

1 **Growth, mortality, and reproduction of the oblique-banded snapper**
2 **(*Pristipomoides zonatus*) in Guam**

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20 **Abstract**

21 Deepwater snapper fisheries in the Mariana Archipelago are important commercial, recreational,
22 and subsistence fisheries. *Pristipomoides zonatus*, one of the top four deepwater snapper species
23 harvested in Guam, lacked life history information. To fill this gap, a comprehensive life history
24 assessment for *P. zonatus* which included age, growth, mortality, and reproduction was
25 conducted in Guam. The size range of *P. zonatus* sampled for life history was from 11.5 cm to
26 40.4 cm (fork length), with ages ranging from 0.5 to 30 years. Von Bertalanffy growth model
27 combined sex parameters were $L_{\infty} = 36.91$ cm, $K = 0.29$. Males obtained a larger average size
28 and a larger asymptotic size (+3.03 cm) compared to females. *Pristipomoides zonatus* matures at
29 a small size and age ($L_{50} \leq 24.0$ cm and $A_{50} \leq 2.1$ yr) relative to their maximum size (40.4 cm) and
30 age (30 yr). Additionally, *P. zonatus* has a long spawning season and short spawning interval,
31 suggesting high reproductive output. Our results expand knowledge on *Pristipomoides* life
32 history (fast early growth, moderately long-lived, high productivity), providing the necessary
33 information for the management of *P. zonatus* in Guam.

34 **Introduction**

35 Deepwater fisheries, composed mainly of snappers (Lutjanidae), groupers (Epinephelidae), and
36 emperors (Lethrinidae), are found in subtropical and tropical waters throughout the Indo-Pacific
37 in rocky seamounts or continental slopes from 90–360 meters (Anderson and Allen 2001). Many
38 of these species, especially snappers, are commercially and culturally valued and are an
39 important food source for local residents (Dalzell 1996; Williams *et al.* 2012).

40 Most deepwater snapper fisheries are small-scale and considered data limited (Williams *et al.*
41 2013). Therefore, it is not surprising that deepwater snapper fisheries lack much of the biological
42 information needed for sustainable management (Newman *et al.* 2016; Williams *et al.* 2012).
43 Available life history information for deepwater snappers suggests moderate to slow growth,
44 high longevity, and low natural mortality (Williams *et al.* 2012; Newman *et al.* 2016; O'Malley
45 *et al.* 2019). These characteristics make deepwater snappers more vulnerable to overexploitation,
46 even at relatively low fishing levels (Williams *et al.* 2013; O'Malley *et al.* 2019).

47 The Oblique-banded Snapper (*Pristipomoides zonatus*) is a deepwater snapper that has a wide
48 distribution across the Indo-Pacific. Maximum length recorded for *P. zonatus* is 57.7 cm
49 (Kamikawa *et al.* 2015), and recent research using radio-carbon dating indicates that this species
50 can live up to 30 years in Hawaii (Andrews and Scofield 2021). Some work was done on age and
51 growth by Raslton and Williams 1989, however the otolith enumeration techniques used in the
52 study have been found to be incorrect. Studies on reproduction of *P. zonatus* is limited to
53 spawning seasonality, with no information at size and age at maturity (Raslton and Williams
54 1989). Therefore, there are significant data gaps in the biology and life history of this species.

55 *Pristipomoides zonatus* is one of the most commonly caught deepwater snapper species in the
56 Mariana Archipelago (Guam and Commonwealth of the Northern Mariana Islands (CNMI))
57 (Langseth *et al.* 2019). The deepwater snapper fishery in the Marian Archipelago plays a vital
58 role in recreational, subsistence, and commercial fisheries (Myers 1993). Fishing is primarily
59 focused around the islands of Guam, Rota, Tinian, and Saipan but extends north to Zealandia
60 Bank (O’Malley *et al.* 2019). The fishery is composed of commercial and subsistence fishers and
61 employs vessels less than 8 meters (Langseth *et al.* 2019). Total annual catch in 2017 was
62 estimated at 7,196 kg (Coefficient of Variation (CV) 0.22) for Guam and 31,855 kg (CV 0.83)
63 for CNMI (Langseth *et al.* 2019).

64 *Pristipomoides zonatus* is managed as part of a multi-species complex composed of deepwater
65 snapper, grouper, jacks, and emperors and are termed “bottomfish”. The recent stock
66 assessments of the bottomfish fishery in the Mariana Archipelago, conducted by the United
67 States National Marine Fisheries Service, are cause for concern. The 2019 stock assessment
68 determined the Guam bottomfish fishery was in an overfished state but was not undergoing
69 overfishing. In CNMI, the bottomfish fishery (composed of the same species as Guam) was not
70 overfished and overfishing was not occurring, but there was large uncertainty in stock status
71 (Langseth *et al.* 2019). These recent stock assessments raise concerns over the sustainability of
72 the fishery and emphasize the need for additional regional biological and life history information
73 for deepwater snapper species such as age, growth, mortality, and reproduction to update stock
74 assessments and management strategies (Hilborn and Walters 2013). Biological and life history
75 data are particularly valuable for length-based assessments which are often used for fisheries that
76 have limited or poor catch and effort information (Nadon *et al.* 2015).

77 This study assessed the life history of *P. zonatus* to fill critical biological and life history
78 information needed for management. To determine the accuracy and validity of our assessed
79 ages, we applied ageing criteria for *P. zonatus* following methods that have been developed for
80 deepwater snappers (Newman *et al.* 2015). We then estimated the age precision (between-reader
81 agreement, average percent error, and coefficient of variation). Then using fishery-dependent
82 data and biological samples we assessed length at age, growth, mortality, spawning season, size
83 (L_{50}) and age (A_{50}) at maturity. Finally, we compared the length frequency of our samples to the
84 fishery length data to ensure a representative sample was selected from the fishery. This regional
85 biological and life history data for *P. zonatus* will guide future stock assessments and
86 management efforts.

87 **Materials and methods**

88 *Data and sample collection*

89 Fishery-dependent *P. zonatus* length and weight information was collected from 2000-2019
90 (n=923) according the methods described by Sundberg *et al.* 2015. Biological samples were
91 collected from 6 September 2014 to 15 January 2017 (otoliths n= 317, gonads n= 242).

92 Biological samples were sampled from markets or donated by fishers. Of the individuals selected
93 for age and growth, 208 had corresponding gonad collections and could therefore be assigned
94 sex. Additionally, macroscopic sex identification was done by the appearance of gonads for 255
95 out of the 317 individuals sampled. However, when macroscopic identification of sex was
96 compared to histological identification of sex, macroscopic identification was found to be
97 inaccurate 23.4% of the time thus only histologically identified gender was used for all sex
98 specific analyses.

99 Fork length (FL (0.1 cm)) and fish weight (W (g)), were measured, and gonads and otoliths
100 extracted. Otoliths were cleaned, weighted (OW (0.001 g)), and stored in plastic vials. Gonads
101 were weighted (GW (0.001 g)) and a midsection of the gonad from one of the lobes was removed
102 and stored in 10% buffered formalin.

103 *Otolith processing and ageing criteria*

104 One otolith (either right or left, randomly chosen) was examined for condition (not broken or
105 chipped) and, if suitable, the otolith was weighed (0.001 g), and the sagitta was marked to
106 identify the primordium on the medial surface along the sulcus acusticus. Each individual otolith
107 was mounted and transversely sectioned, perpendicular to the sulcus acusticus using a Buehler
108 precision Isomet saw with two blades separated by a 400 μm spacer (Usseglio et al 2015) or
109 affixed by thermoplastic adhesive to a slide and ground along the primordium using a
110 GEMMASTA GFL8 lapping wheel to a thickness less than 400 μm (O'Malley *et al.* 2019). The
111 otolith sections were hand ground and polished to a thickness of 0.18 - 0.25 mm using lapping
112 film in decreasing size from 30 to 0.3 μm until the banding pattern was clear.

113 Daily growth increments (DGI) for a selection of individuals (< 20 cm) were examined using a
114 compound microscope to identify the location of the first annulus. Otoliths assigned for DGI
115 assessment were further polished using 3, 0.3, and 0.1 μm lapping film until daily growth
116 increments were visible. A compound microscope was used to count DGI on three different
117 occasions to get mean DGI count to the location of the first annual growth increment and total
118 DGI (mean age (days)) for each individual.

119 Ageing criteria was developed and ageing accuracy assessed using a reference set of 100 otoliths
120 from the Mariana Archipelago. Two readers came to agreement on the location of the first annual
121 mark prior to reading. Blind readings of the reference collection of sectioned otoliths were done
122 using a compound microscope by two readers on four separate occasions. Between reader
123 agreement was assessed using the coefficient of variation and average percent error as described
124 in O'Malley *et al.* (2016). The coefficient of variation (CV) is the ratio of the standard deviation
125 over the mean (Chang 1982; O'Malley *et al.* 2016). A mean CV was estimated by averaging the
126 individual CV of all aged fish. The average percent error (APE) was assessed from all aged fish.

127 The index of average percent agreement (IAPE; (Beamish and Fournier 1981)) was determined
128 by averaging the average percent error across all fish aged.

129 Annual growth increments have been validated for *P. zonatus* using bomb carbon ($F^{14}C$;
130 Andrews and Scofield 2021). Our ageing criteria was applied to the $F^{14}C$ validated otolith
131 collection (n = 40) housed at NOAA Pacific Islands Science Center to further confirm that the
132 ageing criteria are acceptable (Andrews and Scofield 2021).

133 Final ages for *P. zonatus* were estimated from counts of opaque bands by a single reader
134 following the aging criteria. Samples were read blind, with no knowledge of FL, weight, or date
135 of capture. Samples were read twice with a minimum of two weeks between readings. Ages were
136 accepted when they were the same and read a third and occasionally a fourth time if different.
137 One individual was removed from the age and growth assessment because it was considered an
138 outlier (age = 2, FL = 37.1 cm).

