) examined each section on at least two separate occasions. When

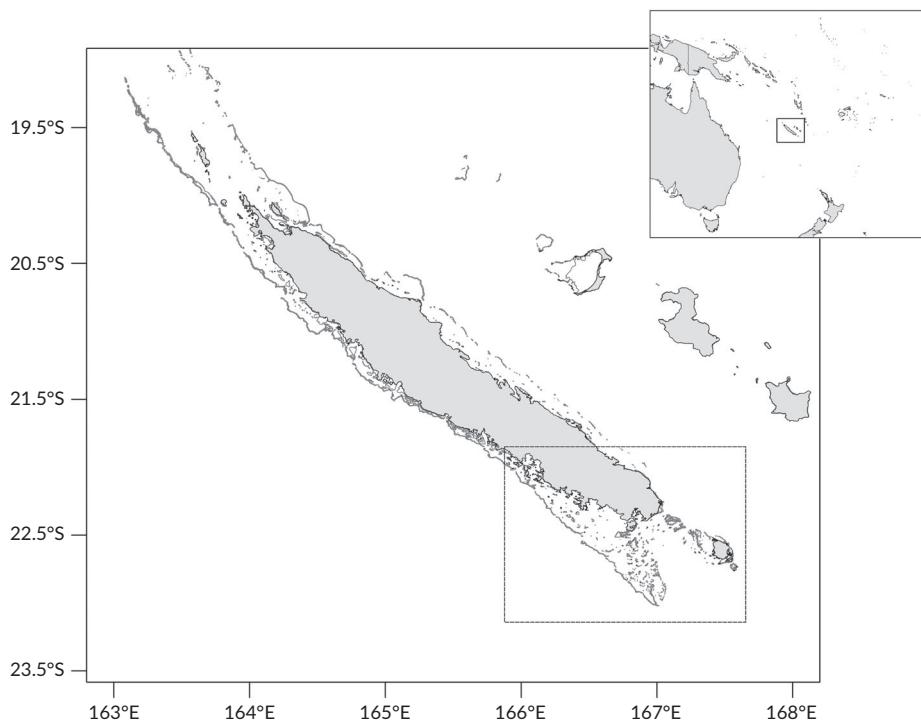


FIGURE 1 Map of New Caledonia showing the approximate area (----) from which samples of *Lutjanus gibbus* were obtained

opaque increment counts from these two occasions agreed, the count was taken as the number of opaque increments. When the two opaque increment counts for an individual differed, a third count was performed and the final opaque increment number was assigned when at least two counts agreed. Final agreed counts were compared against those of a second experienced reader (reader 2), who read each otolith at least once. Histograms of ageing differences, the coefficient of variation (CV; Chang, 1982) and age bias plots (Campana *et al.*, 1995) were used to evaluate precision and systematic differences in opaque increment counts between readers.

For analyses of growth and age at maturity, a decimal age was estimated for each individual using the birth date, the time of year when the opaque increments on the otoliths of the majority of *L. gibbus* became delineated (*i.e.*, 1 January, see §3.1), the number of otolith increments and the date of capture. The birth date for all samples was assumed to be 1 January, coinciding with the peak of female spawning, as determined from monthly trends in gonadosomatic indices (I_{GS}) and prevalence of spawning capable and running ripe developmental stages of gonads.

To test the assumption that opaque increments were laid down on an annual basis, the outermost otolith margin was classified into one of three categories: (1) opaque, whereby an opaque increment was forming or had formed around the edge of otolith, with no translucent material beyond the last opaque increment; (2) narrow translucent, whereby a translucent band was encountered on the otolith edge comprising less than half the width of the previous translucent band; and (3) wide translucent, whereby a translucent band was encountered on the otolith edge comprising roughly half or more the width of the previous translucent band. The proportion of otoliths with opaque increments on their edge in each month was plotted

across the calendar year to assess periodicity of opaque increment deposition. Mean daily sea surface temperatures (SST) were plotted alongside the proportion data, based on satellite-derived data for the period January 2000 to December 2015 (www.esrl.noaa.gov/psd/), to assess the relationship between opaque increment formation and SST.

2.3 | Gonad histology

A subsample of gonads was selected for histological examination to validate macroscopic sex assignments and determine the developmental stage. Preference for selection was given to ensuring samples came from a wide range of lengths and ages. Medial transverse sections of gonads were embedded in paraffin wax, sectioned at 5 µm, mounted on slides and stained with Mayer's haematoxylin and eosin. Slides were viewed under a compound microscope and gonads were classified into the developmental stages adapted from Brown-Peterson *et al.* (2011) described above (§2.1).

2.4 | Growth, length and age distributions

Length and age-frequency distributions were constructed for each sex. Kolmogorov-Smirnov tests were used to compare length and age distributions between sexes.

