Age, growth, and reproduction of the yellow-edged lyretail *Variola louti* (Forssakal, 1775)

Eva Schemmel · Kristen Dahl

Abstract Groupers (Family Epinephelidae) are important to commercial, subsistence, and recreational fisheries throughout the world. Grouper species have complex life histories that make them more vulnerable to exploitation. While there has been extensive research on some, the majority of groupers lack sufficient life history information for proper management. The yellow-edge lyretail grouper, *Variola louti*, has life history gaps that need to be filled and lacks regional life history information for Guam. Age, growth, and reproduction were assessed from fishery-dependent samples collected from around Guam from 2010 to 2017. *Variola louti* ranged from 19.4 to 49.7 cm fork length (FL) and 2 to 17 years old. Due to the size selectivity of the fishery, a Bayesian von Bertalanffy growth model was applied. The von Bertalanffy growth parameters were $L_\infty = 43.7$ cm FL, $k = 0.28$, and $t_0 = -0.2$. Protogynous hermaphroditism was confirmed with females reaching reproductive maturity at 26.0 cm FL (L_{50}) and 2.6 years (A_{50}) and female to male sex change at 35.3 cm FL ($L_{\Delta 50}$) and 6.1 years ($A_{\Delta 50}$). Sex ratio was 1.5 females per male, excluding transitional individuals. Using Hoenig's method, natural mortality was estimated at 0.37 $year^{-1}$. The life history of *Variola louti* suggests that it is a relatively fast growing and early maturing grouper that is not as vulnerable to exploitation as larger bodied, slower growing groupers. However, future monitoring of sex ratio, size at maturity, and size at sex change is recommended to track and manage fishery effects, such as the recent scuba spear ban in Guam, on the life history and population status of this species.

Keywords Grouper · Life history · Growth · Reproduction

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Introduction

Groupers (Family Epinephelidae), further defined as the subfamily Epinephelinae, are currently considered to contain 9 genera (*Alphestes*, *Cephalopholis*, *Dermatolepis*, *Epinephelus*, *Gonioplectrus*, *Hyporthodus*, *Mycteroperca*, *Plectropomus*, and *Variola*) and are found throughout the world in many different ocean habitats (Ma and Craig 2018). Traditionally, grouper species were considered to be comprised of 15 genera; however, molecular phylogeny research suggests the 9 genera above which include 167 species (reviewed in Félix-Hackradt et al. 2022). Groupers exhibit a diverse array of life histories with some of the larger species reaching sexual maturity as late

as 10 years of age, and longevity exceeding 50 years (Andrews et al. 2019; Craig et al. 2011). Groupers also exhibit a diverse array of reproductive patterns; however, they tend to exhibit monandric protogynous hermaphroditism (i.e., all males derive from adult females by sex change). Some exceptions to this hermaphroditic pattern exist which can include bisexual juvenile reproductive development, diandry (primary males and secondary males derived by sex change), and gonochorism (Sadovy and Colin 1995).

Groupers are a commercially important assemblage of species in several markets including the aquarium and live fish trades, as well as many recreational, commercial, and subsistence fisheries throughout the world. Unfortunately, their complex life histories can make them more vulnerable to exploitation (for review see Sadovy de Mitcheson et al. 2020). In general, grouper life history and reproductive biology traits result in low resilience to exploitation and increased vulnerability to overfishing (Coleman et al. 2000; Sadovy de Mitcheson et al. 2020), especially for those that are large-bodied, long-lived, slow-growing, and form spawning aggregations (Sadovy de Mitcheson et al. 2020). Despite this, the life histories and reproductive strategies of many species of groupers remain unknown, making efforts to effectively manage such species difficult.

The genus *Variola* is part of a monophyletic clade shared with genera *Plectropomus* and *Gonioplectrus* (Ma and Craig 2018). There are only two identified species within the genus *Variola: Variola louti* and *Variola albimarginata*. *Variola* spp. have a wide Indo-Pacific distribution and are found in coral reef, reef crest, and outer slope habitats at depths of 15–250 m (Nair et al. 2017). Reported maximum size is 65 cm fork length (FL) for *V. albimarginata* and 81 cm FL for *V. louti* (Craig et al. 2011), and prior research suggests that both are relatively short-lived (Grandcourt 2005; Nair et al. 2017). For example, Grandcourt (2005) reported a maximum size of 60 cm FL, a maximum age of 15 years, $L_\infty = 51.0$ cm FL, and $k = 0.48$ for *V. louti* from Seychelles. *Variola* spp. are also believed to be hermaphroditic, but this has yet to be confirmed. Their reproductive strategy, including size and age at maturity and size and age at sex change, is currently unknown.

Variola louti are captured in multiple fisheries and with multiple gear types throughout their range (Galal et al. 2002; Grandcourt 2005). In Guam, *V. louti* are part of a shallow water reef fishery (predominantly spear fishing) and a shallow water bottomfish fishery (using hook and line in depths that are outside of spear and scuba depth limits and < 135 m). The minimum size reported is around 20.0 cm FL, and the maximum size previously reported is 49.0 cm FL (Kamikawa et al. 2015). Estimated annual landings are highly variable for this species around Guam ranging from 19 to 3159 kg (mean = 688 kg; Bohaboy and Matthews 2023). Management action in March 2020 saw the banning of spearfishing on scuba for all fish species in response to research which indicated the overall size, as well as the ratio of large to small individuals, had declined in Guam over the past 25 years (Houk et al. 2018). This highlights the need for more information on *V. louti* life history in order to better assess population status and future management strategies, in particular, the impact of the scuba-spear ban.

This study investigated the age, growth, natural mortality, and reproduction of *Variola louti* using biological samples collected from the reef and bottomfish fisheries in Guam from 2010 to 2017. This information fills life history gaps for the species and adds to the collective understanding of the biology of groupers in the Pacific which is an important component of population monitoring and sustainable fisheries management.

Methods

Sample collection

A biological sample collection program was established in Guam in 2010 (Sundberg et al. 2015). This Commercial Fisheries Biosampling Program collected fishery-dependent length observations ($n = 1147$) and biological samples (otoliths [$n = 287$] and gonads [$n = 255$]) of *V. louti* from the waters around Guam from 2010 to 2017. Additionally, during research surveys in summer 2014, five *V. louti* were caught in Asuncion, Maug, Pagan, and Uracus (Fig. S1), Commonwealth of the Northern Marianas Islands (CNMI). These fish were aged and compared to the ages of those from Guam. Ultimately, they were not included in the growth model because they came from locations that are considered lightly fished and may not be representative of fish in Guam.

Comparisons between Guam and these lightly fished areas serve as a check on potential fishery effects on growth and length-at-age.

Length distributions of the biological samples ($n = 287$) were compared to the entire fishery-dependent length observations for *V. louti* ($n = 1147$) using a Kolmogorov–Smirnov test to determine if biological samples constituted a representative sample of the fishery. Additionally, a Student's *t* test was performed to compare mean length from the biological samples to fishery-dependent length observations.

All fish were measured for FL (0.1 cm), weighed (W [g]), and gonads and otoliths extracted. Otoliths were cleaned, weighed (OW [0.001 g]), and stored in plastic vials. Gonads were weighed (GW [0.001 g]) and a midsection of the gonad from one of the lobes was removed and stored in 10% buffered formalin.

Fishery-dependent length observations were analyzed to determine if gear or fishing method (hook and line [shallow water bottomfish fishery] or freediving spear and scuba spear [reef fishery]) impacted length frequencies. A Kolmogorov–Smirnov test was used to determine if there were differences in *V. louti* length distributions between the bottomfish fishery and reef fishery. The percent of the samples from the shallow water bottomfish fishery and reef fishery were assessed to determine the fishery's contribution of the field-dependent length data and biological samples.

