


Life-history characteristics of an exploited bonefish *Albula glossodonta* population in a remote South Pacific atoll

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Abstract

Bonefishes *Albula* spp. are important components of subsistence fisheries and lucrative sport fishing industries throughout their circumtropical distribution. In Oceania, however, *Albula* spp. have historically been overexploited and there is a growing need to balance the demands of competing fishing sectors, making the description of their life history a regional priority. To this aim, we collected biological samples from *Albula* spp. of Anaa atoll, French Polynesia, to identify the species that compose the stock and estimate their life-history parameters including age, growth, reproduction and natural mortality. Our results indicate that *Albula glossodonta* is the species of bonefish present, with a maximum age that is below the, 20 year longevity of the genus (8 years in males and 10 years in females). Differential growth patterns existed between the two sexes ($L_{\infty} = 58, 78$ cm fork length (L_F) and $K = 0.38, 0.21$ for males and females, respectively). Males attained sexual maturity at 43 cm L_F (c. 3 years) whereas females matured at 48 cm L_F (c. 4 years) and oocyte production was significantly related to body mass, with a maximum batch fecundity of 1,133,767 oocytes in a 4406 g (70 cm L_F) female. The gonado-somatic index of harvested fishes indicated that the spawning season extends from March through September. Based on the observation of a, 20 year bonefish at the proximate Tetiaroa Atoll and several empirical models, estimates of natural mortality ranged from 0.21 to 0.68; however, an estimate of 0.21 was deemed most appropriate. This information facilitated the resurgence of a *Rahui* (temporary fishing closure) and community-based management to protect *A. glossodonta* during a critical portion of their spawning season and in this context our results provide an important demographic baseline in evaluating the recovery of this fishery.

KEYWORDS

age and growth, *Albula glossodonta*, artisanal fishery, reproduction, spawning aggregation

1 | INTRODUCTION

Bonefishes *Albula* spp. are neritic benthivores that frequent shallow coastal sandflats and seagrass beds of tropical seas (Adams *et al.*, 2007; Bowen *et al.*, 2007). In addition to providing important services

to these coastal ecosystems, they are a cornerstone of subsistence fisheries and support ecotourism throughout their worldwide distribution, rendering them a culturally and economically important species (Adams *et al.*, 2014; Allen, 2014; Moret, 2007). Despite the considerable efforts to understand and protect bonefishes in the Atlantic

Ocean, congeneric species in less developed regions of the world have received little attention (Adams *et al.*, 2014). The life history of roundjaw bonefish *Albula glossodonta* (Forsskål 1775) in the Pacific Ocean has only been studied in Hawaii and Palmyra Atoll a nearly pristine marine reserve in the central Pacific Ocean (Donovan *et al.*, 2015; Friedlander *et al.*, 2007; Kamikawa *et al.*, 2015). Nevertheless, the species remains a foundation of many artisanal fisheries, particularly in sparsely populated Pacific islands and atolls with small communities that target and harvest albulids from spawning aggregations (Allen, 2014; Friedlander *et al.*, 2007; Johannes & Yeeting, 2000). The practice of fishing on spawning aggregations can destabilise fish populations, altering their abundance, sex ratio, body size and reproductive success (De Mitcheson *et al.*, 2008; De Mitcheson & Erisman, 2012; Sadovy and Domeier, 2005). In many Pacific islands, the intensive exploitation of albulid spawning aggregations has led to declines in their populations and regionally few protective measures have been implemented for these species (Adams *et al.*, 2014; Beets, 2000; Friedlander *et al.*, 2007; Johannes & Yeeting, 2000; Kamikawa *et al.*, 2015).

Development of ecotourism in the remote Pacific islands has been proposed as a sustainable economic alternative to extractive fisheries harvest that could improve both the quality of life for the residents of these remote communities and the conservation of their fisheries resources (Barnett *et al.*, 2016; Wood *et al.*, 2013). This is reflected in valuations of albulids. In some Pacific island locations such as Kiritimati (Christmas Island), which employs up to 20 local guides in a fishery valued at approximately US \$2.5 million year⁻¹ to the island's economy (Campbell & Hanich, 2014). However, recreational fishing in these remote communities competes with artisanal fisheries that harvest albulids for food security (Allen, 2014). Consequently, local governments have had to regulate the harvest of these species in the absence of scientific data (Cook Islands Government, 2010) and there is a growing need to balance both the subsistence and recreational demands on *Albula* spp. in the Pacific islands. Making the description of their life history a regional fisheries management priority.

Understanding the life-history demographics of *Albula* spp. in Oceania is critical for the development of management and conservation plans (Beverton & Holt, 1959; Quinn & Deriso, 1999; Ricker, 1954). Life history characteristics that describe age and life-time growth such as the von Bertalanffy growth parameters, maximum size and longevity are often used to predict natural mortality (Hoenig, 1983; Pauly, 1980), evaluate the age structure of a population, estimate regeneration time (Depczynski & Bellwood, 2006) and predict a stock's ability to deliver sustainable yield at a given harvest rate (Carruthers *et al.*, 2014; Goodyear, 1993). Reproductive characteristics such as the length and age of maturity provide fisheries managers with an understanding of the critical size a fish must obtain for it to replace itself and reduce growth overfishing (Cope & Punt, 2009; Froese, 2004). Furthermore, the identification of the seasonal and lunar timing of spawning can help identify periods where these species are vulnerable to overharvest and temporal closures are required (Adams *et al.*, 2018).

Anaa is a small coralline atoll in the South Pacific, where an emerging recreational fly-fishing industry shares the *Albula* spp. resource with a customary artisanal fishery. An initial assessment of this atoll's fisheries indicates that *Albula* spp. constitute 25% of the catch and are overexploited, with fishing mortality estimated to be three times the rate of natural mortality for albulids (Filous *et al.* 2019). To help fill information gaps that could aid in the development of management strategies locally and regionally, we collected biological samples from *Albula* spp. harvested at Anaa atoll to identify the species that compose the stock and estimate their life-history parameters including allometric growth, age and growth, reproduction and empirical estimates of natural mortality.