The relationship between L_F and W_T was modelled for those fish with whole mass available using a power function of the form $W_T = a L_F^b$. The effect of sex on the L_F-W_T relationship was examined using generalised linear mixed-effects models (GLMM), following the approach of Williams *et al.* (2017). Length and mass data were log-transformed to satisfy the assumption of linearity. Sex was modelled

as a fixed factor, while fishing set (fisher and date of capture) was modelled as a random effects term in all models to eliminate potential bias or pseudoreplication resulting from the non-independence of samples collected during the same set. Akaike's information criterion for small sample sizes (AICc; Burnham & Anderson, 2002) was used to determine the models best supported by the data. Support for sex-specific relationships between L_F and W_T were evaluated by comparing the AICcs between the model including a sex effect and the model excluding a sex effect.

Growth of female and male *L. gibbus* was modelled using the von Bertalanffy growth function (VBGF) fitted by nonlinear least-squares regression of L_F on age. The form of the VBGF used to model length-at-age data was: $L_t = L_\infty(1 - e^{-K(t-t_0)})$. No random effect of fishing set was included in the growth models as most sets had two or fewer individuals of each sex (80% of sets for females, 64% for males). Support for sex-specific growth curves was evaluated using the approach of Kimura (2008), whereby sex was added as a covariate on each of

the three VBGF parameters, such that:
$$\begin{pmatrix} L_{\infty i} \\ K_i \\ t_{0i} \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_i \beta_{1L} \\ \beta_{0K} + x_i \beta_{1K} \\ \beta_{0t} + x_i \beta_{1t} \end{pmatrix},$$

where x_i is a dummy variable for sex (female or male) for the i th fish and β_0 and β_1 are covariates for each of the three VBGF parameters. To assess sex-specific differences in growth, a growth model fitted to all data without the effect of sex was compared with a growth model fitted to all data with sex as a covariate using AICc.

2.5 | Mortality

The instantaneous rate of total mortality (Z) for *L. gibbus* was estimated using the GLMM estimator of Millar (2015). This method is considered to outperform the Chapman-Robson and weighted-regression estimators, particularly in cases where there is variability in recruitment to the fishery and annual survival, autocorrelated recruitment, ageing error and sampling randomness (Millar, 2015). Random-intercept Poisson loglinear models were fitted using GLMMs separately for females and males and both sexes combined, with the frequency of fish in each age class as the response variable, age as a fixed factor and a random intercept. All models were fitted to data for age classes equal to or greater than the modal age. The estimate of Z was the negative of the maximum likelihood estimator of the slope coefficient from each model.

The natural mortality rate (M) for female and male *L. gibbus* and for both sexes combined, was estimated by fitting the linear equation $\log_e(M) = 1.46 - 1.01(\log_e t_{max})$, where t_{max} is the maximum age observed (Hoenig, 1983). Estimates of fishing mortality (F) were calculated as the difference between Z and M .

2.6 | Spawning season and maturity

Sex-specific monthly trends in gonadosomatic index ($I_{GS} = W_G/W_T * 100$) and the proportion of individuals in each histological gonad development stage of III and above across the calendar year were examined for both sexes to determine the spawning period for *L. gibbus* in southern New

Caledonia. I_{GS} and histological stage data were grouped by calendar month, pooling all sampling years, as inter-annual sample numbers were too small to detect reproductive patterns.

Generalised linear models were used to model the length and age at maturity of female and male *L. gibbus*. Maturity state (§2.1) as determined from the histological sections was treated as a binomial response variable with logit link function and modelled as a function of either L_F or age. No random effect of fishing set was included in the maturity models due to small sample sizes of each sex in most sets.

All statistical analyses were performed in R 3.5.0 (www.r-project.org). GLMMs were conducted using the glmer function in the lme4 package (Bates et al., 2015), while non-linear modelling of the VGBF was conducted using the nls function in the stats package in R.

3 | RESULTS

3.1 | Age determination and length and age distributions

The average CV in opaque increment counts between the two readers was 4.19%, indicating a high level of precision between readers. Differences in increment counts between readers, where they occurred, were typically in the order of 1 to 2 annuli, with no systematic biases evident, although it should be noted that there were few individuals with opaque increment counts >30 (Figure 2). Therefore, increment counts from the first reader were used in age estimates.

Patterns of otolith edge classification clearly demonstrated an annual periodicity in the formation of opaque increments (Figure 3), confirming that increments were laid down on an annual basis. Rather than coinciding with peak low SST, annuli deposition was observed to begin towards the austral summer, commencing in some individuals in November, with the greatest proportion of individuals displaying opaque marginal increments in January (Figure 3). Annuli were found to be fully deposited in all sampled individuals by April (Figures 3, 4).

Sampled populations of *L. gibbus* were male biased, with a sex ratio of 1 female to 1.78 males. The length distributions differed between sexes ($D = 0.42$, $P < 0.001$), though no difference was observed in age distributions ($D = 0.18$, $P > 0.05$). Pooling both sexes, the modal length class was 28 cm L_F , while the modal age class was 3 years (Figure 5). Modal length and age classes differed between sexes. For females, the modal length class was 25 cm L_F , while for males the modal length class was 34 cm L_F . The modal age class for females was 3 years, while the modal age class for males was 6 years (Figure 5). The largest female was 34.3 cm L_F , while the largest male was 44.1 cm L_F . The oldest observed female was 38 years, while the oldest observed male was 36 years.

