



Comparative growth, age at maturity and sex change, and longevity of Hawaiian parrotfishes with bomb radiocarbon validation

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1 Comparative growth, age at maturity and sex change, and longevity of Hawaiian
2 parrotfishes, with bomb radiocarbon validation

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19 Running head: Comparative growth and longevity of parrotfishes

20 **Abstract:** Growth rates and longevities were estimated for five major fishery species of
21 parrotfishes (“uhu”) at Oahu, Hawai’i. All species grew rapidly with von Bertalanffy Growth
22 Formula (VBGF) k values $\geq 0.4 \text{ yr}^{-1}$. Longevities were found to range broadly among the three
23 SMALL species—4 yr in *Calotomus carolinus* and 6 and 11 yr in *Scarus psittacus* and *Chlorurus*
24 *spilurus*—and to 15-20 yr in *S. rubroviolaceus* and *Chlorurus perspicillatus* for the two LARGE
25 species. Age-reading and growth curves for the latter two LARGE species were validated using
26 bomb radiocarbon dating. Median ages at sexual maturity as females (A_{M50}) and at sex change
27 (from female to terminal phase male, $A_{\Delta 50}$) were estimated using logistic models. Sexual
28 maturation occurred at 1–2 yr for the SMALL species and at 3–3½ yr in the LARGE species. $A_{\Delta 50}$
29 estimates ranged from 2–4 yr in the SMALL species and were about 5 and 7 yr in *S.*
30 *rubroviolaceus* and *C. perspicillatus*, respectively. Estimated milestones poorly corresponded to
31 the current minimum legal size for uhu in Hawai’i (12" or 30.5 cm fork length). Pooling these
32 parrotfishes for management seems generally inappropriate, especially for the two LARGE
33 species. Age-based metrics are more informative than size-based metrics for these fishes.

34

35 Keywords: Scaridae, Labridae, life-history variation, minimum size regulations, age-based
36 metrics

37 Introduction

38 Parrotfishes (Labridae, tribe Scarinae: Choat et al. 2012) are of major ecological and
39 economic importance throughout the tropical central and western Pacific, including the Hawaiian
40 Archipelago, and at many other tropical reef areas worldwide (Bellwood and Choat 1990; Houk
41 et al. 2012; Bonaldo et al. 2014). As esteemed food fish and preferred fishery targets,
42 parrotfishes are often highly- if not over-exploited in many regions (Bellwood et al. 2012;
43 Edwards 2013; DeMartini and Smith 2015). Despite the importance of parrotfish in tropical reef
44 fisheries, little information exists on their growth rates, ages at sexual maturity and sex change,
45 and longevities. Estimates of these parameters plus body sizes at maturity and sex change
46 (DeMartini and Howard 2016) are needed for providing comprehensive demographic input to
47 accurate, modern stock assessments. Age-based assessments are increasingly recognized as
48 important for managing stocks of tropical reef species like parrotfishes in which demographics
49 often vary appreciably over small (regional, local; Pinca et al. 2012; Taylor and Choat 2014;
50 Taylor 2014) and basin-wide (Heenan et al. 2016) spatial scales.

51 Prior to a recent paper by DeMartini and Howard (2016), little published information on vital
52 rates existed for the parrotfishes of Hawai'i. DeMartini and Howard (2016) estimated body sizes
53 at sexual maturity and at female-to-male sex change for five major parrotfish species (three
54 small-bodied or "SMALL" species: palenose *Scarus psittacus* Forsskål [henceforth *S. psittacus*],
55 stareye *Calotomus carolinus* (Valenciennes) [henceforth either *Calotomus* or *C. carolinus*],
56 Pacific bullethead *Chlorurus spilurus* (Valenciennes) [henceforth *C. spilurus*]; and two large-
57 bodied or "LARGE" species: redlip or ember *Scarus rubroviolaceus* Bleeker [henceforth *S.*
58 *rubroviolaceus*], and spectacled *Chlorurus perspicillatus* (Steindachner) [henceforth *C.*
59 *perspicillatus*]) among the seven parrotfish species that occur in the Hawaiian Archipelago

60 (Randall 2007). Six of these species are generally reported on and managed as a single unit taxon
61 (classified by its local name “*uhu*”) with a single minimum legal body length for extraction in all
62 Hawaiian fisheries, comprising commercial, recreational, and artisanal. One species (*C.*
63 *carolinus*) has no minimum legal size at present in Hawai'i (DeMartini and Howard 2016).

