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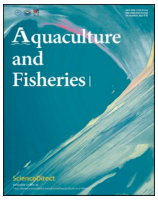

Original research article

Preliminary age-based life history characteristics of the dogtooth tuna, *Gymnosarda unicolor* (Ruppell, 1838), in the southwest Pacific Ocean

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ABSTRACT

Dogtooth tuna, *Gymnosarda unicolor* were sampled off the east coast of Australia (southwest Pacific Ocean) from 2007 to 2012. Ages were determined by examining thin transverse sections of their sagittal otoliths and were based on counts of alternating opaque and translucent zones (annual growth increments). Growth was rapid during the first year of life, after which growth in length was much reduced. Parameters of the constrained von Bertalanffy growth function (fork length-at-age) were $L_\infty = 1164.77$ (mm, FL) and $K = 0.44$ year^{-1}. Preliminary estimates of longevity indicate a maximum observed age of at least 20 years. There was a high degree of variation in the observed length and age of sexual maturity for *G. unicolor*. Despite this variation, the size at 50% maturity for female *G. unicolor* estimated in this study was 713 mm FL (<2 years of age). The diet of *G. unicolor* is very broad and covers a range of fish species. The life history characteristics of *G. unicolor* overall, indicate that this species may be somewhat resilient to fishing. However, reports of localised depletions, in association with heavy targeting by sports fishers, low effective population sizes and patchy recruitment indicate that this species is particularly vulnerable to overfishing.

1. Introduction

The dogtooth tuna, *Gymnosarda unicolor,* is an iconic, large, epipelagic, coral reef-associated fish endemic to the Indo-Pacific region. It is found primarily in tropical waters from the east coast of Africa and the Red Sea, north to Japan, and westwards to the islands of the central Pacific, however they are not found in waters around Hawaii (Anon, 2005; Collette, 2001; Collette & Nauen, 1983; Silas, 1963). They are generally found offshore associated with coral reefs, often on steep drop-offs and seamounts, and are reported to occur to depths of at least 300 m, and are observed as solitary individuals, in small groups and occasionally in small schools up to 10 or more individuals (Collette & Graves, 2019; Silas, 1963). The preferred temperature profile of *Gymnosarda unicolor* is in the range of 20 °C to 28 °C (Kishinouye, 1923). Unlike the name suggests, although they belong to the Family Scombridae like other tuna species, taxonomically they are more closely related to bonito (Tribe Sardini) (Pepperell, 2010). Their common name is derived from its large, conical teeth (Collette & Nauen, 1983). The diet of *G. unicolor* is reported to be generally small fishes, such as scads (*Decapterus*), unicornfish (*Naso*) and fusiliers (*Caesio* and *Pterocaesio*) (Collette & Graves, 2019).

While captured in commercial fisheries, *Gymnosarda unicolor* are not the target species of any specific fisheries in the Western Pacific region (Anon, 2005). They are a popular sports fish known for their exceptional fighting characteristics (Collette & Graves, 2019), and this popularity has increased in recent years. Most of the reported landings between 1963 and 2006 were from the Indian Ocean (Joshi et al., 2012), and the global reported catch has risen from an annual average during the 1970s of ∼220 t to an annual average of ∼1610 t for the period 2010–18 (http://www.fao.org/fishery/statistics/en; accessed 5th June 2020).

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Despite rising catches, very little is known about the biology of *G. unicolor* (Collette & Graves, 2019). Given their large size, their relatively low historic catch levels and the fact they are mostly caught in remote locations, studies on *G. unicolor* are limited. Further, a recent study listed *G. unicolor* as a key priority scombrid species for life history studies due to their data-poor status and their capture across multiple fisheries (Juan-Jordá et al., 2013). The study of Juan-Jordá et al. (2013) highlighted the lack of age-based demographic parameters for *G. unicolor*.

One of the earliest studies, a synopsis on *G. unicolor*, highlighted the lack of biological knowledge as early as 1963 (Silas, 1963). Joshi et al. (2012) examined the biology of *G. unicolor* from Indian waters. Individuals up to 162 cm fork length (FL) were sampled, but this species has been reported to reach a maximum length of approximately 2.5 m FL, although this has not been verified. Indeed, the IGFA world record for a recreationally line caught *G. unicolor* is 107.5 kg, landed in Tanzania in 2015 (https://igfa.org/igfa-world-records-search/; accessed June 5, 2020), while a larger specimen taken by a spearfisher in Indonesia in 2010 weighed 110 kg. It is feasible that Joshi et al. (2012) did not sample the complete size range of *G. unicolor*, and this may be related to fishing effects in Indian waters. Joshi et al. (2012) derived the following von Bertalanffy growth parameter estimates using length-based methods (use of ELEFAN from the FiSAT software); $L_\infty = 163.6$ cm, $K = 0.43$ yr^{-1}, $t_0 = -0.12$ and estimated a longevity of at least 12 years of age for *G. unicolor*.

In the Western Pacific, the Coral Sea area has been regarded as the centre of the distribution of *G. unicolor* (Pepperell, 2010). The Australian Government recently formed the Coral Sea Marine Park (CSMP) with the aim of conserving biodiversity and other values, as well as for ecologically sustainable use of natural resources (Director of National Parks, 2018). In order to address sustainable conservation and management needs of *G. unicolor*, knowledge of their ecology and life history relevant to the region is required. Bentley et al. (2014) reported on the stock structure of *G. unicolor* and observed that individuals were more closely related at similar sites, despite genetic homogeneity across the Indo-West Pacific region, suggesting high dispersal capabilities of larval and/or juvenile stages, with limited adult movement. They concluded that management of this species should include harvest strategies that limit the potential for localised depletion events. This further highlights the need for detailed information regarding the life history and ecology of *G. unicolor* to inform best practice management in significant areas such as the Coral Sea. Currently, there are no prescriptive management measures specific to *G. unicolor* in the CSMP or indeed elsewhere in the wider Pacific region, despite an increasing sports fishery for them.