139 *Demographics, growth and mortality*

140 Growth was estimated using the von Bertalanffy (VBGF) (von Bertalanffy 1938), Gompertz
141 (Gompertz 1825), Schnute (Schnute 1981), and Ricker (Ricker 1975) models. The best fit model
142 was determined using the Akaike Information Criteria for small sample sizes (AICc) (Burnham
143 and Anderson 2002). Both the VBGF (1371.0) and Gompertz (1371.7) had the lowest AICc.
144 However, the VBGF was selected because of the AICc model support and because of the
145 prevalence of the von Bertalanffy growth model in deepwater snapper studies (Mees 1993;
146 Newman and Dunk 2003; Williams *et al.* 2017; O'Malley *et al.* 2019).

147 The VBGF sex-specific (histologically confirmed sex) and pooled sex age-length data was fit
148 using non-linear least squares using the following model:

$$149 \quad L_t = L_\infty(1 - e^{-K(t-t_0)})$$

150 where: L_t = the predicted mean length at age t (years)

151 L_∞ = the asymptotic length in cm

152 K = the growth coefficient

153 t = the estimated age in years

154 t_0 = the theoretical age at which the fish would have zero length

155 Residual sum of squares was used to test for differences between sex-specific growth curves
156 (Haddon 2010). If differences were found, likelihood ratio tests were used to identify which

157 growth parameter (t_0 , K , L_∞) was significantly different (Kimura 1980). Female and male growth
158 curves were also compared using 95% bivariate confidence ellipses (Kimura 1980); comparison
159 of confidence intervals is a conservative yet effective measure of significance (Schenker and
160 Gentleman 2001). The Kolmogorov-Smirnov test was used to compare size and age frequency
161 distributions between sexes. T-tests were used to compare mean sizes between sexes.

162 Age composition and the instantaneous rate of total mortality (Z) were estimated using age
163 frequency distributions. To assess the population age frequency distribution, we applied an Age
164 Length Key (ALK) following the methods of Kimura (1977) by using the aged *P. zonatus*
165 ($n=316$ from this study) and applied it to the fishery-dependent length observations ($n=923$),
166 which we term the un-aged population. Aged samples were divided into 2 cm bins ranging from
167 the minimum to the maximum length of the un-aged population, and the probability of age given
168 the length interval was estimated. The individuals were then assigned an age based on the
169 expected proportion of individuals in each age category. Decimal ages were rounded to whole
170 years. The age composition from the un-aged population with the applied ALK was used to
171 assess the instantaneous rate of total mortality (Z) using a weighted linear regression of the
172 negative natural log of catch at age with age three set as the age at full recruitment and without
173 right age truncation (Smith *et al.* 2012).

174 Natural mortality (M) was estimated using 2 estimators. The first was the Pauly's (1980) updated
175 estimator (Then *et al.* 2015):

$$176 \quad M = 4.118K^{0.73}L_\infty^{-0.33},$$

177 where K and L_∞ are growth parameters from the combined sex VBGF as defined above.

178 The second was the Hoenig's (1983) updated method (Then *et al.* 2015):

$$179 \quad M = 4.899t_{max}^{-0.916},$$

180 where: t_{max} = maximum age. We estimated Hoenig's natural mortality based on $t_{max} = 30$ yr.

181 *Reproduction*

182 *Pristipomoides zonatus* gonad samples (135 females, 87 males) were embedded in paraffin,
183 sectioned at 5 μ m, and stained with hematoxylin and eosin counter staining at the John A. Burns
184 Medical School at the University of Hawaii. Female reproductive state was diagnosed following
185 criteria by Brown-Peterson *et al.* (2011) (Table 1). Regenerating females were differentiated
186 from immature females by having two or more diagnostic criteria of prior spawning activity such
187 as thick ovary wall, atretic oocytes, post ovulatory follicles, muscle bundles, brown bodies, or

188 enlarged blood vesicles. Males were classified as immature or mature by the presence of
189 spermatozoa.

190 Two criteria were used to assess female reproductive maturity (1) physiological maturity (L_{50p}):
191 presence of cortical alveoli, and (2) functional maturity (L_{50f}): onset of vitellogenesis (Brown-
192 Peterson *et al.* 2011). Because there is no standard for maturity criteria in deepwater snappers,
193 both physiological and functional maturity were assessed to allow for comparisons to prior and
194 future studies. Female reproductive maturity (L_{50p} & L_{50f}) and male reproductive maturity was
195 assessed using samples collected during the spawning season (April – September; as identified
196 following methods below and supported by Raslton and Williams 1989). A total of 182 gonad
197 samples were collected during the spawning season consisting of 111 females and 71 males.

198 Size at sexual maturity (L_{50}) and age at maturity (A_{50}), the size and age at which 50% of
199 individuals of a given sex are mature, was assessed for each sex using a logistic regression model
200 with binomial family and logit link function (Chen and Paloheimo 1994). Estimates of L_{50} and
201 A_{50} were generated using 1000 bootstrapped replicates of the model coefficients. Likelihood ratio
202 tests were done to determine if size or age at maturity differed between sexes and if the estimates
203 of L_{50} based on L_{50p} and L_{50f} varied.

204 Monthly gonadosomatic index (GSI) was assessed from histologically-identified females to
205 determine reproductive investment with size and from functionally mature females ($n = 87$) and
206 males ($n = 76$) with gonad weights to identify the spawning season:

$$207 \quad GSI = \frac{\text{gonad weight (g)}}{\text{gonad free body weight (g)}} \times 100$$

208 The proportion of females in spawning capable and actively spawning reproductive phases was
209 assessed along with monthly GSI values to identify the spawning season. Additionally, the
210 spawning fraction was estimated by assessing the frequency of individuals spawning using the
211 hydrated oocyte method (DeMartini and Fountain 1981) and the post ovulatory method (Hunter
212 and Macewicz 1985) during the spawning season. Lastly, the spawning interval, the time period
213 between spawning events, was estimated as the inverse of the spawning fraction (Lowerre-
214 Barbieri *et al.* 2011).

215 *Data evaluation*

216 Biological samples were randomly collected from the fishery. However, there may have been a
217 tendency toward choosing some of the extremes of the size distribution. This type of size
218 selective sampling can result in bias (Chang *et al.* 2019a; Goodyear 2019); therefore, we used a
219 Kolmogorov-Smirnov test to determine if the sample length distribution was representative of
220 the fishery by comparing it to the entire fishery-dependent length observations. Additionally, the

221 von Bertalanffy growth parameters, which were estimated by using a sub-sample of the fishery
222 length observations with an applied age-length-key (ALK (described above) were compared with
223 parameters estimated using all of the aged samples. The proportional sub-sample was selected by
224 grouping 316 samples into 2 cm length bins and applying a weight to each bin based on the
225 proportion of the fishery-dependent length observation in each size bin. The residual sum of
226 squares was used to test for differences between our aged biological sample and the proportional
227 otolith sample growth curves (Haddon 2010). If differences were found, likelihood ratio tests
228 were used to compare growth parameter estimates from the different growth models (Kimura
229 1980).

230 All analyses and statistical tests were performed in R (R Development Core Team 2018).

231 **Results**

232 *Otolith processing and ageing criteria*

233 Thin sections between 180–250 μm produced the reliable between reader age estimates. If the
234 section was too thin, then the annuli became washed out; if the section was too thick, the
235 translucent zone became difficult to discern and multiple annuli appeared to be lumped together.

236 Daily increment analysis validated that the first annual mark begins at the inflection point of the
237 otolith (Table 2; Fig. 1). There is a wide opaque mark immediately following the inflection point
238 (Fig. 1). There were on average 164 daily increments counted before the inflection point (Table
239 2). Given the summer spawning season (peak spawning in June and July), this translates to the
240 annual mark being deposited in winter with an average of 164 days equating to deposition
241 beginning in December and January. A remaining pattern of annual marks were relatively wide
242 through the first 3 to 5 years, after which the annuli spacing becomes narrower and more regular
243 (Fig. 1).

244 Otolith weight was not a good predictor of age for *P. zonatus*. There was not a strong linear
245 relationship between otolith weight and age (Fig. 2).

246 Index of average percent error (IAPE) was assessed for a reference set of 100 *P. zonatus* from
247 the Mariana Islands. The between reader agreement was 61.2% and within 1 year was 80.0%, the
248 coefficient of variation was 16.5%, and the average percent error was 11.7%. This indicated a
249 concordance between readers and is within the acceptable range (Newman and Dunk 2003). The
250 ageing error between the two readers and the estimated age of Hawaii fish from bomb
251 radiocarbon dating was lower (8.6% APE), indicating a moderately high level of precision can be
252 expected among readings and the ageing protocol established is replicable. The percent error for
253 the Guam ages was highest for mid-sized fish within an otolith range from 0.20 to 0.35 g and

254 ages 3 to 5 years (Fig. 3). Age bias plots indicated that there was not an under- or overestimation
255 of ages relative to the other reader (Fig. 3).

256 *Demographics, growth, and mortality*

257 All available otolith samples ($n = 317$) from the Guam Commercial Fisheries Biosampling
258 Program were aged. The size of *P. zonatus* sampled for biological specimens ranged from 11.5
259 cm to 40.4 cm and the ages ranged from 0.5 to 30 years. Significant differences were found
260 between the size frequency of males and females ($D = 0.444$, $p\text{-value} < 0.01$) and age ($D =$
261 0.327 , $p\text{-value} < 0.01$) (Fig. 4). The mean male size was larger than females (+4.4 cm, $t = 7.11$,
262 $df = 184.14$, $p\text{-value} < 0.001$). Male mean size (FL) was 31.3 cm and female mean size was 26.9
263 cm. Males become larger than females starting at age 3, with an average of +2.8 cm per age class
264 (min +1.2 cm, max +4.8 cm). Maximum estimated ages were also larger for males (30 yr)
265 compared to females (19 yr).

