

Age-based life history of Pacific longnose parrotfish *Hipposcarus longiceps* from New Caledonia

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Abstract

The Pacific longnose parrotfish, *Hipposcarus longiceps*, is a medium- to large-bodied scarine labrid that is among the most commonly harvested species in mixed reef fisheries across the Indo-Pacific. Despite its ecological and fisheries importance, assessments of stock status and development of appropriate management strategies for the species have been limited by an absence of biological information. To date, the only detailed studies of the biology of *H. longiceps* have occurred in tropical regions. This study examined the biology of *H. longiceps* in southern New Caledonia, towards the southernmost extent of the species' distribution. In addition, resulting estimates of longevity and asymptotic length were compared against those derived for the species elsewhere in the Pacific, and regional patterns in these parameters were explored for correlation with sea surface temperature (SST). A total of 212 *H. longiceps* were collected from commercial fishers or fish markets between September 2015 and March 2017. Sampled individuals ranged from 28.2 cm fork length (L_F) to 57.3 cm L_F , and from 424 g to 3773 g. Examination of sectioned otoliths showed a clear pattern in increment formation, with opaque zones forming annually in most individuals between July and August (*i.e.*, austral winter). Estimated longevity was similar between sexes, at ~18 years for females and ~19 years for males. These estimates extend the reported longevity of *H. longiceps* by at least 5 years. Despite this species being a diandric protogynous hermaphrodite, sex ratios were only slightly female biased, with 1 female:0.6 males. Primary males (*i.e.*, those individuals that are male at first sexual maturity) constituted 30% of all sampled individuals and 79% of all males. A clearly defined, yet protracted, spawning season was evident, with peak spawning occurring from December–February, extending from November to April in some individuals. The estimated median length (L_{50}) and age (A_{50}) at female maturity were 38.9 cm L_F and 5.7 years, respectively, while the estimated length at which females changed sex to secondary males was 52.5 cm L_F . Reported longevity and asymptotic length were found to exhibit considerable regional variation, and both were negatively associated with SST. The results highlight the importance of geographically disparate studies into the species' biology, inform future assessments for

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the species, provide key baseline information for comparative work and improve understanding of spatial patterns of the life history of parrotfish species.

KEYWORDS

fisheries management, growth, mortality, New Caledonia, parrotfish, reproduction

1 | INTRODUCTION

Parrotfish (Family Labridae, Subfamily Scarinae) are an abundant and diverse component of fish communities on coral reef ecosystems around the world. As a group, parrotfish fill a wide variety of functional roles within reef ecosystems. Through their feeding actions, parrotfish modify the benthic biota by reducing macroalgae growth, cropping epilithic algal turf and providing areas of bare substrate for coral recruitment (Bellwood, 1996; Green & Bellwood, 2009). Parrotfish also play an important role in the production, reworking and transport of sediments in reef ecosystems (Bellwood, 1996).

Parrotfish exhibit a range of body sizes, display high plasticity in growth and vary considerably in their life spans, with maximum longevity spanning from just a few years to over 40 years (Andrews *et al.*, 2015; Choat & Robertson, 2002). Parrotfish display complex mating systems and a wide range of reproductive strategies, including classical gonochorism (e.g., Robertson *et al.*, 1982), functional gonochorism (e.g., Taylor *et al.*, 2018a), whereby all male recruitment occurs through pre-maturational sex change, and dual hermaphroditic development pathways, namely (a) diandry, whereby two types of males are present in a population, primary males, or those that are males at first sexual maturation, and secondary males, or those that originate from a sex change in functional females, and (b) monandry, whereby all males originate from functionally mature females (Sadovy De Mitcheson & Liu, 2008).

The Pacific longnose parrotfish, *Hipposcarus longiceps* (Valenciennes 1840), is a medium- to large-bodied scarine labrid that occurs from the eastern Indian Ocean westwards to French Polynesia (Randall *et al.*, 1990). The species is an important component of commercial, artisanal and subsistence mixed-reef fisheries across the Indo-Pacific, and is one of the most harvested reef fishes of the Pacific Islands region. In Micronesia, for example, *H. longiceps* constitutes the third, sixth and seventh highest species by mass in commercial reef fisheries catches from Yap, the Commonwealth of the Northern Mariana Islands, and Guam, respectively (Houk *et al.*, 2012), and forms a significant component of spear (now the dominant fishing method) and net catches in Pohnpei (Rhodes *et al.*, 2008, 2018). Moore *et al.* (2015) observed *H. longiceps* to be the top-ranked species in night spearfishing catches landed at Koror, Palau, representing over 25% of surveyed catches by weight. The species plays a key ecological role on coral reefs as a scraper/small excavator and browser, reducing turf- and macro-algae cover and generating bare substrate through its feeding actions (Green & Bellwood, 2009; Mantyka & Bellwood, 2007a, 2007b).

Hipposcarus longiceps is a diandric protogynous hermaphrodite and occurs in two contrasting colour phases: initial phase (IP) and terminal phase (TP) (Taylor & Cruz, 2017; see also Moore & Colas, 2016). Individuals in IP colouration can be immature females, mature females

or primary males, while individuals in TP colouration can be secondary males (i.e., those that have originated from functional females) or primary males. The species inhabits shallow water and forms large schools for reproduction, foraging, and sleeping (Colin, 2012; Taylor & Cruz, 2017). Combined with their relatively large body size, these aspects greatly enhance the species' susceptibility to fishing via increased catchability (Bejarano *et al.*, 2013).

Despite the species' importance to coral reef ecological processes and fisheries across its broad geographical distribution, and behavioural predisposition to overharvesting, detailed studies into the biology of *H. longiceps* have been limited to a small number of locations. In Pohnpei, Federated States of Micronesia (at approximately 6°53'N), Taylor and Choat (2014) observed a maximum length of 430 mm fork length (L_F) and a maximum age of 6 years, while Taylor and Cruz (2017) observed a maximum length of 514 mm L_F and a maximum age of 10 years for individuals collected from market sampling in Guam (at approximately 13°28'N). However, parrotfish have been shown to display high levels of plasticity in demographic parameters between locations across even small spatial scales (Gust *et al.*, 2002; Paddock *et al.*, 2009; Taylor, 2014), raising concerns about the appropriateness of using life-history parameters from these locations for assessments elsewhere across the species distribution.

This paper examines the age-based life history of *H. longiceps* from reefs of southern New Caledonia, including growth, longevity, mortality, spawning seasonality, length and age at female maturation and length at sex change. In addition, regional variation in maximum observed age and asymptotic length are explored using data from the current study and the published literature, and patterns in these life-history variables are assessed for correlation with sea surface temperature (SST); a key driver of coral reef fish life history (Robertson *et al.*, 2005; Taylor *et al.*, 2019). Data from southern New Caledonia, towards the southernmost extent of the species distribution, provide an opportunity to contrast biological parameters against those observed from low-latitude locations. The derived results provide a preliminary insight to stock status, facilitate future stock assessments and the development of appropriate management strategies, and further the understanding of spatial variability in life-history traits of *H. longiceps* and parrotfish species more broadly.