2 | MATERIALS AND METHODS

2.1 | Study site

Anaa is a small Atoll (38 km²) 350 km east of Tahiti, in the Tuamotu Archipelago of French Polynesia and represents a Pacific island community in which *Albula* spp. are targeted by both subsistence and recreational fisheries (Figure 1). The atoll is bordered by a coral reef that drops off into the open ocean and surrounds a shallow lagoon (c. 8 m

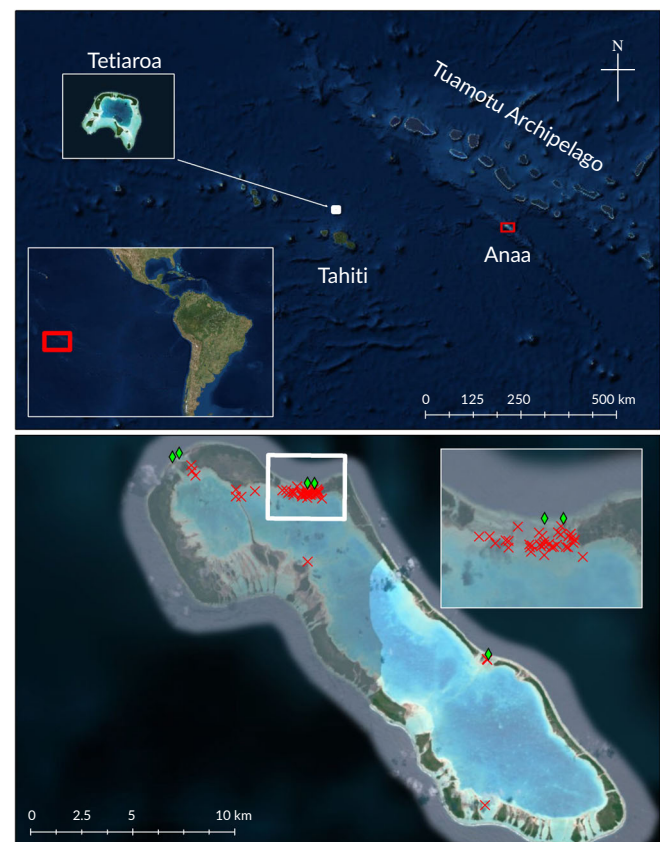


FIGURE 1 The location of Anaa and Tetiaroa Atolls in relation to the Tuamotu Archipelago of French Polynesia, ♦, The locations of passes through the outer reef that are used by migrating albulids during spawning events; ×, the locations of artisanal fish traps

maximum depth) with 11 small islands known as *motu* and fringing sandflats. Unlike most atolls in the archipelago, Anaa is closed, meaning that it lacks a deep oceanic pass that connects its interior lagoon to the outer reef. The reef crest forms a barrier around the atoll and there is limited tidal influence on the water movement in the lagoon. Instead its water level is determined by the size and direction of the prevailing swell, which can fill or drain the lagoon through small shallow channels called *hoa* among the coral ring. Several shallow breaks in the reef crest are situated in the large *hoa* north-east of the Atoll, adjacent to Tukahora village and allow movement of fish between the lagoon and oceanic habitats (Figure 1). An artisanal trap fishery, comprising heart-shaped weirs constructed from dead coral, targets the spawning migrations of *Albula* spp., which are concentrated in this migratory passage during their reproductive migrations. Catches from these traps provide sustenance and economic opportunities for the atoll's c. 500 residents.

2.2 | Collection of biological samples

Albula spp. landed in the artisanal trap fishery at Anaa Atoll were randomly sampled from 2015–2018. In addition to these fish, supplementary collections of young of the year *Albula* spp. (< 20 cm fork length, L_F) were made with hook and line in the marinas and boat harbours adjacent to Tukahora village. To estimate longevity (t_{max}) in the absence of fishing mortality, samples were collected from nearby Tetiaroa Atoll in 2014. Tetiaroa is a closed atoll in the Society Islands, 53 km north of Tahiti with no permanent inhabitants, a relatively unexploited *Albula* population and a predator composition similar to that of Anaa Atoll (Figure 1). During sampling events, we recorded the capture method, standard length (L_S , cm), L_F (cm), total length (L_T , cm), total somatic mass (M_T , g), sex and gonad mass (M_G , g). Along with these measurements, we collected sagittal otoliths, fin clips and cross sections of gonad tissues from a sub-sample of these fish. *Albula* spp. and their gonads were weighed to the nearest gram with an Acculab Vicon scale (Model VIC-612; www.acculab.balances.com), whereas otoliths and gonadal sub-samples of female oocytes were weighed to the nearest 0.01 g and 0.1 g, respectively, with an Ohaus Pioneer scale (Model PA124C; www.ohaus.com). In these analyses, all values are given as mean \pm SD unless otherwise stated. All statistical analyses were conducted using R 3.4.3 (www.r-project.org).

2.3 | Allometric growth

Length–length relationships between L_S , L_F and L_T , as well as a length–mass relationship between $\log-L_F$ and \log -total somatic mass (M_T) were developed with linear least-squares regression. To define the length–mass relationship, the a and b parameters from the $\log-L_F$ – M_T equation were converted back to the untransformed relationship by taking the anti-log of the linear regression, to derive the equation: $M_T = aL_F^b$, where b is the allometric growth parameter and a is a scaling constant (Hayes *et al.*, 1995).

2.4 | Age and growth

To estimate age and growth rates, the right sagittal otoliths of sampled fish were cleaned with water and 95% ethanol, weighed to the nearest 0.01 g and measured to the nearest 0.10 mm with Johnson 1889–0600 digital callipers (Johnson Level & Tool Co.; www.levelsupply.com). Once measured, the otoliths were mounted to a 2 x 2 cm square piece of plywood with super glue and a transverse section was taken through the primordium with an IsoMet low speed saw (Buehler, Inc.; www.buehler.co.u). The otolith sections were then mounted to a glass slide with crystal bond heat activated glue and polished with 15 μ m lapping film (Usseglio *et al.*, 2015). After sectioning, the age of each fish was evaluated by counting annuli under x4 magnification with a compound microscope. Prior to counting, the approximate distance of the year one annulus was validated for each fish by counting the daily growth rings of young of the year bonefish under x40 magnification, measuring their otolith length and dividing the total otolith length by age plus a 57 day estimated post-larval duration from Friedlander *et al.* (2007). These daily estimates of growth were averaged and multiplied by 365 to obtain the approximate distance of the year one annulus. Finally, the maximum age observed in Tetiaroa Atoll was taken as an estimate of t_{max} .

Age and growth curves were developed from these age-at-length data for both male and females to provide a prediction of a fish's age based on a given length. Seven different von Bertalanffy growth models with combinations of potential sex specific growth parameters including mean asymptotic length (L_∞), growth rate (K) and the theoretical age at which length is zero (t_0) were generated with nonlinear least squares using the `nls()` function in R, following the von Bertalanffy equation: $L_t = L_\infty (1 - e^{-K(t - t_0)})$, where L_t is length at age t , L_∞ is mean asymptotic length, K describes how fast the asymptote is reached, t is the age in years and t_0 is the theoretical age at which length is 0 (Ricker, 1987; von Bertalanffy, 1938).

To determine if male and females exhibit sexually dimorphic growth and select the most appropriate model, statistical comparisons were conducted among the seven models with a series of likelihood ratio tests (Kimura, 1980), using the `lrt()` function in the `fsa` package in R. We first compared a general unisex model to the sex-specific model in which all growth parameters L_∞ , K and t_0 differed. We then sequentially tested this sex-specific model against a series of more parsimonious nested models, until we identified the model that was statistically different from all simpler alternatives (Ogle, 2016).

2.5 | Reproduction

The sex ratio (F:M) was taken across all biological samples for which sex could be identified and tested with a χ^2 -test using the `chisq.test()` function in R, to determine if the sample differed significantly from a 1:1 sex ratio. Differences between the mean size of males and females were tested with a Welch's two-sample t -test using the `t.test()` function in R. To visualise the relationship between size at first maturity, the gonado-somatic index (I_{GS}) values of male and females were

plotted against L_F ; $I_{GS} = 100M_G M_T^{-1}$, where M_G is total mass (g) of both gonads and M_T is the total somatic mass (g).