Therefore, the aim of this study was to estimate preliminary life history parameters for *G. unicolor* that would inform management. We complement the biological data with observations on their diet that further advances knowledge of the ecological role of *G. unicolor* in tropical oceans.

2. Materials and methods

2.1. Sample collection and processing

The collection of *G. unicolor* was carried out opportunistically between 2007 and 2010 in the north-eastern Australian and Coral Sea region (Fig. 1), although a single fish was collected in 2012. Individuals were primarily collected between August and December (Table 1), which is the main fishing season for this species in the region, partly due to the favourable prevailing weather conditions at that time of the year.

Individual fish were sourced primarily from recreational spearfishers, while four were line caught. The date and location of capture were also recorded. Due to the large size of these fish, samples provided often were comprised of heads with guts attached, accompanied by length and weight measurements where practicable. Each sample was given a unique identifying code. Samples were dissected in the laboratory, and relevant measurements and observations recorded. Where whole frames (fish skeletons) were provided, fork length (FL, mm) and total length (TL) were recorded. Where possible, total weight (kg) was also recorded. Upper jaw length (UJL) was measured since this has been shown to be a good proxy for FL in other scombrid species (Fig. 2; see Welch et al., 2009).

Gut contents were also examined and where possible the prey species and/or type were recorded, and photos taken. Sagittal otoliths were removed from each sample of *G. unicolor*, washed, dried and then stored for later examination. During dissections, sex was macroscopically determined as male, female or immature. The maturity stage was determined using a simplified macroscopic staging system developed for

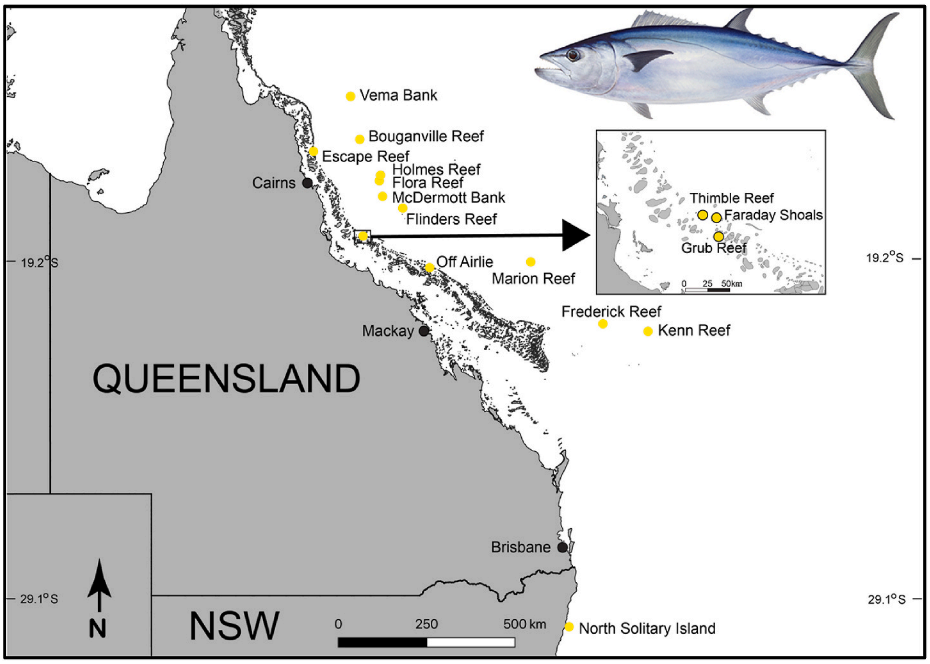

Fig. 1. Sample locations on the Great Barrier Reef, Coral Sea (southwest Pacific Ocean), and northern New South Wales, Australia.

Table 1

Summary of the number of *G. unicolor* samples collected for each location, and the type of data obtained from each sample (not all reproductive samples were able to be used for all analyses).

Location	Number	Size data	Age data	Reproductive data
Bouganville Reef	2	2	2	2
Escape Reef	1	1	1	1
Faraday Shoals	5	5	5	5
Flinders Reef	20	20	20	20
Flora Reef	3	3	2	0
Frederick Reef	1	1	0	1
Grub Reef	1	0	0	0
Holmes Reef	3	3	3	3
Kenn Reef	1	1	1	0
Marion Reef	15	15	14	15
McDermott Bank	1	1	1	0
North Solitary Island	1	1	1	1
Off Airlie (outer GBR off Bowen)	3	3	3	0
Thimble Reef	3	3	3	3
Vema Bank	9	9	9	9
Total:	**69**	**68**	**65**	**60**

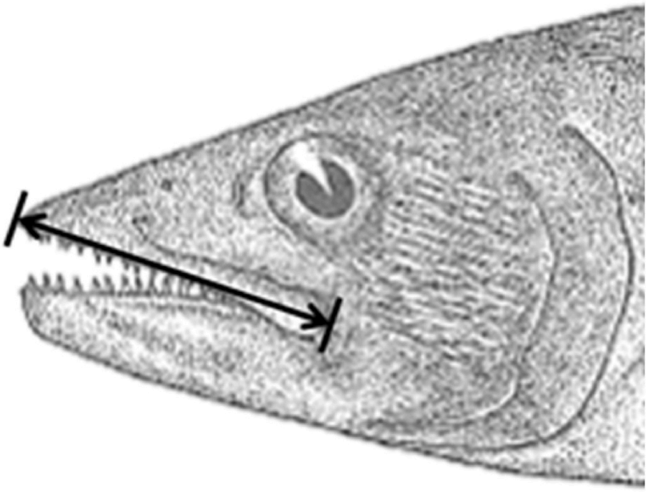

Fig. 2. Measurement taken for the upper jaw length (UJL) of *Gymnosarda unicolor* samples. Image adapted from: Silas (1963).

another large scombrid, the Spanish mackerel, *Scomberomorus commerson* (Mackie et al., 2005; Mackie & Lewis, 2001). Gonad weights were also measured and recorded where possible.