2 | MATERIALS AND METHODS

2.1 | Study area and sample collection

Samples of *H. longiceps* were collected from commercial net fishers who fished in southern New Caledonia (Figure 1) or from two vendors at the Nouméa central fish market, where the fisher, location of

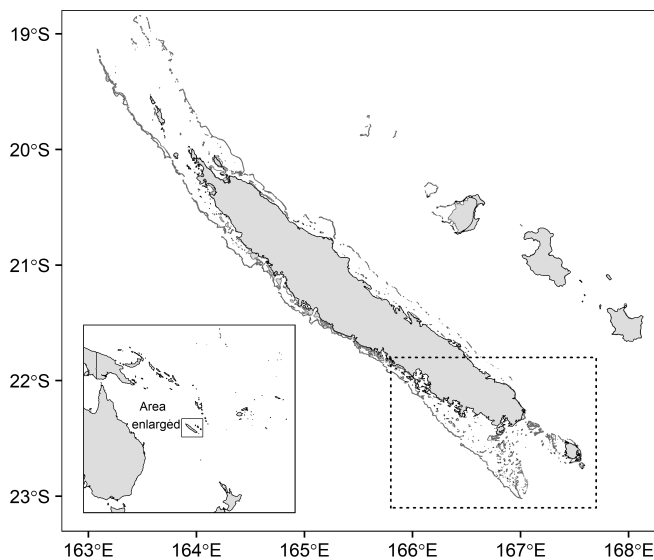


FIGURE 1 Map of New Caledonia showing the approximate area where *Hipposcarus longiceps* were collected (dashed rectangle)

fishing and date of capture could be assured. Sampling was typically conducted once per week (occasionally twice per week) between September 2015 and March 2017. For each fish, the standard length (L_S , measured from the tip of the snout to the posterior edge of the last scale), L_F (measured from the tip of the snout to the end of the middle caudal rays), total length (L_T , measured from the tip of the snout to the end of the longest caudal fin ray) and whole weight (W_W) were recorded, unless damaged. All fish length measurements were recorded to the nearest 0.1 cm and W_W to the nearest 1 g. Sagittal otoliths (hereafter otoliths) were removed, cleaned, dried and stored in plastic vials. Gonads were dissected, weighed to the nearest 0.1 g, sexed and staged macroscopically. Gonads were classified into developmental stages adapted from Brown-Peterson *et al.* (2011): immature, developing, spawning capable, running ripe (*i.e.*, actively spawning subphase), regressing, and regenerating, using criteria therein. Most gonads were fixed fresh in 10% buffered formalin for histological processing, although a small number were frozen prior to fixation. The colour phase (*i.e.*, IP or TP) was recorded for each individual.

2.2 | Age determination

A single otolith from most individuals was embedded in casting resin and sectioned on the transverse axis through the primordium, in a direction perpendicular to the sulcus acusticus. Sections were cut using a modified high-speed gem-cutting saw with a diamond impregnated blade. Up to three sections were cut for each otolith, with otoliths cut thinly (*c.* 0.3 mm) to improve the clarity of the growth increments. Sections were cleaned, dried and mounted on glass slides with a cover slip using casting resin. Opaque increments were counted with a compound microscope using a combination of reflected and



FIGURE 2 Photomicrographs of transverse otolith sections of *Hipposcarus longiceps* under transmitted light. Top, a 42.0 cm fork length (L_F) female caught in June 2016 with four opaque increments (white circles) and a translucent otolith margin; bottom, a 51.5 cm L_F female caught in May 2016 with 16 opaque increments and a translucent otolith margin. Black circles with white outlines indicate the presumed 6 month increment

transmitted light, with enumeration following the approach of Taylor and Choat (2014) and Taylor and Cruz (2017) (Figure 2). Each otolith was read at least twice by the author. When there was agreement in the counts of opaque increment from these two reads, the count was taken as the number of opaque increments. A third count was performed when the two counts for an individual differed, and the final opaque increment number was assigned when any two of the three counts agreed. Counts for two individuals could not be agreed through this process. In each of these instances opaque increment counts differed by 1 (*e.g.*, 6, 7, 8) so the middle value was taken, following Taylor and Cruz (2017).

The timing of opaque and translucent increment deposition in *H. longiceps* otoliths was examined using edge-type analysis, following the approach by Moore (2019). The margin of each otolith was categorized as opaque, whereby an opaque band was evident around the edge of otolith, narrow translucent, whereby a translucent band comprising <50% of the width of the previous translucent band was encountered, or wide translucent, whereby a translucent band comprising $\geq 50\%$ of the width of the previous translucent band was encountered. The proportion of fish with opaque margins was calculated for each month and plotted across the calendar year to assess the timing of opaque zone deposition in otoliths. Satellite-derived mean daily SSTs (in $^{\circ}\text{C}$) were collated for the southern New Caledonia region between January 2000 and December 2015 (obtained from NOAA/OAR/ESRL PSL, Boulder, Colorado, USA; <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>) and were plotted alongside the proportion data to assess the relationship between opaque increment formation and SST.

Following confirmation of the timing of opaque zone deposition, a decimal age was calculated for each individual. Decimal ages were based on the assumed birth date, the peak of opaque increment deposition (*i.e.*, 1 July; see Results), the number of opaque increments and

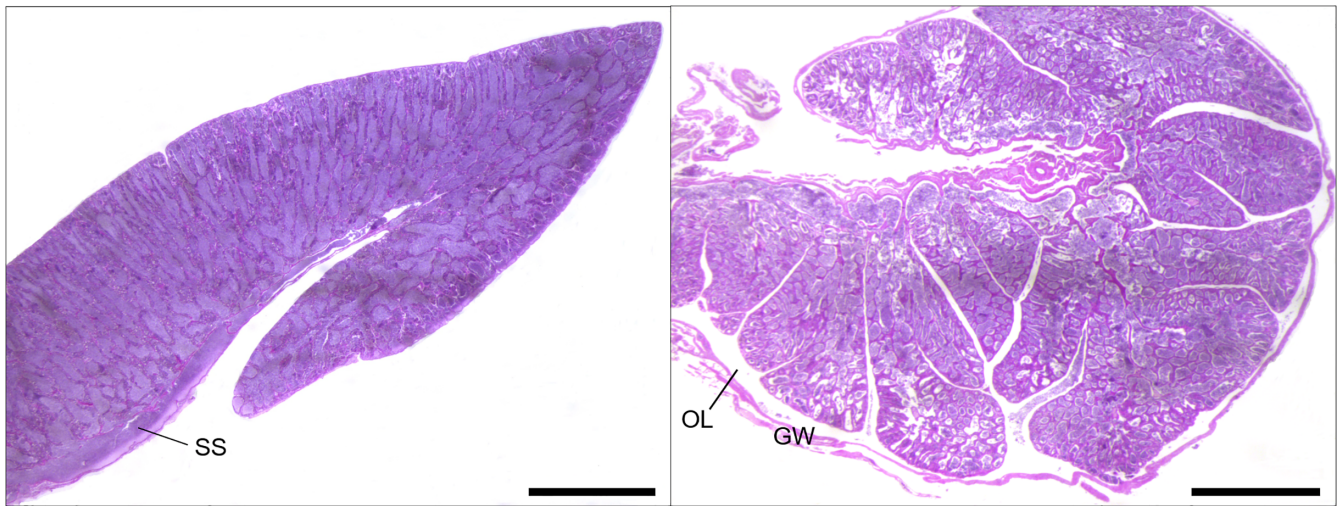


FIGURE 3 Testes of male *Hipposcarus longiceps*. Left, primary male, displaying prominent sperm sinuses (SS); right, secondary male, displaying obvious ovarian lumen (OL) and a thick former ovarian gonad wall (GW). Scale bars: left, 2 mm; right, 1 mm

the month of capture. An assumed birth date of 1 January (the peak of female spawning) was used for all samples, as determined from monthly patterns in gonadosomatic indices [GSI, (gonad weight/ W_W) \times 100] and patterns of developmental stages of gonads. Accordingly, formation of the first opaque increment was considered to take place ~6 months after birth (Figure 2). This first increment was often difficult to delineate and thus the first counted opaque increment was considered to form one and a half years after birth. Thus, an individual with five annual bands and a narrow translucent otolith margin caught in July was considered to be 5.5 years old, while an individual caught in January with five annual bands was considered to be 6 years old. A full year was added to those individuals caught in July–August that had a wide translucent otolith margin.