Length and age at first maturity were calculated based on the proportion of reproductively mature individuals in 2 cm size classes determined by histology and macroscopic assessment. Maturity was determined macroscopically, by the occurrence of developed oocytes or spent ovaries in females and sperm in males. To further examine these samples, cross-sections of gonads were taken from male and females and preserved in a solution of 10% buffered formalin for field storage. Upon return to the laboratory, gonad samples were removed from the formalin solution and washed overnight with fresh water. The samples were then stored in 70% ethanol after soaking for 30 min in a series of graded solutions (30% ethanol, 50% ethanol, 70% ethanol). The samples were then embedded in paraffin wax, sectioned with a microtome and mounted on a glass slide where the cells were stained with haematoxylin and eosin (h&e). After sample preparation, the gonad cells were viewed under a compound microscope and assigned reproductive stages based on the characteristics of the reproductive cycle published by Brown-Peterson *et al.* (2011). Maturity was validated based on the presences of vitellogenic oocytes, advanced stages of oocyte maturation, hydrated oocytes, atresic oocytes, or post-ovulatory follicles in females and sperm in males (Brown-Peterson *et al.*, 2011). After the identification of maturation state, the ages of each sample were determined with length–age conversions using the previously identified sex-specific growth parameters: L_∞ , K and t_0 . After data preparation, the length (L_{50}) and age (A_{50}) at which 50% of individuals became sexually mature and the length (L_{95}) and age (A_{95}) at which 95% of individuals became sexually mature was determined for male and females by fitting a logistic model to the proportion of mature fish v. immature fish by 2 cm size and yearly age classes. The proportion of mature fish were fitted by iteratively reweighted least squares using the `glm()` function and confidence intervals for the model parameters were estimated by bootstrapping with 1000 iterations, where the logistic model is described by the equation; $\log((p1^{-1}) - P) = a + \beta L_F$, where P is the probability of being mature, L_F is the fork length (or age class) and a and β are fitting constraints.

Total batch fecundity was estimated with the gravimetric methods defined in Murua *et al.* (2003). Gravid females were collected, weighed and measured following the methods described above. The gonads were then extracted, weighed and 0.1 g sub-samples of oocytes were taken from the anterior, middle and posterior sections of the gonad and placed into small 5 cm diameter Petri dishes. A solution of 33% glycerol and water was added to the samples to break down the tissue encasing the oocytes and a laboratory spoon was used to manipulate the oocytes until all of them were separate and individually distinguishable from each other. After dispersing the oocytes, the samples were magnified x4 and photographed with a Dino-Lite digital microscope (model Edge, AM4515ZTL; www.dino-lite.com). The number of individual oocytes per sample was counted with ImageJ 1.51j8 (NIH; www.imagej.nih.gov) software's multipoint counting tool (Abramoff *et al.*, 2004). The number of oocytes in each sub-sample were then applied to the following equation to estimate

the total annual fecundity of an individual fish: $F = \left[\sum_i \frac{O_i}{M_i} \right] n^{-1} M_G$, where F is batch fecundity, O_i is the number of oocytes in sample, M_i is sample mass, n is number of samples and M_G is total ovary mass (Murua *et al.*, 2003). Linear regression was then used to describe the relationship between batch fecundity and M_T (Crabtree and Harnden, 1997).

Albula spp. movement at Anaa Atoll's artisanal fish trap complex is hypothesised to be associated with reproductive migrations and the I_{GS} of fish harvested from these traps should reflect reproductive activity in this closed atoll. Therefore, we evaluated the seasonality of reproduction by calculating the monthly mean I_{GS} for both male and females that were harvested in the artisanal trap fishery for the duration of the study. We plotted these values to show seasonal patterns in reproduction and significant differences in the mean I_{GS} across the months of the year were tested with linear models. The location of the significant differences in mean I_{GS} between the months of the year were then identified with a Tukey's honest significant difference (HSD) test and the `glt()` function in the `multcomp` package in R. Finally, to describe reproductive activity in relation to lunar cycle, we plotted the I_{GS} from a sub-sample of females in relation to the lunar day of the date they were harvested in the migratory passage (*i.e.*, number of days following the full moon) and tested for significant differences in I_{GS} between moon phase with a `kruskal.test()` function.

2.6 | Empirical estimates of natural mortality

To obtain empirical estimates of natural mortality at Anaa, we used the life-history parameters L_∞ , K , t_{max} and the mean annual water temperature collected by a HOBO water temp (Pro v2 model #; www.hobodataloggers.com) that was located in the lagoon. These parameters were applied to the M empirical function in the R package `fishmethods` to obtain estimates of natural mortality based on the length equation described in Pauly (1980) when accounting for schooling behaviour: $\log M = 0.654 \log K - 0.28 \log L_\infty + 0.463 \log T$, where M is the estimated natural mortality rate, K is the von Bertalanffy growth coefficient, L_∞ is the mean asymptotic length and T is the mean annual water temperature in °C. If the species of interest is a schooling fish, the M estimate is multiplied by 0.8 (Pauly, 1980).

Also, the fish equation described in Hoenig (1983): $\ln M = 1.46 - 1.01 \ln t_{max}$, where M is the estimated natural mortality rate and t_{max} is the longevity of the species (Hoenig, 1983).

For comparison, an additional estimate of natural mortality was obtained with the Hoenig_{nls} equation described by Then *et al.* (2015): $M = 4.899 t_{max}^{-0.916}$, where M is the estimated natural mortality rate and t_{max} is the longevity of the species (Then *et al.*, 2015).

3 | RESULTS

3.1 | Species identification

All of the *Albula* spp. we examined matched the phenotypic description of *Albula glossodonta* (Forsskål 1775) morphology provided by

Donovan *et al.* (2015), being distinguished from other species of sharp jawed *Albula* spp. by a broadly rounded lower jaw and absence of yellow pigmentation under the pectoral fin (Donovan *et al.*, 2015). The tests of DNA sequences extracted from a small sub-sample of five *Albula* spp. correspond to the phylogeny of *A. glossodonta*, suggesting that although other species may remain to be discovered, *A. glossodonta* is the species captured in the artisanal fishery of Anaa Atoll (Appendix S1 Figure S1 and Table S1).

3.2 | Allometric growth

Length and mass measurements were obtained for 741 *A. glossodonta* from Anaa Atoll ranging in size from 11 to 71 cm L_F with a mean (\pm SD) length of 48 ± 10 cm L_F . The smallest individual weighed 14 g, the largest was 4792 g and their mean mass was 1604 ± 809 g. From these data, length-length relationships were generated (Table 1) and described by: $M_T = 0.01L_F^{3.06}$ ($r^2 = 0.99$, $P < 0.01$).