64 Detailed life-history information is generally lacking for tropical coral reef fishes, not just
65 parrotfishes. Clearly, detailed studies are not possible or practical for most species comprising
66 these notoriously diverse ecosystems, but that should not preclude conducting such studies for
67 some species of great ecological and economic importance like the parrotfishes (DeMartini and
68 Smith 2015). Managing multiple species (such as the parrotfishes) with likely disparate life
69 histories (Choat and Robertson 2002; DeMartini and Howard 2016) as compound taxa would not
70 be acceptable practice in higher-latitude fisheries, yet such is the norm in tropical fisheries. In the
71 present paper we hopefully can help to begin raising the bar by setting new precedent for detailed
72 input as a basis for tropical fisheries management.

73 We herein provide the first comprehensive estimates of growth (size-at-age) for any of the
74 parrotfishes in Hawai'i—with the first growth curves validated anywhere for two of the
75 species—and corresponding estimates of median age at sexual maturity and at sex change. Our
76 major focus was to compare and contrast their growth metrics with the intent of evaluating
77 whether it is reasonable that all of the species should be managed as a single unit taxon in
78 Hawai'i.

79

80 **Methods**

81 **Fish specimen collection and metrics**

82 Specimens were obtained using both fishery-independent and fishery-dependent (market
83 sampling) means during March 2005 to April 2007 (Hawai'i Cooperative Fishery Research Unit
84 2008; Howard 2008) and complemented by additional market specimens obtained during
85 September 2012 to August 2014, as described by DeMartini and Howard (2016); these
86 collections were supplemented by additional market fish obtained during March-August 2015.
87 Fork length (FL, to the nearest 0.1 cm) was measured in the laboratory, as was round body mass
88 (RM) to the nearest 10 grams for fish > 0.5 kg (A&D Weighings, San Jose, California, Model
89 FG-60-KBM) and to the nearest gram for fish \leq 500 g (Mettler Instrument Corporation,
90 Highstown, New Jersey, Model PE-600), with gonad mass (GM) weighed to 0.01 g (A&D
91 Weighings, San Jose, California, Model GR-202). Because all parrotfish species in Hawai'i
92 include distinctly colorful terminal phase (TP) male fish (Randall 2007), the sexual identity of
93 TP fish was assigned using external body coloration, corroborated by testes histology (DeMartini
94 and Howard 2016). Sexual identities of initial phase (IP) fish were first assessed based on
95 macroscopic appearance of gonads when dissected and was later corroborated by histology
96 (DeMartini and Howard 2016).

97 **Otolith preparation and visual age counts**

98 Otoliths were obtained from fresh or frozen-thawed fish by removing the brain case using
99 either a scalpel for smaller juveniles or a mallet plus butcher knife or hand saw for large
100 juveniles and adult fish. The largest pair of otoliths (sagittae) was extracted and cleaned of all
101 attached tissue under a dissecting microscope, rinsed in water, disinfected in 95% ethanol, and
102 air dried before dry storage in labeled vials. All available otoliths were weighed on a micro-
103 balance to 0.1 mg prior to further preparation. One member of each pair of otoliths (either left or
104 right, random choice; Choat et al. 1996) was prepared and aged using the following series of

105 steps. The otolith was first mounted sulcus side-down near one end of a standard glass
106 microscope slide using Crystalbond[®] (Electron Microscopy Sciences, Hatfield, Pennsylvania).
107 The otolith was manually sanded using a Gemmasta Faceting Machine (Shelley's Lapidary
108 Supplies, South Australia) to expose the nucleus. The slide was then heated to melt the
109 Crystalbond[®] and free the specimen, and the section flipped over and remounted with the flat
110 sanded side against the slide. The otolith was then further sanded to produce a thin (~200–300
111 µm), transverse cross-section. The cross-section was then covered again in Crystalbond[®] for
112 viewing and enumeration of either or both daily and annual age features. Annuli, defined as an
113 alternating pair of opaque and translucent zones (Lou 1992), were counted under a dissecting
114 microscope, using transmitted light at an average magnification of 20x. An equal number (3) of
115 independent and non-consecutive age readings for annuli were made for each specimen by a
116 single reader without reference to any prior reading and the mean of these three reads used as the
117 best estimate of age, expressed in decimal-years.

118 For select yearling specimens of *C. carolinus* < 20 cm FL, and for select juvenile-sized
119 specimens of *C. perspicillatus* and *S. rubroviolaceus* < 30 cm FL, the second otolith, if available,
120 was prepared for evaluation of daily growth increments (DGIs: Lou and Moltschaniwskyj 1992).
121 Otolith specimens to be used for DGI counting were further polished using a progression of
122 lapping film (9.0, 3.0, and 0.3 µm grit). All visible DGIs, including those formed both prior to
123 and after the settlement check (Wilson and McCormick 1999) were counted by 3 independent
124 and non-consecutive age readings by a single reader and the mean of the 3 readings used as the
125 best estimate of age in days. DGI counts also were related (as fractional years) to age in years
126 estimated from counts of annuli as a means of verifying age.