2.3 | Gonad histology

Gonads from most individuals were subjected to histological examination to verify the macroscopic sex assignments. For females, a secondary goal was to determine the developmental stage for assessing maturity schedules and spawning seasonality. Transverse sections of gonads (up to three per individual) were embedded in paraffin wax, sectioned at 5 μ m, mounted onto microscope slides and stained with haematoxylin and eosin. Slides were examined using both dissecting and compound microscopes with transmitted light. Female gonads were classified into the same developmental stages as used for the macroscopic assessments. Ovary development staging was based on criteria detailed by West (1990), using the terminology in Brown-Peterson *et al.* (2011). Following Taylor and Cruz (2017), consideration was given to (a) presence or absence of post-ovulatory follicles (POFs) as an indicator of prior spawning, (b) proliferating spermatogenic material in the presence of degenerative vitellogenic oocytes as an indicator of post-maturational sex change and (c) characteristics of an ovarian lumen in male testes signifying secondary versus primary

male development, based on the criteria outlined in Sadovy and Shapiro (1987) and Shapiro and Rasotto (1993) (Figure 3). Additional features used to assess prior spawning and thus maturity of females included the structural appearance of lamellae, intra-lamellar stromal tissue, the presence of atretic oocytes and brown bodies, and the thickness of the ovarian wall (Sadovy & Shapiro, 1987).

2.4 | Growth and mortality

Relationships between L_S , L_F and L_T were assessed using linear models. The relationship between L_F and W_W was modelled using a power function of the form $W_W = a \times L_F^b$, where a is the coefficient of the power function and b is the exponent. Length and weight data were log-transformed prior to analysis to satisfy the assumption of linearity.

Growth of *H. longiceps* was initially modelled using the standard von Bertalanffy growth function (VBGF) fitted by nonlinear least-squares regression of L_F on the decimal age data. The VBGF took the form:

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

where L_t is the predicted mean L_F (cm) at age t (years), L_∞ is the hypothetical asymptotic length, k is the growth coefficient and t_0 is the age at which fish would have a theoretical length of zero. Corresponding 95% confidence intervals (CIs) were generated by bootstrap resampling through 1000 iterations. Separate VBGFs were run using data for all individuals combined, primary males, and females and secondary males combined. A second series of VBGFs were run where growth curves were constrained (y intercept) to a common length at settlement (L_0) of 1.5 cm L_F to account for the growth of small juveniles which were missing from the dataset and to facilitate

comparisons with studies in other regions (e.g., Taylor & Choat, 2014; Taylor & Cruz, 2017). Following the recommendation of Taylor *et al.* (2018b), a re-parameterized VBGF (rVBGF; Francis, 1988) was run in parallel to each unconstrained VBGF model. The parameters selected for the rVBGF were L_5 , L_{10} and L_{15} , providing estimates of mean length-at-ages 5, 10 and 15 years.

Support for developmental path- (*i.e.*, female and secondary male vs. primary male) specific VBGF growth curves was assessed using the approach of Kimura (2008), whereby development strategy was added as covariates (β) on each of the three VBGF parameters, such that:

$$\begin{pmatrix} L_{\infty i} \\ k_i \\ t_{0i} \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_i \beta_{1L} \\ \beta_{0k} + x_i \beta_{1k} \\ \beta_{0t} + x_i \beta_{1t} \end{pmatrix}$$

where x_i is a dummy variable for developmental path, set to either 0 or 1, for the i th fish. To evaluate the occurrence of developmental path-specific differences in growth, the Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) of a standard VBGF model fitted without the effect of developmental path was compared with the AICc of a standard VBGF model fitted with developmental path included as a covariate. Models with an AICc value within two of that of the best approximating model (lowest AICc) were considered to be equivalent (Burnham & Anderson, 2002).

The instantaneous rate of total annual mortality (Z) for *H. longiceps* was estimated using the generalized linear mixed-effect model (GLMM) estimator of Millar (2015), based on samples collected in 2016 only. A single random-intercept Poisson loglinear model was fitted to data for age classes equal to or greater than the modal age class for all individuals combined (*i.e.*, pooling across sexes), with the frequency of fish in each age class as the response variable, age as a factor and a random intercept. The negative of the maximum likelihood estimator of the slope coefficient from the model was taken as an estimate of Z .

The natural mortality rate (M) for *H. longiceps* was estimated by solving the linear equation of Hoening (1983) for fish, where $\log_e(M) = 1.46 - 1.01 \times \log_e(t_{\max})$, where t_{\max} is the maximum age. A maximum age of 19 years was cautiously applied, reflecting the maximum age class observed for the species (this study). An estimate of fishing mortality (F) was calculated as the difference between Z and M .

2.5 | Reproductive biology

Generalized linear models (GLMs) were used to model the length and age at maturity of female *H. longiceps*, and the length and age of female to secondary male sex change. All females with gonads in stages developing-regressing as verified by histology were considered to be mature. Maturity state (*i.e.*, immature or mature) and sex (*i.e.*, female or secondary male) were treated as binomial response variables and modelled as a function of L_F and age with logit link. Corresponding 95% CIs for each parameter were derived by bootstrap resampling using 1000 iterations.

Monthly trends in the proportion of histologically verified mature females and GSI values of both mature females and mature males across the calendar year were examined to determine the seasonality of *H. longiceps* spawning in southern New Caledonia. GSI and stage data were aggregated by month across years.

2.6 | Regional variation in longevity and asymptotic length

Estimates of life span and asymptotic L_F from the present study were compared against those derived for *H. longiceps* from the northern Great Barrier Reef (GBR), Australia (Choat & Robertson, 2002; J. Choat, pers. comm.), Guam (Taylor & Cruz, 2017), Palau (Kitalong & Dalzell, 1994), Pohnpei (Taylor & Choat, 2014) and the Solomon Islands (Sabetian, 2010) to examine regional variation in age-based life history. Where reported as L_S or L_T , asymptotic length estimates were converted to L_F using correlation coefficients of the present study (see Results). Following Taylor and Cruz (2017), maximum age and asymptotic L_F estimates were regressed against satellite-derived SST data for each location using linear regression to explore correlations of each variable with SST.

All statistical analyses were conducted in R version 4.0.2 (R Core Team, 2020). All linear models, GLMs and nonlinear modelling of the VBGF were conducted using the *stats* package (R Core Team, 2020). The re-parameterized VBGFs were generated using the package *fishmethods* (Nelson, 2019).

3 | RESULTS

3.1 | Age determination

A clear annual periodicity in the formation of opaque increments in *H. longiceps* otoliths was evident from patterns of otolith edge classifications (Figure 4), indicating that increments were deposited annually. Opaque increment deposition was observed to begin towards the austral winter, commencing in May in some individuals, and peaking between July and August. Opaque increments were fully deposited by October (Figure 4).

3.2 | Length and age distributions

A total of 212 *H. longiceps* were collected during the sampling period. Catch samples were female biased, with a sex ratio of 1 female:0.6 males. The modal length class of all sampled individuals was 45 cm L_F and the modal age class was 7 years (Figure 5). The largest individual sampled was 57.3 cm L_F and weighed 3.73 kg, while the oldest individual was 19.8 years of age. Sampled female *H. longiceps* ranged from 28.2 to 55.1 cm L_F and 3.3 to 18.9 years of age. Primary males constituted 79% of all males sampled and were observed across most length and age classes, and across both IP and TP colour forms. Secondary males ranged from 48.8 to 57.3 cm L_F and 8.2 to 18.5 years (Figure 5).