266 Sex-specific growth was identified for *P. zonatus* ($F\text{-value} = 25.42$, $df=1$, $p\text{-value} < 0.01$; Fig.
267 6). Males reached a larger L_{∞} (+3.03 cm) compared to females ($\chi^2 = 15.92$, $df = 1$, $p\text{-value} <$
268 0.01 ; Table 3; Fig. 5). However, there was no difference in K ($\chi^2 = 0.16$, $df = 1$, $p\text{-value} = 0.69$)
269 or t_0 ($\chi^2 = 1.33$, $df = 1$, $p\text{-value} = 0.25$). Out of the 242 individuals sampled for reproduction, 208
270 *P. zonatus* (123 females, 85 males) had both histologically verified sex and age information.
271 Therefore, 108 aged individuals of unknown sex were included in the combined (both the female
272 and male) growth curve. Combined sex L_{∞} was 36.91 cm (95% CI: 36.12 cm, 37.75 cm) and K
273 was 0.29 (95% CI: 0.26, 0.32) (Table 3).

274 Total mortality (Z) for *P. zonatus* estimated from the catch curve analysis resulted in a Z of 0.32
275 (95% CI: 0.25, 0.40) (Fig. 6). Pauly's estimate of M was higher (0.51) than Z . Hoenig's estimate
276 of M was 0.22 and thus the resulting fishing mortality (F) was 0.10.

277 *Reproduction*

278 *Pristipomoides zonatus* was found to have asynchronous oocyte development, with multiple
279 oocyte stages present at the same time. Twenty six percent of the collected females were
280 immature ($n = 35$), ranging in size from 17.4 cm to 27.2 cm. Immature female gonads typically
281 had both chromatin nucleolar and perinucleolar oocytes present with oogonia present in some of
282 the smaller individuals (Fig. 7a). Seven percent ($n = 9$) of females were virgin females
283 undergoing early development (developing I: cortical alveolar oocytes most advanced oocyte
284 stage) (Table 1; Fig. 7b) and 11% ($n = 15$) of females were in the developing II phase. Ten
285 percent of females were actively spawning ($n=14$) and 16% ($n=21$) were spawning capable (Fig.
286 7c & d). Eight percent ($n = 11$) were regressing, with ovaries containing a large proportion of
287 atretic oocytes and with old post ovulatory follicles present in many of the individuals (Fig. 7e).

288 Twenty two percent ($n = 30$) of females were regenerating and often displayed evidence of prior
289 spawning activity such as scattered delta and/or gamma oocyte atresia (Fig. 7f).

290 Male and female physiological size at maturity were not significantly different ($\chi^2 = 5.183$, $df =$
291 1 , p -value = 0.08), nor were the male and female functional size at maturity ($\chi^2 = 2.642$, $df = 1$,
292 p -value = 0.27). The combined sex size and age at maturity ranged from 23.324.0 cm and 1.7–
293 2.1 yr (Table 3). We reported female physiological and functional L_{50} and A_{50} , and female and
294 male L_{50} and A_{50} as the baseline for future research (Table 3; Fig. 8).

295 Female L_{50p} and L_{50f} maturity and size at first spawning were compared to better understand the
296 size and timing of female reproduction. Physiological maturity marks the onset of oocyte
297 maturation, while functional maturity is the onset of oocyte vitellogenesis. Female size and age
298 at L_{50f} were not significantly different from female L_{50p} (L_{50} : $\chi^2 = 1.71$, $df = 1$, p -value = 0.19
299 and A_{50} : $\chi^2 = 1.413$, $df = 1$, p -value = 0.24). However, despite not being statistically different, L_{50f}
300 was estimated at 1.12 cm larger and 0.6 yr older. This suggests rapid oocyte growth from cortical
301 alveolar to vitellogenic oocyte stages. The smallest actively spawning female observed was 25.8
302 cm. However, a smaller regressed female (22.4 cm) and a smaller spawning capable female (22.7
303 cm) were observed, showing variability around size at maturity and suggesting a potential for
304 smaller size at first spawning.

305 Gonadosomatic index increased with reproductive developmental phases from immature to
306 actively spawning, and subsequently decreased in regressing and regenerating females (Table 1).
307 Overall, female gonad weight increased with fish size and, for spawning capable and actively
308 spawning individuals, there was a strong relationship between log gonad weight with gonad free
309 body weight ($\log GW = 0.6821 + GFBW * 0.0026$, $df = 27$, $R^2 = 0.66$; Fig. 9).

310 Guam *P. zontatus* has a protracted spawning season in which multiple spawning events occur.
311 Increased GSI was observed from May through September (Fig. 10). Spawning capable females
312 were present during this time and actively spawning females were observed in May, July,
313 August, and September, providing further evidence of the spawning season (Fig. 11). Effort was
314 made to sample *P. zontatus* year-round; however, sample sizes were lower in the winter ($n < 13$
315 females per month). However, we did not find evidence of spawning in the winter (October–
316 March).

317 Females with either post ovulatory follicles and/or hydrated oocytes were relatively common
318 during the spawning season (May–September). During the spawning season, 16.2% of mature
319 female ovaries contain POFs or hydrated oocytes (8.1% POFs and 9.0% hydrated oocytes). The
320 resulting spawning frequency was estimated to be approximately 11-12 days. However, the
321 presence of both hydrated oocytes and recent POFs at the same time suggests that *P. zontatus* is
322 capable of daily spawning (Fig. 7 d).

323 *Data evaluation*

324 The Kolmogorov-Smirnov test found some evidence that the length distribution of the sample
325 differed from the fishery-dependent length observations ($D = 0.09$, p -value = 0.05; Fig. 12);
326 however, a t-test found no difference in mean size ($t = 1.14$, $df = 490.51$, p -value = 0.26).
327 Therefore, we determined that there were no differences. Furthermore, there no difference in
328 growth curves between proportional otolith samples and all of the samples ($df = 1$, $F = 1.26$, p -
329 value = 0.26). Therefore, we considered the sample distribution adequate and representative of
330 the fishery and don't believe that sampling bias is impacting our results.

331

332 **Discussion**

333 In Guam, *Pristipomoides zonatus* is similar to other deepwater snappers in that it is moderately
334 fast growing and moderately long-lived (Newman *et al.* 2016; O'Malley *et al.* 2019; William, *et*
335 *al.* 2013). The oldest *P. zonatus* sampled from the Guam deepwater snapper fishery was 30
336 years. Male *P. zonatus* obtained a larger average size and a larger L_{∞} than females.
337 *Pristipomoides zonatus* mature at a small size and age ($L_{50} \leq 24.0$ cm and $A_{50} \leq 2.1$ yr) relative to
338 their maximum size and age (40.4 cm, 30 yr). Additionally, *P. zonatus* has a long spawning
339 season, with a high spawning fraction and a short spawning interval, suggesting high
340 reproductive productivity.

341 Thin sections have been shown to reduce ageing error in eteline snappers (Wakefield *et al.* 2017)
342 and *P. zonatus* is no exception. Therefore, we assessed our ageing accuracy and developed
343 ageing criteria using thin otolith sections. We found that otolith sections widths ranging from
344 180 μm to 250 μm were acceptable. Our APE was high (11.7%) but acceptable (Newman and
345 Dunk 2003). However, most of the variability in our age estimates was within 1 year (80.0%).
346 The highest variability was between 3 to 5 year old individuals, but the variability was non-
347 directional (i.e. age estimates had an equal chance of being younger or older). Documentation of
348 ageing accuracy and using thin otolith sections supports that standardized comparison of life
349 history characteristics for deepwater snappers.

350 The largest aged *P. zonatus* (40.4 cm) happened to be the oldest individual aged (30 yr).
351 However, as with most lutjanids, there is a decoupling of length with age after L_{∞} is reached
352 (Newman *et al.* 2016; O'Malley *et al.* 2019). Individuals greater than the combined sex L_{∞} of
353 36.91 cm ranged in age from 6 to 30 yr. Research on *P. zonatus* growth in the Hawaiian Islands
354 suggests that longevity is approximately 30 yr and the growth parameters differed from this
355 study (Allen and Scofield 2021). However, the Hawaiian Island estimates should be considered
356 preliminary given the small sample size and size selective sampling design which is known to
357 inflate L_{∞} (Chang *et al.* 2019a; Goodyear 2019). In a previous study of *P. zonatus* across the

358 Mariana Archipelago, Ralston and Williams (1989) estimated $L_{\infty} = 46.4$ cm, which is nearly 10
359 cm greater than the L_{∞} observed from Guam in this study. However, Ralston and Williams
360 (1989) numerical integration of daily growth increments technique does not produce reliable
361 ages so the resulting growth curves are inaccurate. Recent advances in age reading clearly
362 indicate that most *Pristipomoides* reach greater maximum ages than previously thought (>30
363 years) (Newman et al. 2016; Uehara et al 2020; Allen and Scofield 2021). Although we
364 document *P. zonatus* up to 30 years old around Guam, the maximum age is likely higher given
365 the rarity of old individuals given our sample size, and because fishing is known to cause age
366 truncation (Newman and Dunk 2003, O'Malley et al. 2019).

