Preliminary life history of the Critically Endangered bottlenose wedgefish *Rhynchobatus australiae* from Southeast Asia

Brooke M. D'Alberto[1,2,*], Naomi Clark-Shen[3,4], Kathy Xu Tingting[4],
Madeline E. Green[2], Neil Hutchinson[3], Andrew Chin[1], Colin A. Simpfendorfer[1]

[1]Centre for Sustainable Tropical Fisheries and Aquaculture & College of Science and Engineering,
James Cook University, Townsville, 4811 Queensland, Australia
[2]CSIRO Oceans and Atmosphere, Hobart, 7000 Tasmania, Australia
[3]Tropical Futures Institute, James Cook University, Singapore 387380
[4]The Dorsal Effect, Singapore 573969

ABSTRACT: The bottlenose wedgefish *Rhynchobatus australiae* has experienced substantial population declines throughout its range. However, there is a lack of life history information (age, growth, and maturity) available for this species to inform conservation and management efforts. A total of 48 *R. australiae* samples were purchased from 2 fishing ports in Singapore between July 2018—July 2019. Species identification was confirmed by mtDNA barcoding using the NADH2 region. Length of specimens ranged from 506—1645 mm total length (TL), and ages ranged from 0—11 yr. Multi-model analysis was used to estimate growth parameters using a Bayesian approach with informative priors. The von Bertalanffy model was the best fitting growth model for the combined sexes (L_∞ = 2814 mm TL; L_0 = 517 mm TL; k = 0.07 yr^{-1}), for females only (L_∞ = 3053 mm TL; L_0 = 504 mm TL; k = 0.06 yr^{-1}), and for males only (L_∞ = 2741 mm TL; L_0 = 497 mm TL; k = 0.07 yr^{-1}). Preliminary results indicate that females and males may mature at different ages and lengths, with females (A_{50} = 3.25 yr; L_{50} = 1014 mm TL) matured younger and at smaller sizes, than males (A_{50} = 5.03 yr; L_{50} = 1197 mm TL). *R. australiae* has an estimated theoretical longevity of 40 and 47 yr for males and females, respectively. This study provides the first preliminary species-specific life history information for *R. australiae*, suggesting that this species in Southeast Asian waters is slow-growing. This information will further the biological knowledge available for this species and can be used to help design effective management and conservation measures.

KEY WORDS: Age and growth · Maturity · Reproduction · Bayesian analysis · Multi-model inference method

1. INTRODUCTION

Accurately describing the life history parameters (age, growth, and reproduction) of a species is the foundation for understanding species biology, population dynamics, and status. For species exposed to fishing, characterising these parameters is important for fisheries stock assessment, management, and conservation, especially for long-lived, slow-growing, late-maturing, and less-fecund species, such as chondrichthyans (sharks, rays, skates, and chimaeras) (Cortés 2002). Coupled with available knowledge of distribution, movement, and abundance, this information can be used to predict how a species might respond to fishing pressure (Harry et al. 2011), estimate sustainability of catches (Cailliet 2015), under-

*Corresponding author: brooke.dalberto@outlook.com

stand potential benefits of marine protected areas (Dwyer et al. 2020), and predict how quickly a species could recover from population declines (Dulvy et al. 2014, D'Alberto et al. 2019).

Bottlenose wedgefish *Rhynchobatus australiae* is a large (maximum size: 3230 mm total length [TL]) (Faizah & Chodrijah 2020) shark-like ray widespread throughout tropical and temperate waters in the Indo-West Pacific Ocean from Mozambique to northern and eastern Australia (as far south as Ballina, NSW; Colefax et al. 2021) and Fiji (Giles et al. 2016, Last et al. 2016). It is found primarily in soft benthos areas. The species is frequently observed at depths of 30—40 m (White et al. 2013b), with a depth range of 0—100 m (Kyne et al. 2019a, B. M. D'Alberto unpubl. data). *R. australiae*, like other wedgefish species, is lecithotrophic viviparous, with a reported litter size between 7 and 19 pups (White & Dharmadi 2007, Last et al. 2016, Mull et al. 2020). *R. australiae* is assessed as Critically Endangered on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, as it has experienced significant declines throughout its entire range (Kyne et al. 2019a). It is mainly caught as bycatch in fishing gears such as trawl nets, bottom set longlines, purse seine nets, and gillnets, and is typically retained as valuable by-products of incidental catch (Jabado 2018).

R. australiae is the most commonly caught wedgefish species across Southeast (SE) Asia (Giles et al. 2016). Wedgefish products are consumed domestically in many SE Asian countries (e.g. meat), and are also exported internationally (e.g. fins) (Choo et al. 2021, Choy et al. 2022). *R. australiae*, along with 9 other wedgefish species and 6 species of giant guitarfish (Family Glaucostegidae), were listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2019 due to concerns that international trade of products and subsequent fishing pressure were driving the species declines. Singapore plays a significant role in the global trade of chondrichthyan products, and imported significant amount of wedgefish, mainly from Indonesia and Malaysia, prior to the CITES listing (Boon 2017, Choy et al. 2022). However, the current import and demand, if any, for wedgefishes in Singapore is unknown and requires further research. The high value of the fins in international trade and the high-quality flesh in domestic markets are considered key drivers for their historical and current retention in coastal fisheries (Keong 1996, Wu 2016, Hau et al. 2018, Haque & Spaet 2021), particularly as a protein source in many resource-scarce coastal communities. The development of robust conservation and fisheries management measures for *R. australiae* highlight the need for research on this species, including accurate and regionally appropriate biological information.

Despite its wide distribution and high interaction with fisheries, there is limited life history information available for *R. australiae.* Wedgefish species are typically identified based on snout and fin morphology and pectoral fin spot patterning, and identification between wedgefish species can be difficult (White et al. 2013a, Jabado 2018, Kyne et al. 2020). There have been historical difficulties in identifying the species compared to other 'look-alike' wedgefish species due to similarities in morphology, such as white-spotted wedgefish *R. djiddensis*, eyebrow wedgefish *R. palpebratus*, broadnose wedgefish *R. springeri*, roughnose wedgefish *R. cooki*, and smoothnose wedgefish *R. laevis* (White et al. 2013a, Jabado 2018, Kyne et al. 2020). Substantial errors in life history estimates such as growth completion rates can be introduced when misidentified individuals are included within a life history analysis (Smart et al. 2016a). Life history information for *R. australiae* is limited to 1 study in eastern Australia, where the similar morphological characteristics between wedgefish species have provided variable life history parameters. White et al. (2014) estimated a growth completion rate of 0.40 yr^{-1} for a *Rhynchobatus* spp. species complex of *R. australiae*, *R. palpebratus*, and *R. laevis* at the time of publication. Recent taxonomic revision has resolved this species complex, with *R. laevis* primarily found in the Arabian Sea and the Bay of Bengal in the Indian Ocean, and off China and Japan in the Western Pacific (Last et al. 2016). Meanwhile, further examination of genetic analysis associated with specimens examined by White et al. (2014) has demonstrated that the Australian east coast samples were primarily *R. australiae* (D'Alberto et al. 2019). Upon re-analysis, using 3-parameter frequentist multimodel growth analysis data from White et al. (2014) by D'Alberto et al. (2019), the growth completion rate for *R. australiae* was estimated to be 0.08 yr^{-1}, considerably slower than originally estimated, with the von Bertalanffy growth model (VBGF) as the most appropriate function. The estimated age at maturity of females and males was between 3 and 5 yr old for eastern Australian population (D'Alberto et al. 2019). There is a paucity of information on age, growth, longevity, and reproductive biology for *R. australiae* throughout its distribution, including SE Asia. Life history traits of chondrichthyan species can differ between conspecific populations (Rigby & Simpfendorfer 2015, Bradley et al. 2017). There is evidence of

population separation for *R. australiae* between eastern Australian and SE Asian populations based on genetic analysis (Giles et al. 2016), which may result in intra-specific variations in life history parameters due to regional differences in environment and available resources, reflecting varying population dynamics and resilience to exploitation.

This study aimed to provide preliminary species-specific life history parameters for *R. australiae* sourced from 2 Singaporean fishery ports. A Bayesian growth modelling approach was undertaken, with the use of informative priors to help improve the biological plausibility of the growth estimates, due to the limited sample size and absence of large individuals (Smart & Grammer 2021). DNA barcoding was conducted to validate species identification, as morphological characteristics have proved variable in other studies (White et al. 2014). Species-specific information on the life history of *R. australiae* can be used to build the basis for the development of regional management plans and conservation action for these threatened rays.