Age and growth

One otolith (either right or left, randomly chosen) was examined for condition (i.e., not broken or chipped) and, if suitable, the sagitta was marked to identify the primordium on the medial surface along the sulcus acusticus. Each individual otolith was mounted and transversely sectioned perpendicular to the sulcus acusticus using a Buehler precision Isomet saw with two blades separated by a 400 μm spacer (Usseglio et al. 2015) or affixed by thermoplastic adhesive to a slide and ground along the primordium using a GEMMASTA GFL8 lapping wheel to a thickness of 400 μm (O'Malley et al. 2019). The otolith sections were then polished using lapping film (30 to 0.3 μm grit) to a thickness of 200–240 μm until the banding pattern was clearly visible. Otoliths were cover slipped with casting clear epoxy resin (Fiberglass Hawaii) before reading. Samples were read blind (i.e.,

no knowledge of FL, weight, or date of capture) and were read twice by a single reader with a minimum of two weeks between reads. Ages were accepted when two reads matched and read a third time if they were different. Two age readers read a subset reference collection of the Guam *V. louti* otoliths ($n = 62$) to determine average percent error (APE) and coefficient of variation (CV). The APE and CV were averaged across all individuals to estimate the Index of Average Percent Error (IAPE) and average CV. Age-bias plots were used to assess symmetry and identify any systematic differences in aging between readers (Campana et al. 1995). Edge type analysis (Newman and Dunk 2003) was done to validate increment periodicity and compared to mean monthly sea surface temperature from Guam (NOAA Coral Reef Watch 2022). Linear regression was used to determine the relationship between otolith weight and age.

A Bayesian von Bertalanffy growth model was used with the following model (von Bertalanffy 1938):

$$L_t \sim \text{normal}(L_{t,}\sigma)$$

$$L_t = L_\infty(L_\infty - L_0)e^{-k(t)}$$

$$L_\infty \sim normal(50, 5)$$

$$k \sim uniform(0.0, 0.6)$$

$$L_0 \sim normal(0, 2)$$

$$\sigma \sim \text{uniform}(0, 5)$$

where L_t is the predicted mean length-at-age t (years), L_∞ is the asymptotic FL in cm, k is the growth coefficient, t is the estimated age in years, L_0 is the length at hatch at theoretical time zero (t_0), and σ is the model dispersion/error. Theoretical time zero (t_0) is calculated from L_∞, k, and L_0 using the equation:

$$t_0 = \frac{Ln(1 - L_0/L_\infty)}{k}$$

where a normally distributed prior was used for L_∞ and set to the maximum size encountered in biological samples (50 cm), a half normal prior (truncated at 0) was used for L_0, and a uniform prior was used for k and σ following methods by Smart and Grammer (2021). Markov Chain

Monte Carlo (MCMC) was used to sample the posterior distributions for each growth parameter. Four chains were used with a 1000 iteration warm up (burn in) and 4000 total post-warmup draws with a thin equal to 1. Posterior distribution means and 95% credible intervals (CI) were reported.

Bayesian model fit was assessed with prior sensitivity analyses and posterior predictive distributions, where observed values were compared to the posterior distributions (McElreath 2018; Vehtari et al. 2017). Well-calibrated models should include the observation within the high density of the distribution (McElreath 2018). Trace plots, R-hat, and effective sample size were checked for model convergence (McElreath 2018). Pareto smoothed importance sampling leave-one-out (PSIP-LOO) was used to determine if there were any high-leverage observations (Pareto $\hat{k}$ estimate > 0.7). See Supplemental Information for prior and posterior model checks.

Natural mortality (M) was estimated using Hoenig et al. (1983) updated method (Then et al. 2015), as follows:

$$M = 4.899 t_{max}^{-0.916}$$

where t_{max} = maximum age (17 years).

Reproduction

Gonad samples were embedded in paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin counterstaining at John A. Burns Medical School Histopathology Core Facility at the University of Hawaii. Female and male reproductive phases were assigned following criteria by Brown-Peterson et al. (2011) (Table 1). Regenerating females were differentiated from immature females by having two or more diagnostic criteria of prior spawning activity (e.g., thick ovary walls, atretic oocytes, post ovulatory follicles, muscle bundles, brown bodies, or enlarged blood vesicles). Gonads that contained both ovarian and testicular tissue were classified as transitional or as a functional male with primary oocytes (male with PO) (Sadovy De Mitcheson and Liu 2008; Schemmel et al. 2016). Lastly, hermaphroditic pattern was diagnosed based on Sadovy and Shapiro (1987).

The two criteria used to assess female reproductive maturity were (1) physiological maturity (L_{50p}): presence of cortical alveoli, and (2) functional maturity

(L_{50f}): onset of vitellogenesis (Brown-Peterson et al. 2011). Because there is no universal standard for maturity criteria (Lowerre-Barbieri et al. 2011), both physiological and functional maturity were assessed to allow for comparisons to prior and future studies.

Size (L_{50}) and age (A_{50}) at sexual maturity (i.e., the size or age at which 50% of females are mature), and size ($L_{\Delta 50}$) and age ($A_{\Delta 50}$) at female to male sex change were assessed using a logistic regression model with binomial family and logit link function with 2 cm length bins for size and 1 year bins for age (Chen and Paloheimo 1994). Estimates of L_{50} and A_{50} were generated using 1000 bootstrapped replicates of the model coefficients. Likelihood ratio tests were used to determine if size or age at maturity differed based on physiological or functional maturity criteria.

Gonadosomatic index (GSI) was assessed from histologically identified females to determine reproductive investment with size. GSI was assessed using the following equation:

$$GSI = \frac{\text{gonad weight } (g)}{\text{gonad free body weight } (g)} \times 100$$

Mean monthly GSI was assessed from functionally mature females ($n = 106$) and males ($n = 86$) with gonad weights. Mean monthly GSI and the proportion of females in spawning capable and actively spawning reproductive phases per month were used to identify the spawning season. The relationship between GSI and lunar day was also assessed using a generalized additive model (GAM). Spawning fraction was estimated by assessing the frequency of individuals spawning using the hydrated oocyte method (DeMartini and Fountain 1981). Lastly, spawning interval (i.e., the time period between spawning events) was estimated as the inverse of the spawning fraction (Lowerre-Barbieri et al. 2011).

All analyses and statistical tests were performed in R (R Core Team 2020) using the packages mgcv, FSA, and Stan (Stan Development Team 2023).

Results

Demographics

The majority (76%) of fishery-dependent lengths ($n = 1147$) was measured from the reef fishery (95%