3.2 | Growth

No effect of sex was found on the L_F - W_T relationship of *L. gibbus*, as found by a larger AIC_c and lower Akaike weight for the GLMM that

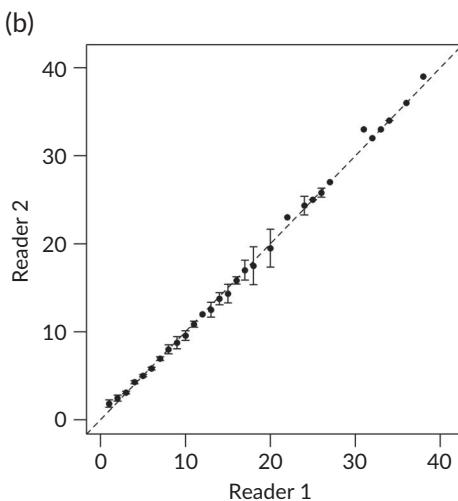
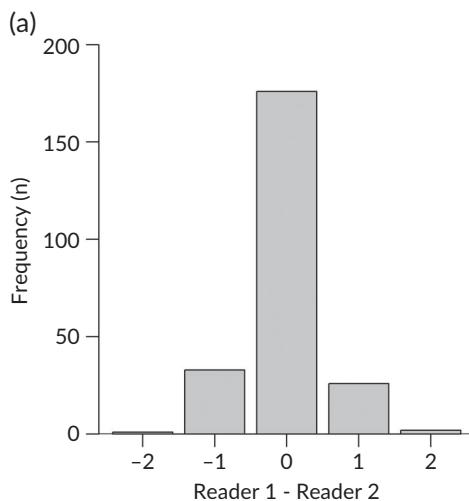


FIGURE 2 (a) Frequency distribution of differences in *Lutjanus gibbus* otolith annuli counts between reader 1 and reader 2 and (b) bias plot comparing otolith annuli counts between the reader 1 (\pm CV) and reader 2 for all ages

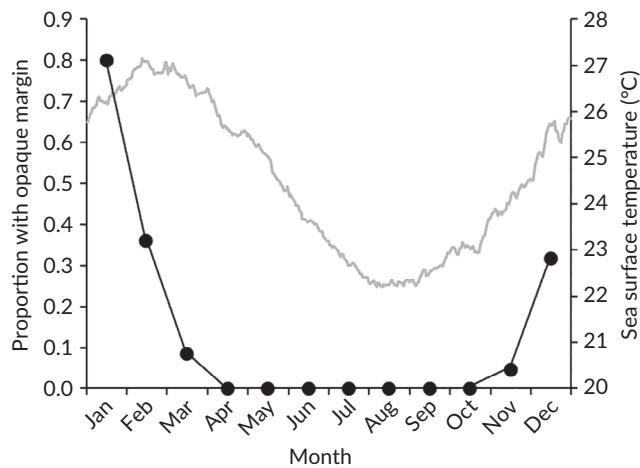


FIGURE 3 Proportion of *Lutjanus gibbus* otoliths with opaque increments by month (●). —, Mean daily sea surface temperature, based on satellite-derived data between January 2000–December 2015

included a term for sex (Table 1). Accordingly, data were pooled across sexes to estimate the L_F - W_T relationship: $W_T = 0.030 L_F^{2.910}$, $P < 0.01$.

Separate sex-specific growth models were supported by the data with a difference of 195.01 between the AICc from the growth model fitted with sex as a covariate on each of the three VBGF parameters (AICc = 904.50) and the AICc from the growth model fitted without the effect of sex (AICc = 1099.51). Overall, males of a given age were considerably larger than females and the predicted mean asymptotic length of males was c. 7 cm greater than that of females (Figure 6).

3.3 | Mortality

Total mortality (Z) for all samples was estimated as 0.13 (Table 2). Estimates of Z were slightly higher for males. Estimates of natural mortality (M) were also slightly higher for males. Fishing mortality was low for both sexes and was estimated as 0.02 for sexed and non-sexed individuals combined.

3.4 | Spawning period and maturity

Gonad characteristics of *L. gibbus* were consistent with gonochorism, with only testicular or ovarian tissue present in any one gonad and no evidence of transitional reproductive tissue or prior bisexual characteristics. Despite low sample sizes, particularly for females, clear trends were evident in both I_{GS} and gonad staging data. Mean monthly I_{GS} values for both mature female and male *L. gibbus* were highest in December to April (Figure 7). Mean monthly I_{GS} values for females peaked in January, while for males, mean monthly I_{GS} values peaked in December–January. Both sexes showed a secondary peak in I_{GS} values in March. Running ripe ovaries were observed between January and March (Figure 7).