3.3 | Growth and mortality

Relationships between L_S , L_F and L_T were defined as:

$$L_F = 1.118 \times L_S - 0.064 \quad (R^2 = 0.99)$$

$$L_T = 1.114 \times L_S + 1.026 \quad (R^2 = 0.99)$$

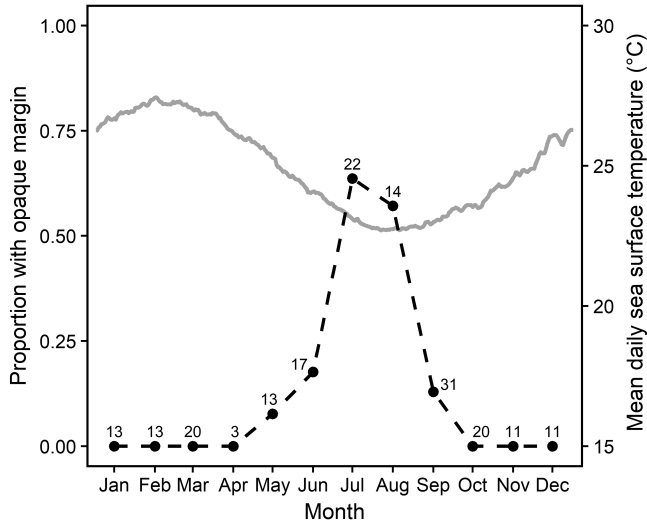
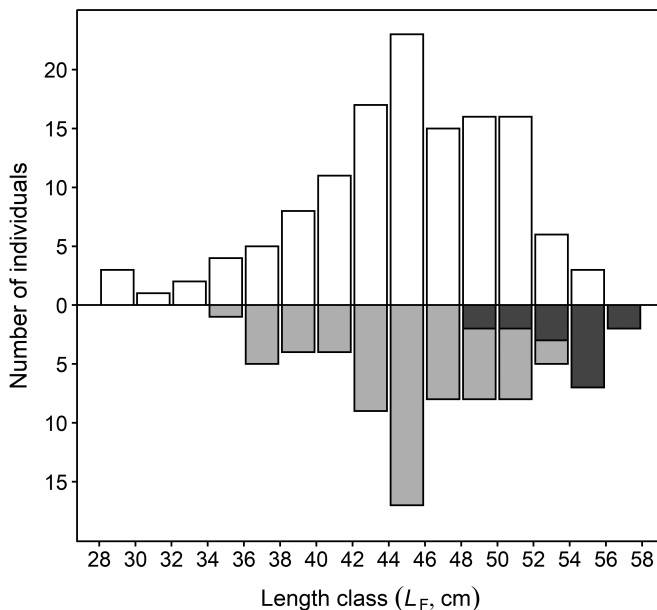


FIGURE 4 Proportion of *Hipposcarus longiceps* otoliths with opaque increments by month. The grey line depicts mean daily sea surface temperature (in °C) based on satellite-derived data between January 2000 and December 2015. Numbers represent sample sizes for each month



$$L_T = 0.996 \times L_F + 1.122 \quad (R^2 = 0.99)$$

The relationship between L_F and W_W was defined as:

$$W_W = 0.020 \times L_F^{2.987}$$

The value of the slope exponent ($b \approx 3$) indicates that *H. longiceps* exhibit an isometric growth pattern in which there is no change in body shape as they grow.

There was no significant effect of developmental path on growth of *H. longiceps*, with the AICc of the growth model including developmental path as a covariate on each of the three VBGF parameters within 2 of that of the growth model fitted excluding development path (927.14 and 926.06, respectively) (see also Table 1). Secondary males were generally larger for a given age than females or primary males (Figure 6). Constraining the growth curve to $L_0 = 1.5 \text{ cm } L_F$ resulted in a slightly reduced estimate of L_∞ relative to the unconstrained growth curve (Table 1). The re-parameterized version of the unconstrained VBGF applied to all individuals irrespective of developmental path yielded L_F estimates of 37.2 (95% CI = 36.3–38.1), 47.5 (95% CI = 47.0–48.0) and 51.2 (95% CI = 50.4–52.0) cm, at ages 5, 10 and 15, respectively (Table 1).

Total annual mortality (Z) for samples from 2016 was estimated as $0.27 (\pm 0.03) \text{ year}^{-1}$. Natural mortality was estimated as 0.22 and fishing mortality estimated as $0.05 (\pm 0.03)$.

3.4 | Reproductive biology

The estimated median length (L_{50}) and age (A_{50}) at female maturity were 38.9 cm L_F (95% CI = 36.8–40.7 cm L_F) and 5.7 years (95%

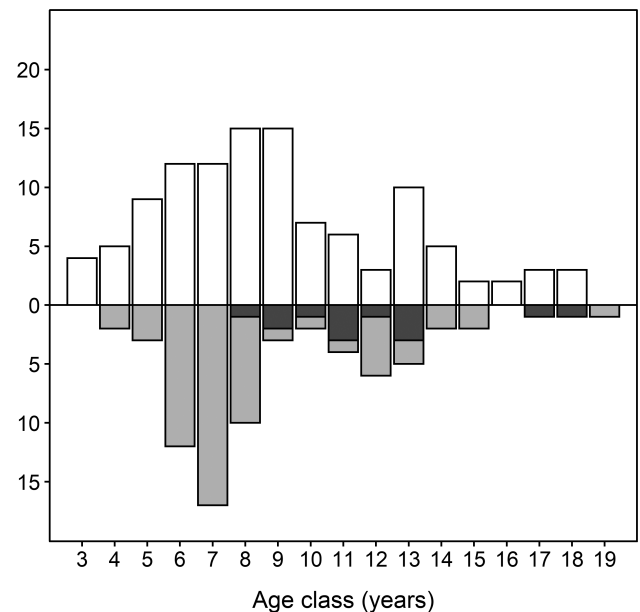


FIGURE 5 Sex-specific fork length (L_F , left) and age (right) frequency distributions for sampled *Hipposcarus longiceps* from southern New Caledonia. Individuals for which sex or developmental path was not determined ($n = 4$) are not shown, (□) females; (■) primary males; (■) secondary males

TABLE 1 Parameter estimates ($\pm 95\%$ CI) from the standard and constrained von Bertalanffy growth functions (VBGFs) and mean lengths at ages 5, 10 and 15 years from the re-parameterized VBGF (rVBGF) for *Hipposcarus longiceps* in southern New Caledonia

Model	Parameter	Females and secondary males	Primary males	All individuals combined
VBGF	L_{∞} (cm)	53.7 (51.8 to 56.4)	52.6 (47.2 to 58.0)	53.2 (51.6 to 55.5)
	k	0.20 (0.15 to 0.26)	0.17 (0.03 to 0.32)	0.21 (0.16 to 0.26)
	t_0	-0.61 (-2.13 to 0.43)	-2.75 (-8.4 to 2.89)	-0.79 (-2.31 to 0.24)
Constrained VBGF	L_{∞} (cm)	53.1 (51.8 to 54.5)	50.5 (48.5 to 52.7)	52.4 (51.3 to 53.6)
	k	0.23 (0.21 to 0.25)	0.27 (0.23 to 0.32)	0.24 (0.22 to 0.26)
	t_0	-0.13 (-0.13 to -0.12)	-0.11 (-0.12 to -0.10)	-0.12 (-0.13 to -0.12)
rVBGF	L_5 (cm)	36.8 (35.7 to 37.8)	38.9 (36.8 to 41.0)	37.2 (36.3 to 38.1)
	L_{10} (cm)	47.7 (47.0 to 48.3)	46.9 (45.8 to 47.9)	47.5 (47.0 to 48.0)
	L_{15} (cm)	51.5 (50.6 to 52.5)	50.2 (48.4 to 51.9)	51.2 (50.4 to 52.0)

CI = 4.8–6.6 years), while the estimated length and age at which 95% of females attained maturity was 42.5 cm L_F (95% CI = 40.7–45.3 cm L_F) and 7.4 years (95% CI = 6.5–8.8 years) (Figure 7). The lengths at which 50% and 95% of females changed sex were 52.5 (95% CI = 50.6–55.2 cm L_F) and 57.2 cm L_F (95% CI = 54.7–58.0 cm L_F), respectively. Due to the large proportion of females in the oldest age classes it was not possible to estimate the age at sex change (Figure 7).