367 Age-based natural mortality estimators such as Hoeing's updated estimator (Then et al. 2015)
368 have been deemed suitable to use for deepwater snappers in the region (O'Malley et al. 2019).
369 Our estimate of M from the Hoeing age-based natural mortality estimator for *P. zonatus* ($M =$
370 0.22) was similar to what was found for the Goldeneye Jobfish (*P. flavipinnis*, $M = 0.22$) and
371 slightly higher than Goldflag Jobfish (*P. auricilla*, $M = 0.18$) from the Mariana
372 Islands (O'Malley et al. 2019). However, age truncation was identified for *P. auricilla* in the
373 Guam and Saipan deepwater snapper fisheries relative to unfished areas in the archipelago
374 (O'Malley et al. 2019). Thus, our estimate of M may be inflated. Our resulting $F = 0.10$, which is
375 smaller than that reported for *P. auricilla* ($F = 0.24$, O'Malley et al. 2019) from the Southern
376 Mariana Islands (Guam and Saipan). Additional assessments from the unfished portion of the
377 Mariana Archipelago are recommended to determine the maximum age for *P. zonatus* in the
378 Mariana Archipelago. This is important because many stock assessments depend on indirect
379 methods to estimate natural mortality such as those described in Then et al. (2015) and its
380 accuracy is highly dependent on an accurate maximum age (O'Malley et al. 2019). If fishing
381 reduced the maximum age of fish around Guam, then the resulting M estimate would increase
382 uncertainty to and potentially bias stock assessment output (Mannini et al. 2020; Punt et al.
383 2021).

384 Males were found to obtain a larger asymptotic size compared to females, but K was not
385 significantly different. We did observe larger males compared to females starting at age 3. This
386 corresponds fairly closely with the age at maturity and may be caused by differential energy
387 investment in reproduction between the sexes (Roff, 1983). However, in eteline snappers, there
388 does not appear to be a clear pattern in sex dimorphism, with males larger than females for some
389 species (*P. sieboldii*, Uehara et al. 2018) and smaller for others (*Etelis carbunculus*, Nichols
390 2019 ; *E. coruscans*, Uehara et al. 2018).

391 *Pristipomoides zonatus* females invest a large amount of energy into reproduction with a
392 relatively high GSI (GW up to 4% of GFBW), long spawning season, and rapid spawning
393 frequency. A 4% or greater ratio of female GW to GFBW is common in eteline snappers and
394 indicates significant investment in reproduction (DeMartini 2017). We also found an exponential
395 increase in gonad allocation (gonad weight and GSI with fish size and weight). Increased gonad
396 allocation with female size is common in fishes; fecundity or total egg production is a more

397 accurate estimate of reproductive investment (Hixon *et al.* 2014). For example, fecundity
398 increases with fish size for *P. argyrogrammicus* with a batch fecundity of 10,016 eggs for 17.7
399 cm female compared to 91,626 eggs for 27.8 cm female (Nanami 2011). Batch fecundity
400 estimates are needed to determine the total reproductive investment of *P. zonatus*. Both the
401 hydrated oocyte and postovulatory spawning frequency methods resulted in a similar spawning
402 frequency of 11-12 days. However, spawning may occur over several days or at a higher
403 spawning frequency given that hydrated oocytes and recent POFs are common in actively
404 spawning females. The high GSI and relatively high spawning frequency suggests a significant
405 investment in reproduction by female *P. zonatus*.

406 While our study lacked sufficient sampling during winter, we did find that *P. zonatus* had a
407 protracted spawning season, occurring at least from May through September. This is similar to
408 the findings of Raslton and Williams 1989 looking at monthly mean GSI across the year for *P.*
409 *zonatus* across the Mariana Islands. Similarly, other eteline snappers have prolonged spawning
410 seasons with multiple spawning events across the season (Grimes 1987; Mees 1993; Nanami
411 2011; Luers *et al.* 2018; Uehara *et al.* 2018). For example, the ornate jobfish, *P.*
412 *argyrogrammicus*, has a spawning season from April through August around Okinawa, Japan
413 (Nanami 2011). The long spawning season further increases the reproductive potential for *P.*
414 *zonatus*.

415 Both physiological and functional maturity are commonly used to assess L_{50} and A_{50} , with
416 preference on which maturity criterion is used depends on the species and the investigator
417 (Brown-Peterson 2003). For *P. zonatus*, the different criteria for estimating female size at
418 maturity (L_{50}) varied by less than 1.12 cm and were not significantly different, indicating rapid
419 oocyte growth for this species and no evidence for skipped spawning or halted maturation.
420 However, even if small differences exist or no differences are found, reporting both commonly
421 used criteria allow for more species, regional, and temporal comparisons of L_{50}/A_{50} (Brown-
422 Peterson 2003).

423 *Pristipomoides zonatus* female functional size at maturity ($L_{50} = 23.6$ cm) was close to functional
424 size at maturity estimates from similar sized eteline snappers *Etelis carbunculus* (23.4–27.2 cm)
425 and *P. sieboldii* (23.8–28.6 cm) in Hawaiian and Okinawan waters (DeMartini 2017; Uehara *et*
426 *al.* 2018). The ratio of the combined sex L_{50} to L_{∞} (0.66) for *P. zonatus* is similar to other
427 estimates for snappers (Nadon and Ault 2016) and holds to the Beverton-Holt life history
428 invariance ratio (Jensen 1996; Prince *et al.* 2015). However, female age at maturity for *P.*
429 *zonatus* is on the younger side for eteline snappers with female A_{50} ranging from around 1-2
430 years for *P. sieboldii* to 11.7 years for *Etelis coruscans* (Uehara *et al.* 2018). Furthermore, our
431 ratio of A_{50} to A_{max} (maximum age) for female *P. zonatus* is 12.1% placing it on the lower end for
432 Lutjanids, which has been found to vary between 11.9% to 30.4% (reviewed in Uehara *et al.*
433 2018).

434 Great effort was made to acquire fishery-dependent samples with monthly temporal resolution.
435 However, in Guam, the deepwater snapper fishery is seasonal with the majority of the effort
436 during the spring and summer when weather conditions are more favorable. Therefore, while
437 sampling effort was year-round, the majority of the samples were collected during the spring and
438 summer. Although the biosampling program worked hard to obtain a representative sample
439 across the length distribution for *P. zonatus* small individuals were not commonly encountered in
440 the Guam fishery. The smallest *P. zonatus* sampled from the Guam fishery was 11.5 cm, but
441 most of the individuals caught in the fishery are greater than 20 cm. The size and age of *P.*
442 *zonatus* at settlement is unknown. Leis and Goldman (1987) observed a 5.0 cm pelagic juvenile
443 *P. sieboldii*, and a 7.0 cm juvenile *P. filamentosus* was found in juvenile habitats (sandy flats at
444 65–100 m) (Moffitt and Parrish 1996). Thus, it is possible that *P. zonatus* juveniles recruit to
445 deep slope habitats after settling and developing in nursery habitats or other areas not targeted by
446 the fishery. Alternatively, size selectivity in fishing gear may also produce a similar pattern in
447 which fish less than 20 cm have a low likelihood of being exploited in the fishery. Given these
448 challenges, the comparison of growth curves using the aged samples versus a proportional data
449 set did not identify any issues that may have negatively impacted our estimates of *P. zonatus* life
450 history.

451 Our research provides the most complete life history assessment for *P. zonatus* for Guam. We
452 provide sex-specific estimates of VBGF parameters and present L_{50} based on multiple common
453 criteria to allow for between study comparisons between species and across regions. This
454 research provides the necessary information for management for *P. zonatus*, an important
455 component of the Guam deepwater snapper fishery.

456

457

458 **Author contributions**

459 Eva Schemmel wrote and conducted the analysis. Ryan Nichols contributed to the analysis and
460 development of ageing criteria. Eric Cruz collected biological sampling and supported the
461 processing of the otoliths, Jane J. J. Boyer contributed to the processing of the otoliths, and Frank
462 F. Camacho provided guidance and oversight on the research.

463 **Conflicts of interest**

464 The authors declare that there are no conflicts of interest.

465 **Availability of data and material**

466 Data and metadata are available at Pacific Islands Fisheries Science Center. 2021. *Life History*
467 *Program Life History Estimates*, <https://inport.nmfs.noaa.gov/inport/item/59002>.

468

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669

Table 1. Female reproductive phase, oocyte stage, criteria for physiological and functional maturity, mean gonadosomatic index (GSI), and diagnostic characteristics for *Pristipomoides zonatus* modified from Brown-Peterson *et al.* 2011.

Reproductive Phase	Most advanced oocyte stage	Physiologically Mature	Functionally Mature	GSI (mean+SE)	Characteristics
Undeveloped	Oogonia, chromatin nucleolar (CN), or perinucleolar (PN)	No	No	0.21 (0.02)	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	0.44 (0.05)	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	0.71 (0.13)	Developing individuals with early vitellogenic oocytes, VTI, and/or VTII present.
Spawning Capable	Late vitellogenic (VTIII)	Yes	Yes	1.78 (0.17)	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	2.29 (0.31)	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	0.71 (0.11)	Ovaries dominated with atretic oocytes. May contain some CA or VT oocytes.
Regenerating	Perinucleolar	Yes	Yes	0.36 (0.32)	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.

Table 2. Daily increment analysis for small Guam *Pristipomoides zonatus* individuals with daily increment counts to the otolith inflection point (location of first annuli) and the average of three counts to the otolith edge (mean age).

Sample ID	Otolith Weight (g)	Fork Length (cm)	Mean Age (days)	Age at Inflection (Days)
GVDP-626	0.1026	18.5	313	155
GVDP-770	0.1005	17.7	312	132
GVDP-597	0.1490	22.9	521	180
GVDP-794	0.0514	11.5	189	189
GECC-408	0.0960	16.4	260	183
GECC-925	0.1527	23.1	546	146

Table 3. Life history traits and 95% confidence intervals for Guam *Pristipomoides zonatus*. Combined VBFG parameters are males, females, and aged individuals with unknown sex, and combined L_{50} and A_{50} are histologically assessed males and females. Lengths are fork length (cm) and ages are in years. There were 208 individuals (n age) with histological verified sex and age information (123 females and 85 males).