2. MATERIALS AND METHODS

2.1. Sample and data collection

Samples were purchased by Singapore-based enumerators (N. Clark-Shen and K. X. Tingting) from fish merchants at 2 government-run facilities: Senoko Fishery Port (SFP) in the north (domestic fishing vessels) and Jurong Fishery Port (JFP) in the south (foreign fishing vessels) (Singapore Food Agency 2019). Sampling trips where wedgefish were purchased were conducted twice per month in July, August, October, and December 2018 and January, February, June, and July in 2019, during surveys reported in Clark-Shen et al. (2021). These ports received whole, fresh products, and are separate from the ports in Singapore that received dried goods such as dried shark fins. Local and regional fishing boats and trucks deliver seafood to the fishery ports during the early morning hours. For half of the survey period, JFP was surveyed before SFP, and for half of the survey period, SFP was surveyed before JFP to gain insights into the port activity at various times. The 2 ports were surveyed on the same morning between 00:30 and 04:00 h (e.g. SFP from 00:30 to 01:30 h, and then JFP from 02:00 to 04:00 h). The country and port of origin recorded by the Singapore-based enumerators was used to assign fishing countries and export points for wedgefish. The purchase prices were converted from Singapore dollar (SGD) to US dollar (USD) prices using an online currency converter (www.xe.com/currencyconverter/; 1 USD = 1.33 SGD as of April 2023) (Table S1 in Section S1 in the Supplement at www.int-res.com/articles/suppl/n053p363_supp.pdf).

Wedgefish collected were brought back to the laboratory and stored frozen until dissection. The wet weight (kg) and length measurements were recorded once the samples were thawed prior to dissections. Stretched TL (length from the tip of the snout to the furthest tip of the tail) was recorded for wedgefish samples with fins attached upon purchasing, as well as fork length (FL; length from the tip of the snout to the centre/fork of the tail) and pre-caudal length (PCL; length from the tip of the snout to the deepest part of the pre-caudal notch). For those specimens with dorsal, second dorsal, and caudal fins removed prior to purchasing, the PCL was recorded and converted to TL using the following equation that was developed from recorded lengths from this study and unpublished data (Fig. S1 and Table S2 in Section S2):

$$TL = PCL \times 1.2175 - 13.305; \; r^2 = 0.99 \qquad (1)$$

A segment of the vertebral column (~10 cm length) was removed from between the cranium and first dorsal fin, including a section of the cervical synarcual, which is a section of fused vertebral column located behind the cranium (Fig. 1A), and stored frozen for subsequent age determination. Photographs were taken of each individual before processing.

2.2. DNA barcoding of tissue samples for species identification

During the vertebral processing, tissue samples for DNA barcoding were excised from the vertebral chord or remaining muscle around the vertebral chord and preserved in 100% analytical-grade ethanol. DNA from vertebral chord or muscle samples was extracted using the DNeasy Blood & Tissue Kit (Qiagen) following manufacturer's instructions and with starting material of approximately 0.25 g. Genetic species identification was undertaken using the NADH2 region of the mitochondrial genome with the primers ILEM (5'-AAG GAG CAG TTT GAT AGA GT-3') and ASMN (5'-AAC GCT AGC TGT TAA TT AA-3') (Naylor et al. 2005). PCRs were undertaken in 25 µl volumes using the Multiplex PCR kit (Qiagen), 10 µM primers, and DNA (15−25 ng). PCR used the following thermocycler parameters: initial hold at 95°C for 15 min, 30 cycles of 94°C for 30 s, 50°C for 90 s, 72°C
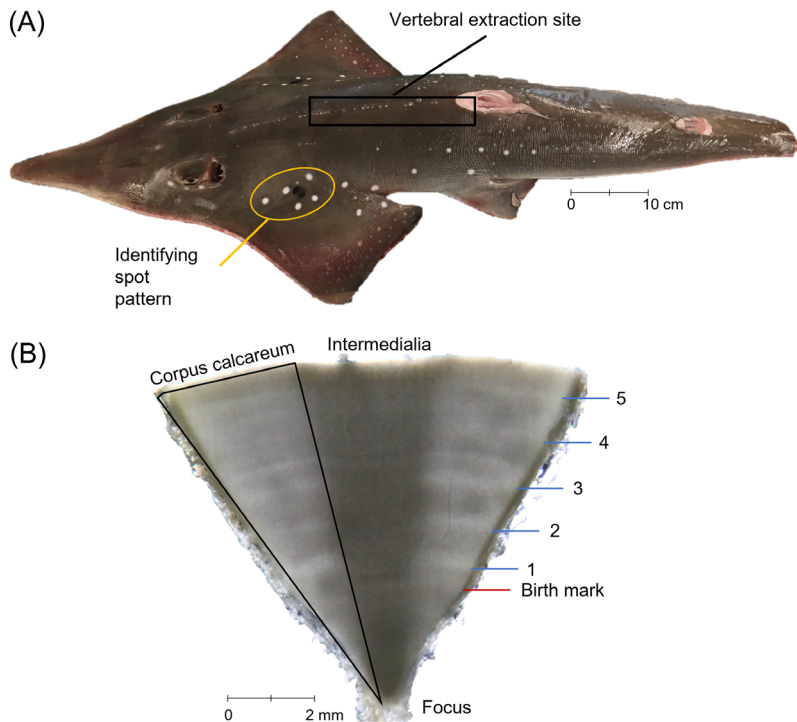
Fig. 1. (A) Illustration of bottlenose wedgefish *Rhynchobatus australiae* highlighting the line of 3 white spots (yellow circle) diagnostic in this species when visible, and location of the vertebral extraction site for age and growth analysis (black rectangle). (B) Photograph of a section of vertebral centra for male *R. australiae*, aged to 5 yr old at 966 mm total length, sampled from Jurong Fishery Port in Singapore in July 2019. The location of the birth mark (red line), corpus calcareum, focus, intermedialia, and estimated vertebral bands (blue lines) is indicated

vertebral centra were separated and soaked in 5% sodium hypochlorite solution for up to 30 min to remove residual soft tissues. Centra were thoroughly rinsed under tap water and dried in an oven at 60°C for 24 h. The largest centrum with no to minimal defects (e.g. scalpel cuts, staining) was selected to be sectioned. A low-speed rotary saw with twin diamond-tipped blades (Buehler) was used to take longitudinal sections (400 µm thick) through the focus (centre of the vertebrae) of individual centra. The sections were mounted onto microscope slides using Crystal Bond adhesive (SPI Supplies) for analysis and storage. Centra that were too small to be loaded into the chuck of the sectioning saw were sectioned by hand sanding. Single centra were mounted onto a microscope slide using Crystal bond adhesive and sanded under 20 mm of water towards the centre of the centrum using 400 grit wet and dry abrasive papers. Once one side was completed, the centrum was remounted and sanded again on the other side until the desired thickness was achieved (Simpfendorfer 1993).

for 90 s, followed by final extension of 72°C for 10 min. Following PCR, products were cleaned with Agencourt AMPure magnetic beads (Beckman Coulter). Successfully amplified PCR products were sent to the Australian Genome Research Facility (AGRF) for bidirectional Sanger sequencing. Forward and reverse sequences were assembled into consensus sequences using Geneious® Prime (Biomatters; www.geneious. com). Consensus sequences were aligned within Geneious and sequence identity was confirmed by using the BLAST module in Geneious against known and validated ND2 sequences of *Rhynchobatus springeri*, *R. palpebratus*, and *R. australiae* provided by G. Naylor.

2.3. Vertebrae preparation and processing

Vertebral preparation and sectioning followed standard protocols detailed in Cailliet & Goldman (2004). After thawing, the haemal arch, neural arch, and muscle flesh were removed using a scalpel. Individual

2.4. Age determination

Digital images of sectioned centra were taken under transmitted light using a Leica M165C dissecting microscope with a Canon EOS 6D (WG) digital camera. Samples were counted independently by 3 experienced readers (B. M. D'Alberto, C. A. Simpfendorfer, and A. Chin) without any prior knowledge of the length or sex of the individual to minimise bias in the age estimates. The birth mark was identified by the change in angle of the inner margin of the corpus calcareum, demonstrating the transition from pre- to post-natal growth and was considered to be age zero (Fig. 1B). Age estimates were generated by counting the visible opaque bands in the corpus calcareum. The spacing and clarity of bands, inflections near the outside and inside edges of the corpus calcareum, and band continuity across the intermedialia were used to help distinguish true bands from checks (McPhie & Campana 2009). Marginal increment analysis was not conducted to validate the periodicity of the growth band pair formation, as samples could not be col-

lected every month. Band pairs were assumed to be annual, based on the marginal increment analysis of a similar-sized species of shark-like rays, blackchin guitarfish *Glaucostegus cemiculus* (Enajjar et al. 2012), and considered preliminary (Fig. 1A). Section quality was rated on a scale of 0 (unreadable) to 4 (very clear banding), with quality being dependent on criteria such as band clarity along the corpus calcareum and closeness of the sagittal cut to the focus (McPhie & Campana 2009).