The estimated length and age at which 50% of females attained maturity was 25.8 cm L_F and 3.9 years of age, while the estimated length and age at which 50% of males attained maturity was 26.8 cm L_F and 3.4 years of age (Figure 8). The largest immature female sampled was 26.6 cm L_F , while the oldest immature female was 4.71 years old. The smallest and youngest mature female sampled was 24.9 cm L_F and 3.11 years old. The largest immature male sampled was 28.5 cm L_F , while the oldest immature male was 4.96 years old. The smallest mature male sampled was 26.8 cm L_F , while the youngest mature male was 2.10 years old.

4 | DISCUSSION

The lack of age-based life history information is a key limitation in the development of effective assessments of population status and appropriate management and harvest strategies for many tropical coral-reef fishes (Marriott *et al.*, 2007; Newman *et al.*, 2000a, 2000b). In particular, for many exploited species, there is a general lack of key biological information in the absence, or near-absence, of fishing pressure (Marriott *et al.*, 2007). This study provided age-based life-history information of an exploited lutjanid species in southern New Caledonia where the species is considered to be lightly fished. In southern New Caledonia, *L. gibbus* was found to display strong sexual

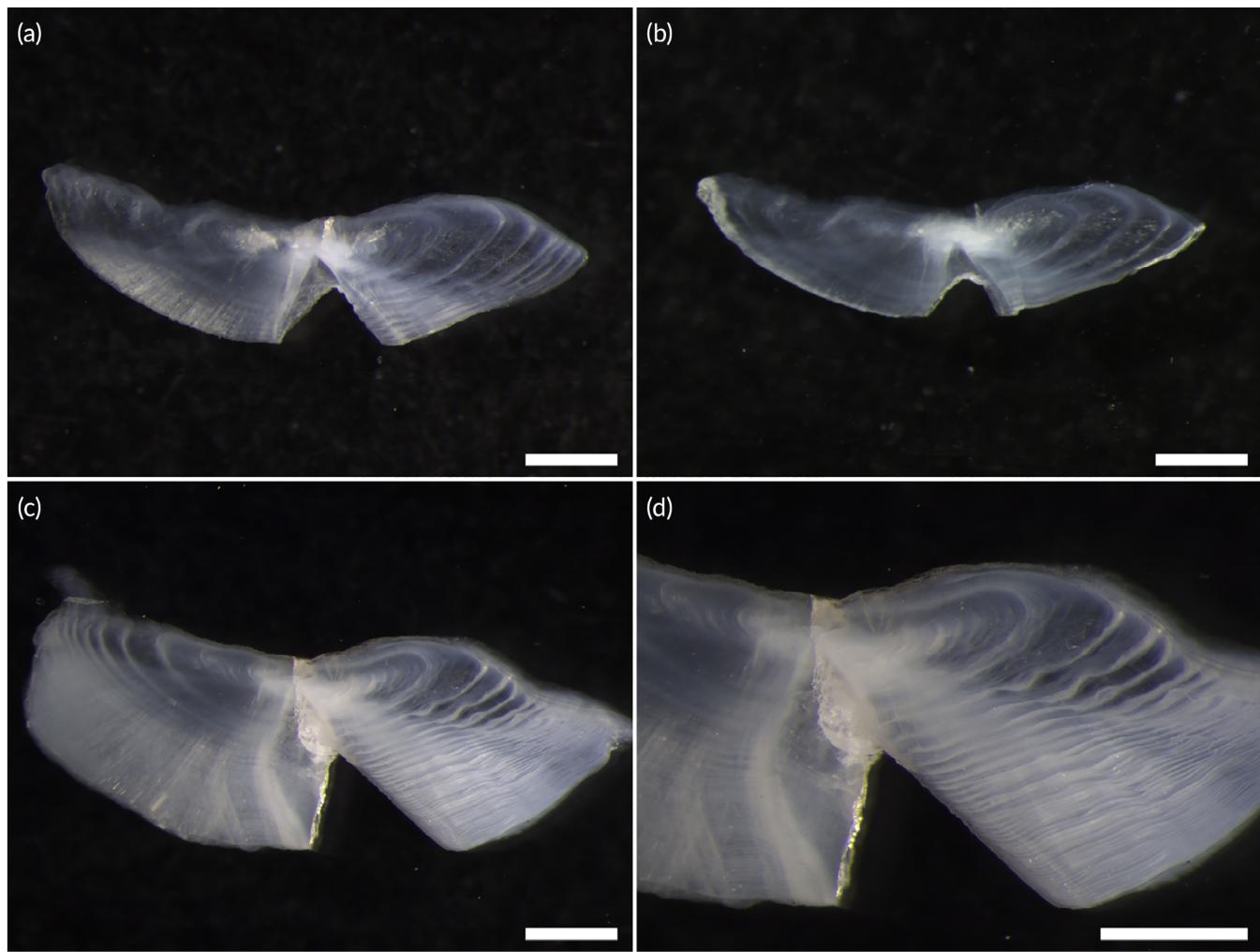


FIGURE 4 Photomicrographs of transverse otolith sections of *Lutjanus gibbus*. (a) A 34.6 cm fork length (L_F) male collected in November 2015, displaying a wide translucent otolith margin and 7 completed opaque bands; (b) a 27.9 cm L_F male collected in February 2016, displaying a narrow translucent margin with 4 completed opaque bands; (c) and (d) a 44.1 cm L_F male collected in January 2015, displaying an opaque otolith margin and 36 completed opaque bands. Scale bar 1 mm

dimorphism in growth and have an observed maximum life span of at least 38 years.