Trait	Females	Males	Combined
L_{∞} (cm FL)	35.31 (34.29, 36.45)	38.34 (37.06, 39.78)	36.91 (36.12, 37.75)
K (yr ⁻¹)	0.27 (0.23, 0.32)	0.29 (0.22, 0.36)	0.29 (0.26, 0.32)
t_0	-2.03 (-2.66, -1.53)	-1.54 (-2.50, -0.85)	-1.46 (-1.75, -1.21)
n age	123	85	316 (208)
Maximum age	19	30	30
Maximum FL	37.2	40.4	40.4
L_{50} physiological	22.52 (22.10–23.72)	24.12 (23.20–26.20)	23.34 (23.0–24.35)
L_{50} functional	23.60 (23.20–24.52)		24.04 (23.71–24.80)
A_{50} physiological	1.54 (1.30–2.12)	1.79 (1.43–2.54)	1.68 (1.47–2.19)
A_{50} functional	2.11 (1.92–2.54)		2.11 (1.95–2.47)

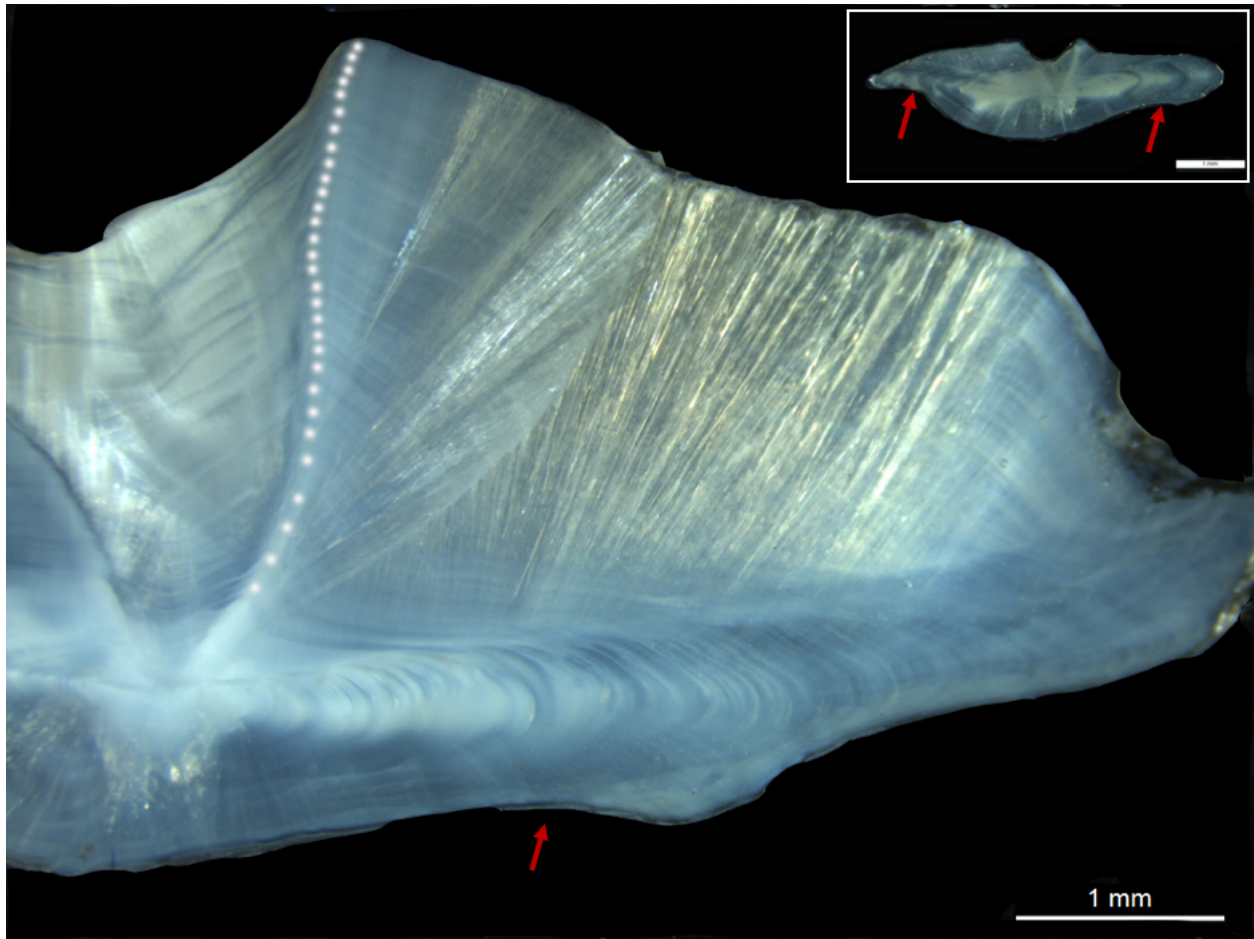


Fig. 1. A 30-year-old *Pristipomoides zonatus* showing the first five thick annual bands with the first annual mark at the inflection point (red arrow) and the inset showing a one-year old (312 days) *P. zonatus* with the first annual mark formation starting immediately after the inflection point (red arrows). White scale bars are 1.0 mm.

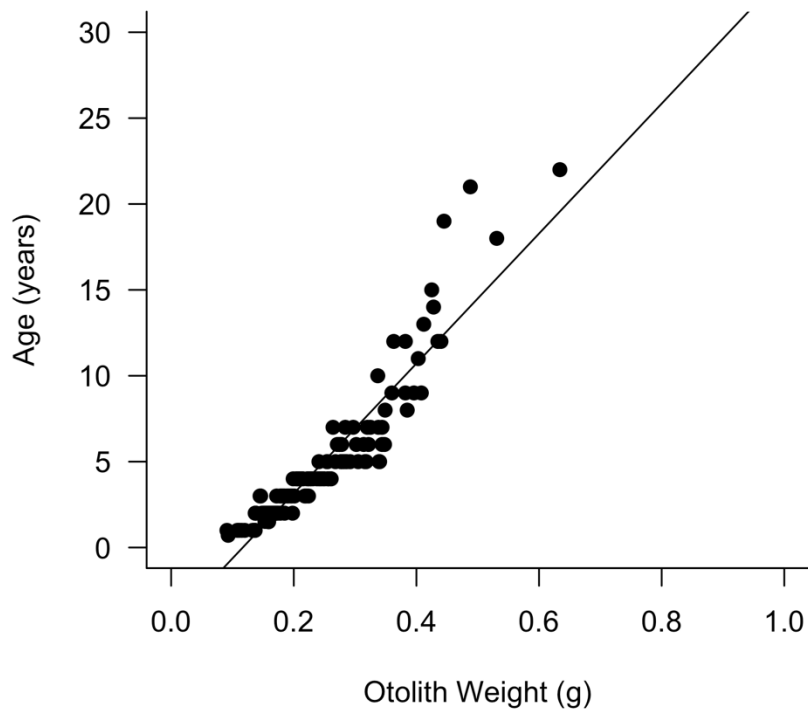


Fig. 2. Relationship between otolith weight to age for *Pristipomoides zonatus* estimated from thin sectioned otoliths ($y=37.83x-4.42$, $R^2=0.86$).

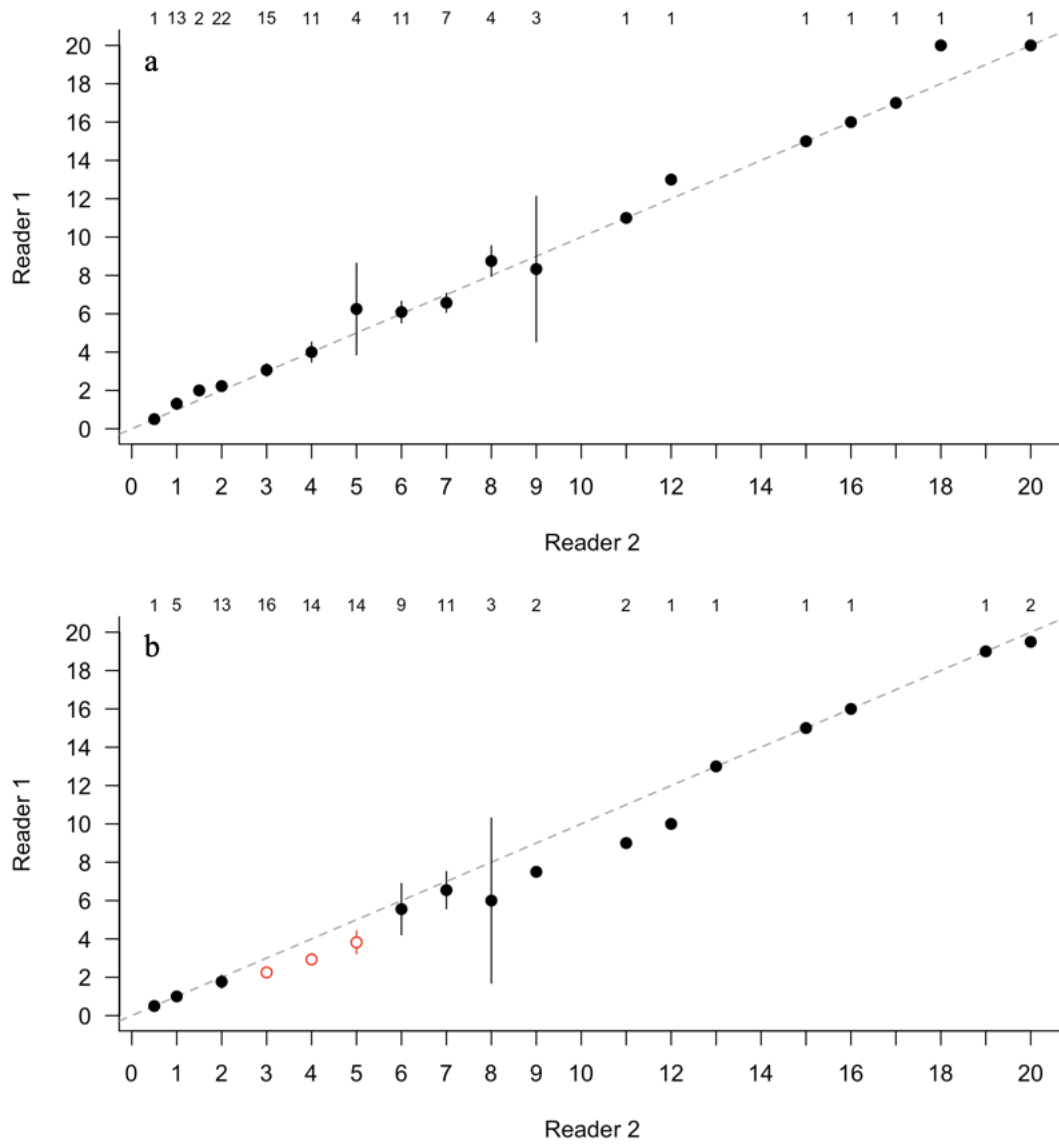


Fig. 3. Age-bias plots comparing Reader 1 and Reader 2 *Pristipomoides zonatus* ages of thin sections from the Mariana Islands from two separate reads (a & b). Each error bar represents the 95% confidence intervals. Number on top of the plots indicates the number of individuals at each age.