Samples with differing counts between readers were re-examined collaboratively and a consensus age was agreed upon. If no consensus age could be agreed, then the samples were excluded from the analysis. Systematic bias of the growth band estimates between the 3 readers (1 vs. 2, 1 vs. 3, and 2 vs. 3) was investigated with the unpooled Bowker's tests of symmetry, using the 'ageBias' function in the FSA package (Ogle et al. 2020). Pairwise age bias plots were generated for each iteration of reader estimates. Inter-reader precision was assessed using percentage agreement of samples for which all age estimates perfectly agree (PA), Chang's coefficient of variation (CV), and average percentage error within a sample using mean as the divisor (APE), with the 'agePrecision' function in the FSA package (Ogle et al. 2020).

2.5. Growth modelling

A multi-model framework was applied to the length-at-age data for 3 candidate growth functions chosen *a priori*: VBGF, Gompertz, and logistic growth models (Thorson & Simpfendorfer 2009, Smart et al. 2016b) (our Table 1). The use of a multi-model framework generates the most robust growth estimates and

avoided the possibility of using an inappropriate model, as the use of a single model such as the VBGF can bias growth estimations if it is unsuitable for the species' growth (Katsanevakis 2006, Smart et al. 2016b).

Growth was estimated in a Bayesian framework using Markov chain Monte Carlo simulation (MCMC) to overcome the low number of length-at-age observations and the absence of large individuals. A frequentist approach was also applied; however, due to the lack of large individuals, the Bayesian approach was deemed more appropriate (see Text S1, Table S3, and Fig. S2 in Section S3). Bayesian models were fit using the 'BayesGrowth' package (v. 0.3.5) (Smart 2021) by using R statistical software (v. 4.2.2, R Core Team 2021), in accordance with the methods described in Smart & Grammer (2021). Four MCMC chains with 10000 iterations, with a burn-in period of 1000 iterations, were used to determine the parameter posterior distributions. A thinning rate of 10 was applied to overcome autocorrelation between iterations. Model convergence was assessed by computing the Gelman-Rubin statistic *Rhat* and assessment of the mixing of the 4 MCMC chains, with diagnostic plots generated using the 'Bayesplot' package (v. 1.10.0) in R.

Models were fit to length-at-age data for both sexes combined, females only, and males only. Each model was fit with a normal residual error structure (σ). Prior distribution for asymptotic length (L_∞) was informed by reported maximum length for females (3230 mm TL) (Faizah & Chodrijah 2020). It was assumed that males reached a maximum size of 3000 mm TL, based on the previous known maximum size of the species (Kyne et al. 2019a), and the assumption of sexual dimorphism where male *R. australiae* attain a smaller maximum size than females (Cortés 2000). The reported length at birth (L_0) was 460−500 mm (White & Dharmadi 2007) and the smallest individual in this study was 506 mm. Given this information, normally distributed priors (μ, σ) were set at $L_\infty \sim N(3230, 323)$ and $L_0 \sim N(488, 25)$ for sexes combined and females only. Additionally, a prior of $L_\infty \sim N(3000, 300)$ was used for males only. The parameter estimates for growth-completion coefficient (k for VBGF, g_{Gom} for Gompertz, and g_{Log} for logistic) of each growth model were estimated using the 'Estimate_MCMC _growth' wrapper function. A non-

Table 1. Model equations of the 3 candidate growth functions used to estimate the growth parameters of bottlenose wedgefish *Rhynchobatus australiae* collected at 2 Singapore fish markets. VBGF: von Bertalanffy growth function; L_T: length at age T; L_∞: asymptotic length; L_0: length at age 0; k, g_{Log}, and g_{Gom}: growth-completion coefficients of the respective models

Model	Growth function equation	Reference
VBGF	$L_T = L_0 + (L_\infty - L_0)[1 - \exp(-kT)]$	Von Bertalanffy (1938)
Logistic function	$L_T = \dfrac{L_\infty - L_0\,[\exp(g_{\text{Log}})]}{L_\infty - L_0\,[\exp(g_{\text{Log}} - 1)]}$	Ricker (1979)
Gompertz function	$L_T = L_0\,e\ln\left(\dfrac{L_\infty}{L_0}\right)(1 - e^{-g_{\text{Gom}}})$	Ricker (1975)

informative prior was used for σ and a common non-informative prior was used for the growth coefficients of the 3 candidate models (Table 1). A lower and upper bound was nominated for uniform distribution of k of 0 and 1.0 yr^{-1} respectively. An upper bound was nominated for the uniform distribution of σ of 1000. The common non-informative prior for the growth coefficients allowed for the comparison of 3 candidate growth functions, each with identical priors (Smart & Grammer 2021).

The best fitting growth model was identified using the 'Compare_Growth_Models' function in the 'BayesGrowth' package (Smart 2021). This was conducted by using the 'leave one out' (LOO) cross validation analysis and the widely applicable information criterion (WAIC). The leave-one-out information criterion (LOOIC) and LOOIC weights (LOOICw) were calculated, of which the model with the lowest weights was selected to be the most appropriate growth model. These 2 functions are equivalent to Akaike's information criterion weights (AICw) (Akaike 1998) for frequentist model selection (Smart & Grammer 2021). The growth curves for all 3 models were constructed using the 'Calculate_MCMC_growth_curve' function in the 'BayesGrowth' package (Smart 2021).

Where the VBGF was the best fitting growth model, estimates of longevity were calculated:

$$T_{max} = \left(\frac{1}{k}\right) \times \ln\left[\frac{L_\infty - L_0}{(1-x) \times L_\infty}\right] \qquad (2)$$

where T_{max} is the longevity in years, k is the growth coefficient of the VBGF, L_∞ is the asymptotic length, L_0 is the length at birth, and x is the proportion of L_∞ reached at T_{max} for which age at which 95% and 99% of L_∞ is reached (Dureuil et al. 2021).

2.6. Reproductive biology

The internal reproductive condition and maturity were recorded for all samples. For males, clasper calcification was recorded (Table 2) and clasper lengths were measured from the tip of the clasper to the point at which the clasper joins the pelvic fin. Males were internally inspected for flowing sperm from the cloaca upon pressure applied to the seminal vesicle or presence of sperm in the clasper groove flowing freely (Stehmann 2002). For females, the uterus condition was inspected internally (Table 2). The number of yolky ova present in the ovary were recorded, where the yolky ovum have a distinct yellow colouration whereas non-yolky ovum were white. The maximum ova diameter (MOD) for the largest ova present in the ovary was measured to the nearest mm.

The maturity of each individual was staged using an index modified from Walker (2005) (our Table 2). For males, the maturity was staged based on the clasper condition and the maturity stage of females were based on the uterus condition (Table 2). The maturity stage data were converted to a binomial maturity category (immature = 0, mature = 1) for statistical analysis. Population estimates of length at maturity were produced for males and females using a logistic regression equation (Walker 2005):

$$P(L) = P_{max} \times \left[1 + e^{-\ln(19)\left(\frac{L-L_{50}}{L_{95}-L_{50}}\right)}\right]^{-1} \qquad (3)$$

where $P(L)$ is the proportion of the population mature at total length (L) and P_{max} is the maximum proportion of mature individuals. The lengths which 50% (L_{50}) and 95% (L_{95}) of the population were mature were estimated using a generalised linear model (GLM) with a binomial error structure with a logit-link func-

Table 2. Reproductive indices used for staging the maturity condition of oviparous and viviparous cartilaginous fishes. Adapted from Walker (2005)

Organ	Index	Description	Binary maturity condition
Females			
Uterus	U = 1	Uteri uniformly thin and white tubular structure. Small ovaries and with no yolked ova	Immature
	U = 2	Uterus thin, tubular structure that is partly enlarged posteriorly. Small yolked ova developing in ovary	Immature
	U = 3	Uterus uniformly enlarged tubular structure. Yolked ova developing in ovary	Mature
	U = 4	Uterus enlarged with *in utero* eggs or embryos macroscopically visible — pregnant	Mature
	U = 5	Uterus enlarged, flaccid and distended tubular structure — post-partum	Mature
Males			
Clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

tion using the Estimate_Len_Maturity function in the AquaticLifeHistory package (v. 0.0.9) (Smart 2019) in the R program environment (R Core Team 2021). The probability of each individual of a given length being mature was produced using 1000 bootstrap iterations of the logistic parameters. Population estimates for age at maturity for the ages when 50% (A_{50}) and 95% (A_{95}) of the population were mature were estimated using the same methods and the Estimate_Age_Maturity function in the AquaticLifeHistory package (Smart 2019).