2.2. Age determination

Otoliths were embedded in epoxy resin and cut transversely through the primordium using a diamond-tipped blade on a low-speed saw. Sections approximately 300–400 μm were then mounted on glass slides using a thermoplastic mounting media (Crystalbond 509). A CCD digital camera mounted onto the dissecting microscope (Leica MZ80) was then used to capture images of each otolith, which were saved for age determination. For age determination each otolith was inspected, and the section with the clearest zone pattern was chosen for assessing age. This was usually the section closest to the primordium. The age of each sample was determined by counting the number of assumed annual opaque zones along a count path from the primordium to the otolith edge, either on the dorsal or ventral side of the otolith adjacent to the sulcus.

All otoliths were read once by a single reader to provide age estimates and repeated by a second reader. Age estimates were accepted if these two counts agreed. Otherwise, a third read was undertaken by a third independent reader and agreement between this and any of the first two reads was taken as the accepted age. If all three reads disagreed, the median count was assigned as the accepted age following Heupel et al. (2010). To avoid the potential for biasing age estimates, all counts were made without knowledge of fish size, otolith weight, sex and location. All readers were experienced at ageing a variety of fish species. In addition, each otolith sample was assigned a score to rate the readability of the otolith section on a scale of 1–5 (Table 2).

Marginal edge type was assigned subjectively by each reader based on the optical properties of the edge using the following categories: **I** - intermediate (translucent material past last opaque zone is generally less than 1/3 of previously completed translucent zone); **W** - wide (translucent material past last opaque zone is generally greater than 1/3 of previously completed translucent zone); **N** - new (opaque visible on edge). The edge type is an indicator of the likelihood of zone formation in the next period of deposition. An edge type W indicates that an opaque zone is likely to form soon, an edge type coded I indicates that the last opaque zone was likely to be recently deposited, and edge type N indicates that the new opaque zone is in the process of being deposited on the otolith margin.

The timing of the formation of assumed annuli (see Choat et al., 2009), represented as opaque increments, was estimated by analysis of otolith edge categories in conjunction with the date of sample collection. The approximate birth date was determined from daily counts in a single 0+ aged fish, which was used along with edge categories, to assign final age estimates. To assess any potential systematic bias in otolith counts between the first two readers, who both read all otoliths, we used an age bias plot (Campana et al., 1995). To estimate the precision of counts we used the Index of Average Percent Error, using age estimates from the first two readers (IAPE; Beamish & Fournier, 1981).

The alternating bands of opaque and translucent zones considered as annual growth increments in this study are analogous to those reported as annual growth increments in a range of species (e.g., Newman et al., 1996; Newman, 2002; Wakefield et al., 2013; Newman et al., 2016; Boddington et al., in press). Given that the great majority of age validation studies have confirmed the annual periodicity of increment formation (alternating bands of opaque and translucent zones) across a plethora of fish species, Choat et al. (2009) noted the need for a more strategic approach where growth zones were assumed to be annuli in order to derive basic life history information across a range of tropical fish species.

2.3. Data analysis

Relationships for fork length–total length, fork length–weight and fork length–upper jaw length were estimated using regression analysis. Weight data were log transformed to standardise the residuals. Due to the low sample size, regressions were fitted to pooled data only.

Final age estimates and size (FL) data were used to describe the growth of *G. unicolor* using the von Bertalanffy growth function (VBGF) (Beverton & Holt, 1957). This was plotted using a nonlinear least-squares regression of FL as the explanatory variable on age as the response variable:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$$

Table 2

Readability indices and their interpretation when reading otoliths.

Index	Interpretation
1	Sample is exceptionally clear with unambiguous increments
2	Sample is clear and confident with estimate
3	Sample may be ± one year from determined age
4	Sample is difficult to interpret and subject to multiple interpretations
5	Sample is unreadable due to failed preparation or missing sample

where L_t = the mean length at age t; L_∞ = the asymptotic mean length; K = the rate at which L_∞ is approached (growth coefficient); and t_0 = the theoretical age at length zero.

The VBGF model using a binomial distribution was plotted with t_0 either unconstrained (estimated) or constrained to zero ($t_0 = 0$) to qualitatively examine the effects of few smaller individuals in the sample and produce biologically sensible growth parameter estimates. Confidence intervals for these parameters were constructed through bootstrap methods which has been suggested to perform better for nonlinear regression models, where there are departures from normally distributed variances (Htjet et al., 1990). Homoscedasticity and normality of residuals were also tested accordingly.

Seasonality in spawning was determined by plotting maturity stages by month, and by plotting mean monthly gonadosomatic indices (GSI) for females. GSI was calculated as:

$$GSI = \left(\frac{W}{TW}\right) \cdot 100$$

where W = total gonad weight (grams) and TW = total fish weight (grams). Plotting the mean GSI for each stage was also undertaken as a means to validate the macro-staging methods.