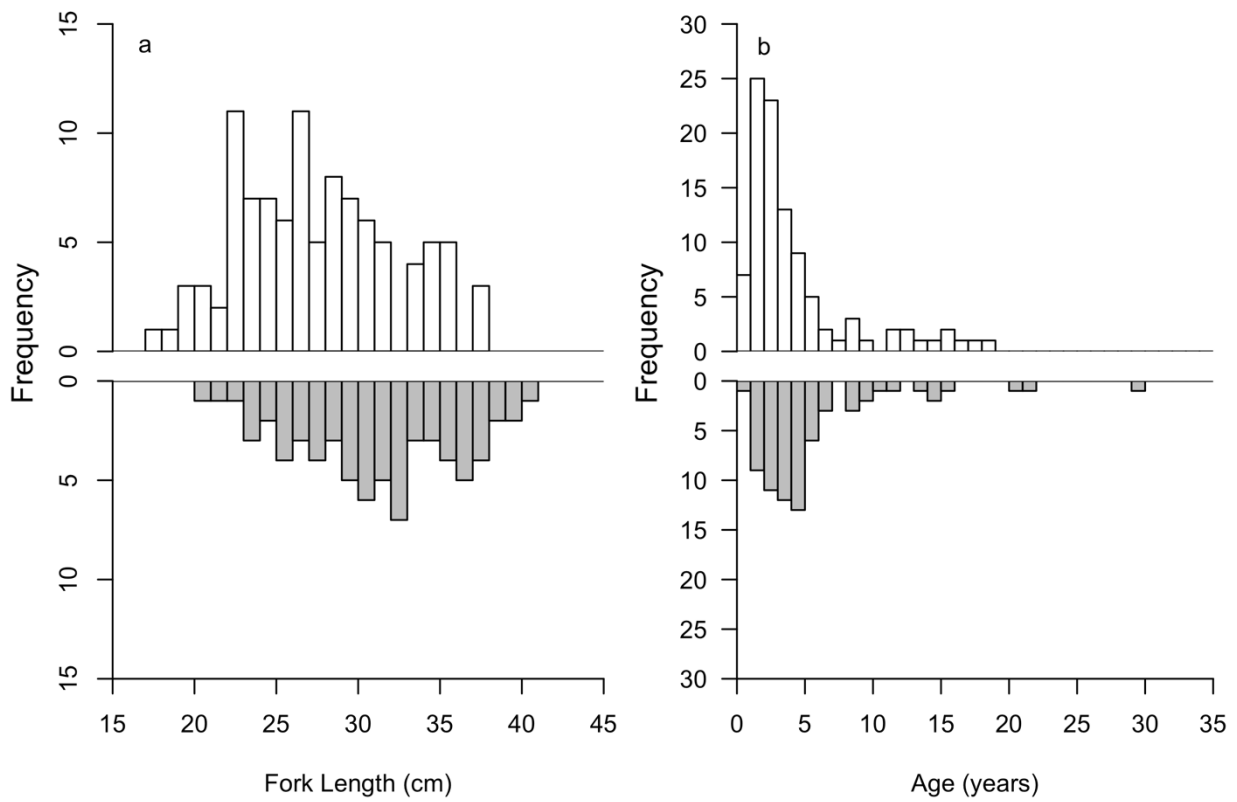


Fig. 4. Comparison of female (white) and male (grey) length distributions (a) and female (white) and male (grey) age distributions (b) for *Pristipomoides zonatus* from Guam.

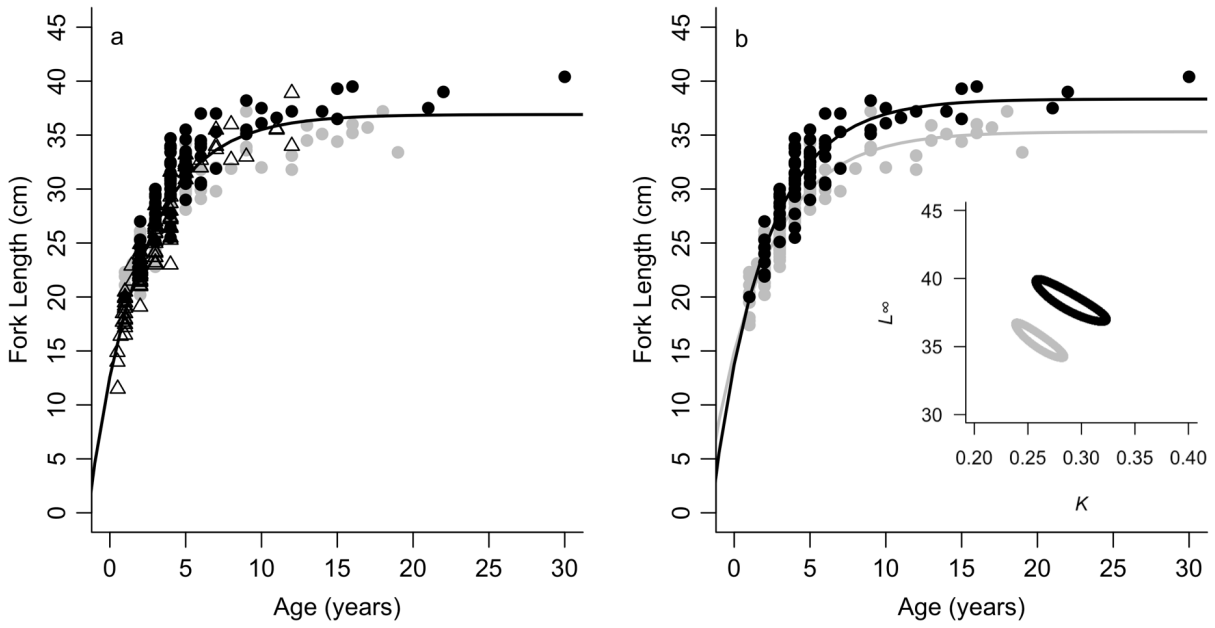


Fig. 5. (A) The von Bertalanffy growth curve for all aged *Pritipomoides zonatus*, including females (grey; $n = 123$), males (black, $n = 85$), and individuals with unknown sex (triangles; $n = 108$) and (B) the von Bertalanffy growth curves and 95% growth parameter confidence ellipses for females (grey; $n = 123$) and males (black, $n = 85$),

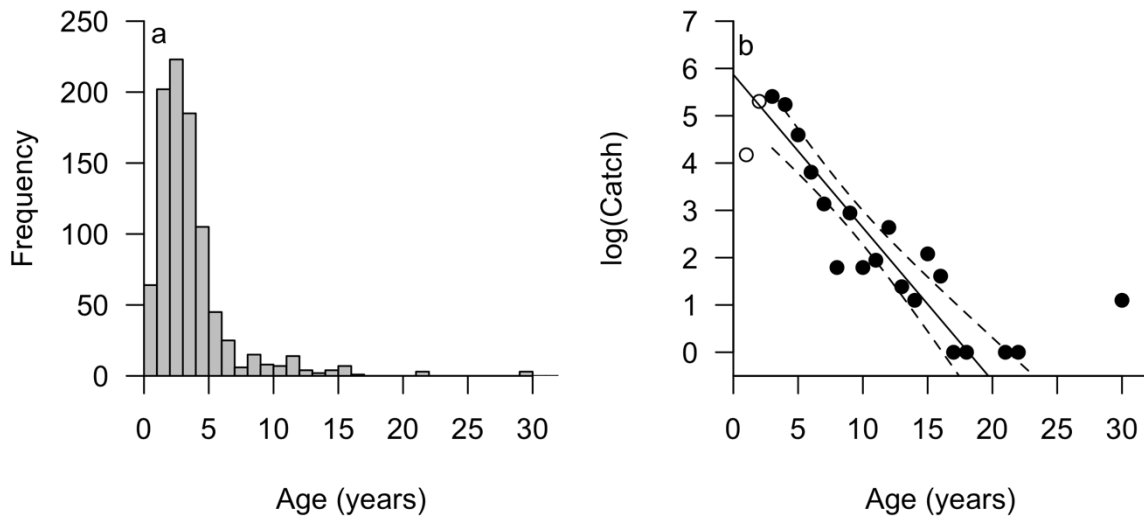


Fig. 6. Frequency of Guam *Pristipomoides zonatus* fishery-dependent age observations from the applied age length key ($n = 923$) (a) and log catch (frequency) for each age class with filled circles representing age classes that are fully recruited to the fishery (b). Total mortality is estimated as the absolute slope of the relationship between log catch and age ($Z = 0.32$ (0.25, 0.40)).