2.7. Comparison of life history estimates

In order to compare the life history characteristics of *R. australiae* to the eastern Australian population (White et al. 2014, D'Alberto et al. 2019), the VBGF fits were reproduced. Life history parameters for similar-sized 2 giant guitarfish species (family Glaucostegidae) that have life history estimates available, *G. cemiculus* and giant guitarfish *G. typus* (Capapé & Zaouali 1994, Enajjar et al. 2012, White et al. 2014, D'Alberto et al. 2019), were used. The theoretical longevity was calculated using the VBGF parameters for the other population and species.

3. RESULTS

3.1. Sample composition

A total of 51 wedgefish specimens were purchased from JFP (n = 31) and SFP (n = 20) (Table S1) over 8 trips. The majority of the wedgefish were reported to have been imported from Indonesia (n = 35), with 4 samples reported to have been imported from Malaysia, and 12 samples had unknown origins; therefore the study samples will be referred to as the SE Asian population.

Genetic sequencing confirmed that 49 of the specimens were *Rhynchobatus australiae* and 2 samples were *R. palpebratus*, which were excluded from the analysis (see Table S4 in Section S4). One female *R. australiae* with its snout removed below the eyes was excluded from the analysis due to concerns about the length conversions. In total, 28 females with a TL range of

506−1417 mm (Fig. 2A) and 20 males with a TL range of 512−1645 mm (Fig. 2B) were analysed for vertebral and maturity analysis. Thirty-nine wedgefish samples (81%; n = 48) had dorsal, second dorsal, and caudal fins removed prior to the sample collection, with TL range of 631−1645 mm. Nine samples were whole with fins attached upon sample collection (19%), with length range of 506−1122 mm TL.

3.2. Age estimates

The age estimates presented in this study are preliminary, as the assumption of annual deposition of the growth band rings could not be verified by methods such as monthly increment analysis. Estimated ages for *R. australiae* ranged between 0 and 10 yr for females (Fig. 2C) and between 0 and 11 yr for males (Fig. 2D). Across the 3 independent readers, no samples were excluded from the lack of consensus and there was no systematic bias of age estimates detected (Fig. 3).

Between Readers 1 and 2, the PA ± 1 yr was 25.5% with slight variation around the 1:1 line, with Reader 2 generally ageing the samples older than Reader 1 (Fig. 3A). The APE and Chang's CV of the age esti-
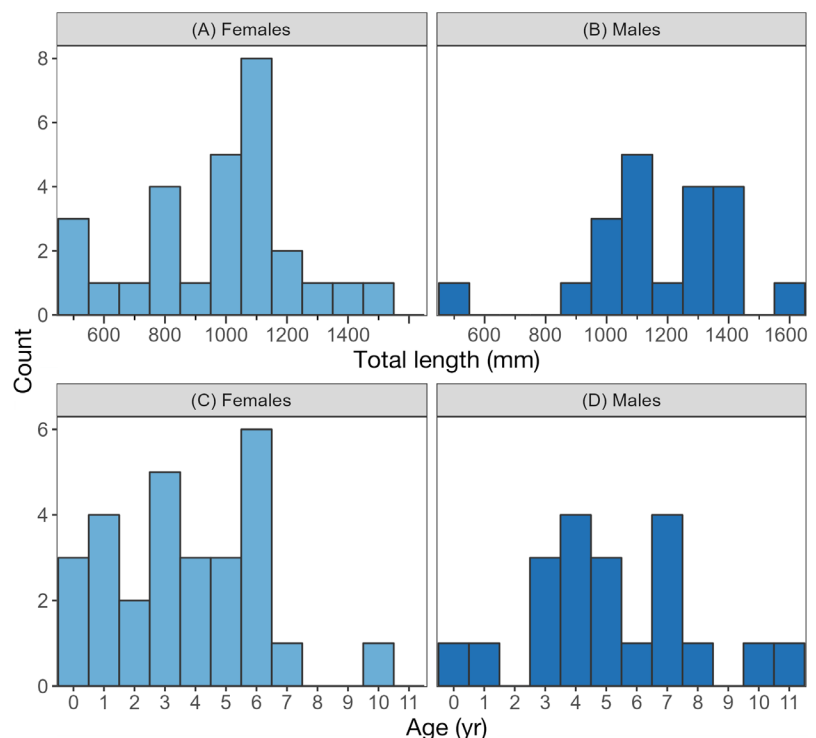

Fig. 2. Sample composition of bottlenose wedgefish *Rhynchobatus australiae* for total length for (A) females and (B) males, and the estimated ages for (C) females and (D) males, from 2 Singapore fish markets, sampled between October 2018 and August 2019
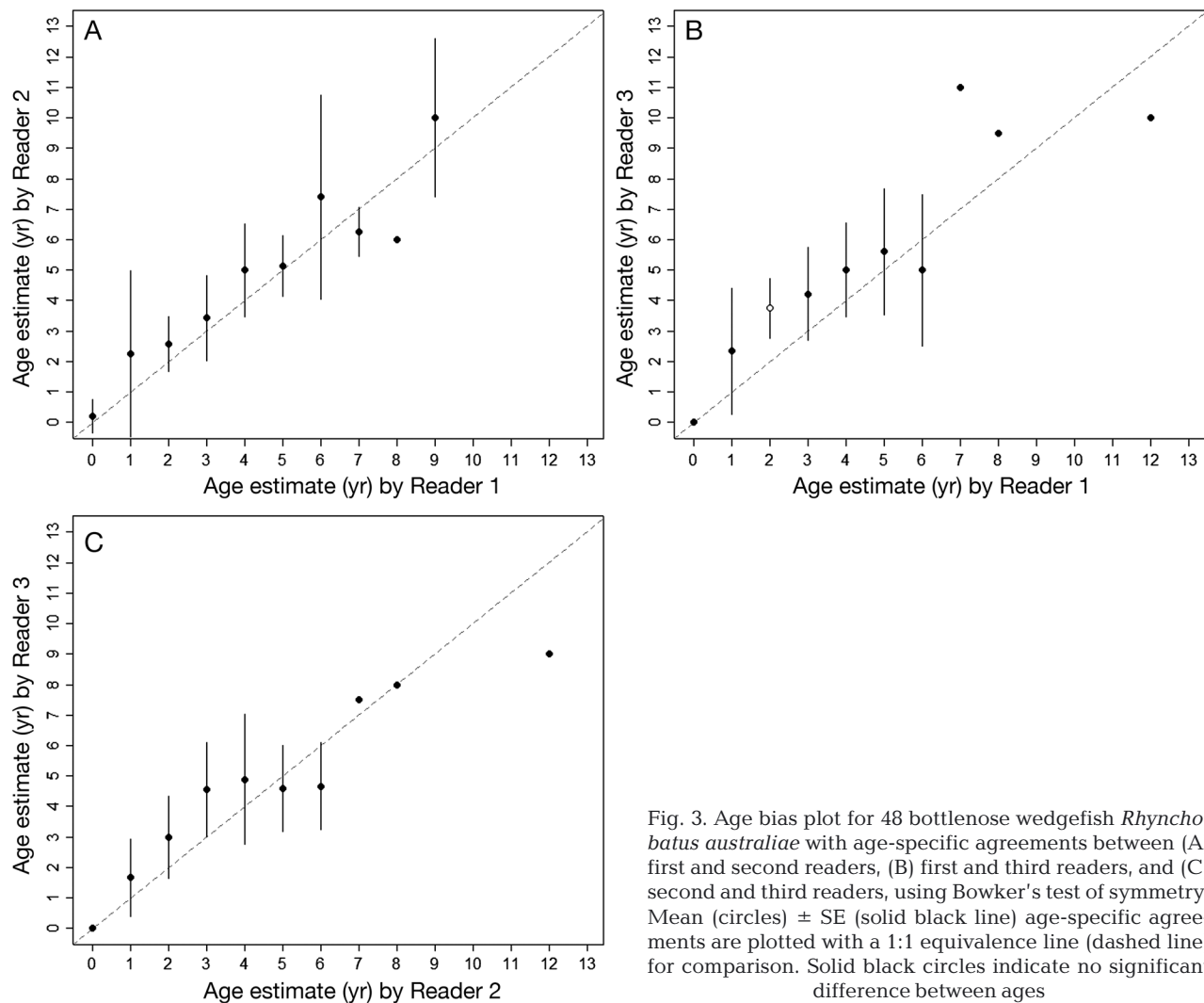
Fig. 3. Age bias plot for 48 bottlenose wedgefish *Rhyncho-batus australiae* with age-specific agreements between (A) first and second readers, (B) first and third readers, and (C) second and third readers, using Bowker's test of symmetry. Mean (circles) ± SE (solid black line) age-specific agreements are plotted with a 1:1 equivalence line (dashed line) for comparison. Solid black circles indicate no significant difference between ages