Table 1 Reproductive phases and their respective oocyte stages, criteria for physiological and functional maturity, and diagnostic characteristics for *Variola louti* (modified from Brown-Peterson et al. 2011). Male with PO (primary oocytes) and male reproductive phases were further classified into developing, spawning capable, and regressing following Brown-Peterson et al. (2011)

| Reproductive Phase	Most advanced oocyte stage	Physiologically Mature	Functionally Mature	Characteristics
Undeveloped	Oogonia, chromatin nucleolar (CN), or perinucleolar (PN)	No	No	Immature individual with chromatin nucleolar (large nucleus (germinal vesicle) surrounded by a thin layer of cytoplasm), and perinucleolar (germinal vesicle increases in size and nuclei appear at its periphery) oocytes. Thin ovary wall
Developing I	Cortical alveolar (CA)	Yes	No	Developing individuals with cortical alveolar oocytes (CA; appearance of cortical alveoli (yolk vesicles) in the cytoplasm and formation of the vitelline membrane)
Developing II	Early vitellogenic (VT I and/or VTII)	Yes	Yes	Developing individuals with early vitellogenic oocytes, VTI, and/or VTII present
Spawning Capable	Late vitellogenic (VTIII)	Yes	Yes	Late stage vitellogenic oocytes (VTIII) present and identified by increased oocyte size and uniform distribution of yolk. May contain late stage post ovulatory follicles (POFs)
Actively Spawning	Germ vesicle migration (GVM), germ vesicle breakdown (GVBD), hydrated oocytes (H), ovulated eggs, POFs	Yes	Yes	Contains one or more of the following: germ vesicle migration, germ vesicle breakdown, hydrated oocytes, ovulated eggs, and/or recent POFs. May contain atretic oocytes, identified by theca membrane breakdown and loss of spherical appearance
Regressing	Perinucleolar, cortical alveolar, and/or vitellogenic	Yes	Yes	Ovaries dominated with atretic oocytes. May contain some CA or VT oocytes
Regenerating	Chromatin nucleolar (CN), perinucleolar (PN)	Yes	Yes	Only primary growth oocytes present (chromatin nucleolar and perinucleolar). May contain unabsorbed material from past spawning events, large muscle bundles, large blood vessels, and thick ovarian wall
Transitional	Chromatin nucleolar (CN), perinucleolar (PN)	Yes	Yes	Similar to regressing phase (dominated by atresia) but may contain a few healthy oocytes. Crypts of spermatogonia and spermatocytes present

Table 1 (continued)

Reproductive Phase	Most advanced oocyte stage	Physiologically Mature	Functionally Mature	Characteristics
Male with PO	Chromatin nucleolar (CN), perinucleolar (PN)	Yes	Yes	Gonad tissue dominated with seminiferous tissue with developed seminiferous crypts. Can contain developed sperm sinuses and spermatozoa can be present in crypts, lumen of lobules, and sperm sinuses. Lumen and melanomacrophage centers often present. Primary oocytes present
Male	NA	Yes	Yes	No primary oocytes present or degrading oocytes. Can be developing, spawning capable, regressing, or regenerating. Melanomacrophage centers may be present

scuba spear; 5% spear), while the shallow water bottomfish fishery (hook and line) accounted for 21% of lengths, and the remaining 3% were categorized as a mixture of both shallow water bottomfish and reef fishing methods. Fishery-dependent length distributions of *V. louti* differed between the reef and shallow water bottomfish fishery ($D = 0.28$, p value < 0.01; Fig. 1). *V. louti* were, on average, 4.2 cm FL larger from the reef fishery compared to the shallow water

bottomfish fishery ($t = -11.23$, $df = 390.81$, p value < 0.01). Similarly, median size of *V. louti* from the reef fishery was 3.4 cm larger than the shallow water bottomfish fishery.

A total of 289 otoliths and 255 gonads were sampled from the waters around Guam. The majority of *V. louti* biological samples were from the reef fishery (59%); the shallow water bottomfish fishery accounted for 39%, and 2% did not have a gear type or fishery specified. Across all individuals, 146 females, 54 males, 42 males with primary

Fig. 1 Length distributions of *Variola louti* sampled from Guam between 2010 and 2017 from the **a** bottomfish fishery ($n = 245$) and **b** reef fishery ($n = 867$) from fishery-dependent observations. Dashed lines indicate mean size observed within each fishery
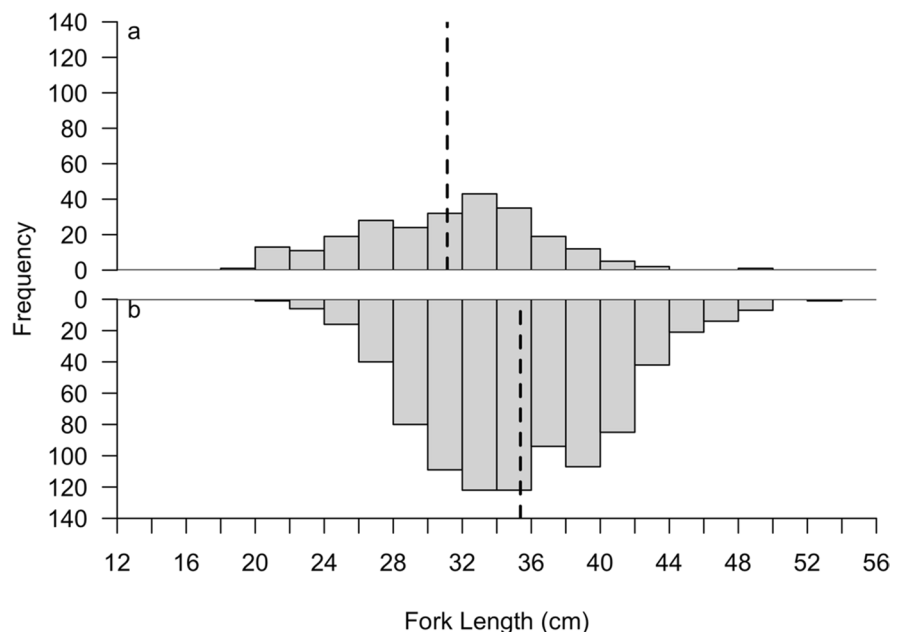
stage oocytes, and 13 transitional individuals (both ovarian and spermatogenic tissue present but inactive) were histologically identified. The male (males and males with PO) to female sex ratio was 40.0%. Fork lengths ranged from 19.4 to 49.7 cm for the biological samples and 19.8 to 53.6 cm for the fishery-length observations. The length distributions of biological samples and fishery-length observations did not differ ($D = 0.06$, p value $= 0.18$) and mean lengths did not differ ($t = 1.12$, $df = 326.87$, p value $= 0.27$), indicating that biological samples collected were representative of the fishery.

Age, growth, and mortality

Opaque marks were visible on otoliths polished to a thickness between 200 and 240 µm (Fig. 2b). Opaque marks were presumed to be deposited annually, the highest proportion of which were deposited December through March which coincided with the lowest mean monthly sea surface temperatures (Fig. 2a). There was a strong relationship between age and otolith weight (Fig. 2b; $y = 0.009 + 0.009*Age$, $R^2 = 0.88$, p value < 0.01). Between reader agreement was 45%, and agreement within 1 year was 84%. The average
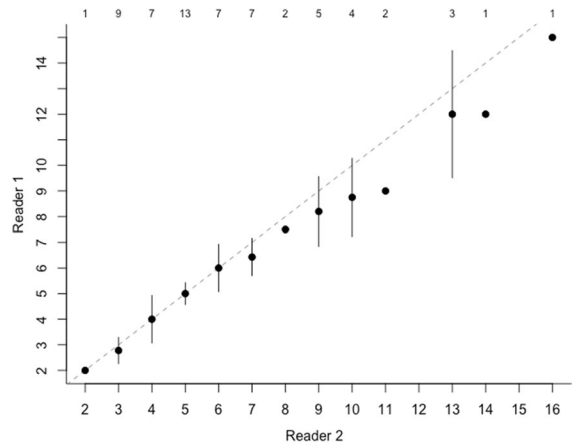
Fig. 3 Age-bias plots comparing reader 1 and reader 2 ages of *Variola louti* from Guam. Each error bar represents the 95% confidence intervals. The number on top of the plots indicates the number of individuals at each age

CV was 8.5% and the IAPE was 6.0%. The age-bias plot shows slight disagreement between readers for individuals over 11 years (Fig. 3).