Despite low sample sizes, monthly trends of both GSI and female gonad staging data showed a clear pattern of annual periodicity. Mean monthly GSI values for mature *H. longiceps* were highest from

November to February for females and November to March for males, the latter coinciding with periods of highest SST (Figure 8). Individuals in the running ripe classification stage (*i.e.*, as evidenced by the presence of oocytes undergoing late-stage germinal vesicle migration, germinal vesicle breakdown, hydration or ovulation; Brown-Peterson *et al.*, 2011) were observed between November and April (Figure 8), although the latter month was represented by a single mature female.

3.5 | Regional variation in longevity and asymptotic length

There was a 5-fold geographic variation in maximum observed age among the six locations for which life-history information was available. Estimates of both maximum observed age and asymptotic L_F decreased with increasing SST (Figure 9). This relationship was significant for maximum age ($R^2 = 0.89$, $P < 0.01$) but not for asymptotic length ($R^2 = 0.55$, $P = 0.09$).

4 | DISCUSSION

The maximum age of *H. longiceps* reported in the current study (~19 years) extends the species' reported life span by at least ~5 years. Previous longevity estimates for the species includes 14 years for an unknown location of the GBR (Sabetian, 2010; A. Sabetian, pers. comm.), 12 years from the northern GBR (based on 14 individuals from the Townsville and Lizard Island regions; Choat & Robertson, 2002; J. Choat, pers. comm.), 10 years from Guam (based on 279 individuals; Taylor & Cruz, 2017), 6 years from Pohnpei (based on 64 individuals; Taylor & Choat, 2014) and 5 years from Solomon Islands (based on 67 individuals; Sabetian, 2010). To our knowledge, this makes *H. longiceps* one of the longest lived parrotfish of the c. 100 currently recognized species to date (Fricke *et al.*, 2020), behind *Bolbometopon muricatum* (~40 years; Andrews *et al.*, 2015), *Scarus trispinosus* (~22 years; Freitas *et al.*, 2019), *Cetoscarus bicolor* (~21 years; Taylor *et al.*, 2018) and *Scarus frenatus* (~20 years; Choat *et al.*, 1996).

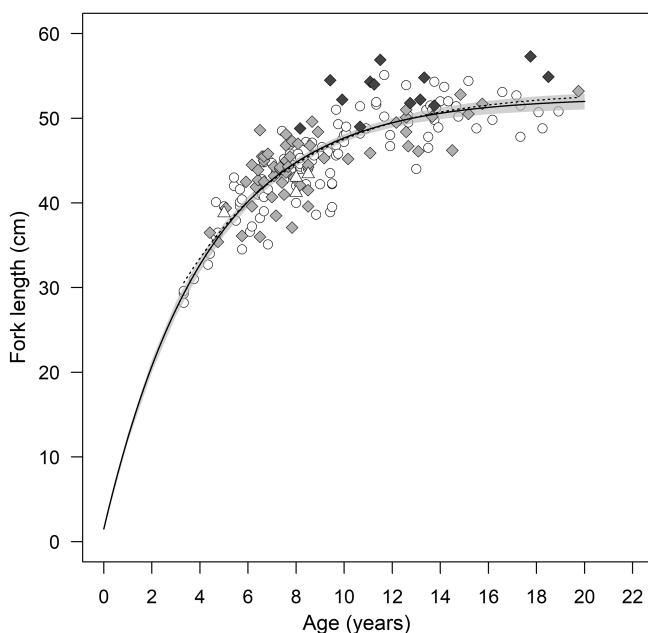


FIGURE 6 Length-at-age data and fitted von Bertalanffy growth function (VBGF) curves for *Hipposcarus longiceps* from southern New Caledonia. Shaded areas represent 95% confidence intervals for the constrained VBGF curve (confidence intervals for the unconstrained VBGF curve are not shown). (○) females; (◆) primary males; (◆) secondary males; (△) unknown; (-----) unconstrained VBGF; (—) constrained VBGF

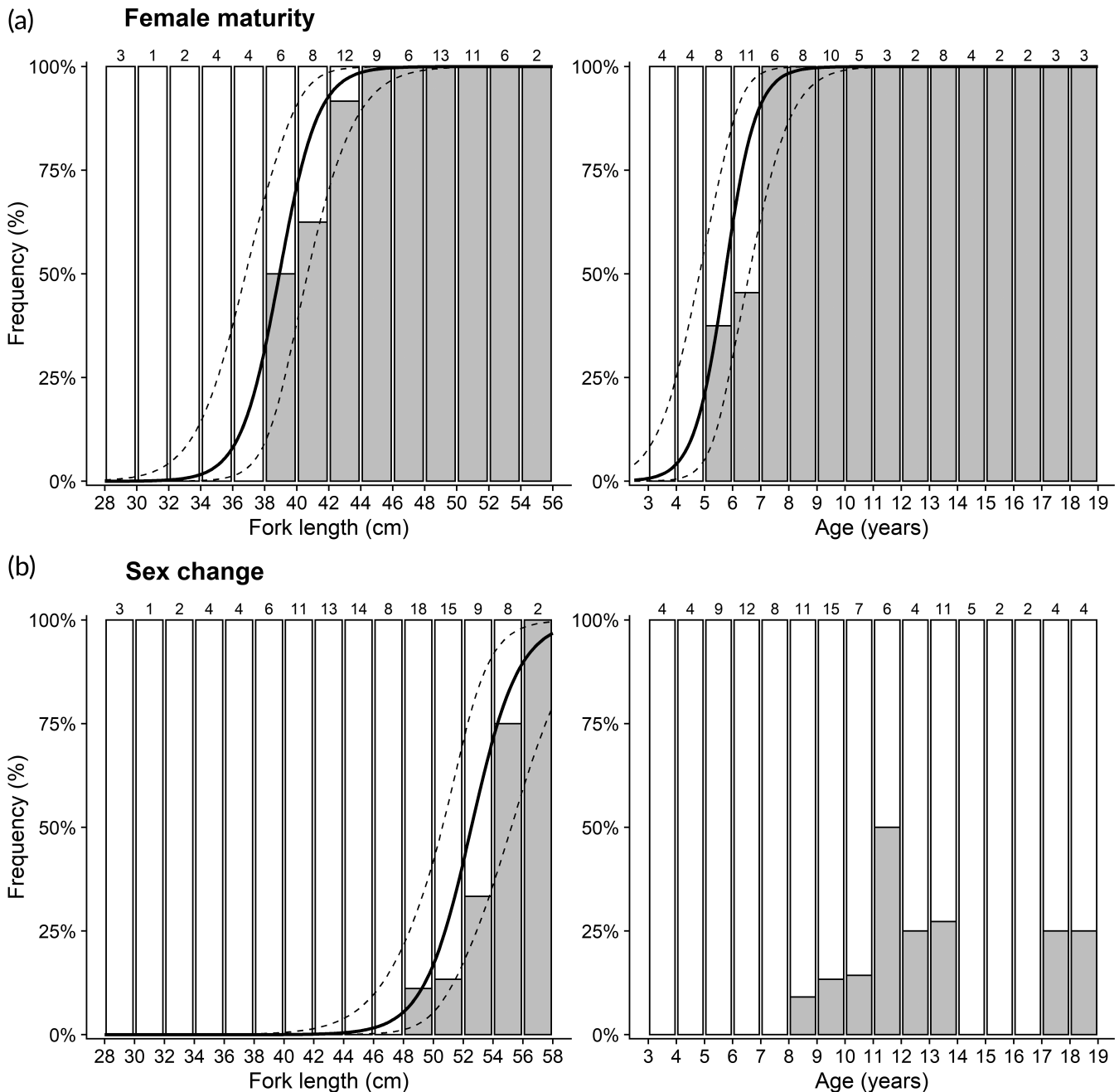


FIGURE 7 Percentage frequency of immature (white bars) and mature (grey bars) female *Hipposcarus longiceps* by sequential 2 cm fork length (L_F) (left) and age (right) classes (top row) and percentage frequency of female (white bars) and secondary male (grey bars) *Hipposcarus longiceps* by sequential 2 cm fork length (L_F) (left) and age (right) classes (bottom row) from southern New Caledonia. Numbers above the bars of both plots represent sample sizes. The solid line represents the logistic curve derived from the probability that a fish of a given L_F is mature (top row) or a secondary male (bottom row). Dashed lines represent the associated 95% confidence intervals