mates were 17.7% and 25.1%, respectively. There was no systematic bias detected across the age range between Readers 1 and 2 (Bowker's test of symmetry, df = 18, χ^2 = 14.5, p = 0.69; Fig. 3A). Between Readers 1 and 3, the PA ± 1 yr was 24.5%. The APE and CV of the age estimates were higher than between Readers 1 and 2 at 22.1% and 31.3%, respectively. There was no systematic bias detected across the age range between Readers 1 and 3 (Bowker's test of symmetry, df = 21, χ^2 = 25.1, p = 0.24; Fig. 3B). Between Readers 2 and 3, the PA ± 1 yr was 20.4%. The APE and CV of the age estimates were higher than between Readers 1 and 2 at 21.4% and 30.3%, respectively. There was no systematic bias detected across the age range between Readers 2 and 3 (Bowker's test of symmetry, df = 21, χ^2 = 20.0, p = 0.52; Fig. 3C). Comparing all 3 reader estimates together, the PA + 1 was 10.2%, APE was 19.6%, and the average CV was 31.5%.

3.3. Growth modelling

Based on the LOOIC weights, the VBGF was the best performing model for the combined sexes, females only, and males only (Table 3). There was no support for either the logistic or the Gompertz growth functions (Table 3). The Bayesian VBGF applied to the observed age-at-length data fit equally well, with priors having normal distributions for combined sexes, females only, and males only (see Figs. S3–S5 in Section S5). There was no auto-correlation detected for combined sexes, females only, and males only (Figs. S6–S8 in Section S5). The Gelman-Rubin diagnostic statistic *Rhat* for the VBGF parameters of L_∞, k, L_0, and σ were 0.999, 1.0001, 1.0008, and 1.0009, respectively, suggesting the length of the burn-in and number of subsequent cycles was sufficient. There was mixing of the 4 MCMC chains (Figs. S3–S5). The

Table 3. Summary of Bayesian model posterior parameter estimates and leave-one-out-information criterion (LOOIC) performance of the 3 models used for the combined (females and males) and separate sexes observed length-at-age data with outlier removed for bottlenose wedgefish *Rhynchobatus australiae*. Samples collected from Singapore fish markets (October 2018−August 2019). The LOOIC weight (*w*) values are similar to the Akaike information criterion weight values and determine the most appropriate growth model (**bold**). VBGF: von Bertalanffy growth function; n: sample size; SE: mean standard error; L_∞: asymptotic length; TL: total length; *k*: von Bertalanffy growth completion rate; *g*: Gompertz/logistic growth completion rate; L_0: length at birth; σ: sigma. Informative priors of $L_0 = 480 \pm 25$ mm was set for combined sexes, females only, and males only. Informative priors were set for combined sexes and females only of $L_\infty = 3230 \pm 323$ mm, and $L_\infty = 3000 \pm 300$ mm were set for males

	Model	n	Model performance			Model parameter estimates								Theoretical longevity
			LOOIC	±SE	w	L_∞ (mm TL)	±SE	*k/g* (yr^{-1})	±SE	L_0 (mm TL)	±SE	σ	±SE	
Combined	**VBGF**	**48**	**612.7**	**13.5**	**0.97**	**2814.2**	**6.54**	**0.066**	**0.0003**	**517.53**	**0.382**	**140.32**	**0.273**	40.30
	Logistic	48	620.7	14.5	0.02	1757.4	6.78	0.334	0.0015	522.31	0.428	144.97	0.373	
	Gompertz	48	621.4	13.5	0.01	2338.8	8.45	0.159	0.0009	527.38	0.422	149.44	0.336	
Females	**VBGF**	**28**	**359.3**	**10.6**	**0.96**	**3053.5**	**5.96**	**0.056**	**0.0002**	**504.46**	**0.389**	**142.75**	**0.375**	46.92
	Logistic	28	372.5	8.2	0.00	2956.3	6.17	0.196	0.0004	519.96	0.436	181.51	0.519	
	Gompertz	28	365.9	8.6	0.04	2977.7	6.18	0.114	0.0003	513.87	0.406	162.08	0.406	
Males	**VBGF**	**20**	**260.5**	**9.03**	**0.97**	**2741.4**	**5.54**	**0.073**	**0.0003**	**496.92**	**0.453**	**157.21**	**0.484**	39.94
	Logistic	20	273.5	8.80	0.00	2484.1	7.91	0.236	0.0009	504.78	0.408	208.93	0.794	
	Gompertz	20	267.4	8.91	0.03	2601.5	6.71	0.140	0.0006	502.99	0.409	186.48	0.666	

mixing of the MCMC chains and *Rhat* values for all parameters indicates that there was no evidence for non-convergence of the model.

There were small differences in the growth parameters between combined sexes, females only, and males only, where females were estimated to have a slightly greater asymptotic length and slower growth completion coefficients than males (Table 3, Fig. 4). The length-at-birth estimates for males were within the known documented range, while the length-at-birth estimates for combined sexes and females only were slightly greater than the known size at birth (Table 3, Fig. 4). The results indicated that growth of wedgefish was relatively slow, taking 4 yr to double in size from birth (~500 to 1000 mm).

3.4. Reproductive biology

There were 13 and 9 mature female and males, respectively, as well as 11 immature males and 7 immature females in the samples. Five female *R. australiae* were observed to have ova in their ovaries and were observed to be at maturity stage 4. The lengths of the mature females with ova ranged from 1019 to 1473 mm TL. The mean (±SE) maximum ova diameter was 11.00 ± 2.86 mm, ranging between 2 and 18 mm. The number of yolky ova in the ovaries ranged from 7 to 15. No embryos were observed.

The average length of fully calcified claspers of male *R. australiae* was 213 ± 20 mm (n = 7; range: 165−292 mm). The average length for partially and non-calcified claspers was 120 ± 10 mm (n = 5; range: 94−145 mm) and 45.7 ± 20.7 mm (n = 3; range: 11−100 mm), respectively. For 3 male samples, claspers had been removed prior to the sample being purchased and maturity was staged from internal dissections. Clasper calcification was not recorded for 2 samples, and based on the clasper lengths (175 and 250 mm), these 2 samples were assumed to be mature individuals. Running sperm was observed for 8 male samples, absent in 9 samples, and not recorded for 4 samples.

The maturity estimates presented in this study are considered preliminary due to the low sample size. The estimates indicate that female and male *R. australiae* may mature at different ages and lengths (Fig. 5). The largest immature female was 1145 mm TL and estimated to be 5 yr old, while the smallest mature female was 1019 mm TL with an estimated age of 3 yr old. The mean (±SE) maximum likelihood estimates for length of maturity of L_{50} and L_{95} for females was estimated to be 1014.21 ± 52.99 and 1203.04 ± 93.68 mm TL, respectively (Fig. 5A). The median age (±SE) of maturity for A_{50} and A_{95} for females was 3.25 ± 0.56 and 5.58 ± 1.13 yr, respectively (Fig. 5C).