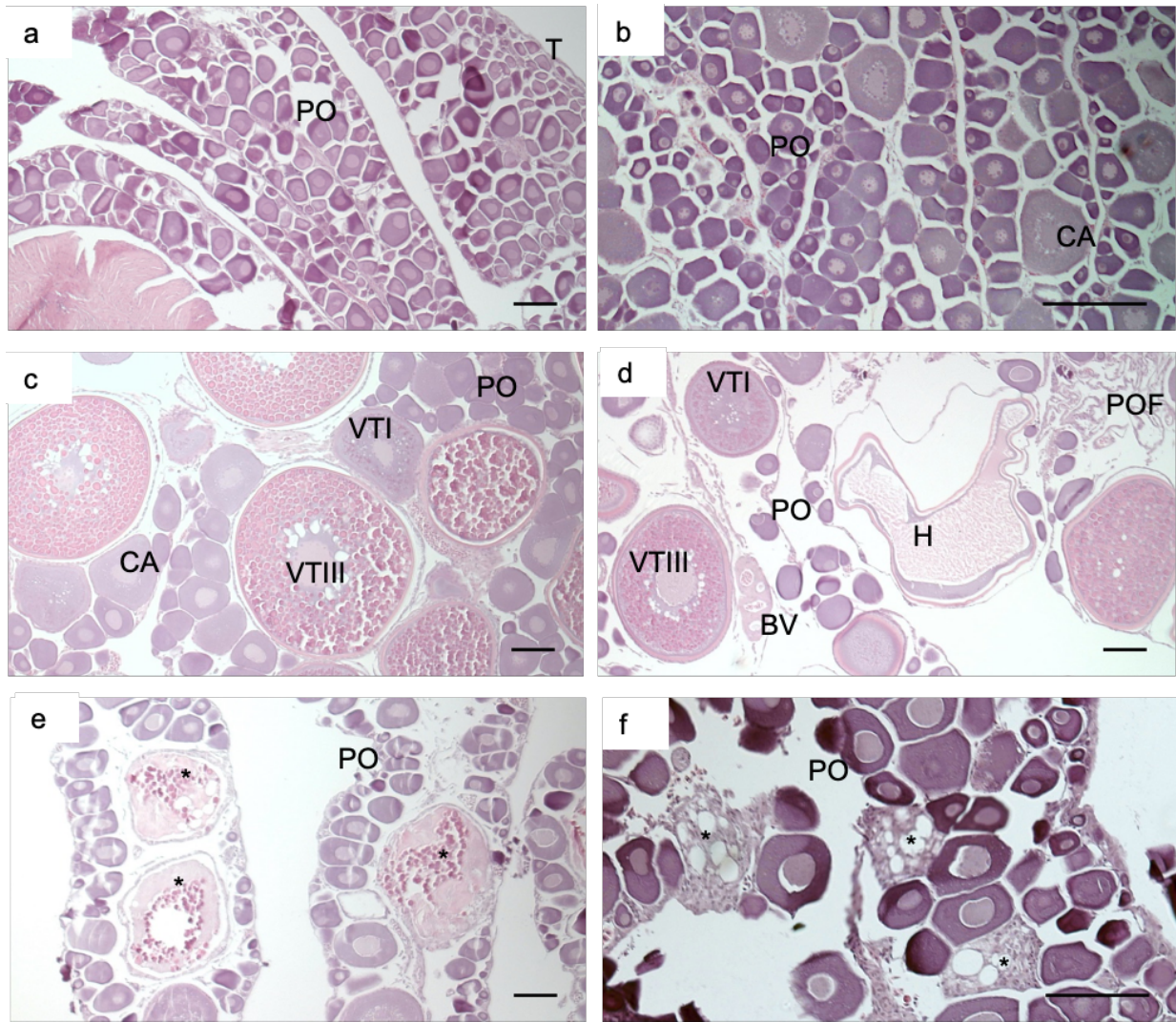


Fig. 7. Stages of Guam *Pristipomoides zonatus* oogenesis and reproductive phases following Brown-Peterson *et al.* 2011). (a) Immature female with primary stage oocytes (PO) and a thin tunica (T), (b) developing female with PO and cortical alveoli (CA) oocytes, (c) spawning capable female with stage I and III vitellogenic oocytes (VTI & VTIII, respectively), (d) actively spawning female with hydrated oocytes (H), recent post ovulatory follicles (POF), VTIII, VTI, CA and PO, (e) regressing female with beta atresia (*) and PO, (f) regenerating female with delta atresia (*) and PO. All scale bars are 100 μm .

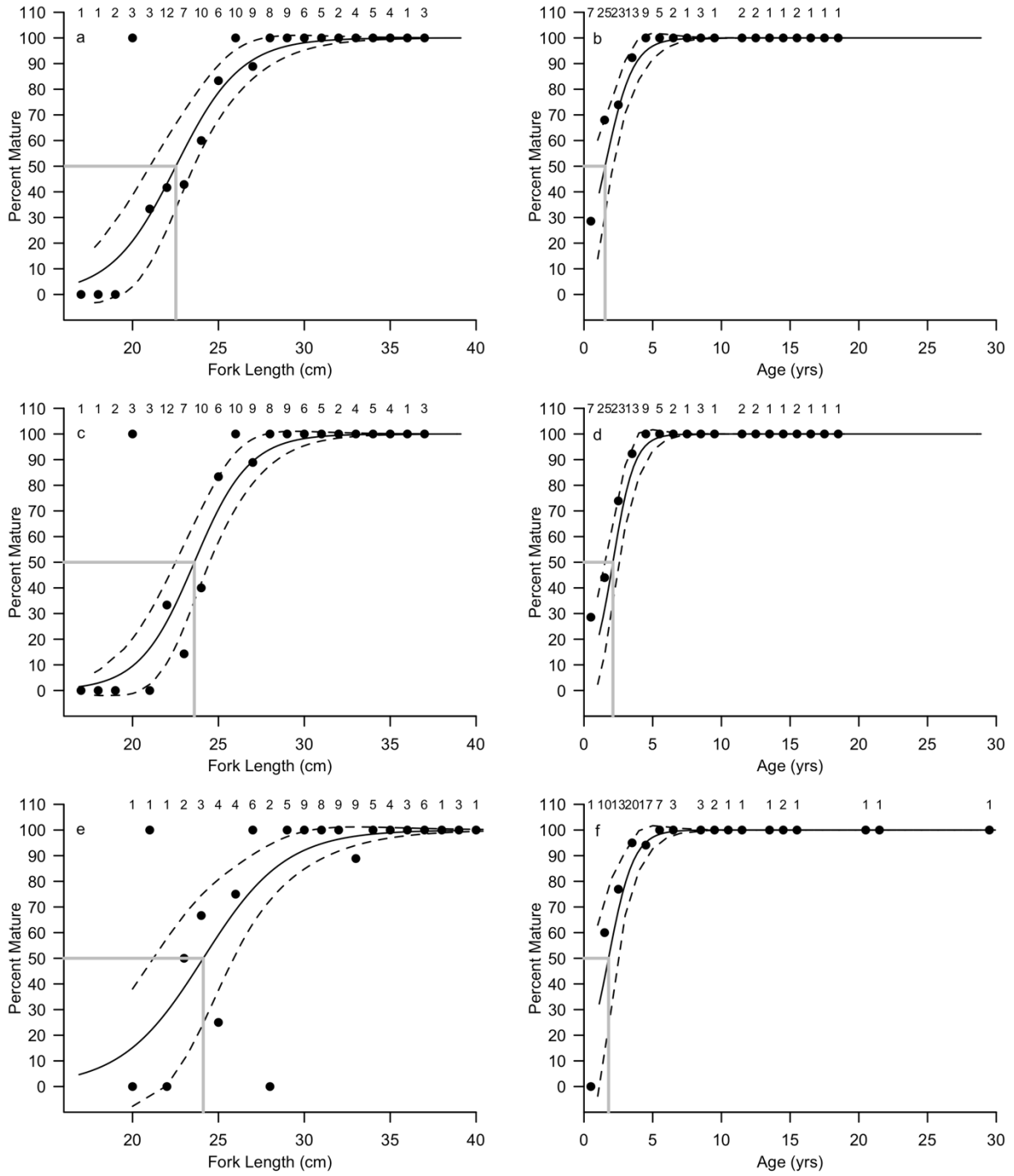


Fig. 8. Maturity ogive for Guam *Pristipomoides zonatus*. Female physiological length (a) and age at maturity (b), female functional length (c) and age at maturity (d), and male length (e) and age at maturity (f). Dashed lines indicate 95% confidence intervals and gray lines indicate L_{50} and A_{50} .

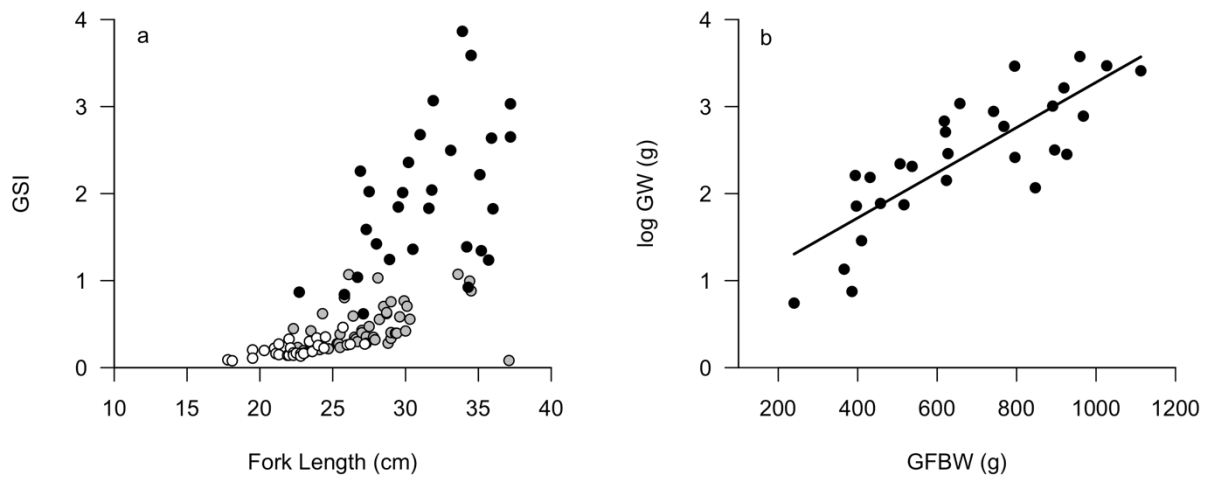


Fig. 9. Female Guam *Pristipomoides zonatus* gonadosomatic index with fork length (a) and spawning capable and actively spawning female log gonad weight (GW) with gonad free body weight (GFBW) ($\log GW = 0.6821 + GFBW * 0.0026$, $df = 27$, $R^2=0.66$; (b). Spawning capable and actively spawning females are black, immature females are white, and all other female reproductive phases are grey.