Ages of *V. louti* ranged from 2 to 17 years. Males were larger (7.4 cm, $t = -13.16$, p value < 0.01) and older (2.5 years, $t = -8.21$, p value ≤ 0.01) than
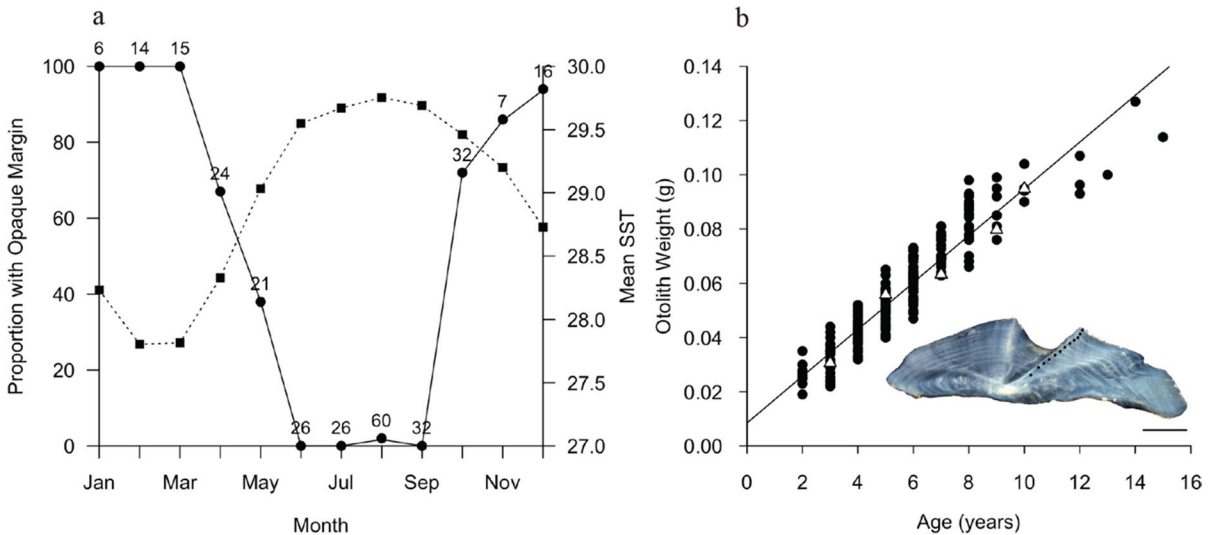

Fig. 2 Edge analysis showing proportion of *Variola louti* otoliths with opaque margin (solid line) and mean sea surface temperature by month (dashed line) for fish sampled from Guam between 2010 and 2017, and **b** relationship between otolith weight and age ($n = 247$) of *V. louti* from Guam (black circles) and CNMI (white triangles). Plotted line is a linear regression fit to the data ($y = 0.009 + 0.009*Age$, $R^2 = 0.88$, p value < 0.01). Inset image is a *V. louti* polished otolith showing opaque marks (age $= 12$ years) from a 39.1 cm FL female with 1 mm scale bar (inset image is enlarged in Supplemental Material Fig. S2)

Fig. 4 Percent frequency of *Variola louti* reproductive stages by fork length (cm) and age (years) for fish sampled from Guam between 2010 and 2017. Developing stages (Developing I & Developing II) were grouped together into "Developing." Male reproductive phases are grouped into "Male." Males with PO (primary oocytes) are separated into their own group regardless of the reproductive phase (developing or spawning capable)
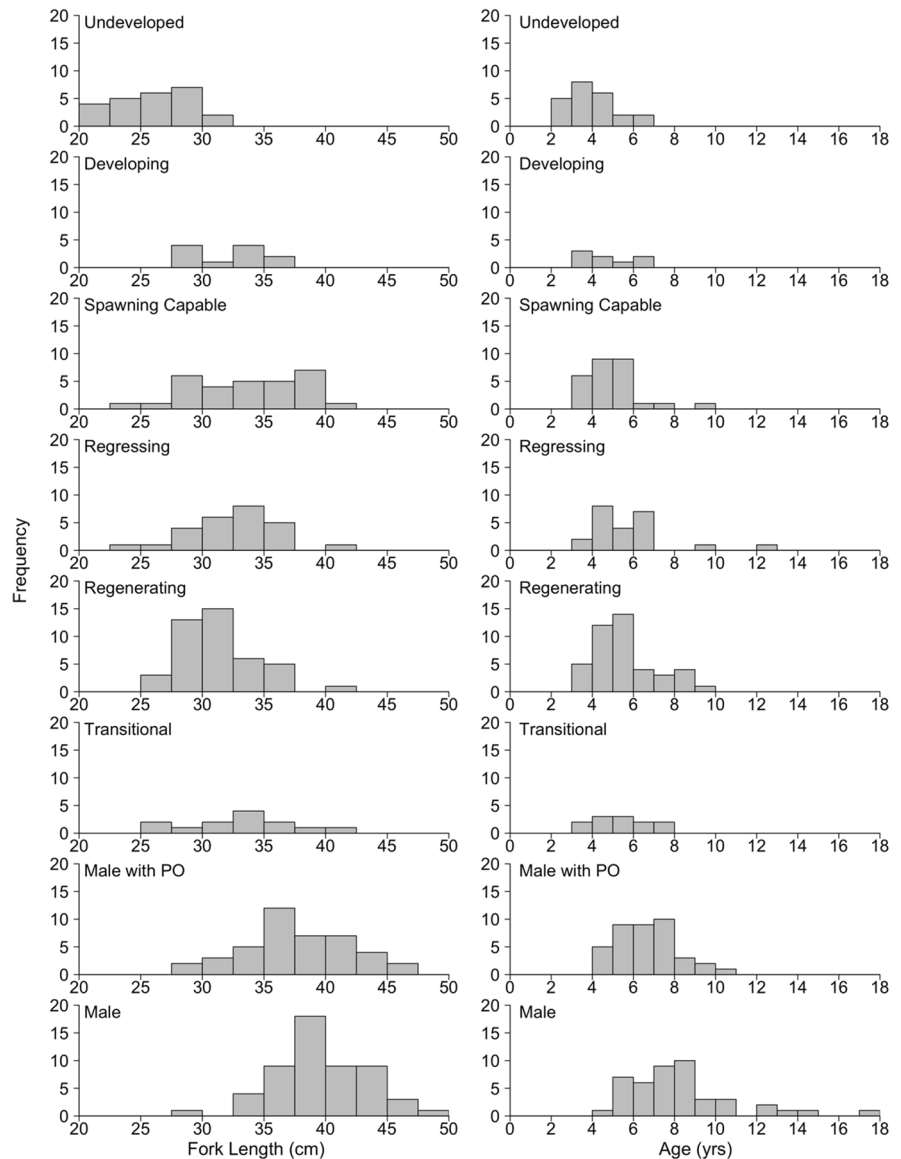
females (Fig. 4). The maximum age was 12 years for females and 17 years for males. The mean age was 4.7 years for females and 7.1 years for males. There was significant variability in length-at-age (Fig. 5; see Supplemental Information for table of means and CV). The estimated von Bertalanffy growth function parameters (95% CI) were $k=0.28$ (0.24–0.32), $L_\infty=43.7$ cm FL (42.0–45.8 cm FL), and $t_0=-0.2$ years (−0.5–0.0) (Table 2; Fig. 5). The length-at-age of the fish from CNMI fell within the range of fish from Guam (Fig. 5). As expected for size selected sex change for protogynous hermaphrodites,

sex-specific growth was observed with males reaching a larger L_∞ than females (Supplemental Information Table S3 and Fig. S5); however, we focus on combined sex growth parameters as these are comparable to other studies. Natural mortality estimated using Hoenig's method was 0.37 years^{-1}.