Age and growth parameters for the *A. glossodonta* population were estimated by analysing the sagittal otoliths from a sub-sample of 474 *A. glossodonta* that consisted of 249 females 11–71 cm L_F and 225 males 11–62 cm L_F (Figure 2). Prior to aging, the year 1 annulus was validated from the daily growth rings of eight young-of-the-year *A. glossodonta*. Their estimated daily otolith growth of $5.44 \pm 0.78 \mu\text{m day}^{-1}$ was multiplied by 365 to obtain the approximate distance of the year one annulus (c. 1986 μm). The maximum age observed in females was 10 years and 8 years in males, with an average age of 4.7 ± 1.7 and 4 ± 1.2 years, respectively (Table 2). In addition to these fish from Anaa, we aged five *A. glossodonta* from Tetiaroa Atoll, ranging in size 53–70 cm L_F , with a maximum age of, 20 in a 70 cm L_F female and an average age of 11 ± 5 years.

Results of the likelihood-ratio tests indicate that male and female *A. glossodonta* exhibit sexually dimorphic growth ($df = 3$, $\chi^2 = 96.16$, $P < 0.01$; Appendix S1 Table S2). Of the possible growth models tested, the model that specified different L_∞ and K parameters for male and female *A. glossodonta* with a unisex t_0 was the most appropriate ($df = 1$, $\chi^2 = 3.22$, $P > 0.05$; Appendix S1 Table S2). Assuming growth follows the von Bertalanffy growth function, this model provides a body growth coefficient $K = 0.21$ (95% CI 0.18–0.25) for females and 0.38 (95% CI 0.32–0.44) for males. The maximum average size of an infinitely old fish (L_∞) was also different between sexes

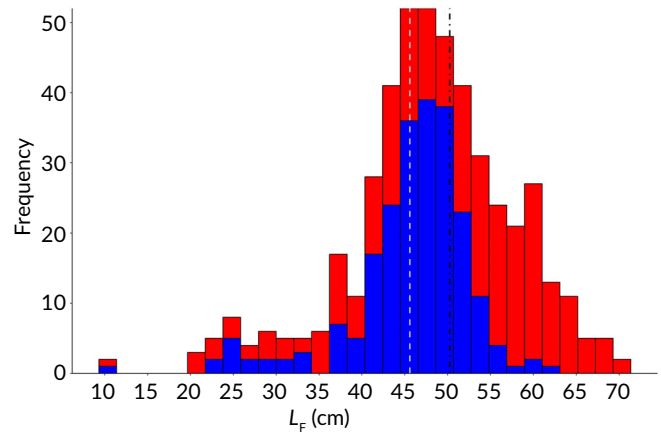


FIGURE 2 The size frequency distribution of *Albula glossodonta* for which we examined otoliths, with the mean fork length (L_F) of males (■) 46 cm and mean L_F of females (■) 50 cm. (-----) male, and (-----) female

with female $L_\infty = 78$ cm (95% CI 74–83 cm) for females and male = 58 cm (95% CI 56–61 cm; Table 2). The unisex theoretical age at which length is zero (t_0) was estimated at -0.40 years (95% CI -0.64 to -0.20 years; Table 2 and Appendix S1 Table S3).

3.3 | Reproduction

We evaluated the size, sex, gonad mass and reproductive state from a sub-sample of 674 *A. glossodonta*, with a sex ratio of 334:331 (F:M), which was not significantly different from 1:1 ($\chi^2 = 1.25$, $P > 0.05$). Females were on average (52 ± 10 cm L_F) 13% larger than males (46 ± 6 cm L_F) and this difference was statistically significant ($t = 8.0$, $P < 0.01$), with females obtaining a larger maximum size (71 cm L_F) than males (62 cm L_F). Ovarian development in immature females was characterised by primary growth (PG) oocytes, while developing females exhibited both PG and cortical alveolar (CA) oocytes. In addition to these two development stages, mature females capable of spawning exhibited vitellogenic oocytes and actively spawning oocytes including those undergoing germinal vesical migration (GVM) and germinal vesical break down (GVBD) whereas mature regressing (i.e., spent) individuals exhibited PG, CA oocytes and post ovulatory

TABLE 1 Parameters of linear length-length and log-linear length-mass relationships for *Albula glossodonta* at Anaa Atoll following the model $y = ax + b$

x	y	a (SE)	b (SE)	r^2	P
L_F	L_S	0.892 (0.003)	0.365 (0.166)	0.99	< 0.01
L_T	L_S	0.804 (0.003)	-1.545 (0.207)	0.99	< 0.01
L_S	L_F	1.109 (0.004)	0.108 (0.185)	0.99	< 0.01
L_T	L_F	0.898 (0.003)	-1.955 (0.206)	0.99	< 0.01
L_F	L_T	1.100 (0.004)	2.820 (0.218)	0.99	< 0.01
L_S	L_T	1.225 (0.005)	2.738 (0.245)	0.99	< 0.01
$\text{Log}_{10}L_F$	$\text{Log}_{10}M$	3.063 (0.012)	-1.99 (0.02)	0.99	< 0.01

L_F : fork length (cm); L_S : standard length (cm); L_T : total length (cm); M : total somatic mass (g).

TABLE 2 Life-history parameter estimates (95% CI) for male and female *Albula glossodonta* at Anaa atoll. (n.b., A t_{\max} of 20 years was used in the calculations of mortality with longevity-based methods, as a specimen of 20 years was found on Tetiaroa Atoll and fishing is a significant source of mortality that probably biased our observations of t_{\max} on Anaa Atoll)

Life-history parameter	Definition	Female	Male
L_{∞}	Mean length of infinitely old fish	78 (74 to 84)	58 (56 to 61)
K	Growth rate	0.21 (0.18 to 0.25)	0.38 (0.32 to 0.44)
t_0	Theoretical age at zero length	-0.40 (-0.64 to 0.20)	-0.40 (-0.64 to 0.20)
M_{Hoening}	Instantaneous natural mortality rate	0.21	0.21
$M_{\text{Hoeningls}}$	Instantaneous natural mortality rate	0.32	0.32
M_{Pauly}	Instantaneous natural mortality rate	0.37	0.68
a_M	Parameter a for mass-at-length equation	0.01	0.01
b_M	Parameter b for mass-at-length equation	3.06	3.06
L_{50}	Length at which 50% of individuals have reached maturity	48 (47-49)	43 (43-44)
L_{95}	Length at which 95% of individuals have reached maturity	51 (50-52)	47 (46-48)
A_{50}	Age at which 50% of individuals have reached maturity	4.19 (4.02-4.31)	3.32 (3.17-3.49)
A_{95}	Age at which 95% of individuals have reached maturity	4.73 (4.16-4.94)	4.41 (4.16-4.64)
a_F	Parameter a for fecundity at mass equation	-123,146	-
b_F	Parameter b for fecundity at mass equation	300	-
t_{\max} Anaa	Oldest fish found at Anaa Atoll	10	8
t_{\max} Tetiaroa	Oldest fish found at Tetiaroa Atoll	20	-

Length estimates are in fork length (cm), age estimates in years.

follicles (Figure 3). Immature male *A. glossodonta* were characterised by the presence of primary spermatogonia whereas mature males exhibited spermatozoa (Appendix S1 Figure S2).