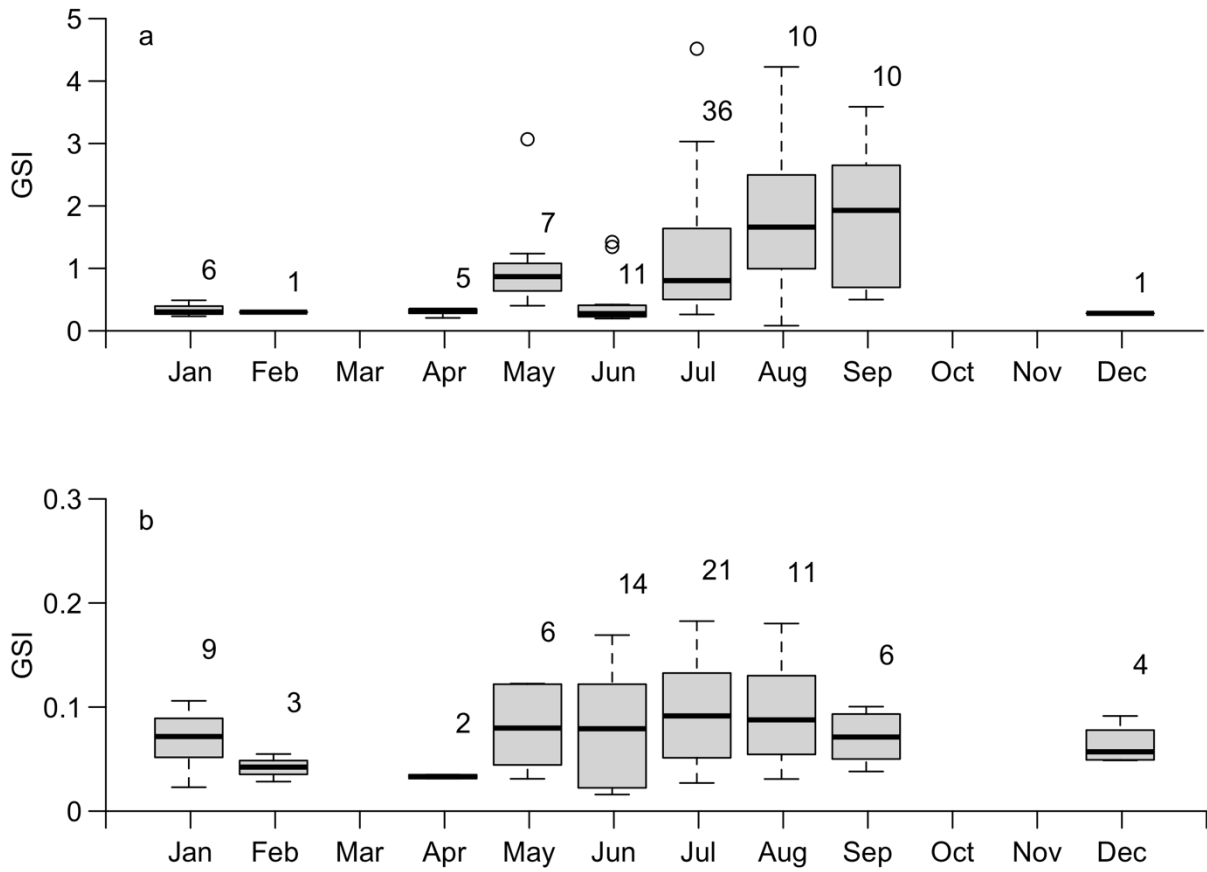


Fig. 10. Median and interquartile range for Guam *Pristipomoides zonatus* gonadosomatic index (GSI) from functionally mature females (a) and mature males (b). Numbers represent sample size.

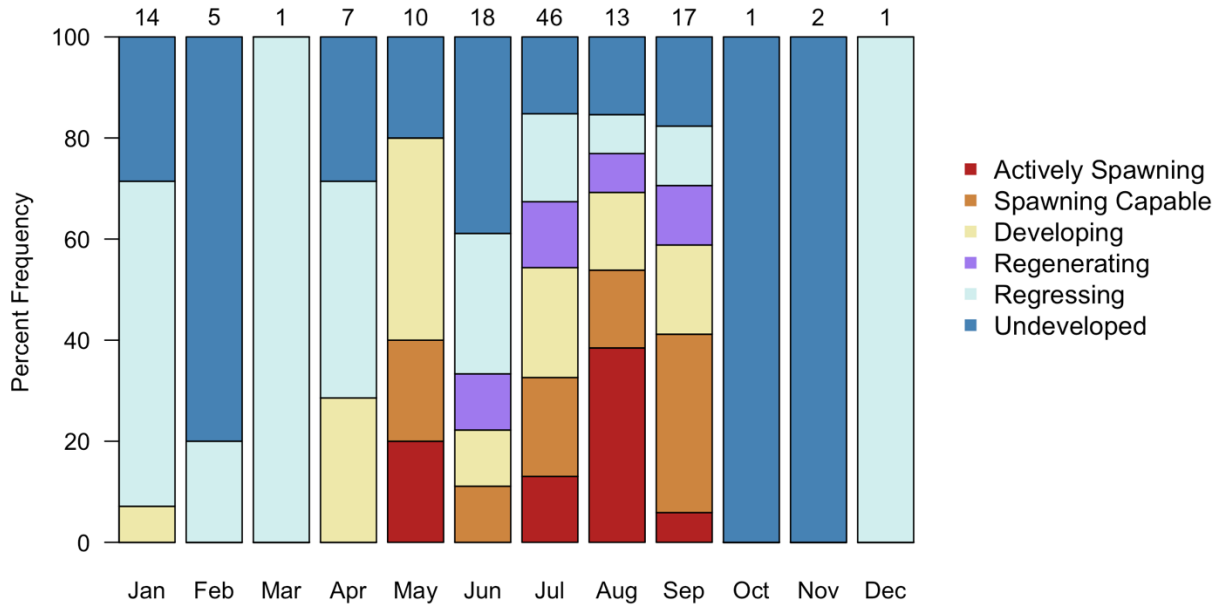


Fig. 11. Percent frequency of Guam female *Pristipomoides zonatus* reproductive phases per month. All years of sampling are combined. Sample sizes per month are indicated above the bars.

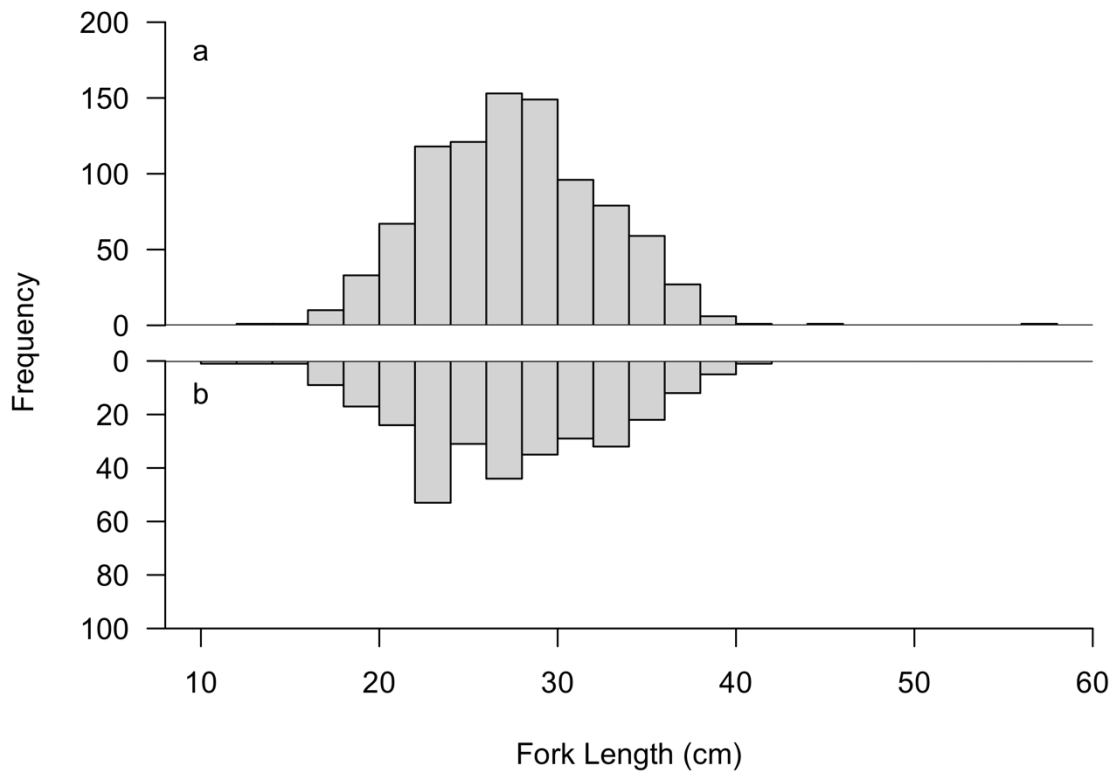


Fig. 12. Comparison of Guam *Pristipomoides zonatus* fishery-dependent length observations ($n = 923$) (a) to the life history samples collected ($n = 316$) (b).