Length and age at which 50% and 95% of fish reach maturity (L_{50}, L_{95}, A_{50} and A_{95} respectively) were estimated for female fish only using logistic regression analysis of the type:

$$\log\left(\frac{p}{1-p}\right) = \alpha + \beta_1 X$$

where log (p/1-p) represents the proportion of mature vs. immature individuals linearized using the *logit* function, α denotes the intercept, β_1 denotes the regression slope coefficient, and X denotes the explanatory variable (size or age). This was used to model the relationship between fish length and age categories with the proportion of mature fish in each category (Maturity stage >1). Thus, fish length and age were taken as the explanatory variables and tested for normality, while maturity was used as the response variable. The validation of the binomial distribution models was confirmed by checking using the Cook's distance, the normal Q-Q plot, the back transformation of the log coefficients and a goodness of fit with the Pearson Chi-Square test for the model residuals and the residual deviance. Due to a low sample size, we used the derived length based on UJL, where a measured FL was not available.

3. Results

A total of 69 *G. unicolor* samples were obtained from throughout the southwest Pacific spanning a latitudinal distance of approximately 2300 km. The smallest fish was collected from the very southern limit of the species known range in Australia, at Coffs Harbour in northern New South Wales (Fig. 1; Table 1). All samples were used in all data analyses depending on the extent of data collected from each sample. Only 60 individuals were sexed, comprising 7 immature fish, 42 females and 11 males (Table 3). Where FL was not provided, this was derived using the upper jaw length, since this relationship was shown to be consistent (see below). The size, age and weight range for each gender, and overall varied considerably (Table 3). Fish for which maturity data were obtained ranged from 423 to 1632 mm FL, corresponding to ages from 0+ to 18 years, and from 4.5 to 60 kg in weight (one individual weighed 75 kg and was 20 years of age but did not come with any morphometric measurements; Table 3). The total sample numbers were low due to the logistical difficulty associated with obtaining these fish. Given the wide size and age range sampled it was considered that these data were sufficient to provide preliminary estimates of the key morphometric and life history parameters (Figs. 3 and 4).

Table 3
Summary of the size, age and weight ranges for immature, female and male fish collected. Mean values are shown in parentheses, * = only two weights recorded.

Gender	n	Size range (FL, mm)	Age range (years)	Weight range (kg)
Immature	7	423–980 (779)	0+ – 7	4.5–6.0*
Female	42	660–1632 (1079)	1–18	7.0–60.0 (23.3)
Male	11	700–1287 (872)	1–17	5.5–35.0 (12.2)

The age bias plot indicated that there was very little systematic bias between the two main otolith readers (Supplementary material). The IAPE was estimated to be 5.14%, which approximates with the recommendation of 5% and suggests that otoliths of *G. unicolor* are of moderate complexity, depending on the sectioning technique (Morison et al., 1998). Due to the low sample size, there was insufficient information to determine the timing of otolith zone formation based on otolith margin criteria. Direct observation of samples for given months suggested that the marginal increment may be at a maximum width by early summer.

There was a good fit for the relationships between UJL:FL, FL:TL and FL:Weight (Table 4; Supplementary material). Individual *G. unicolor* can reach a large size and are often found in remote locations which can make sample collection difficult. The ability to measure UJL and still be able to reliably derive FL and TL estimates will be beneficial to any future sample collection strategy.

Estimates of length at age for *G. unicolor* were highly variable. The relationship between size and age estimated (unconstrained) with the von Bertalanffy growth model resulted in the following growth parameters: $L_\infty = 1341.20$, $K = 0.143$, $t_0 = -3.17$ (Fig. 5). The confidence intervals of L_∞, K and t_0 ranged from 1169.10 to 2046.57, 0.039 to 0.280 and −10.84 to −0.48, respectively. The confidence intervals of K displayed a normal distribution, which was not the case for L_∞ and t_0 (Supplementary material). Hence, the difference between the asymptotic and bootstrapped confidence intervals are much greater for L_∞ and t_0, than for K. The relationship between size and age from the model with t_0 constrained to zero (constrained) resulted in the following estimated growth parameters: $L_\infty = 1199.00$ and $K = 0.321$ (Fig. 6). The confidence intervals of L_∞ and K ranged from 1120.11 to 1320.77 and 0.234 to 0.426, respectively. All confidence intervals of these parameters showed a normal distribution (Supplementary material).

Due to low sample numbers, we were limited in the months across which reproductive status could be assessed. Nevertheless, there were several individuals with gonads in spawning condition during the months that fish were sampled, suggesting the sampling periods covered at least a portion of the spawning period. Given that we used macroscopic reproductive staging methods of a different yet similar species, we compared the mean GSI estimates with each reproductive stage to validate the staging method. There was an increase in GSI with increasing reproductive stage suggesting the method was valid (Supplementary material). Fish sampled during September were primarily of reproductive Stage 2 (mature resting) with approximately 15% in Stage

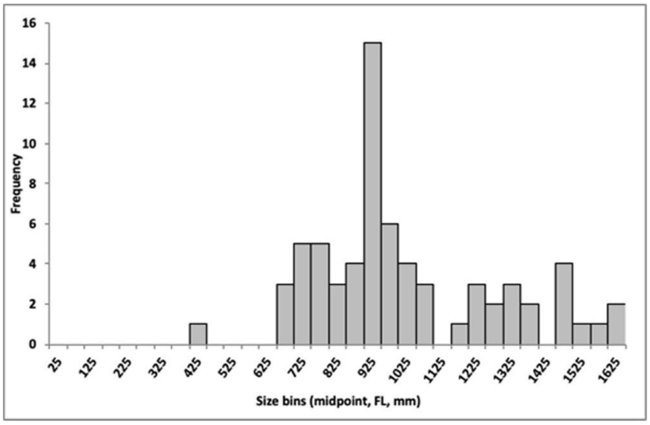

Fig. 3. Size frequency distribution of the *G. unicolor* sampled from the southwest Pacific Ocean (size bins used were 50 mm). n = 68.