In southern New Caledonia, opaque increment formation in *L. gibbus* otoliths was found to coincide with spawning season, rather than during the period of peak low SST. This observation is consistent with those of Nanami *et al.* (2010) for *L. gibbus* and Shimose and Tachihara (2005) for *Lutjanus fulviflamma* (Forsskål 1775), both in southern Japan, but somewhat contrasts that of Taylor *et al.* (2018) for *L. gibbus* in American Samoa, who observed annuli deposition to occur during periods of peak low SST. Although Taylor *et al.* (2018) provide no information on the spawning seasonality for the species in American Samoa, unpublished data suggest little evidence for spawning seasonality at that location (B. Taylor, pers. comm.). For populations in New Caledonia and southern Japan, the presence of annuli in immature individuals suggests that opaque increment formation, though coinciding with spawning season, is not necessarily dependent on spawning. However, the stimulus for opaque increment formation may be correlated with external factors that also initiate

spawning in mature individuals (Newman *et al.*, 1996), such as an increase in SST from the peak annual low.

Considerable sex-specific differences in length at age were evident in the present study, with males attaining a much larger length at a given age than females. This result is consistent with those reported for *L. gibbus* by both Nanami *et al.* (2010) and Taylor *et al.* (2018) and similar patterns have been observed in a range of *Lutjanus* Bloch 1790 species, including *Lutjanus adetii* (Castelnau 1873) and *Lutjanus quinquefasciatus* (Bloch 1790) (Newman *et al.*, 1996), *Lutjanus carponotatus* (Richardson 1842) (Kritzer, 2004; Newman *et al.*, 2000a), *Lutjanus sebae* (Cuvier 1816) (Newman & Dunk, 2002). The greater length at age and asymptotic length for male *L. gibbus* is likely a function of the lower energetic costs involved with producing sperm than eggs (Wootton, 1985), providing a mechanism for males to allocate more energy into growth than females. Additionally, it may be that males forage more actively than females. Assuming that sex ratios of *L. gibbus* in coral-reef ecosystems are approximately equal, the considerable male bias observed in the current study suggests that