The binomial logistic model for male age- and length-at-maturity data was not able to converge due to the spread of the data with no overlap between mature and immature samples, as well as low sample size (n = 20) (Fig. 5B,D). A quasibinomial logistic model was used for the preliminary male maturity analysis, with a bin width of 1 yr for age-at-maturity analysis, and 100 mm for the length-at-maturity analysis to generate confidence intervals. The 1-sided confidence intervals
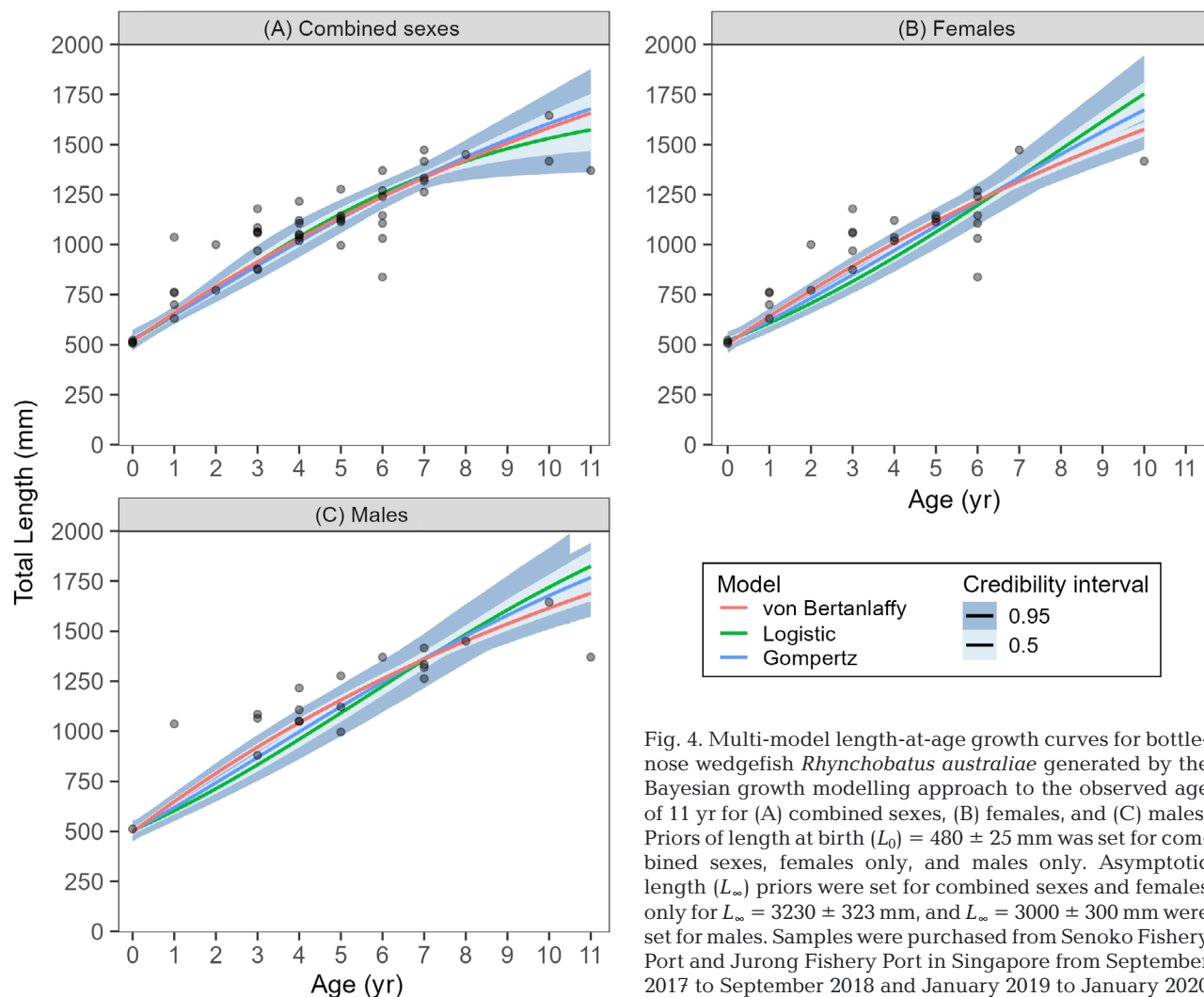
Fig. 4. Multi-model length-at-age growth curves for bottle-nose wedgefish *Rhynchobatus australiae* generated by the Bayesian growth modelling approach to the observed age of 11 yr for (A) combined sexes, (B) females, and (C) males. Priors of length at birth (L_0) = 480 ± 25 mm was set for combined sexes, females only, and males only. Asymptotic length (L_∞) priors were set for combined sexes and females only for L_∞ = 3230 ± 323 mm, and L_∞ = 3000 ± 300 mm were set for males. Samples were purchased from Senoko Fishery Port and Jurong Fishery Port in Singapore from September 2017 to September 2018 and January 2019 to January 2020

for the quasibinomial model are the result of the spread of the maturity data for the males (Fig. 5B,D). The largest immature male was 1216 mm TL and estimated to be 4 yr old, while the smallest mature female was 1263 mm TL with an estimated age of 7 yr old. The mean length (±SE) at maturity of L_{50} and L_{95} for males were estimated to be 1197.1 ± 0.05 and 1209.5 ± 0.15 mm TL, respectively (Fig. 5B). The mean (±SE) estimates of A_{50} and A_{95} for males were 5.03 ± 0.0004 and 5.16 ± 0.0024 yr, respectively (Fig. 5D).

3.5. Comparison of life history estimates

There were similar growth completion rates of *R. australiae* from SE Asia, compared to the population from the eastern Australia estimated by D'Alberto et al. (2019) using the data from White et al. (2014) (our Table 4, Fig. 6). Life history parameter estimates from the eastern Australian population were generated using the frequentist approach, while estimates in this study were generated using informative priors for L_∞ and L_0 with a Bayesian approach (Fig. 6). The oldest observed age was similar between studies, at 11 yr age. However, the maximum observed size of *R. australiae* was different between the studies (Table 4). L_∞ estimates were similar between the 2 populations (Fig. 6). The theoretical longevity of the SE Asian population of *R. australiae* was greater than the theoretical longevity of the eastern Australian population. The age-at-maturity estimates for females was similar between the 2 populations (Table 4). Size at birth was similar between the 2 populations (Fig. 6, Table 4). The populations of *R. australiae* from SE Asia and eastern Australia had considerably slower growth compared to 2 giant guitarfish species (family Glaucostegidae) that have life history estimates available, *Glaucostegus cemiculus* and *G. typus* (Capapé & Zaouali 1994, Enaj-
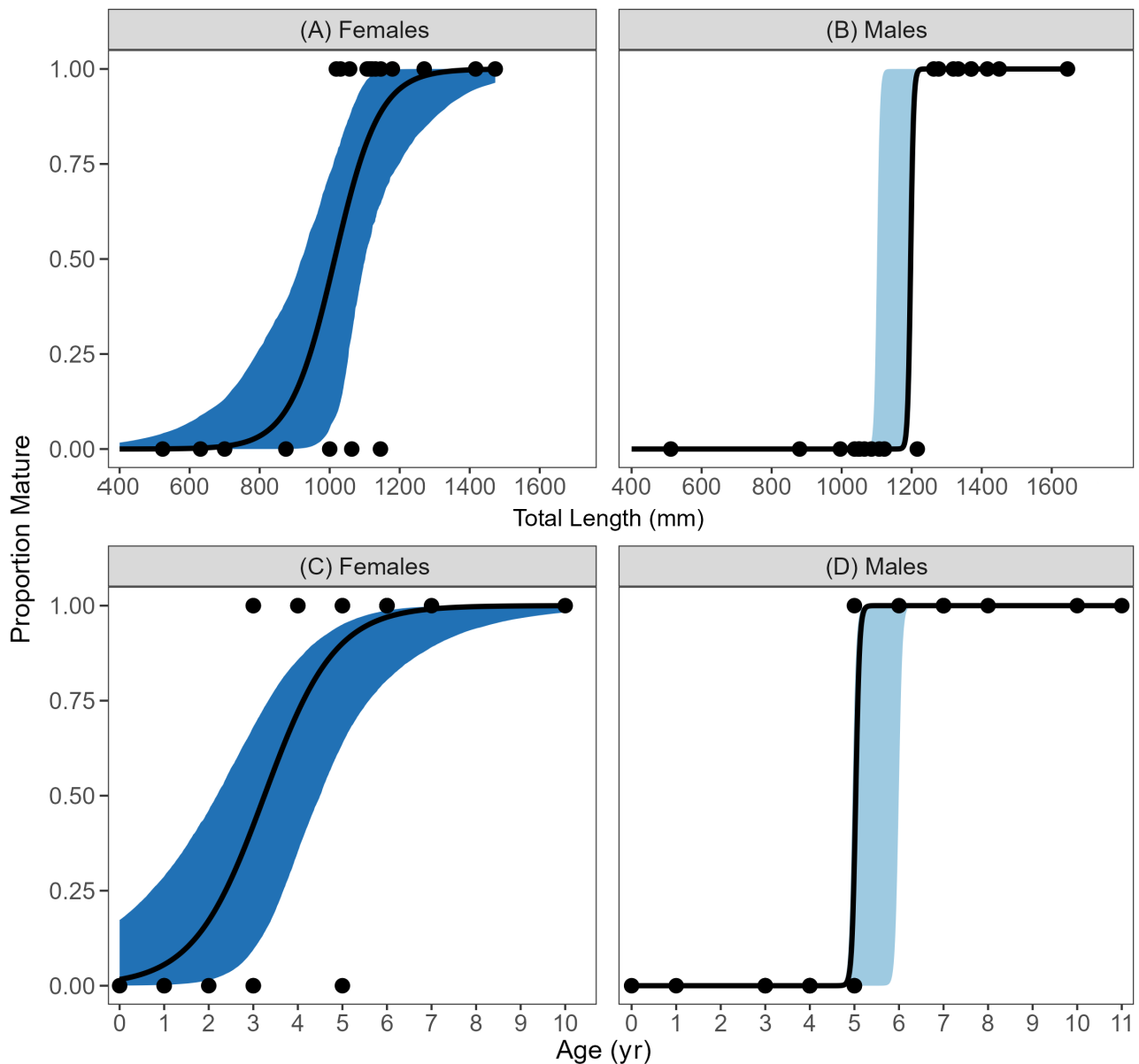
Fig. 5. Maturity ogives for length at maturity of (A) females (n = 19) and (B) males (n = 20) and age at maturity of (C) females and (D) males for bottlenose wedgefish *Rhynchobatus australiae* sampled from Senoko Fishery Port and Jurong Fishery Port in Singapore from September 2017 to September 2018, and January 2019 to January 2020. Sample observations (black circles) are represented on the figure