The size and age at maturity estimated by logistic regression indicated that males matured earlier and at smaller sizes than females. Fifty per cent of females were mature (L_{50}) at 48 cm L_F (95% CI 47-49 cm) and an age of 4.19 years (95% CI 4.02-4.31 years) whereas males reached sexual maturity at 43 cm L_F (95% CI 43-44 cm) and 3.32 years of age (95% CI 3.17-3.49 years). These size at maturity estimates were consistent with increased variability of I_{GS} at the specified L_F (Appendix S1 Figure S3).

Batch fecundity was estimated using gravimetric methods for 57 mature females, ranging from 1315-4406 g. Oocyte developmental stage of the primary cohort was homogeneous in all samples and estimates of batch fecundity ranged from 253,930 to 1,133,767 individual oocytes, with the maximum batch fecundity observed in a 4406 g (70 cm L_F) *A. glossodonta*. Oocyte production was significantly related to body mass and can be described by the equation $y = 300x - 123,146$ ($r^2 = 0.93$, $P < 0.01$).

The I_{GS} of *A. glossodonta* captured in the atoll's artisanal fish traps suggests that *A. glossodonta* at Anaa exhibited a protracted spawning season. The I_{GS} of female *A. glossodonta* harvested March-September was, on average, almost five times higher than those harvested during the months October-February ($r^2 = 0.318$, $F_{10,259} = 11.02$, $P < 0.01$). In addition, male I_{GS} was one to two times higher during the same period ($r^2 = 0.40$, $F_{11,257} = 15.68$, $P < 0.01$). These figures suggest that spawning lasts throughout the austral autumn and winter (Figure 4). Although there is still some spawning activity from October-December, the low I_{GS} observed during these months is due to the

harvest of juvenile *A. glossodonta* in the fish traps. These events are a separate phenomenon not related to spawning and most often occur during prolonged periods of high southerly wind ($>80 \text{ km h}^{-1}$) when the lagoon becomes turbid. Local ecological knowledge suggests that during these high wind events, sexually immature fish seek refuge in the trap complex and are captured (Figure 3(a),(b)).

Unlike the movements of juveniles, the movement of adults are associated with spawning and follow the lunar cycle. Typically, gravid females first appear in the trap complex during the waning gibbous moon, approximately 3-4 days after the full moon. The I_{GS} of female *A. glossodonta* peaks during the second night of the run (i.e., 5-6 days after the full moon). These fish presumably spawn and return to the lagoon over the next several days, as spent fish with low I_{GS} were observed from 7-18 days after the full moon and significant differences in I_{GS} were observed between the waning gibbous and last quarter moon ($\chi^2 = 8.69$, $df = 1$, $P < 0.01$; Figure 5); these I_{GS} values correspond to three oocyte development stages. Firstly, during the initial day of the spawning migration, *A. glossodonta* are spawning capable and their primary cohort of oocytes has progressed into vitellogenic stage 3 (Figure 5(a)). After traversing the trap complex and reaching the oceanic passes, the oocytes of these actively spawning fish progress into the advanced stages of oocyte maturation including germinal vesical migration (GVM), germinal vesical break down (GVBD) and hydration when spawning is imminent (indicated by the peak in I_{GS} 6 days after the full moon; Figure 5(b)). Finally, returning females with spent gonads are characterised by a low I_{GS} with post ovulatory follicles (POF), primary growth (PG) oocytes and cortical alveolar (CA) oocytes (Figure 5(c)). Upon examination, the gonads of these spent females were completely empty, with POFs

FIGURE 3 Ovarian histology samples from *Albula glossodonta* stained with haematoxylin and eosin in various stages of reproductive development. (a) An immature 31 cm fork length (L_F) fish; (b) a developing 50 cm L_F fish harvested in a artisanal fish trap during a high wind event prior to its first reproductive season; (c) a mature regenerating 57 cm L_F fish harvested in the lagoon before the start of the spawning season; (d) a mature spawning-capable 59 cm L_F fish harvested in the artisanal fish traps during the initial pulse of a spawning migration that coincides with the start of the actively spawning subphase; (e) a mature spawning-capable 54 cm L_F fish undergoing oocyte maturation and hydration that was netted from a spawning aggregation staging in the passage way on the seaward side of the trap complex several hours before spawning; (f) a mature spent 59 cm L_F fish with a regressing ovary and was harvested in the artisanal fish traps while returning from spawning. A, artresia; CA, cortical alveolar oocyte; GVBD, germinal vesicle breakdown; GVM, germinal vesicle migration; PG, primary growth oocyte; POF, postovulatory follicles; VTG1, primary vitellogenic oocyte; VTG2, secondary vitellogenic oocyte; VTG3, tertiary vitellogenic oocyte

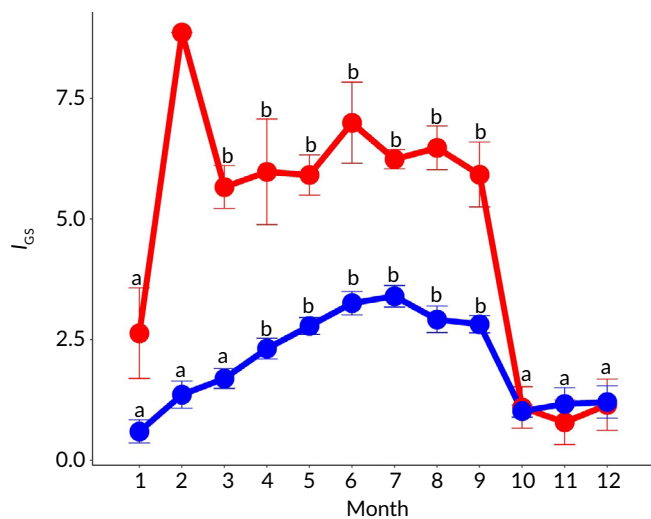
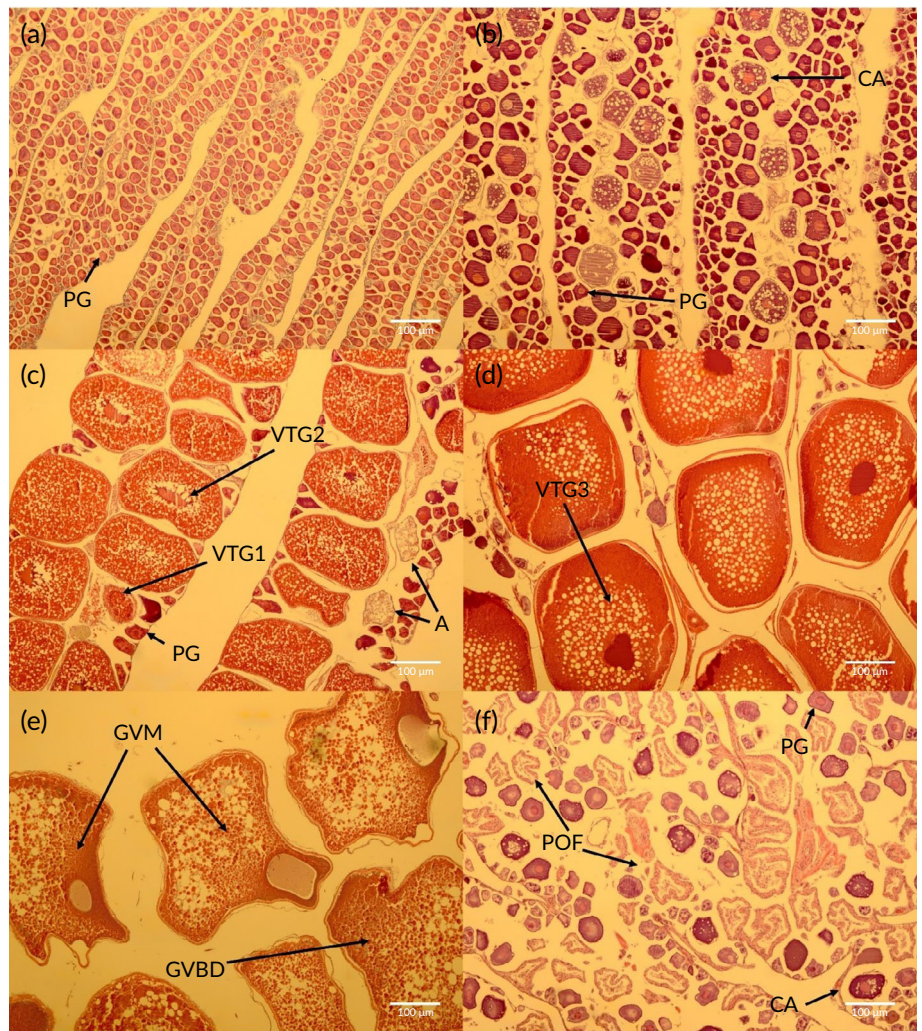