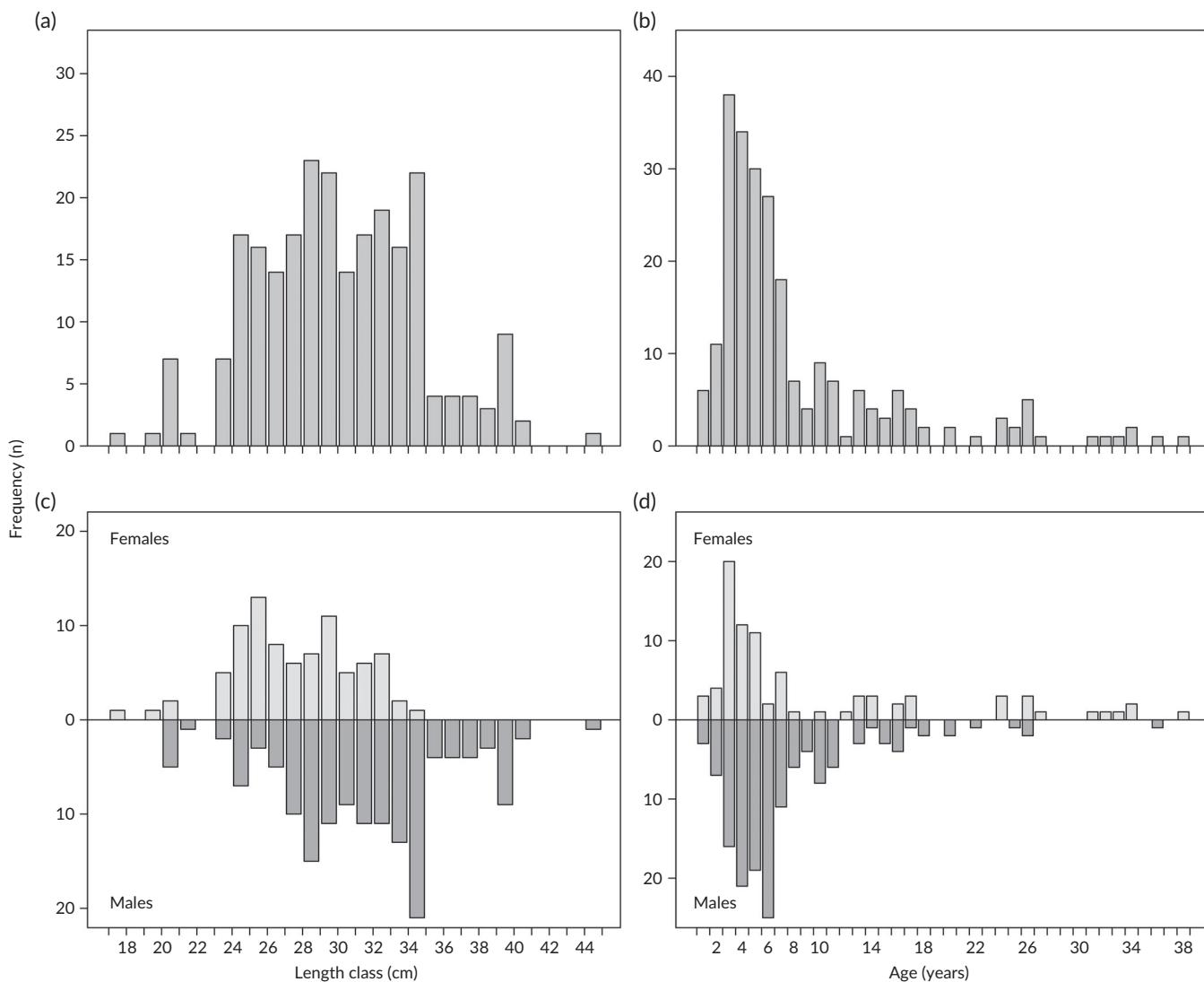


FIGURE 5 Combined (a) fork-length and (b) age-frequency distributions; for *Lutjanus gibbus* from southern New Caledonia. Also, the sex-specific (c) length and (d) age-frequency distributions

TABLE 1 Summary of generalised linear mixed effect models (GLMM) used to examine the effects of sex on the relationship between fork length (L_F) and mass (W_T) for *Lutjanus gibbus* from southern New Caledonia

Model	K	AICc	ΔAICc	w
$\log W_T = \log L_F + \beta_{\text{set}} + \varepsilon$	4	-345.71	0	0.99
$\log W_T = \log L_F + \text{sex} + \beta_{\text{set}} + \varepsilon$	5	-336.70	9.00	0.01

Note: K: The number of estimated parameters; AICc: the small-sample bias-corrected form of Akaike's information criterion; ΔAICc : the Akaike difference; w: the Akaike weight; β_{set} : the random effect of fishing set; ε : an error term.

individuals of this sex may have a greater tendency to take baited fishing gear, supporting this hypothesis. Williams *et al.* (2017) provided a similar hypothesis to explain higher growth rates of female *Etelis carbunculus* Cuvier 1828, a deepwater lutjanid. Patterns of sexual dimorphism, such as that observed for *L. gibbus*, can complicate

assessments of population status, especially in cases where the primary data source is abundance and length frequencies from fishery-dependent or independent surveys (Taylor *et al.*, 2018).

Prior to the present study, the maximum reported age of *L. gibbus* was 27 years, based on samples from American Samoa (Taylor *et al.*, 2018). The current study extends the maximum reported age for the species by 11 years, to at least 38 years. The extended longevity observed for *L. gibbus* in southern New Caledonia relative to that reported for the species elsewhere is likely a function of environmental influences (including water temperature, food availability and competition), fishing pressure, genetics, or, most probably, a combination of factors (Conover *et al.*, 2006). The ability of individuals to reach greater longevity and larger body sizes at higher latitudes, where water temperature are generally cooler, has been documented in a number of shallow and deep-water fish species with distributions spanning broad latitudinal and temperature ranges (Andrews *et al.*, 2016; Berumen *et al.*, 2012; Robertson *et al.*, 2005; Trip *et al.*, 2008;

Williams et al., 2017). At c. 22°–23° S, the sampling area in southern New Caledonia is amongst the southernmost extent of the distribution of *L. gibbus* and the relatively low water temperatures probably