jar et al. 2012, White et al. 2014, D'Alberto et al. 2019). Age and length at maturity were similar between the wedgefish and giant guitarfish species (Table 4).

4. DISCUSSION

Accurate life history estimates or a quantifiable uncertainty around them is vital for developing science-based population management and conservation strategies. Globally, populations of *Rhynchobatus aus-*

traliae are in steep decline, driven by extensive fishing pressure, especially within the SE Asian region (Kyne et al. 2020). This study presented the first life history parameters for *R. australiae* in SE Asia, and a second study for age and growth information for this Critically Endangered species (White et al. 2014, D'Alberto et al. 2019). *R. australiae* in this study were estimated to have a slow growth completion rate (combined sexes and males only, $k = 0.07$ yr^{-1}; female only, $k = 0.06$ yr^{-1}). Species with a growth completion rate of <0.10 yr^{-1} tend to be particularly vulnerable to population decline

Table 4. Comparative life history parameters for bottlenose wedgefish *Rhynchobatus australiae* from Southeast (SE) Asia, sourced from Senoko Fishery Port and Jurong Fishery Port in Singapore and imported from Indonesia and Malaysia, *R. australiae* from eastern Australia, as well as similar species of blackchin guitarfish *Glaucostegus cemiculus* from central Mediterranean, and giant guitarfish *G. typus* from eastern Australia. n: sample size; TL: total length; L_{obsv}: observed maximum size in the study; VBGF: growth model of von Bertalanffy (VBGF), and the numbers indicating the number of parameters estimated: 2 parameters with fixed size at birth (-2), and standard 3-parameter model (-3); k: growth completion rate; L_∞: asymptotic total length; L_0: length at birth; A_{mat}: age at maturity for 50% of the population (A_{50}) and 95% of the population (A_{95}); L_{mat}: length at maturity for 50% of the population (L_{50}) and 95% of the population (L_{95}); A_{max}: maximum age/longevity for observed samples (O_{max}) and recalculated theoretical estimates based on the von Bertalanffy growth completion rate (T_{max})

Species	Region	Sexes	n	L_{obsv} (mm TL)	Growth model	k (yr^{-1})	L_∞ (mm TL)	L_0 (mm TL)	A_{mat} (yr) A_{50}	A_{95}	L_{mat} (mm TL) L_{50}	L_{95}	Litter size Min.	Max.	A_{max} (yr) O_{max}	T_{max}	Reference
R. australiae	SE Asia (Indonesia, Malaysia)	Combined	48	1645	VBGF-3	0.07	2814	517	–	–	–	–	–	–	11	40	Current study
		Female	28	1473	VBGF-3	0.06	3053	505	3.3	5.6	1014	1203	–	–	10	47	
		Male	20	1645	VBGF-3	0.07	2741	497	5.0	5.2	1197	1209	–	–	11	40	
	Eastern Australia	Combined	47	2630	VBGF-2	0.40	–	500	–	–	–	–	–	–	12	–	White et al. (2014)
					VBGF-3	0.08	3178	525	3.0	6.0	–	–	–	–	12	31	D'Alberto et al. (2019)
G. cemiculus	Central Mediterranean (southern Tunisia)	Female	247	2020	VBGF-3	0.20	1987	265	5.1	–	1381	–	–	–	14	14	Enajjar et al. (2012)
		Male	299	1680	VBGF-3	0.27	1790	354	2.9	–	1118	–	–	–	10	11	
	Central Mediterranean (SE Tunisia)	Female	407	2300	–	–	–	300–350	–	–	1100	–	5	12	–	–	Capapé & Zaouali (1994)
		Male	390	1920	–	–	–	300–350	–	–	1000	–	–	–	–	–	
G. typus	Eastern Australia	Combined	23	2840	VBGF-2	0.15	–	400	–	–	–	–	–	–	–	–	White et al. (2014)
					VBGF-3	0.06	4021	499	6.5	8.0	–	–	–	–	19	48	D'Alberto et al. (2019)

(Cailliet & Goldman 2004). While there is evidence of population separation between the eastern Australian and SE Asian populations based on genetic analysis (Giles et al. 2016), the life history parameters between the 2 regions are relatively similar, with comparable estimates of growth rates. There still may be intra-specific variation occurring due to regional differences in environment, as well as methodological differences between studies, including sampling size, gear selectivity, methods of age estimation, verification, validation, and type of growth model applied (Stevens et al. 2000, Cailliet & Goldman 2004).

R. australiae were aged to a maximum of 11 yr for males (1370 mm TL) and 10 yr for females (1417 mm TL), and approximately at half the maximum length for this species (3000–3230 mm TL). The theoretical longevity, estimated from the VBGF growth completion rate, was 40 yr for males and 47 yr for females. Annual growth band pair deposition was assumed for *R. australiae*, based on the marginal increment analysis of a similar-sized species of shark-like rays, *Glaucostegus cemiculus* (Enajjar et al. 2012). Underestimation of longevity and overestimation of growth is a serious concern for developing effective management strategies for fisheries. Numerous reviews have reported sampling biases and failures in ageing protocols, including lack of validation (Cailliet et al. 2006, Cailliet 2015), that often result in overestimation or underestimation of age and growth parameters (Harry 2018). Without comprehensive age validation studies (e.g. mark and recapture using tetracycline injection or bomb radiocarbon dating) to validate the periodicity of the growth band pairs, the ages presented could be inaccurate. Therefore the age, growth curves, and age-at-maturity estimates are considered preliminary. The uncertainties highlight the need to further research the life history parameters for this species.