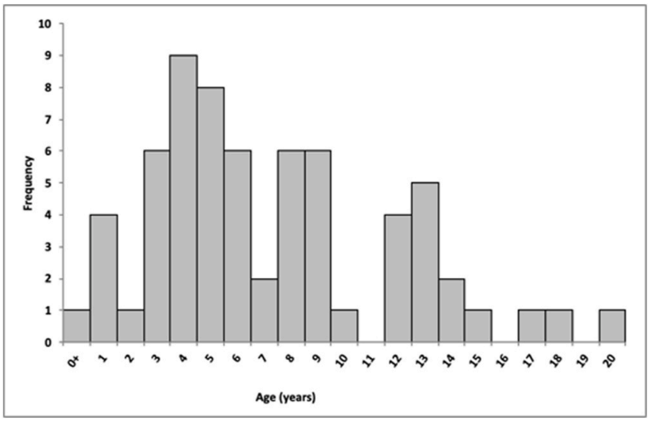

Fig. 4. Age frequency distribution of the *G. unicolor* sampled from the southwest Pacific Ocean. n = 65.

Table 4
Linear equations describing the relationships for UJL:FL, FL:TL and FL:Weight respectively, along with the coefficient of determination (r^2 values) and sample size (N); UJL = upper jaw length (mm); FL = fork length (mm); TL = total length (mm); and weight is expressed as the logarithmic (kg).

Relationship	Equation	r^2	N
UJL:FL	UJL = 6.8554(FL) + 71.978	0.9621	55
FL:TL	TL = 1.0196(FL) + 50.498	0.9982	24
FL:Weight	Weight = 0.0007($FL^{1.0799}$)	0.9679	37

3 (developing). Mean GSI was also relatively low during September. By November and December fish were predominantly Stage 3 with an increasing proportion becoming Stage 4 (developed) suggesting the onset of spawning was imminent. Despite there being no Stage 5a or 5 b (pre-spawning and spawning respectively) females, some males were Stage 4 (spawning). Mean GSI also increased sharply during the months of sampling with a peak in December (Fig. 7).

The smallest mature female *G. unicolor* in the collected samples was 660 mm FL, while the largest immature fish was 980 mm FL, suggesting a relatively wide range in size for the onset of maturity. Model parameters for both size and age models were validated. The Cook's distance value was less than 0.08 and the normal Q-Q plot did not show any unusual patterns. Pearson Chi-Square values of 0.99 for size and 0.98 for age indicate that our models are a very good fit and that we can explain 99.9% or 98.9% of our data, respectively. The size model coefficients show significant effects of increasing size with increasing levels of maturity (intercept = 0.001, slope = 1.009), similar to the age model (intercept = 0.440, slope = 1.653). The estimate of size at which 50% of the female population is mature was 716 mm FL and 95% are mature at 1022 mm FL (Supplementary material). The age at which 50% of the female population is mature was 1.6 years and 95% are mature at 7.5 years of age (Supplementary material).

4. Discussion

This study provides the first age-based estimates of the life history parameters for *G. unicolor* and provides a foundation for effective management of this species, particularly in the Australian-southwest Pacific Ocean region. In particular, the results of this study will inform future management for the responsible and sustainable use of this valuable resource in the Coral Sea Marine Park where they are a popular species of sports fish. The biological characteristics of *G. unicolor* include moderate longevity, rapid initial growth in the first year, and early maturation. These traits, along with information regarding gene flow and connectivity (Bentley et al., 2014), provides information that can direct appropriate management arrangements.

Growth in *G. unicolor* was found to be very rapid on average in the first year of life, with the smallest fish at 423 mm FL estimated to be only 155 days old. Growth slowed rapidly after 2–3 years of age at which a mean estimated size range of 568–741 mm FL was attained (constrained model, Fig. 5; Table 5). This size range approximates the estimated size at 50% maturity of 716 mm FL (females; 780 mm TL), and so growth attenuation may be linked to the diversion of some surplus energy from somatic growth into reproduction once maturity is reached. This is consistent with many fish species (Roff, 1983); however, some studies have shown how the influence of seasonality can disrupt this relationship, resulting in variability in the energy allocation budget and the timing of maturity (e.g., Kozłowski & Teriokhin, 1999). A high variation in both growth and the timing of sexual maturity was observed for *G. unicolor* in this study. One immature fish was 882 mm FL and estimated to be 7 years of age, while the largest immature fish was 980 mm FL, and the smallest mature male and female fish were 700- and 650-mm FL respectively (Table 3).

There was a large variability in the observed length-at-age. Despite this, the data fit the growth curves reasonably well. While this is consistent with other scombrid species (Ballagh et al., 2006; Farley et al., 2006; Griffiths et al., 2010; Williams et al., 2012; but see Newman et al., 2012), in this study a small part of the variation observed may be related to the difficulty in interpreting the growth zones in some of the otolith sections prepared. We used commonly applied methods for the otolith preparation which may not be ideally suited to *G. unicolor* otoliths. Otolith preparation methods, including criteria such as: optimal