Reproduction

There was clear evidence that *V. louti* are protogynous hermaphrodites. Length and age distributions differed between sexes (Fig. 4) and histology revealed
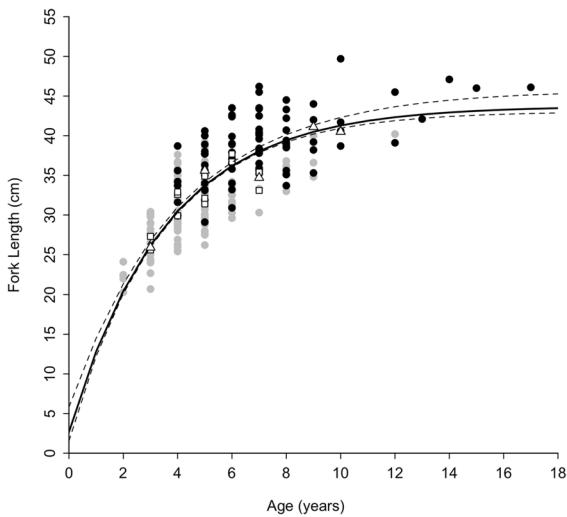
Fig. 5 Bayesian von Bertalanffy growth curve for Guam *Variola louti* ($L_\infty = 43.7$ [42.0–45.8], $k = 0.28$ [0.24–0.32], and $t_0 = -0.2$ [−0.5–0.0]) sampled between 2010 and 2017. Black line is mean and dashed lines are 95% credible intervals. Females (grey circles), transitional (squares), males (males and males with primary oocytes; black circles), and CNMI individuals of unknown sex (triangles) which were not included in the growth model estimation

Table 2 Life history traits and 95% credible intervals for *Variola louti* from Guam

Trait	Value
L_∞ (cm FL)	43.7 (42.0–45.8)
k (year^{-1})	0.28 (0.24–0.32)
t_0	−0.2 (−0.5–0.0)
Maximum age (year)	17
Maximum FL (cm)	53.6
Sex Ratio (F:M)	1.5
L_{50} physiological (cm FL)	25.8 (25.4–27.1)
L_{50} functional (cm FL)	26.0 (25.6–27.3)
A_{50} physiological (year)	2.4 (2.1–3.1)
A_{50} functional (year)	2.6 (2.4–3.1)
$L_{\Delta50}$ (cm FL)	35.5 (35.1–36.4)
$A_{\Delta50}$ (year)	6.1 (5.9–6.7)

the presence of transitional individuals (Fig. 6). The presence of a central lumen in the testes and the fact that the smallest males are larger and older than the smallest transitional individuals further support monandric protogynous hermaphroditism. The smallest transitional individual was 25.6 cm FL and the

youngest was 3 years (Fig. 4). The smallest male with primary oocytes was 27.5 cm (age unknown) and as young as 4 years. The smallest male (without primary oocytes) was 29.1 cm and as young as 5 years.

Gonad histology showed a transition from a female functioning ovary to a male functioning testis (Figs. 6 and 7). The transition from female to male appears to begin in the regressing reproductive phase with the appearance of spermatogenic tissue in the form of small pockets of spermatogonia and spermatocytes scattered throughout the gonad and intermingled with ovarian tissue (Fig. 6a, b). One transitional individual had a few remaining hydrated oocytes, several degenerating vitellogenic oocytes, and small pockets of spermatocytes (Fig. 6a). Primary oocytes appeared to remain in the testes of developing and spawning capable males for extended periods as the lumen shrinks and spermatogenesis progresses (Fig. 6d).

Female GSI was influenced by reproductive phase as well as fish size (Fig. 8a). Mean ($\pm$ SE) GSI of females was 0.11 ($\pm$0.02) for undeveloped, 0.37 ($\pm$0.70) for developing, 1.99 ($\pm$0.28) for spawning capable, 0.35 ($\pm$0.09) for regressing, 0.16 ($\pm$0.01) for regenerating, and 3.12 ($\pm$0.70) for actively spawning phases. Spawning capable and actively spawning females had variable GSI across fish sizes (Fig. 8a). There was a weak relationship between reproductive output (i.e., log gonad weight) and gonad free body weight (Fig. 8b; log GW = 1.3860 + GFBW * 0.0016, df = 40, R^2 = 0.23).

Spawning capable females were encountered throughout the year (Fig. 9). GSI peaked from November through March (Fig. 10a). However, spawning appeared to occur most of the year. Spawning peaked during the first quarter and last quarter of the lunar phase (F value = 3.865, edf = 5.331, rdf = 6.428, p value < 0.01; Fig. 10b). The spawning fraction (i.e., the number of actively spawning females out of the total number of mature females) was 0.11 which translated to a spawning interval of approximately 9 days.

Female size at maturity (L_{50}) was estimated physiologically at 25.8 cm FL (CI: 25.4–27.1 cm FL) and functionally at 26.0 cm FL (CI: 25.6–27.3 cm FL) (Table 2, Fig. 11). Physiological age at maturity was 2.4 years (CI: 2.1–3.1 years) and functional age at maturity was 2.6 years (CI: 2.4–3.1 years) (Table 2, Fig. 11). Female size and age at physiological maturity were not significantly different from functional

Fig. 6 Transitional and male reproductive phases of *Variola louti*: **a** transitional phase with degenerating vitellogenic oocytes (A), a few remnant hydrated oocytes (H), and spermatogonia (SG) and spermatocytes (SC); **b** male with PO primary stage oocytes (PO), lumen (L), melanomacrophage centers (MMC), and spermatogonia and spermatocytes; **c, d** spawning capable male with PO with developed sperm ducts with spermatozoa (SZ), scattered primary stage oocytes throughout the gonad; and **e, f** spawning capable male with sperm sinuses full of spermatozoa and melanomacrophage centers scattered throughout the gonad. Scale bars in all panels are 250 μm
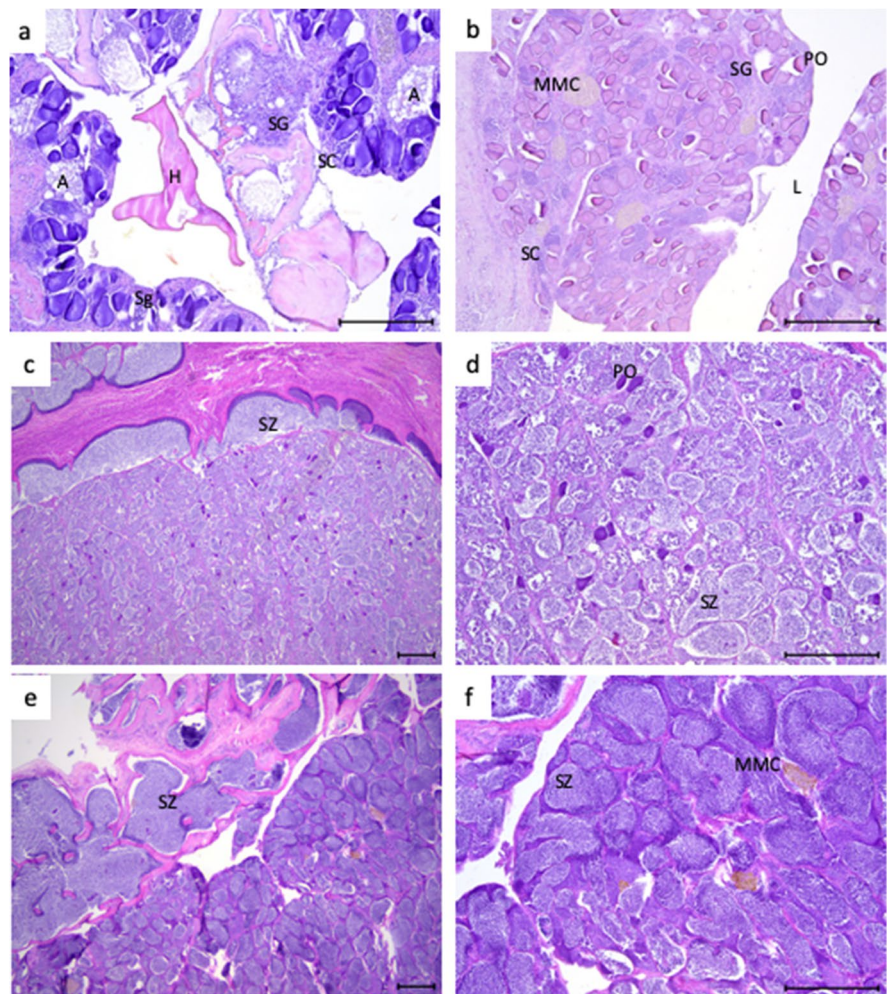
maturity (L_{50}: $\chi^2 = 0.042$, $df = 1$, p value $= 0.84$ and A_{50}:$\chi^2 = 0.031$, $df = 1$, p value $= 0.86$). Size at sex change was 35.5 cm FL (CI: 35.1–36.4 cm FL) and age at sex change was 6.1 years (6.1–6.7 years) (Table 2; Fig. 11).