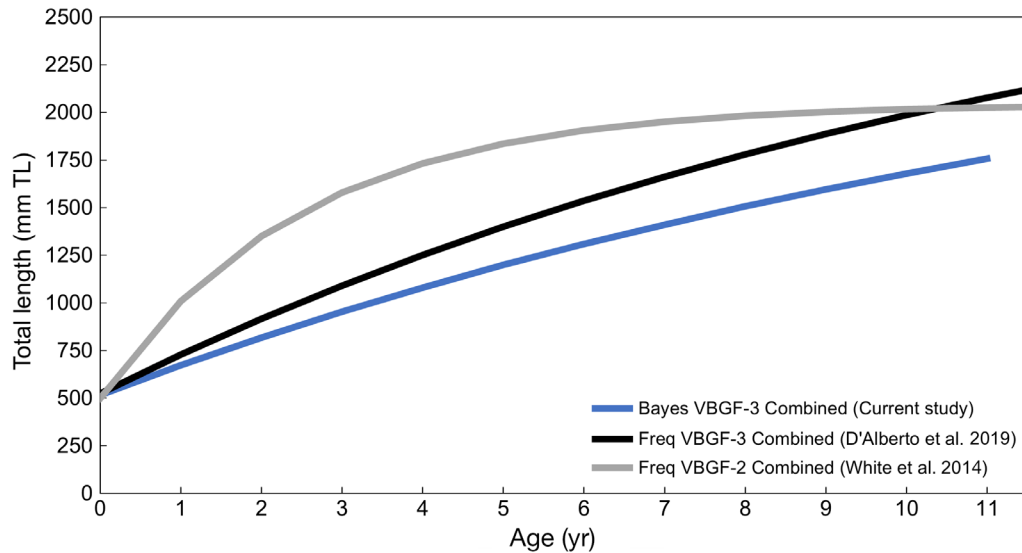Generating life history information for threatened and rare species can be

Fig. 6. Comparison of growth completion rates for the combined sexes (female and male) bottlenose wedgefish *Rhynchobatus australiae* between 2 populations, Southeast Asia from this current study using a Bayesian (Bayes) 3-parameter von Bertalanffy growth function (VBGF-3; blue solid line), and eastern Australia from D'Alberto et al. (2019) using a frequentist (Freq) VBGF-3 (black solid line), and frequentist 2-parameter VBGF (VBGF-2; grey solid line) from White et al. (2014)

difficult, as it traditionally relies on samples collected through lethal sampling, and this may pose a threat to some populations (Heupel & Simpfendorfer 2010). Collection of samples for threatened species are often opportunistic and limited, as in this study, which were limited to the animals available for purchase with limited knowledge of the fishing location, introducing potential biases in the results. Biases in size or age distributions in the sample can reduce the accuracy of life history parameters. They are caused by sampling data from different locations or populations, size-selective gear types, as well as small sample sizes (Thorson & Simpfendorfer 2009). The Bayesian growth modelling approach uses known biological traits of a species as explicit components of a growth model with informative priors for asymptotic length and size at birth, and can be used to overcome some biases, such as absence of large individuals (Pardo et al. 2013, Smart & Grammer 2021). If there are few or no large size classes in the sample, a traditional frequentist approach can considerably underestimate L_∞, leading to an overestimated growth competition rate and size at birth (Goldman 2005, Cailliet et al. 2006, Smart et al. 2016b). The largest individual in the present study was 1645 mm TL, whereas *R. australiae* have been recorded to have a maximum TL of 3230 mm in eastern Indonesia (Faizah & Chodrijah 2020). The Bayesian approach in this study provided a biologically realistic estimate of the asymptotic length and size at birth, compared to a frequentist growth modelling approach with the same data (Table S3).

These results were also similar to the eastern Australian population using a frequentist approach and larger observed individual length of 2630 mm TL (White et al. 2014, D'Alberto et al. 2019). The Bayesian growth modelling approach used in this study appeared to overcome some limitations of missing larger length classes and can help to reduce biases in the estimation of the growth completion rate for a data-limited threatened species. However, there is still uncertainty surrounding the priors used, including ensuring the samples come from the same population, confirming the male maximum size, and assumption of sexual dimorphism that males attain a smaller maximum size than females. There is a need for better life history information for these data-poor species, as there is limited species-specific information, with high levels of uncertainty associated with the life history parameters that are available.

Across all rhinid species, reproductive parameters are generally poorly defined, where the maturity size and age, litter size, and reproductive periodicity are unknown for most species (Last et al. 2016). Life history patterns and correlations, like those presented in Cortés (2000), have not been investigated for rays. *R. australiae* was estimated to mature at a younger age between 3 and 6 yr old for both sexes, which is considerably younger than 50% of the maximum age (~12 yr) that is estimated from the relationship between age at maturity and maximum age for sharks (Cortés 2000). Early maturity for both female and males are also reported for *G. typus*, *G. cemiculus*, and the largetooth

sawfish *Pristis pristis* (Capapé & Zaouali 1994, Enajjar et al. 2012, White et al. 2014, D'Alberto et al. 2019, Kyne et al. 2021). Female *R. australiae* from SE Asia in the current study were estimated to mature at a younger age and smaller length than males, similar to maturity estimates for the eastern Australian population (D'Alberto et al. 2019). This is unusual for chondrichthyans, as females typically mature at an older age than males (Cortés 2000). The reported litter size for *R. australiae* is between 7 and 19 pups, with size at birth between 46 and 50 cm (White & Dharmadi 2007). A positive relationship between litter size and maternal size in chondrichthyans can occur, where larger individuals have more uterine space available to carry a larger litter size and/or larger-sized pups (Kyne et al. 2021). The early maturity of *R. australiae* in SE Asia and in eastern Australia suggests that this species has an above-average population productivity, as a result of earlier maturity, large litter sizes, and large size at birth, compared to other chondrichthyans of similar maximum length (e.g. dwarf sawfish *P. clavata*) (D'Alberto et al. 2019).

Assuming the life history estimates presented here are realistic, then this would suggest that this species may be able to recover from population declines, if fishing pressure is reduced drastically (D'Alberto et al. 2019). However, due to the low sample size for the maturity analysis, it is unknown if the earlier maturity is a result of the small and limited sample size across age and length classes, or inaccurate age estimation, or a unique trait to wedgefishes and giant guitarfishes, compared to other chondrichthyan species. The maturity and reproductive estimates of the current study must be viewed with caution due to the limited number of samples, especially in the larger length classes, and mature male samples in this study. There is crucial reproductive data missing for all wedgefish species, particularly in terms of estimated length and age of maturity for females and males, litter sizes, gestation length, and reproductive periodicity, warranting further directed research.

The misidentification of species and the use of inaccurate surrogate information can have a significant effect on life history parameters (Smart et al. 2016a), which compromises any stock assessments conducted and the sustainability of fisheries (both harvest and discards), as well as impacting conservation-related research and management initiatives (Garcia-Vazquez et al. 2012). There are a number of wedgefish species from the genus *Rhynchobatus* that have overlapping distributions in SE Asia with *R. australiae*, including clown wedgefish *R. cooki* (Kyne et al. 2019b), Taiwanese wedgefish *R. immaculatus* (Kyne & Ebert 2019),

R. springeri (Kyne 2019), *R. laevis* (Kyne & Jabado 2019), and *R. palpebratus* (Kyne & Rigby 2019). In SFP and JFP, wedgefishes are landed in fresh condition, with the majority of samples with fins removed, and on some occasions, snouts removed prior to sale (Clark-Shen et al. 2021), whereas in other fishery ports across SE Asia, wedgefishes are often landed in poor and degraded condition, which results in visual species identification being especially difficult (D'Alberto et al. 2021). Genetic sequencing for this study confirmed that all but 2 samples were *R. australiae*, whereas the 2 samples excluded from the analysis were visually distinct to other *R. australiae* samples and were genetically identified as *R. palpebratus*. *R. springeri* were not observed during the period of this study. The species was recorded at JFP and SFP during the market surveys conducted in Clark-Shen et al. (2021), which covered a greater time period, between September 2017 and September 2018 and between January 2019 and January 2020. The distribution of *R. australiae* overlaps with *R. palpebratus* in Papua New Guinea and northern Australia (Last et al. 2016). The presence of *R. palpebratus* in the 2 Singapore fish markets, where the majority of wedgefish species were imported from Indonesia and Malaysia, indicates that either the individuals originated from waters around Papua New Guinea, or the range for this species is broader than previously documented and requires further investigation. The overlapping ranges of wedgefish species has compounded the misidentification of these rays, especially as some species are rarer in landings and possibly have more of a restricted and/or fragmented spatial distribution.

5. CONCLUSION

To achieve population recovery for species exposed to fishing, managers and conservation practitioners need to understand their population status, risk exposure, and resilience to fishing pressure and other threats. Using Bayesian growth analysis, this study has provided the first and preliminary life history information for *Rhynchobatus australiae* from SE Asia. This Critically Endangered species is estimated to have slow growth and early maturity, compared to other similar-sized chondrichthyans. There is still considerable uncertainty for the age, growth, and maturity parameters, due to the small sample size and limited size distribution. There is a need for further research on life history information for these data-poor species, as there is limited species-specific information, with high levels of uncertainty associated with the life history

parameters that are available. The results of this study provides guidance to help implement management and conservation measures, while highlighting the lack of information available for these species.

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