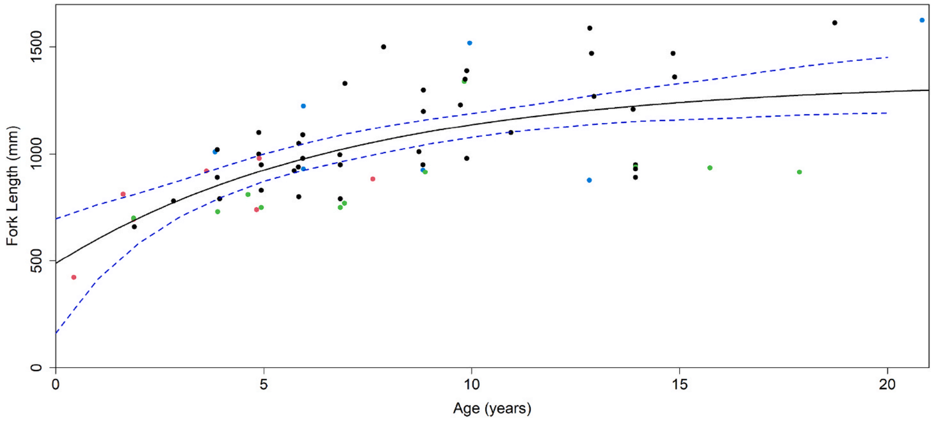

Fig. 5. Length at age data and the unconstrained von Bertalanffy growth curve for the *G. unicolor* sampled. Data points are colour coded to indicate sex (Green = male; Black = female; Red = immature; and Blue = sex not known). The dotted blue lines represent the 95% confidence intervals. n = 65. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

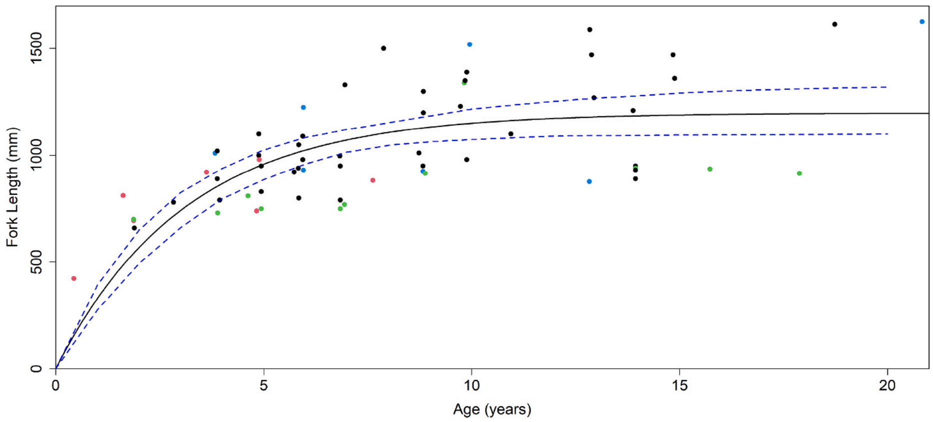

Fig. 6. Length at age data and the von Bertalanffy growth curve with the parameter t_0 constrained to zero for the *G. unicolor* sampled. Data points are colour coded to indicate sex (Green = male; Black = female; Red = immature; and Blue = sex not known). The dotted blue lines represent the 95% confidence intervals. n = 65. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

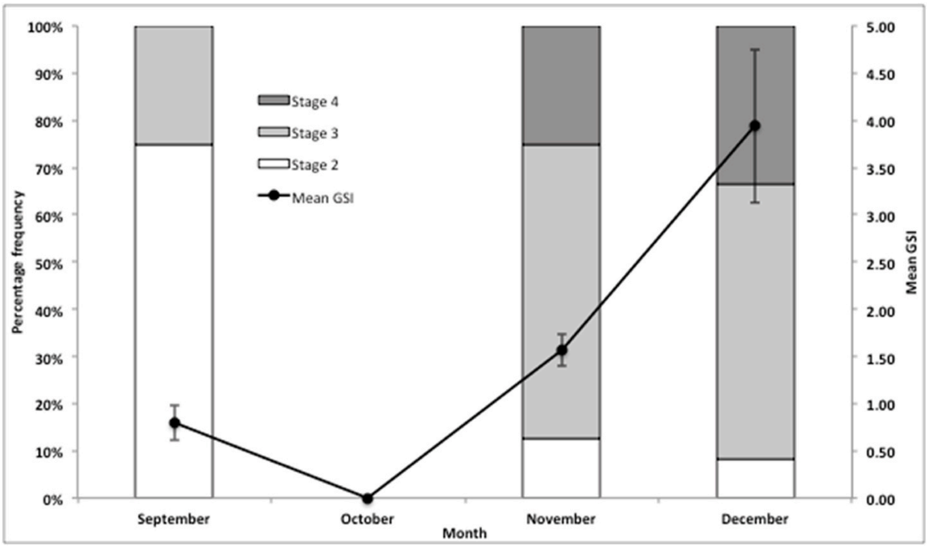

Fig. 7. Macroscopic gonad stages of *G. unicolor* for the sample collection months and the associated mean GSI values (+/− SE; September, November and December samples sizes are 4, 24 and 12).

section thickness; quality control in sectioning orientation; calibration of equipment; and post section treatments (e.g., polishing, acid dipping) has recently been refined in order to maximise growth zone clarity and to facilitate improved estimates of fish age (e.g., Newman et al., 2017, 2015; Wakefield et al., 2017). For species such as *G. unicolor*, where samples hold a large individual value due to the difficulties in obtaining adequate sample sizes, the preparation of otoliths for age estimation becomes increasingly more important to improve the clarity of growth zones. The additional knowledge gained in this study about the potential timing of otolith zone formation, as well as information on spawning and maturation, will allow the development of an improved ageing protocol for this species to be developed. This would further increase the precision and accuracy of the otolith-based age estimates. Moreover, future studies need to focus on increasing both the sample size, collecting explicit sex-specific data and improving the sectioning methodology to improve estimates of length-at-age and subsequent estimates of growth and maturity parameters.