The timing of opaque increment formation (*i.e.*, ~winter) for *H. longiceps* in southern New Caledonia is consistent with that reported for the species in Guam by Taylor and Cruz (2017), yet often contrasts that observed of other scarid species. For example, from tetracycline marks, Choat *et al.* (1996) inferred that opaque increment formation occurs in spring–early summer for *Chlorurus sordidus* (now considered to be *C. spilurus* in the eastern Indian and western and central Pacific Oceans; Bray, 2020; Fricke *et al.*, 2020), *Scarus frenatus*, *Scarus niger*

and *Scarus rivulatus* on the neighbouring GBR, with the results for *S. rivulatus* supported by marginal increment analysis. Ebisawa *et al.* (2016) observed opaque increment formation to occur between June and August (*i.e.*, summer) for *Chlorurus microrhinos* in southern Japan. These differences further highlight the need for species- and location-specific studies of parrotfish life history.

The large proportion of primary males (79% of all sampled males) observed in the present study contrasts with that reported for the

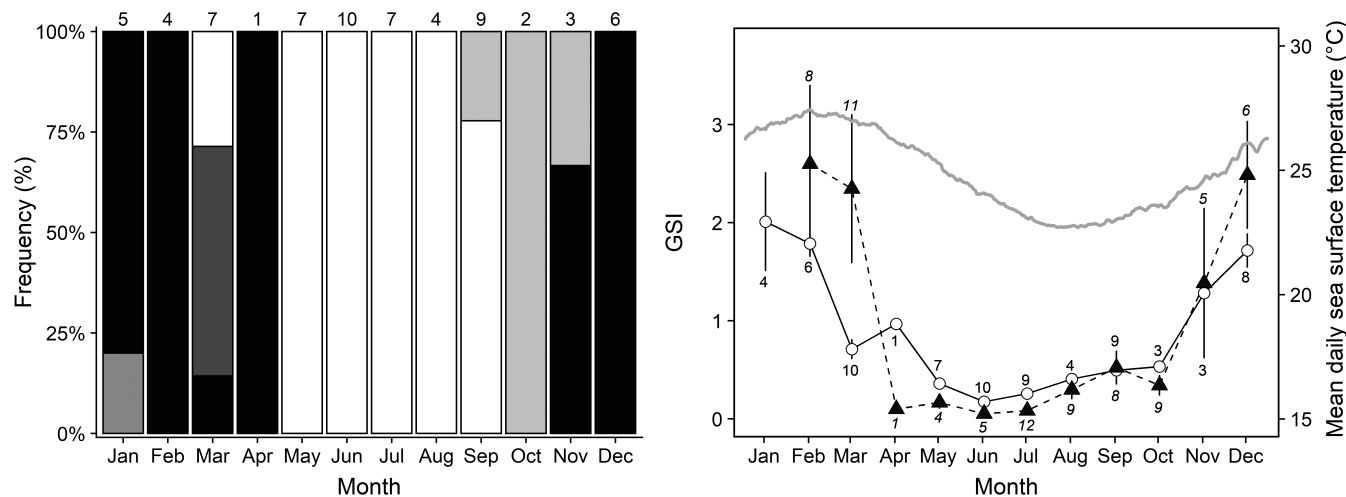


FIGURE 8 Monthly frequencies of mature *Hipposcarus longiceps* ovarian stages (left) and mean monthly gonadosomatic indices (GSI \pm SE; right) for mature female and male *H. longiceps* from southern New Caledonia. The grey line depicts mean daily sea surface temperature (in $^{\circ}$ C) based on satellite-derived data between January 2000 and December 2015. Numbers represent sample sizes for females (normal text) and males (italics) in each month. Left: (□) developing; (▨) spawning capable; (■) spawning; (▩) regressing; (◻) regenerating; Right: (—○—) female; (—▲—) male

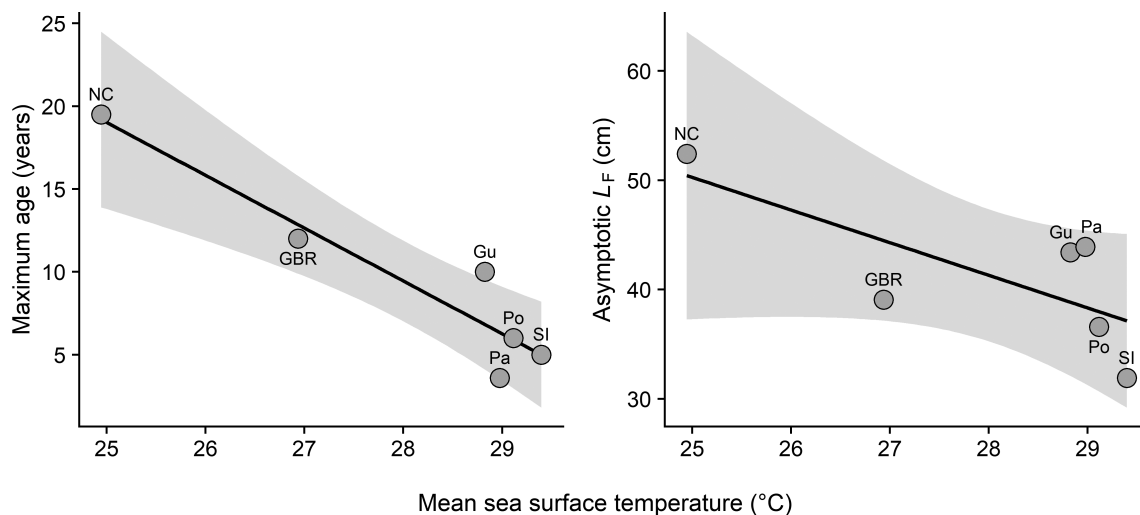


FIGURE 9 Linear regressions of sea surface temperature with maximum observed age (left) and asymptotic fork length (L_F) (right) across six populations of *Hipposcarus longiceps*. GBR, Great Barrier Reef; Gu, Guam; NC, New Caledonia; Pa, Palau; Po, Pohnpei; SI, Solomon Islands. Shaded areas represent 95% confidence intervals

species in Guam, where primary males accounted for 16% of all males (Taylor & Cruz, 2017), but is similar to that observed for the species in Pohnpei, where primary males accounted for 61% of all males (Taylor & Choat, 2014). In diandric labrids, including parrotfish, the proportion of initial phase primary males has been demonstrated to have a strong social basis, with higher proportions of primary males associated with increased group size (Gust, 2004; Munday *et al.*, 2006a). As such, the relatively high proportion of primary males observed in the current study potentially suggests that group sizes of *H. longiceps* in southern New Caledonia may be larger than those in populations sampled elsewhere. Such an effect may be exacerbated by the extended longevity and low mortality of *H. longiceps* in southern New Caledonia, coupled with the species' mating strategy. For

those species in which sex change is plastic and can respond to local conditions, sex allocation theory predicts that sex change should occur when an individual's reproductive value would be greater for the opposite sex than for their current sex (Munday *et al.*, 2006b). Like many diandric labrids, terminal phase male *H. longiceps* appear to patrol territories and adopt a harem mating system, engaging in courtship behaviour and spawning with individual or small groups of females (Colin, 2012; Colin & Bell, 1991). Accordingly, rather than competing for reproductive success with a large number of females for many years, it may be more advantageous for younger individuals in large, stable *H. longiceps* populations to become primary males to increase their individual reproductive value. Further studies into the spawning behaviour of *H. longiceps* in New Caledonia, and linkages

between group size, overall population size and the proportion of primary males within the population, are required to explore these hypotheses.