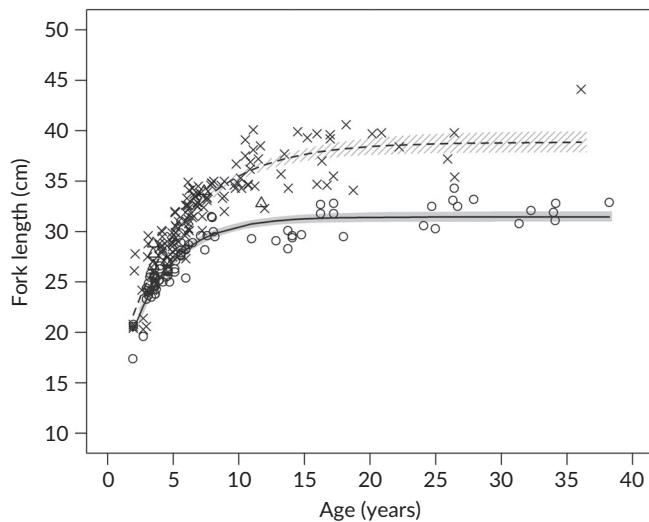


FIGURE 6 Sex-specific length at age data and fitted von Bertalanffy growth curves for *Lutjanus gibbus* from southern New Caledonia: females (\circ) $L_t = 31.46 \pm 0.27$ cm, $K = 0.31 \pm 0.03$, $t_0 = -1.40 \pm 0.44$ years; males (\times) $L_t = 38.88 \pm 0.54$ cm, $K = 0.20 \pm 0.02$, $t_0 = -2.09 \pm 0.43$ years; both sexes combined $L_t = 35.13 \pm 0.39$ cm, $K = 0.29 \pm 0.03$, $t_0 = -1.00 \pm 0.37$ years; solid and line shaded areas indicate 95% CI for females and males, respectively. \triangle , Sex not determined

TABLE 2 Mean (\pm SE) estimates of total mortality (Z), natural mortality (M) and fishing mortality (F) for *Lutjanus gibbus* in southern New Caledonia

Sex	Z	M	F
Female	0.11 ± 0.01	0.11	<0.001
Male	0.16 ± 0.02	0.12	0.04
All individuals combined	0.13 ± 0.01	0.11	0.02

facilitates the extended life span of the species at this location, in accordance with the metabolic theory of ecology (Brown et al., 2004). Supporting this hypothesis, Nanami et al., (2010) observed a maximum age of only 24 years for *L. gibbus* caught off Ishigaki Island in southern Japan, despite their sampling site being at a comparable latitude to that of the current study. Water temperatures around Ishigaki Island often exceed 30°C during summer months and rarely drop below 23°C in winter, whereas they seldom exceed 27°C in summer and often fall below 23°C in winter in southern New Caledonia (www.esrl.noaa.gov/psd/).

Fishing is widely known to result in age truncations of exploited species, with subsequent alterations in biological processes such as growth rates or reproductive schedules (e.g. Harris & McGovern, 1997; Moore et al., 2017; Platten et al., 2002). Fishing pressure on *L. gibbus* in southern New Caledonia is considered to be relatively low compared with other locations in the Pacific Ocean, potentially providing a mechanism for *L. gibbus* to attain the observed extended lifespans. Supporting this assumption, only seven commercially-registered fishers reported landings of the species in 2017 (T. Tiburzio, Département de l'aquaculture et des pêches, pers. comm.) and only a very small number of individual *L. gibbus* (and frequently zero) were landed on a given fishing trip during the sampling (B. Moore, pers. obs.). The low fishing pressure on *L. gibbus* in southern New Caledonia is further highlighted by the sampling undertaken in this study, with only 243 individuals collected despite sustained sampling over a period of 4 years. The species is also generally avoided by recreational or subsistence fishers in New Caledonia, largely due to concerns over ciguatera fish poisoning.

Decoupling the relative influence of various factors such as water temperature or fishing pressure on growth and longevity in fishes can prove difficult, although one such way this has been achieved is with common-garden experiments, whereby individuals are raised under controlled environmental variables so that the environmental and genetic components of phenotypic variation is revealed (Conover et al., 2006). Such experiments may be possible for small, sedentary species with relatively short lifecycles, but are likely to be impractical

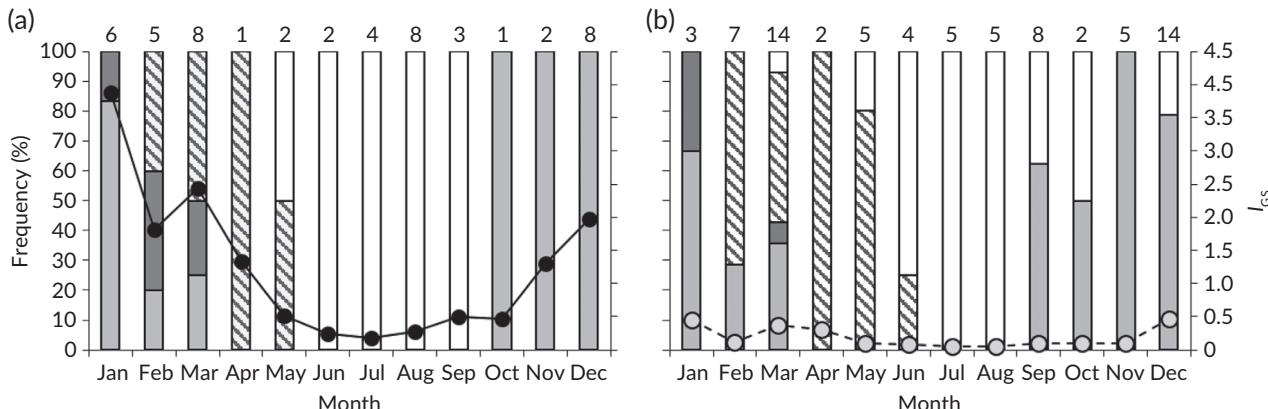


FIGURE 7 Mean monthly (a) female *Lutjanus gibbus* gonadosomatic index (l_{GS} ; —●—) and frequency distribution of maturity stages; (b) male l_{GS} (—○—) and maturity stages. Numbers above the bars represent the number of fish examined in each month. ■ Spawning capable, ▨ Running ripe, □ Regressing and ▨ Regenerating