Growth rates can be affected by several natural factors including gender, environmental conditions and genetics. In this study there were insufficient samples obtained to reliably estimate growth separately by gender, however all males collected (except one) were smaller than 1000 mm FL, despite one of these smaller fish estimated to be 17 years of age. Despite low sample numbers, this is consistent with a study in Fiji, which found that all fish larger than 1000 mm were females and suggested the occurrence of sexual dimorphism for this species (Lewis et al., 1983). They also found that females outnumbered males by 2:1 and in our study that ratio was ~4:1 (noting the small sample size).

The size at 50% maturity estimated in this study was 716 mm FL and almost the entire population was mature by the time they reached approximately 1000 mm FL (Supplementary material). These results are consistent with the few other studies conducted on this species. Lewis et al. (1983) estimated that they first reach maturity from around 650 mm FL, while Joshi et al. (2012) estimated 50% maturity at 690 mm FL. Sivadas and Anasu Koya (2005) also reported that all fish under 700 mm FL were immature, and Silas (1963) reported a mature male of 685 mm TL. This study is the first to use age-based estimates for *G. unicolor* and we estimated that the age at 50% maturity is only 1.6 years of age, while almost all females were mature by 7.5 years of age. This further supports a large variation in the timing of when these fish attain maturity. Further, there is a need for the preservation of fresh gonad tissues in any future studies for detailed microscopic examination and refinement of the maturity estimates described herein.

The largest fish sampled in this study was 75 kg in weight and estimated to be 1625 mm FL (~1708 mm TL) and was also the oldest fish

Table 5

Mean fork length per age for *G. unicolor* estimated for the unconstrained and constrained growth models.

Age (yrs)	Mean fork length (mm); unconstrained model	Mean fork length (mm); constrained model
1	601.93	329.16
2	700.39	567.95
3	785.73	741.18
4	859.72	866.84
5	923.84	958.00
6	979.43	1024.14
7	1027.61	1072.11
8	1069.38	1106.91
9	1105.58	1132.16
10	1136.96	1150.48
11	1164.17	1163.76
12	1187.74	1173.40
13	1208.18	1180.39
14	1225.90	1185.47
15	1241.26	1189.14
16	1254.57	1191.81
17	1266.11	1193.75
18	1276.11	1195.16
19	1284.78	1196.17
20	1292.30	1196.91

sampled with an estimated age of 20 years. This is the first study to provide estimates on the longevity of this species. One previous estimate of maximum age was 12 years based on a fish that was 1620 mm FL using length-based methods (Joshi et al., 2012). Previous studies have reported that *G. unicolor* grows to a maximum size of 2400 mm TL and approximately 80 kg (Silas, 1963). Since those studies, larger specimens have been landed by recreational fishers (e.g. a 110.2 kg fish landed in Indonesia in 2010 (https://www.spearblog.com/2010/11/24/pending-world-record-dogtooth-tuna/). This specimen equates to a fish of approximately 1850 mm FL, and it is therefore likely that *G. unicolor* can live for longer than the maximum age of 20 years observed in this study.

The spawning season in the southwest Pacific Ocean region was determined to be during late Spring-early Summer. It is likely that spawning is extended since samples were not collected during the months following December when GSI peaked. However, using daily counts from the single 0+ fish sampled a birthdate was estimated that corresponds to a December–January spawning. This is consistent with one previous study in Fiji which found that *G. unicolor* spawn during summer months (Lewis et al., 1983). Other studies using only macro-staging methods have suggested that spawning in some parts of the northern hemisphere is year-round (e.g., India and Japan; Joshi et al., 2012). Okiyama and Ueyangi (1977) sampled *G. unicolor* larvae and revealed that they were concentrated along the shallow coastal waters of islands across a large area of the tropical and subtropical Pacific Ocean, between 10 °N and 20 °S. They collected *G. unicolor* larvae in surface and subsurface tows and found greater numbers in the sub-surface tows at depths between 20 and 30 m.

Gymnosarda unicolor is the only tuna species with a true direct association with coral reefs. This is not surprising given that they are not in the same taxonomic grouping as 'true' tunas (Tribe Thunnini), although the differences are otherwise technical (Pepperell, 2010). *Gymnosarda unicolor* are likely to occupy a niche more similar to other reef-associated pelagic predators such as the related Spanish mackerel (*Scomberomorus commerson*), which overlaps their distribution globally to a large extent and also feeds around coral reefs. The main difference is likely to be their depth preferences, with *S. commerson* rarely found in depths greater than 100 m, mostly occupying depths of 10–30 m (Collette & Nauen, 1983), while *G. unicolor* have previously been reported to occupy depths of at least 300 m or greater. Further, although based on limited information, a study in Tuvalu in the Pacific Ocean found a positive correlation between size and depth for this species, with larger individuals being found at progressively greater depths (Anon, 2005). This is consistent with the observations of some of the authors of this study. More recent evidence supports the notion that *G. unicolor* occupy far greater depths than previously reported with one specimen recorded at a depth of 805 m at Pitcairn Island in the Indian Ocean (Friedlander et al., 2014). Previous reports that fish are generally solitary or in small schools of six or less is also consistent with multiple observations by the authors of this study. The affinity of *G. unicolor* to many oceanic coral reefs suggests they may be useful indicator species (see Newman et al., 2018) to monitor the effects of harvest.