The strong negative correlation between maximum age and SST observed in the present study is consistent with the Metabolic Theory of Ecology (MTE), which predicts that much of the variation in life-history attributes can be accounted for by thermally-driven changes in metabolic performance (Brown *et al.*, 2004; Munch & Salinas, 2009). Under the MTE, life span is predicted to increase with lower ambient SST due to reduced metabolism at lower temperatures (Clarke & Johnston, 2002). The results of the present study add to the growing body of literature documenting these associations in coral reef fishes, for example *Acanthurus bahianus* (Robertson *et al.*, 2005), *Centropyge bispinosa* (Lowe *et al.*, 2021), *Ctenochaetus striatus* (Trip *et al.*, 2008), *Naso unicornis* (Taylor *et al.*, 2019) and *Scarus rubroviolaceus* (Taylor & Cruz, 2017). For *H. longiceps*, failing to account for the relationship between life span and ambient SST in assessments could result in considerable over- or underestimates of mortality, exploitation and yield.

In parallel, growth rate, body size and maturation rate in ectotherms covary with temperature under the temperature-size rule (TSR; Atkinson, 1994). Under this rule, slower initial growth rates and increased asymptotic lengths are expected at lower temperatures. While regional patterns in *H. longiceps* asymptotic length displayed a negative correlation with SST, with larger asymptotic lengths observed at locations exposed to cooler water, the trend lacked statistical significance. This may be explained in part by the small sample sizes for some locations, as well as differences in reef geomorphology, productivity, resource availability and competition among sampling sites (Gust *et al.*, 2002; Robertson *et al.*, 2005; Munch & Salinas, 2009; Caselle *et al.*, 2011; Barnett *et al.*, 2017; Taylor *et al.*, 2018; Lowe *et al.*, 2021). For example, the northern GBR sampling location, where parrotfish are unfished, showed the largest deviation from the expected asymptotic length, a likely artefact of the limited sampling at this location ($n = 14$; Choat & Robertson, 2002). Further sampling across geographically disparate locations encompassing gradients of latitude, reef geomorphology, SST and fishing pressure would help to disentangle the relative influence of various environmental and anthropogenic factors on *H. longiceps* longevity and life history (Taylor & Choat, 2014; Moore 2019).

The results of this study signal that at the time of sampling, *H. longiceps* in southern New Caledonia was unlikely to be subject to over-fishing (*i.e.*, fishing mortality was low). Nevertheless, the species' extended life span, coupled with several behavioural aspects, indicate *H. longiceps* may be among the more susceptible of the parrotfish species that are harvested from this region. Accordingly, ongoing monitoring and regular evaluation of stock status is recommended. The life-history information supplied herein provides a foundation for improved assessments and the development of harvest strategies for this species in New Caledonia. Moreover, the extended longevity observed for *H. longiceps* in the current study relative to previous research further confirms the occurrence of large geographic variability of life-history traits and indicates that

local management efforts for this species across the Indo-Pacific would greatly benefit from additional, geographically disparate, age-based research.

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REFERENCES

- Andrews, A. H., Choat, J. H., Hamilton, R. J., & DeMartini, E. E. (2015). Refined bomb radiocarbon dating of two iconic fishes of the Great Barrier Reef. *Marine and Freshwater Research*, 66, 305–316. <https://doi.org/10.1071/MF14086>.
- Atkinson, D. (1994). Temperature and organism size – A biological law for ectotherms. *Advances in Ecological Research*, 25, 1–58.
- Barnett, L., Branch, T., Ranasinghe, R., & Essington, T. (2017). Old growth fishes become scarce under fishing. *Current Biology*, 27, 2843–2848. <https://doi.org/10.1016/j.cub.2017.07.069>.
- Bejarano, S., Golbuu, Y., Sapolu, T., & Mumby, P. J. (2013). Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series*, 482, 197–215. <https://doi.org/10.3354/meps.10270>.
- Bellwood, D. R. (1996). Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia. *Marine Biology*, 125, 795–800. <https://doi.org/10.1007/BF00349262>.
- Bray, D. J. (2020). *Chlorurus spilurus*. In: Fishes of Australia. Retrieved from <https://fishesofaustralia.net.au/home/species/5300>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. <https://doi.org/10.1890/03-9000>.
- Brown-Peterson, N. J., Wyanski, D. M., Saborido-Rey, F., Macewicz, B. J., & Lowerre-Barbieri, S. K. (2011). A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 3, 52–70. <https://doi.org/10.1080/19425120.2011.555724>.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