Discussion

While *Variola louti* are present in many fisheries around the tropics, little was known about the species' life history and vulnerability to exploitation. In this study, *Variola louti* exhibited moderate growth ($k = 0.28$) and reach L_∞ at 43.7 cm FL within 8–10 years. Protogynous hermaphroditism was confirmed for this species; females reach reproductive maturity at a small size (26.0 cm FL) and young age

(2.6 year), and female to male sex change occurs, on average, at 35.3 cm FL and 6.1 years of age. These life history characteristics suggest that *V. louti* are not as vulnerable to exploitation compared to larger, slower growing hermaphroditic groupers such as Galapagos grouper (*Mycteroperca olfax*, Usseglio et al. 2015), Hawaiian grouper (*Hyporthodus quernus*, Andrews et al. 2019; DeMartini et al. 2011), and Nassau *grouper* (*Epinephelus striatus*, Sadovy and Eklund 1999).

There is debate on the best approach to deal with juveniles missing from von Bertalanffy growth models (Kritzer et al. 2001; Pardo et al. 2013) because small changes in the value used to fix t_0 can cause large changes in the other von Bertalanffy growth parameters k and L_∞ (Pardo et al. 2013; Schemmel et al. 2022). A Bayesian growth model with

Fig. 7 Female reproductive phases of *Variola louti*: **a**, **b** undeveloped female ovary with primary oocytes (PO) and tunica (T); **c** spawning capable female with PO, cortical alveolar (CA), vitellogenic II (VTII), and vitellogenic (VTIII) oocytes; **d** actively spawning female with hydrated oocytes (H); **e** regressing female with atretic vitellogenic oocytes (A), space in the lumen (L), and large mussel bundles (MB); and **f** regenerating female with PO and large blood vessels (BV). Scale bars in all panels are 250 μm
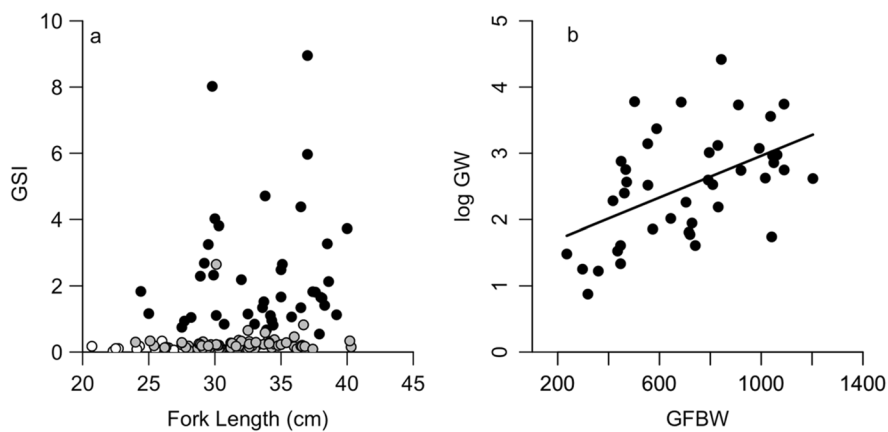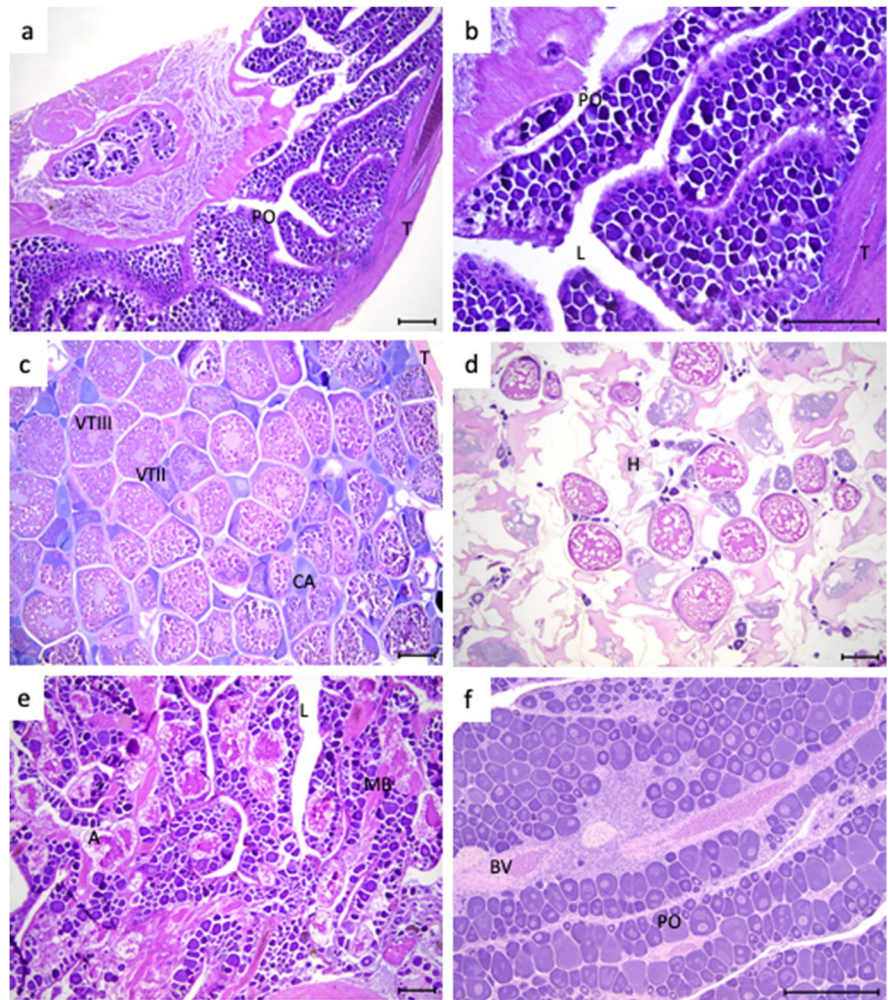
Fig. 8 a Female Guam *Variola louti* gonadosomatic index (GSI) versus fork length, and **b** spawning capable and actively spawning female log gonad weight (GW) versus gonad free body weight (GFBW) (log GW = 1.3860 + GFBW * 0.0016, df = 40, $R^2 = 0.23$) for fish sampled from Guam between 2010 and 2017. Spawning capable and actively spawning females are black, immature females are white, and all other female reproductive phases are gray