Previous studies also report on the diet of *G. unicolor*, however most of these reports appear to be based on third-party reports rather than direct observations. These studies report that *G. unicolor* are a 'voracious predator' and have a diverse range of finfish species in their diet, including scads (*Decapterus*), unicornfish (*Naso*) and fusiliers (*Caesio* and *Pterocaesio*) (Collette & Graves, 2019). In this study we found a range of reef-associated species in the gut contents of *G. unicolor* samples ranging from small pelagic species to more benthic reef attached species. These included: a 600 mm TL whole emperor (Family Lethrinidae) found in the stomach of a 52.5 kg female individual, several fusiliers (Family Caesionidae), a peacock cod (*Cephalopholis argus*), a small tuna (Scombridae), a 570 mm FL sawtail surgeonfish (*Naso* sp.) in the stomach of 60 kg individual, a *Priacanthus* sp. (Bigeye), and a juvenile leatherjacket (Family Monacanthidae) in a 730 mm FL individual. Furthermore, online searches reveal the presence of other species in the gut of *G. unicolor* including rainbow runner (*Elagatis bipinnulata*), small groupers (Family Epinephelidae) and even a ~700 mm FL deep water red snapper (*Etelis* sp.), commonly found in depths of 200–300 m, in the gut of a 200 lb (approx. 91 kg) *G. unicolor* taken in Indonesia. These observations and those reported from this study provides further evidence of a diverse diet across a broad depth range and expands the knowledge of the ecology of *G. unicolor*.

4.1. *Implications for conservation and management*

In this study, we provide essential biological information that better informs fisheries managers on the likely impact of fishing on populations of *G. unicolor*. The life history characteristics described herein are of a generally fast-growing fish that reaches maturity at a relatively small size and young age, on average, with moderate longevity. They are not dissimilar to other scombrid species in their life history and are not expected to be particularly vulnerable to fishing based on these characteristics in isolation.

Because there is no dedicated fishery for this species anywhere, and they are generally captured in remote locations, obtaining samples for evaluation has historically been difficult. These are the key reasons why no population size estimates are available for this species. Despite this, there are numerous anecdotal reports of localised declines and Lewis et al. (1983) reported that: '*The catches are usually not maintained and it is likely that stocks of this species are susceptible to rapid local depletion*'. A recent stock structure study conducted across the Indo-Pacific basins found that there was no significant genetic differentiation between fish from the Indian and Pacific Oceans, however at smaller spatial scales fish from isolated reefs and atolls tended to be more closely related to each other. This was interpreted to suggest that the eggs and larvae of *G. unicolor* are dispersed widely by ocean currents and that potentially at least some juvenile *G. unicolor* may travel large distances before recruiting to isolated coral atolls (although this remains to be confirmed). This type of reproductive pattern is likely to result in patchy recruitment over broad areas which could make isolated populations vulnerable to fishing over short time periods, but not prone to permanent local depletion (Bentley et al., 2014). Moreover, Bentley et al. (2014) determined that this pattern is consistent with a phenomenon known as 'ephemeral genetic patchiness', which is due to a high variance in reproductive success and local recruitment patterns. Furthermore, Bentley et al. (2014) also estimated a low effective population size for the Pacific Ocean, which is also consistent with high variability in reproductive success. Despite this, further research should assess the demographic connectedness of adjacent populations to confirm patterns of connectivity.

The study by Bentley et al. (2014) provides a crucial insight into the spatial scale required for management of *G. unicolor*, with the basic spatial unit of stocks for management purposes determined by dispersal and connectivity with adjacent populations (Secor, 2005). Reports of localised declines in *G. unicolor* populations are consistent with the observed stock structure patterns and provide a strong basis that the spatial scale of management be reef-based or on groups of adjacent reefs and/or atolls (the latter to ensure that there is an effective spawning biomass to contribute recruits).

The age-based estimates of growth and maturity provided herein greatly advance the biological knowledge of *G. unicolor*. Currently there are no management measures that control *G. unicolor* harvest levels, despite the observation and risk of localised depletion. This study details the basic age-based life history information and knowledge available for *G. unicolor*. This will contribute to the next phase of applying data-limited approaches to assessment and ultimately management arrangements for this species. Although the timing of maturity for this fish is variable in size and age, a robust and simple management measure is to introduce a minimum size limit that approximates the size at 50% maturity. For the southwest Pacific Ocean region, we estimated this to be 716 mm FL for females (780 mm TL) and on this basis a minimum size limit of at least 800 mm TL could be implemented. For line caught fish this size should allow these smaller fish to be retrieved and released relatively quickly, thereby minimising post release mortality due to barotrauma. It is worth noting that this assumes a high resilience to the effects of barotrauma for *G. unicolor* at this size, which is currently not known. For spear fishers a conservative approach is to recommend a target size of at least 1000 mm TL (approximately 14 kg).

While the capacity for future studies on this species is always likely to be challenging, the validation of the use of an upper jaw length measurement in this study will be useful for future studies that will be able to obtain head and gut samples only and still reliably obtain an estimate of the length of an individual fish. Nevertheless, with the increasing interest in *G. unicolor* as a target species for sports fishers, as well as the obligation for ecologically sustainable use of natural resources in places like the CSMP, this study provides the sound basis to inform the implementation of simple management measures. In the absence of formal management measures, we would encourage the adoption of voluntary measures by fishers based on recommendations provided in this study so that they can continue to target this species.

Declaration of competing interest

The authors declare that there are no conflicts of interest.

CRediT authorship contribution statement

David J. Welch: Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Adam K. Smith:** Data curation, Methodology, Formal analysis, Investigation, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Kyne Krusic-Golub:** Methodology, Writing – review & editing. **Sandra Erdmann:** Formal analysis, Investigation, Writing – review & editing. **Stephen J. Newman:** Methodology, Formal analysis, Investigation, Supervision, Writing – original draft, Writing – review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aaf.2021.12.004.

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