- Caselle, J. E., Hamilton, S. L., Schroeder, D. M., Love, M. S., Standish, J. D., Rosales-Casián, J. A., & Sosa-Nishizaki, O. (2011). Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 288–303. <https://doi.org/10.1139/F10-140>.
- Choat, J. H., Axe, L. M., & Lou, D. C. (1996). Growth and longevity in fishes of the family Scaridae. *Marine Ecology Progress Series*, 145, 33–41. <https://doi.org/10.3354/meps145033>.
- Choat, J. H., & Robertson, D. R. (2002). Age-based studies. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 57–80). San Diego, CA: Academic Press.
- Colin, P. L. (2012). Longnose parrotfish – *Hipposcarus longiceps*. In Y. Sadovy de Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research and management* (pp. 496–502). Dordrecht, The Netherlands: Springer.
- Colin, P. L., & Bell, L. J. (1991). Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidae) at Enewetak Atoll, Marshall Islands with notes on other families. *Environmental Biology of Fishes*, 31, 229–260. <https://doi.org/10.1007/BF00000690>.
- Clarke, A., & Johnston, N. M. (2002). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905. <https://doi.org/10.1046/j.1365-2656.1999.00337.x>
- Ebisawa, A., Ohta, I., Uehara, M., Nakamura, H., Kanashiro, K., & Yasui, R. (2016). Life history variables, annual change in sex ratios with age, and total mortality observed on commercial catch on Pacific steephead parrotfish, *Chlorurus microrhinos* in waters off the Okinawa Island, southwestern Japan. *Regional Studies in Marine Science*, 8, 65–76. <https://doi.org/10.1016/j.rsma.2016.09.008>.
- Francis, R. I. C. C. (1988). Are growth parameters estimated from tagging and age-length data comparable? *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 936–942. <https://doi.org/10.1139/f88-115>.
- Freitas, M. O., Previero, M., Leite, J. R., Francini-Filho, R. B., Mente-Vera, C. V., & Moura, R. L. (2019). Age, growth, reproduction and management of southwestern Atlantic's largest and endangered herbivorous reef fish, *Scarus trispinosus* Valenciennes, 1840. *PeerJ*, 7, e7459. <https://doi.org/10.7717/peerj.7459>.
- Fricke, R., & van Eschmeyer, W. N., (2020). Eschmeyer's catalog of fishes: Genera, Species, References. Retrieved from <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>
- Green, A., & Bellwood, D. R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region*. Gland, Switzerland: IUCN.
- Gust, N. (2004). Variation in the population biology of protogynous coral reef fishes over tens of kilometers. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 205–218. <https://doi.org/10.1139/f03-160>.
- Gust, N., Choat, J. H., & Ackerman, J. L. (2002). Demographic plasticity in tropical reef fishes. *Marine Biology*, 140, 1039–1051. <https://doi.org/10.1007/s00227-001-0773-6>.
- Hoinig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, 82, 898–903.
- Houk, P., Rhodes, K., Cuetos-Bueno, J., Lindfield, S., Fread, V., & McLlwain, J. L. (2012). Commercial coral-reef fisheries across Micronesia: A need for improving management. *Coral Reefs*, 31, 13–26. <https://doi.org/10.1007/s00338-011-0826-3>.
- Kimura, D. K. (2008). Extending the von Bertalanffy growth model using explanatory variables. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 1879–1891. <https://doi.org/10.1139/F08-091>.
- Kitalong, A., & Dalzell, P. (1994). *A preliminary assessment of the status of inshore coral reef fish stocks in Palau* (p. 37). Noumea, New Caledonia: South Pacific Commission.
- Lowe, J. R., Payet, S. D., Harrison, H. B., Hobbs, J.-P. A., Hoey, A. S., Taylor, B. M., ... Pratchett, M. S. (2021). Regional versus latitudinal variation in the life history traits and demographic rates of a reef fish, *Centropyge bispinosa*, in the Coral Sea and Great Barrier Reef Marine Parks, Australia. *Journal of Fish Biology*, 2021, 1–11. <https://doi.org/10.1111/jfb.14865>.
- Mantyka, C. S., & Bellwood, D. R. (2007a). Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs*, 26, 435–442. <https://doi.org/10.1007/s00338-007-0214-1>.
- Mantyka, C. S., & Bellwood, D. R. (2007b). Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series*, 352, 177–185. <https://doi.org/10.3354/meps07055>.
- Millar, R. B. (2015). A better estimator of mortality rate from age-frequency data. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 364–375. <https://doi.org/10.1139/cjfas-2014-0193>.
- Moore, B., & Colas, B. (2016). *Identification guide to the common coastal food fishes of the Pacific Islands region*. Noumea, New Caledonia: Pacific Community (SPC).
- Moore, B., Rechelluul, P., & Victor, S. (2015). *Creel survey and demographic assessments of coastal finfish fisheries of southern Palau: September 2014*. Noumea, New Caledonia: Secretariat of the Pacific Community.
- Moore, B. R. (2019). Age-based life history of humpback red snapper, *Lutjanus gibbus*, in New Caledonia. *Journal of Fish Biology*, 95, 1374–1384. <https://doi.org/10.1111/jfb.14142>
- Munch, S., & Salinas, S. (2009). Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 13860–13864. <https://doi.org/10.1073/pnas.0900300106>.
- Munday, P. L., White, J. W., & Warner, R. R. (2006a). A social basis for the development of primary males in a sex-changing fish. *Proceedings of the Royal Society B*, 273, 2845–2851. <https://doi.org/10.1098/rspb.2006.3666>.
- Munday, P. L., Buston, P. M., & Warner, R. R. (2006b). Diversity and flexibility of sex-change strategies in animals. *Trends in Ecology & Evolution*, 21, 89–95. <https://doi.org/10.1016/j.tree.2005.10.020>.
- Nelson, G. A. (2019). fishmethods: Fishery Science Methods and Models. R package version 1.11-1. Retrieved from <https://CRAN.R-project.org/package=fishmethods>
- Paddack, M. J., Sponaugle, S., & Cowen, R. K. (2009). Small-scale demographic variation in the stoplight parrotfish *Sparisoma viride*. *Journal of Fish Biology*, 75, 2509–2526. <https://doi.org/10.1111/j.1095-8649.2009.02451.x>.
- R Core Team. (2020). R: A Language and Environment for Statistical Computing (Version 4.0.2). R Foundation for Statistical Computing, Vienna. Retrieved from <https://www.R-project.org>
- Randall, J. E., Allen, G. R., & Steene, R. C. (1990). *Fishes of the Great Barrier Reef and Coral Sea*. Honolulu, Hawaii: University of Hawaii Press.
- Rhodes, K. L., Tupper, M. H., & Wichlimel, C. B. (2008). Characterization and management of the commercial sector of the Pohnpei coral reef fishery, Micronesia. *Coral Reefs*, 27, 443–454. <https://doi.org/10.1007/s00338-007-0331-x>.
- Rhodes, K. L., Nernandez-Ortiz, D. X., Cuetos-Bueno, J., & Ioanis, M. (2018). A 10-year comparison of the Pohnpei, Micronesia, commercial inshore fishery reveals an increasingly unsustainable fishery. *Fisheries Research*, 204, 156–164. <https://doi.org/10.1016/j.fishres.2018.02.017>.
- Robertson, D. R., Reinboth, R., & Bruce, R. W. (1982). Gonochorism, protogynous sex-change and spawning in three Sparisomatine parrotfishes from the western Indian Ocean. *Bulletin of Marine Science*, 32, 868–879.
- Robertson, D. R., Ackerman, J. L., Choat, J. H., Posada, J. M., & Pitt, J. (2005). Ocean surgeonfish *Acanthurus bahianus*. I. the geography of demography. *Marine Ecology Progress Series*, 295, 229–244. <https://doi.org/10.3354/meps295229>.
- Sabetian, A. (2010). *Parrotfish fisheries and population dynamics: A case-study from Solomon Islands*. PhD thesis, James Cook University, Townsville, QLD
- Sadovy, Y., & Shapiro, D. Y. (1987). Criteria for the diagnosis of hermaphroditism in fishes. *Copeia*, 1987, 136–156.

- Sadovy De Mitcheson, Y., & Liu, M. (2008). Functional hermaphroditism in teleosts. *Fish and Fisheries*, 9, 1–43. <https://doi.org/10.1111/j.1467-2979.2007.00266.x>.
- Shapiro, D. Y., & Rasotto, M. B. (1993). Sex differentiation and gonadal development in the diandric, protogynous wrasse, *Thalassoma bifasciatum* (Pisces, Labridae). *Journal of Zoology*, 230, 231–245.
- Taylor, B., & Choat, J. (2014). Comparative demography of commercially important parrotfish species from Micronesia. *Journal of Fish Biology*, 84, 383–402. <https://doi.org/10.1111/jfb.12294>.
- Taylor, B. M. (2014). Drivers of protogynous sex change differ across spatial scales. *Proceedings of the Royal Society B*, 281, 20132423. <https://doi.org/10.1098/rspb.2013.2423>.
- Taylor, B. M., & Cruz, E. (2017). Age-based and reproductive biology of the Pacific longnose parrotfish *Hipposcarus longiceps* from Guam. *PeerJ*, 5, e4079. <https://doi.org/10.7717/peerj.4079>.
- Taylor, B. M., Hamilton, R. J., Almany, G. R., & Choat, J. H. (2018a). The world's largest parrotfish has slow growth and a complex reproductive ecology. *Coral Reefs*, 37, 1197–1208. <https://doi.org/10.1007/s00338-018-1723-9>.
- Taylor, B. M., Trip, E. D. L., & Choat, J. H. (2018b). Dynamic demography: Investigations of life-history variation in the parrotfishes. In A. S. Hoey & R. M. Bonaldo (Eds.), *Biology of parrotfishes* (pp. 69–98). Boca Raton, FL: CRC Press.
- Taylor, B. M., Choat, J. H., DeMartini, E. E., Hoey, A. S., Marshall, A., Priest, M. A., ... Meekan, M. G. (2019). Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. *Journal of Animal Ecology*, 88, 1888–1900. <https://doi.org/10.1111/1365-2656.13095>.
- Trip, E. L., Choat, J. H., Wilson, D. T., & Robertson, D. R. (2008). Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Marine Ecology Progress Series*, 373, 97–109. <https://doi.org/10.3354/meps07755>.
- West, G. (1990). Methods of assessing ovarian development in fishes: A review. *Australian Journal of Marine and Freshwater Research*, 41, 199–222. <https://doi.org/10.1071/MF9900199>.

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