FIGURE 4 The monthly mean (\pm SE) gonado-somatic index (I_{GS}) of female (—) and male (—) *Albula glossodonta* captured in the artisanal fish traps from 2015 to 2018. Different lower-case letters indicate significant differences, $P < 0.05$ (Tukey-Kramer HSD multiple comparisons, note but females were removed from statistical comparisons in February due to low sample size)

and a few remnant ovulated oocytes that were loose in their body cavities (Appendix S1 Figure S4). In all actively spawning and post spawning fishes the development of oocytes in the cohort to be spawned was homogenous, but PG and CA oocytes were also present and probably represent newly developing cohorts for additional within-year spawning events or for the following spawning season.

3.4 | Natural mortality

The empirical estimates of natural mortality for *A. glossodonta* at Anaa Atoll ranged 0.21–0.68. Based on a longevity of 20 years, the Hoenig (1983) and Hoenig_{nl5} equations yielded a non-sex specific natural mortality rate of 0.21 and 0.32 respectively. The Pauly (1980) method allowed us to account for differential growth rates between sexes and with a mean annual water temperature of 27.5 °C yielded a natural mortality rate of 0.37 for females and 0.68 for males (Table 2).

4 | DISCUSSION

The verification of the species that comprise a given population is a critical step in the stock assessment of the genus *Albula* because there is considerable variation in life-history characteristics across its

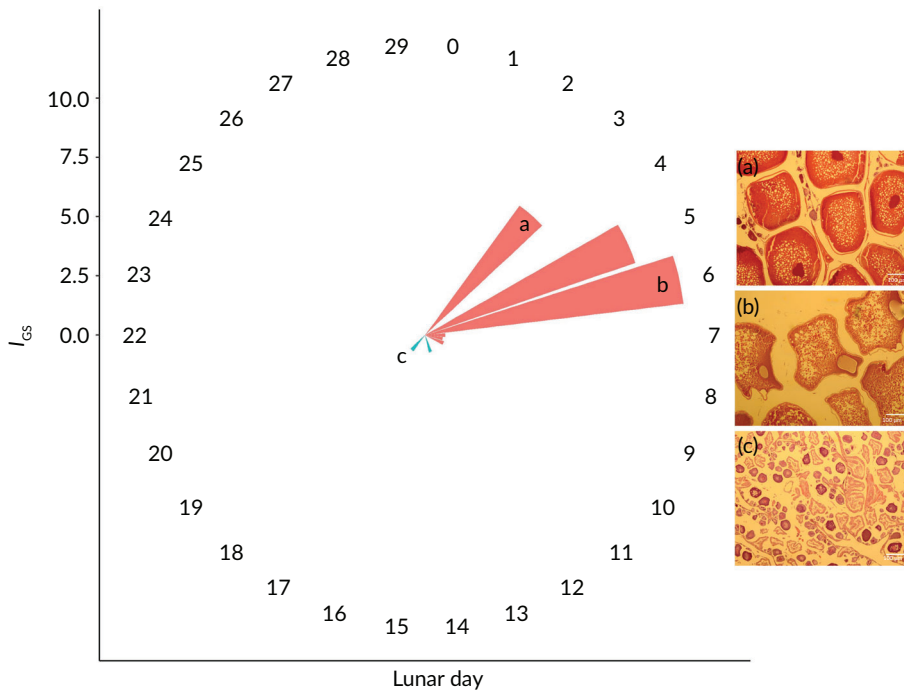


FIGURE 5 Clock diagram of the mean gonado-somatic index (L_{GS}) of female *Albula glossodonta* plotted against the number of days following the full moon (Lunar day 0). ■, The waning gibbous moon phase; ■, the last quarter moon phase; a, b, c, correspond to the histology images of the sampled gonads during the given lunar day: (a) spawning capable vitellogenic stage 3; (b) actively spawning germinal vesicle migration; (c) regressing; i.e., spent

worldwide distribution and *Albula* spp. are a cryptic species complex and can be difficult to identify by their morphological characteristics alone (Adams *et al.*, 2007; Ault, 2007; Burger, 1974; Colborn *et al.*, 2007; Crabtree *et al.*, 1994; Crabtree and Harnden, 1997; Donovan *et al.*, 2015; Pfeiler *et al.*, 2000; Shaklee and Tamaru, 1981). Previous research indicates that *A. glossodonta* is the primary species of *Albula* found on shallow water flats in the atolls of the Indo-Pacific, including the nearby Tetiaroa Atoll (Wallace, 2015). The broadly rounded lower jaw in *A. glossodonta* distinguishes it in the field from *A. virgata* Jordan & Jordan 1922 and other sharp-jawed *Albula* spp. species, with a more angular lower jaw with a pointed symphysis (Colborn *et al.*, 2007; Donovan *et al.*, 2015; Shaklee and Tamaru, 1981). Our field observations of *Albula* spp. were all consistent with this description and genetic tests of a sub-sample of fish indicated that *A. glossodonta* is present on Anaa Atoll. Though it remains possible that other species remain to be discovered, this is a new record for the distribution of this species and here we provide the first description of its life history in a closed atoll in the South Pacific Ocean, where it is threatened by a wide range of anthropogenic activities (Wallace, 2015).