Fig. 9 Trend in reproductive stages of female *Variola louti* by month for fish sampled from Guam between 2010 and 2017. Developing stages (Developing I & Developing II) were grouped together into "Developing." Numbers above each bar indicate aggregate monthly sample sizes
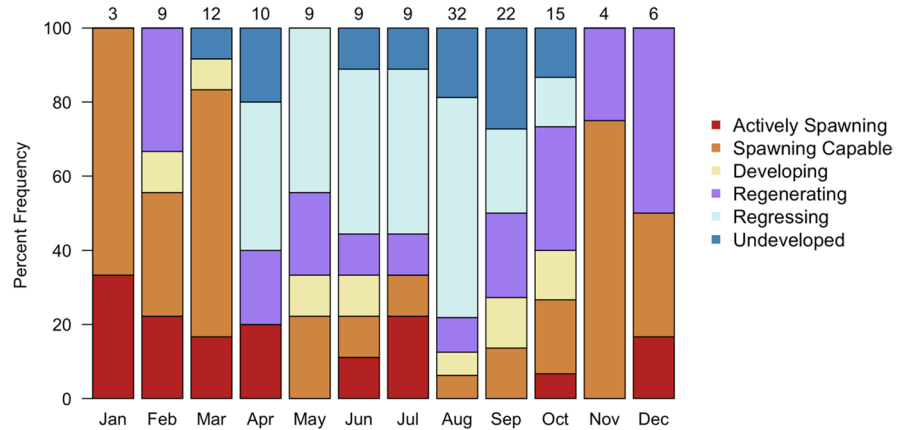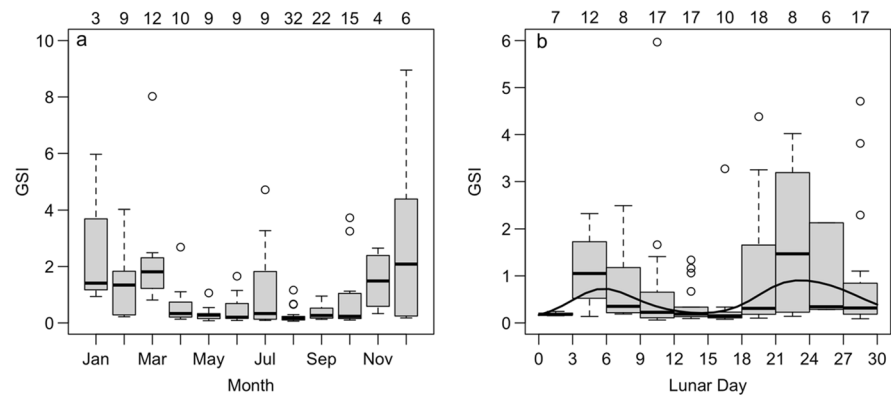

Fig. 10 Median and interquartile range of gonadosomatic index (GSI) for mature female *Variola louti* by month, and **b** generalized additive model GSI ~ fork length + s(Lunar day) fit to raw data points (black line) by lunar day (3 day mean). Numbers on top of the figure represent the sample size of each bin

informed priors was used to improve model fit under minimum size selectivity in the fishery (absence of juveniles under 20.0 cm in the sample). This approach allowed the setting of the L_0 prior to a biologically reasonable range. An alternative approach to deal with minimum size selectivity is to fix or constrain $t_0 = 0$ or fix t_0 to larval size at hatching (Prince et al. 2015). Grandcourt (2005) fixed $t_0 = 0$ for *V. louti* from the Seychelles, with a resulting $k = 0.48$, $L_\infty = 51.0$ cm FL, and max length of 60.0 cm FL. For Guam samples herein, when t_0 was fixed at 0, k was increased to 0.31 and L_∞ was reduced to 42.8 cm FL. Using t_0 fixed to the larval size at hatching, Prince et al. (2015) incorporated 5 studies on *V. louti* and *V. albimarginata*, including Grandcourt (2005), to model life history parameters for *V. louti* in Palau. Parameter estimates reported by Prince et al. (2015) were $L_\infty = 48.3$ cm and $L_{50}/L_\infty = 0.59$. Our study's estimate of L_∞ is within the 95% CI reported by Prince et al. (2015), and

the estimate of L_{50}/L_∞ was the same (0.59). Notably, recent research revealed that when juveniles are missing from the growth curve, constraining $t_0 = 0$ is problematic unless a clear asymptotic length has been reached (Schemmel et al. 2022). Furthermore, there are no estimates of larval size at hatching in Guam. In the case of *V. louti* from Guam, the Bayesian approach helped overcome the low numbers of juveniles encountered and the lack of larval size at hatching information.

When large individuals are missing from the von Bertalanffy growth model, a clear asymptote in growth is not obtained. Our uncertainty in L_∞ is demonstrated by the larger credible intervals around L_∞. While additional older individuals may have helped the fit of the growth model, our sample selection for age and growth was proportional to the fished population. This is an important distinction, because overrepresentation of the largest, oldest individuals can also bias growth parameters (Schemmel et al. 2022).

Fig. 11 *Variola louti* **a** size at functional maturity ($L_{50}=26.0$ cm FL), **b** age at functional maturity ($A_{50}=2.6$ years), **c** size at sex change ($L_{\Delta50}=35.5$ cm FL), and (**d**) age at sex change ($A_{\Delta50}=6.1$ years) for fish sampled from Guam between 2010 and 2017. Solid lines are logistic regression fit to the data and dashed lines are 95% confidence intervals. Sample size is indicated by the size of the grey circles
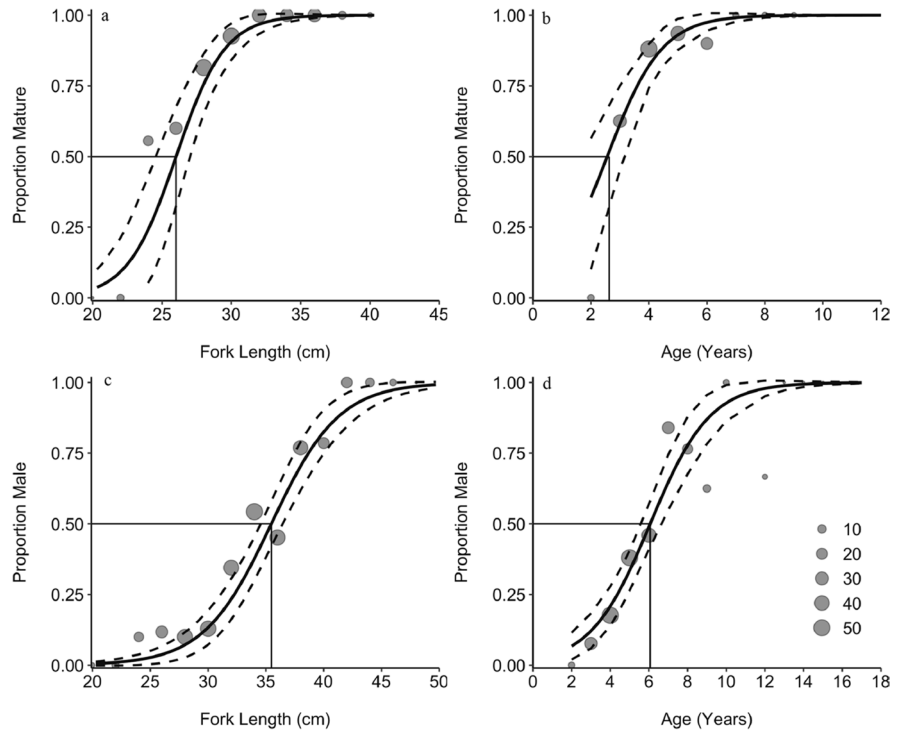
The estimates of maximum age obtained in this study (17 years) are comparable to similar-sized hermaphroditic grouper species. Maximum ages of groupers range from 8 years for the small-bodied leopard coral grouper (*Plectropomus leopardus*; Payet et al. 2020) to 76 years (age validated to 50 years) for the large-bodied Hawaiian grouper (*Hyporthodus quernus*; Andrews et al. 2019). Compared to *V. louti*, the peacock grouper (*Cephalopholis argus*) has a similar geographic range, size (maximum size 49.6 cm FL), and age (maximum age of 16.7 years) (Donovan et al. 2013). Similarly, the squaretail common grouper (*Plectropomus areolatus*; maximum size 80 cm TL) has a reported maximum age of 10 years in Micronesia (Rhodes et al. 2021) and 14 years in the eastern Torres Strait (Williams et al. 2008).