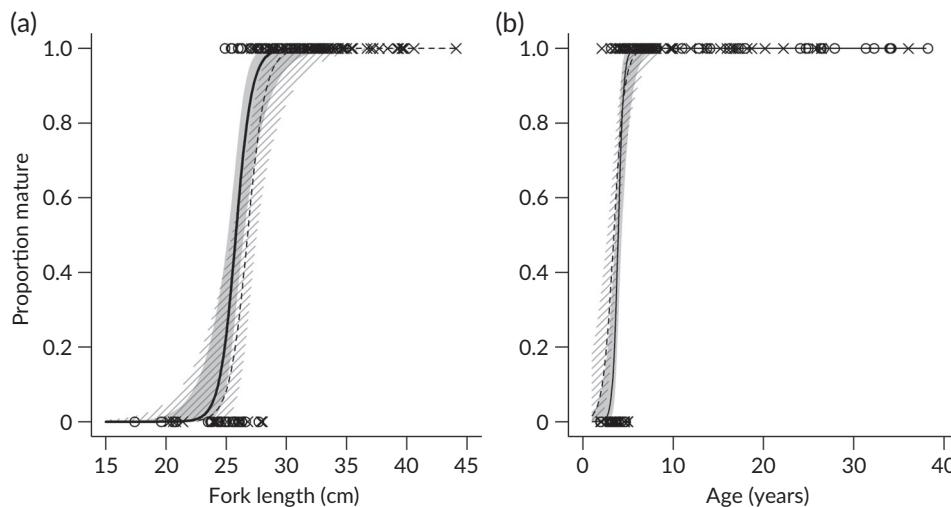


FIGURE 8 (a) Predicted (95% CI) proportion of mature female (○) and male (×) *Lutjanus gibbus* by fork length and (b) age

for *L. gibbus* given the observed longevity. Examination of datasets from geographically disparate locations, covering gradients of latitude and fishing pressure, may help decouple the relative influence of various drivers on *L. gibbus* demography.

The extended longevity observed for *L. gibbus* in southern New Caledonia has significant implications for local assessment and management of the species. Accurate estimates of longevity in fish populations are fundamental to understanding the production potential and status of exploited fish stocks (Newman *et al.*, 2010). For example, maximum age is a key parameter of the Hoenig (1983) estimation of *M*, which is frequently used in a variety of assessment approaches for data-poor and data-rich fisheries, such as catch-curve analyses, yield-per-recruit (Bevetton & Holt, 1957) and surplus-production (Ricker, 1975) models. Errors in estimates of *M* can have significant management implications. Gulland (1970) and Deriso (1987) recommend setting *F* at a value approximately equal to *M* (*i.e.*, an exploitation rate *E* = 1.0) and a number of authors have since advocated this, or more conservative ratios (*e.g.*, *E* = 0.5), as a reference point in catch-curve analyses for data-poor reef-associated fisheries (Newman & Dunk, 2003; Rochet & Trenkel, 2003; Williams *et al.*, 2017). Under this management strategy (*i.e.*, *F* ≈ *M*), the use of an over-inflated rate of *M* for populations in southern New Caledonia, resulting from an underestimation of maximum age (such as by using the maximum age estimate from American Samoa), would then allow *F* to be set too high, potentially leading to recruitment overfishing (*sensu* Newman *et al.*, 2000b). Conversely, however, assuming water temperature is a significant driver of longevity, applying longevity estimates derived from cooler-water populations in assessments of warmer-water populations may increase the likelihood of assessing a stock as being subject to overfishing. Ideally, regional estimates of longevity and natural mortality should be determined, preferably through sampling of areas subject to low or no fishing pressure.

Lutjanus gibbus and other shallow-water lutjanids support significant commercial, artisanal and subsistence fisheries in the tropical Indo-Pacific, yet often little is known of the status of individual species. Results of this study indicate that in southern New Caledonia,

L. gibbus is unlikely to currently be subject to overfishing. The variation in demography of *L. gibbus* observed in published studies suggests a more detailed examination of the spatial patterns in demography will benefit assessments and management of the species within the Indo-Pacific. Moreover, the extended longevity of *L. gibbus* observed in the current study indicates that additional age-based work on the demographics of key harvested species in the absence or near-absence of fishing would be of great benefit to management efforts in the region and elsewhere.

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