Age and growth has been previously studied in the *Albula* genus, yielding von Bertalanffy growth coefficients (K) ranging 0.18–0.30 (Ault *et al.*, 2007; Crabtree *et al.*, 1994; Donovan *et al.*, 2015; Friedlander *et al.*, 2007). The growth parameters $L_{\infty} = 67$ cm L_F and $K = 0.18$ observed in Hawaiian *A. glossodonta*, suggests slower growth than our estimates for both female and male *A. glossodonta* in Anaa. This difference may be attributed to combining male and female *A. glossodonta* into a single growth-rate estimate (Donovan *et al.*, 2015), food availability, or the distance from the equator with Anaa (17.4° S) being closer than Hawaii (21° N) resulting in warmer year-round temperatures and faster growth rates. In the Florida Keys, USA (25° N), Crabtree *et al.* (1994) found slight differences in the growth

rates of female and male *A. vulpes* (L. 1758), with L_{∞} values of 68 and 67 cm L_F and K of 0.279 and 0.242, respectively. In contrast, we found substantial differences in sex-specific growth parameters, with male growth characterised by a rapid approach to their inferior growth asymptote, while females exhibited slow continual growth to a, 20 cm greater difference in their average maximum size. These differences in growth for *A. glossodonta* might be attributed to natural sexual dimorphism that is commonly displayed in broadcast spawners, with females attaining larger sizes to increase potential fecundity (Blanckenhorn, 2005; Parker, 1992).

This study is the first, as far as we are aware, to investigate sex specific age and growth in a exploited *Albula* spp. population and in this context, it is unclear whether the differences in growth are a result of males investing more energetic resources into reproductive behaviour as opposed to somatic growth (Mcbride *et al.*, 2015; Rijnsdorp & Ibelings, 1989), differential rates of fishing mortality between the two sexes (Sinclair *et al.*, 2002), or a combination of these two factors. The artisanal trap fishery at Anaa Atoll is a passive gear that targets *A. glossodonta* spawning aggregations as they move between the lagoon and ocean; sexually dimorphic spawning behaviour, in which males spawn more frequently than females, could increase exposure to the traps and fishing mortality (Henson & Warner, 1997; Secor, 2015). There is some evidence in the literature to support this theory, as in locations where albulid spawning aggregations are harvested (e.g., Tarawa, Kiritimati and Hawaii), females are larger than males (Beets, 2000; Donovan *et al.*, 2015; Johannes & Yeeting, 2000; Kamatie *et al.*, 1995), but no size differences between sexes have been found in localities with limited to no harvest (Ault *et al.*, 2007; Friedlander *et al.*, 2007). Furthermore, in a similar fishery at Tarawa Atoll, significant changes in the species contribution to the overall catch, sex ratio and a 10 cm decline in mean length and size at

maturity were observed over a period of 15 years, suggesting that fisheries can be a significant source of variation in the observations of life-history parameters in exploited *Albula* spp. populations (Adams *et al.*, 2014; Beets, 2000).

Albula spp. are generally thought of as long lived, with the maximum life span of *A. vulpes* estimated at 20 years (Ault *et al.*, 2007). We found *A. glossodonta* of the same age on Tetiaroa Atoll, suggesting that 20 years is an appropriate estimate of t_{\max} for *A. glossodonta*. However, the relatively young maximum and average ages that we observed in the *A. glossodonta* population on Anaa Atoll (despite a much larger sample size from this location) suggests this population is heavily exploited. The age structure of a fished population is often truncated as a result of fishing gears targeting older fish and serially removing them from their population (Beverton & Holt, 1957; Hsieh *et al.*, 2010). This trend has been observed in *A. vulpes* where it is exploited by subsistence fisheries (Rennert *et al.*, 2019) and the oldest *A. glossodonta* we found in our sample was 10 years with 88% of these being <7 years old. In comparison, the maximum observed age of *A. glossodonta* in Hawaii in 2015 was 15 years, with results from a smaller sample size in a location with an active recreational and small-scale commercial fishery (Donovan *et al.*, 2015; Kamikawa *et al.*, 2015). With this in mind, the Hawaii state record for *A. glossodonta* was captured in, 1954 and still stands today at 18 lbs., 2 oz. (c. 8.25 kg; www.hawaiifishingnews.com/records_d.cfm?ID=65). According to the age and growth models presented by Donovan *et al.* (2015), this fish would have been c. 88 cm L_F (well beyond their L_{∞} estimate of 67 cm L_F) and could have been 30+ years old, suggesting a significant decline in the t_{\max} of this population (Donovan *et al.*, 2015). These results and the discrepancy of t_{\max} between Tetiaroa and Anaa (two similar atolls), highlight the importance of obtaining age and growth characteristics from virgin populations and or historical context as a baseline, from which the exploited status of fish populations can be assessed (Jackson *et al.*, 2001; McClenachan, 2009; Taylor *et al.*, 2014). Although some juvenile *A. glossodonta* are harvested during high-wind events on Anaa, *A. glossodonta* are not fully recruited to the trap fishery until they reach sexual maturity and our results suggest that fishing mortality is probably very high and reduces the abundance of older, mature fish in the population. These results are of concern, given the preservation of these larger more fecund fish is essential and a well-established paradigm in sustainable fisheries (Berkeley *et al.*, 2004; Froese, 2004).

The size at maturity for *A. glossodonta* is larger in Anaa than Hawaii, where males are sexually mature at 41 cm L_F and females are mature at 43 cm L_F (Donovan *et al.*, 2015) and this may be attributed to the differential growth rates between the two locations. Our estimate of size and age at maturity were most similar to that of *A. vulpes* in the Atlantic Ocean, where male *A. vulpes* were estimated to be mature at 42 cm L_F (3 years) and 49 cm L_F (4 years) for females (Crabtree & Harnden, 1997). These differences in maturation between sexes indicate that males recruit to the artisanal trap fishery a year earlier than females and are exposed to fishing mortality at a younger

age; another possible explanation for these differences in the size and age structure of the two sexes at Anaa Atoll.

Our results indicate that *A. glossodonta* exhibits group synchronous oocyte development and are consistent with the reproductive physiology of *A. vulpes* (Luck *et al.*, 2018; Mejri *et al.*, 2018). The gonads of all female *A. glossodonta* that had returned from spawning were completely spent with few remnant hydrated eggs loose in the body cavity and only early stages of oocyte development remaining (*i.e.* PG, CA). Additional research is needed to determine the nutritional requirements and the temporal time scale for the recruitment of these under developed oocytes in to the VT3 stage, but our results suggest *A. glossodonta* are capable of multiple spawning events during a given annual cycle. This in conjunction with the significant relationship between body mass and batch fecundity highlights the importance of larger female *A. glossodonta* to the population, as these females could be producing upwards of 3 million eggs year⁻¹ (*i.e.*, 1 million per batch). Furthermore, the concept of a mega-spawner is applicable to the assessment of these fisheries as large older *A. glossodonta* are contributing more eggs per individual than their smaller conspecifics (Froese, 2004).