The occurrence of transitional individuals observed through histological examination of the gonad tissue confirms protogynous hermaphroditism in *V. louti*. The frequency of females and males in the population suggests that the type of hermaphroditic pattern is monandric protogynous hermaphroditism. However, diandry, or the existence of both primary and secondary males, is not uncommon in protogynous grouper species, including *Cephalopholis*, *Epinephelus*, and

Plectropomus species (Adams 2003; Chan and Sadovy 2002; Ebisawa 2013; Fennessy and Sadovy 2002; Liu and de Mitcheson 2009; Liu and Sadovy 2004; Rhodes et al. 2021; Sadovy and Colin 1995). Unfortunately, there were no individuals under 19.4 cm FL with which to determine early gonadal development. However, given the very low frequency of small, young males, diandry is unlikely.

Spawning appeared to occur all year in Guam *V. louti*, as spawning capable or actively spawning females were present in every month. Spawning peaked from November through March; however, the assessment of spawning seasonality is also likely influenced by sample size, sampling location, and the time of sampling. A semi-lunar spawning pattern was observed with peaks occurring during first and last quarter moons. Notably, lunar (full moon) and semi-lunar (new moon) spawning is common in groupers. A few examples include *Plectropomus leopardus* which spawn on new moons (Ebisawa 2013), *P. areolatus* which spawn on full and new moons (Rhodes et al. 2021), and *Epinephelus fuscoguttatus* which spawn on full moons (Pet et al. 2005). Some groupers do not follow a lunar spawning pattern, such as *Mycteroperca jordani*

which spawn most of the month and can for spawn 15 consecutive days (Rowell et al. 2019). While not as common as new and full moon spawning, quarter moon spawning is observed in other groupers and other reef fish species (Rahman et al. 2000; Park et al 2006; Murata et al. 2022). The spawning timing of *V. louti* herein may be specific to Guam, as there can be intraspecific differences in spawning timing (Schemmel and Friedlander 2017; Fukunaga et al. 2020). In some instances, different studies have reported opposite lunar spawning patterns within the same species, for example, *P. areolatus* spawn on either new moons or full moons (for review see Rhodes et al. 2021). The lunar spawning pattern of a species may depend on the environmental, current, and tidal conditions experienced by the population. *Variola louti* seem to prefer the outer reef or slope habitat which may be heavily influenced by environmental conditions (Emslie et al. 2017); however, they can also be found in deeper coastal waters (< 135 m).

Female reproductive output was highly variable and was not strongly correlated with fish size or weight. This may be due to the influence of seasonal and lunar spawning patterns that were not accounted for in GSI analyses. This may also be due to the high rates of sex change observed, where larger females had reduced reproductive output (egg production) and presumably reallocated energy into sexual transition.

Size/age at maturity and size/age at sex change are important indicators of population productivity. This study found *V. louti* to reach maturity at 26.0 cm FL (24.3 cm standard length [SL]). Only one other study examined *V. louti* size at maturity and estimated L_{50} as 29.0 cm SL (~ 33 cm FL); however, assessment of maturity was done using macroscopic (as opposed to histological) methods (Loubens 1980). The differences in size at maturity of *V. louti* from that study (New Caledonia) and ours could stem from differences in methodology, regional environmental conditions, habitat, or exploitation rates. *Variola louti* age at maturity was comparable to other similar-sized protogynous groupers. *Variola louti* matured at 2.5 years compared to *C. argus* which matured at 1.2 years (Schemmel et al. 2016) and *P. areolatus* which matured at 2.9 years (Rhodes et al. 2021). *Variola louti* size and age at sex change was 35.5 cm FL and 6.1 years, respectively. The ratio of size at sex change to L_{∞} was within the range of other similar-sized

grouper species (*V. louti* = 0.81, *C. argus* = 0.79, *P. leopardus* = 0.98); however, the ratio of age at sex change to maximum age was slightly lower (*V. louti* = 0.38, *C. argus* = 0.66, *P. leopardus* = 0.55). It is unclear how long the transitional, inactive, and reproductive phases last for *V. louti*. The prevalence of primary stage oocytes in functioning males suggests full oocyte degeneration is a lengthy process. However, males with primary oocytes appeared to be spawning capable. Primary oocytes have been seen in spawning capable males of other protogynous grouper species including *C. argus* (Schemmel et al. 2016). Future research to monitor size and age at sex change and size at maturity would be beneficial for monitoring shifts in population productivity, as shifts in size at sex change can indicate fishery effects.

Additionally, sex ratio and reproductive behavior are important indicators of exploitation vulnerability in hermaphroditic groupers. Of particular concern for protogynous groupers is the fishery removal of large individuals since most of them are male. This can lead to skewed sex ratios, eventual sperm limitation, and population collapse (Alonzo and Mangel 2004; Coleman et al. 1996). Many grouper species are known to form large, predictable spawning aggregations which make them easily targeted by fishers (Sadovy De Mitcheson et al. 2008; Sadovy De Mitcheson et al. 2020). Hermaphroditic groupers that form spawning aggregations can experience large shifts in sex ratios due to exploitation, with the percent of males declining to as low as 1% of the population (Coleman et al. 1996; Usseglio et al. 2015). However, sex ratios in hermaphroditic groupers can also be influenced by fishing gear type (Wyanski et al. 2000), spatial variability in demographic parameters (Lowerre-Barbieri et al. 2020), and reproductive behavior (Lowerre-Barbieri et al. 2020). *Variola louti* are described as roving serranids, meaning that they are often observed roving or patrolling their habitat (Pears 2005). This type of behavior differs from what has been described for several *Cephalopholis* spp. that are more cryptic and sedentary, exhibiting defined territories with several residing females (Schemmel et al. 2016). The relatively high proportion of males in the Guam population (40%; this study) and 30% in New Caledonia (Loubens 1980) indicates that *V. louti* are unlikely to form group spawning aggregations. Observations of *V. louti* reproductive behavior are needed to better understand the reproductive biology of the species

and its vulnerability to fishery exploitation (Biggs et al. 2021).

The life history information presented here is invaluable for fisheries management and monitoring the impact of the management actions such as scuba spearfishing bans. The Guam scuba spearfishing ban may offer significant protection for *V. louti* as the majority of the catch of large individuals comes from scuba spear fishing in relatively shallow (< 40 m) water. This management action may go a long way toward reversing the declines in average fish size that Houk et al. (2018) documented in Guam. The relatively small size (26.0 cm FL) and young age (2.6 years) at maturity, and the relatively high proportion of males (40%) suggest that *V. louti* are considerably less vulnerable to exploitation than slower-growing and late-maturing groupers. Furthermore, this research fills critical knowledge gaps in growth and reproduction for this species and supports a collective understanding on the biology of groupers.

Declarations

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