The size-selective mortality of the artisanal fishery probably limits both the reproductive output of this population to other atolls in the Tuamotu Archipelago and larval self-recruitment to Anaa Atoll. *Albula* spp. leptocephali exhibit extended planktonic larval durations from 41 to 72 days (Friedlander *et al.*, 2007; Mojica, 1995); larval exchange can therefore occur across a wide seascape (Zeng *et al.*, 2018). A source-sink dynamic may facilitate the persistence of this population under sustained fishing pressure if recruitment from other atolls is high (Armsworth, 2002; Bode *et al.*, 2006; Crowder *et al.*, 2000). However, previous studies have highlighted the importance of self-recruitment to isolated marine ecosystems like that of Anaa Atoll (Abesamis *et al.*, 2016; Almany *et al.*, 2007; Jones *et al.*, 1999, 2005; Mora *et al.*, 2002) and many reef fish are known to spawn in areas with oceanic gyres that permit both short distance dispersal and larval retention within their respective ecosystems (Johannes, 1978). The migratory corridors and small passageways in the reef where *A. glossodonta* presumably exit the atoll to spawn are consistent with this hypothesis, in that they are all located in the north-east of the atoll and the predominate wind and swell direction comes from the south-west, suggesting that a stable eddy pair may facilitate self recruitment (Johannes, 1981). A parentage analysis would yield vital information regarding this aspect of this species management (Planes *et al.*, 2009). Nonetheless, regardless of the mechanism, larval recruitment can be highly variable with environmental conditions, such as prevailing currents and the fishery should be managed on a local scale to insure sustainable yields (Basterretxea *et al.*, 2013; Zeng *et al.*, 2018).

Our results indicate that *A. glossodonta* exhibit a protracted spawning season throughout the austral autumn and winter and this corresponds to the seasonal periodicity of spawning in the northern hemisphere where Hawaiian *A. glossodonta* spawn November–April (Donovan *et al.*, 2015). These findings in *A. glossodonta* are consistent with that of *A. vulpes* in the western Atlantic Ocean, suggesting that

the genus spawns during the cooler months (Crabtree & Harnden, 1997; Danylchuk *et al.*, 2011). The lunar periodicity in albulid spawning is well-documented in the traditional knowledge of Pacific islanders and in Tarawa, pre-spawning aggregations form during the 3 days prior to the full moon and spawning is believed to occur during the full moon (Johannes & Yeeting, 2000). These findings were corroborated on Palmyra Atoll where the highest I_{GS} occurred during the full moon (Friedlander *et al.*, 2007). However, our results indicate that spawning movements and gonad development of *A. glossodonta* at Anaa Atoll occur during the waning gibbous moon, with the night of spawning occurring 5–6 days after the full moon. Prior to this study, the advanced stages of oocyte maturation (*i.e.*, GVM, GVBD and hydration) indicative of an imminent spawning event had never been observed in albulids. Previous authors have hypothesised that these final development stages occur during the transition from pre-spawning aggregation sites to the location of reproductive events over a period of several hours (Adams *et al.*, 2018; Danylchuk *et al.*, 2011, 2019; Luck *et al.*, 2018; Mejri *et al.*, 2018). Our results advance our understanding of the reproductive strategies for this genus and provide the first empirical evidence to support this theory, as oocyte development from VT3 to GVM and GVBD were observed over a period of 12–24 h, while transitioning from pre-spawning aggregation sites to oceanic habitats were they reproduce (Adams *et al.*, 2018; Danylchuk *et al.*, 2011).

Our estimates of natural mortality were variable between the different empirical approaches, a common issue with these methodologies (Hewitt & Hoenig, 2005; Then *et al.*, 2015, 2018; Vetter, 1987). The estimates derived from the Hoenig (1983) and Hoenig_{nlis} equations were the most consistent with previous estimates of natural mortality in the genus, which ranged 0.2–0.3 (Crabtree *et al.*, 1994; Friedlander *et al.*, 2007). Interestingly the Pauly (1980) method yielded sex-specific natural mortality rates based on their differential growth characteristics and it seems plausible that differences in spawning behaviour between the two sexes could increase predation risk or reduce nutrition and result in unequal natural mortality (Gunderson & Dygert, 1988). However, previous research suggests that our Pauly (1980) estimates maybe unreasonably high (Kenchington, 2014; Then *et al.*, 2015). Friedlander *et al.* (2007) analysed the length frequency distribution of the *A. glossodonta* stock in Palmyra Atoll, which provides an estimate of natural mortality (0.27) in a virgin population at a Pacific atoll with high predator densities similar to that of Anaa Atoll (Lennox *et al.*, 2017). Given the uncertainty regarding the estimation of these parameters, historic failure of analogous fisheries and traditional ecological knowledge of the community citing significant declines in *A. glossodonta* abundance, we recommend the more conservative Hoenig (1983) estimate of 0.21 for both sexes in the assessment of this population.

4.1 | Management implications

Thriving ecotourism-based economies exist in the Pacific islands where albulid fisheries have been managed (*i.e.*, Christmas Island and Aitutaki, Cook Islands). However, no long-term recreational fisheries

exist in those island communities where albulid harvest has not been regulated and their artisanal fisheries yields have declined (Allen, 2014; Beets, 2000; Cook Islands Government, 2010; Friedlander *et al.*, 2007). Our results provide biological evidence that the *A. glossodonta* population at Anaa Atoll is heavily exploited and requires a comprehensive fisheries assessment to guide the management of the artisanal trap fishery. To this end, this work provides the basic biological parameters that are prerequisites for the assessment of this fishery and others in the region with data-limited fisheries models such as an age-structured catch curve, the Spawning potential ratio (SPR) or the Froese sustainability indicators (Froese, 2004; Hordyk *et al.*, 2015; Thorson and Prager, 2011).

The documentation of the seasonal reproductive cycle and lunar peaks in gonad development indicates the time of the year and month when this species is most vulnerable to overharvest and could benefit from the resurgence of the community's traditional form of spatio-temporal resource protections known as *Rahui* (Bambridge, 2016; Torrente, 2015). Given the prolonged spawning season, a partial closure of the trap fishery during the waning moon phase for a portion of the annual spawning season would ensure the escapement of a segment of the spawning stock, reduce mortality and improve the sustainability of the fishery.

Ultimately, the results of this research provided the community of Anaa Atoll with the essential prerequisites for the assessment of their fishery. In response to the data provided by this research, the local primary school and government established an educational managed marine area (EMMA) that overlaps with the *A. glossodonta* migratory corridor adjacent to Tukahora village (www.aires-marines.com/content/view/full/16746). This included a plan to institute a temporal *Rahui*, in which the artisanal fish traps are deactivated and *A. glossodonta* spawning aggregations are protected during three months (*i.e.*, ~1/3rd) of the spawning season (www.radio1.pf/anaa-aire-marine-educative/). This resurgence of traditional community-based management will probably improve the sustainability of the artisanal fishery and pave the way for development of community-based ecotourism. In this context our results provide an important demographic baseline in evaluating the recovery of this fishery.

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CONTRIBUTIONS

A.F. contributed to study design, field work, laboratory work (otoliths and gonads), data analysis and manuscript preparation. R.J.L. contributed to field work, data analysis and manuscript preparation. R.R.C. contributed to the analysis bonefish DNA sequences and manuscript preparation. A.M.F. contributed to study design and manuscript preparation. E.E.G.C. contributed to study design and manuscript preparation. Finally, A.J.D. contributed to study design, manuscript preparation and project funding.

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SUPPORTING INFORMATION

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