127 **Bomb radiocarbon dating**

128 Age estimates were validated for a series of specimens of the LARGE species (*S.*
129 *rubroviolaceus*, *C. perspicillatus*). These specimens were randomly selected for bomb ^{14}C dating
130 from across the length distribution of collected fish and spanned the estimated age range (Tables
131 S1, S2 in Supplemental Data, materials available online). To apply bomb ^{14}C dating to the
132 otoliths of each species, the dimensions and weight of whole juvenile otoliths were used to
133 delineate a targeted core or earliest growth within adult otolith specimens. Extraction dimensions
134 and masses for even the smallest otoliths and youngest specimens of each species (*S.*
135 *rubroviolaceus*: 3.4 mg at 1 year; *C. perspicillatus*: 22.6 mg at 2 years) exceeded the threshold
136 values required for bomb radiocarbon analysis. Cross-sectioned adult otoliths indicated that the
137 first few years of growth were at the distal otolith margin and required no surface preparations
138 prior to extraction. A New Wave Research® (ESI–NWR Division; Fremont, CA) micromilling
139 machine was used to extract the earliest otolith growth of adult otoliths: 1) *S. rubroviolaceus*
140 cores were 1.8 mm L \times 1.4 mm W \times 0.20 mm Th and were achieved using a 13-point line scan;
141 and 2) *C. perspicillatus* cores were 2.0 mm L \times 1.6 mm W \times 0.30 mm Th and were achieved
142 using a 20-point line scan. Each extraction was made with a 500 μm Brasseler® (Savannah, GA)
143 bur in a single pass; the targeted extraction mass was near 0.8 mg and 1.2 mg of CaCO_3 for each
144 species, respectively. The extracted otolith samples were submitted as carbonate to the National
145 Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS), Woods Hole
146 Oceanographic Institution (WHOI) in Woods Hole, Massachusetts, for small sample ^{14}C analysis
147 using Accelerator Mass Spectrometry (AMS). Radiocarbon measurements were reported by
148 NOSAMS as Fraction Modern—the measured deviation of the $^{14}\text{C}/^{12}\text{C}$ ratio from a “modern”
149 sample. This reference is defined as 95% of the ^{14}C concentration of the NBS Oxalic Acid I
150 standard (SRM 4990B) normalized to $\delta^{13}\text{C}_{\text{VPDB}}$ (-19‰) in 1950 AD (VPDB = Vienna Pee Dee

151 Belemnite geological standard; Coplen 1996). Fractionation correction was online during AMS
152 processing and corrected values were reported here as $F^{14}\text{C}$ (Reimer et al. 2004), with date
153 corrected $\Delta^{14}\text{C}$ values also reported here (Tables S1, S2).

154 The series of estimated birth dates for each species (youngest to oldest) were compared
155 collectively with the reference $\Delta^{14}\text{C}$ time series in ANCOVA analyses of the slopes and
156 intercepts (SAS Institute Inc. 2006). Known age juveniles were in agreement with the reference
157 data and hence it was reasonable to assume that the core material from older adults would align
158 with the $F^{14}\text{C}$ decline record through ontogeny. The $\Delta^{14}\text{C}$ reference for the Main Hawaiian
159 Islands (MHI) was a collection of coral records, but primarily one record from Kona, Hawai'i
160 Island (Andrews et al. 2016b; Fig. S1). The coral record was supplemented with known age
161 otolith material from juvenile fishes from the region (Andrews et al. 2016a; Table S3).
162 Concordance of the series of measured $\Delta^{14}\text{C}$ values from each species with the trend established
163 by the reference record was used as a tool in determining the validity of age reading criteria—an
164 approach similar to previous age validation studies using the bomb ^{14}C decline period (Andrews
165 et al. 2013; 2016a). In addition, a new approach using whole lapillus $\Delta^{14}\text{C}$ measurements was
166 used to provide a definitive answer regarding whether the sagittal core $\Delta^{14}\text{C}$ value was connected
167 in time to either the ^{14}C rise period (1960s) or the post-peak decline period (after ~1980) of the
168 regional bomb ^{14}C reference record (Fig. S1)—the $\Delta^{14}\text{C}$ value measured in a whole lapillus
169 otolith would be an integrated uptake of ^{14}C through ontogeny (Figs. S2-3, Table S4).

170 **Data processing and statistical analyses**

171 For simplicity and because the numbers of specimens available for ageing were relatively
172 limited for some species, the standard (3-parameter) von Bertalanffy Growth Formula (VBGF)
173 was used to describe growth for all species. A VBGF curve was iteratively fit and defined as:

$$L_t = L_{\text{INF}} \cdot (1 - [e^{-k \cdot (t-t_0)}]),$$

174 where L_t is length (FL, in cm) at age t (in yr), L_{INF} is average asymptotic length, t_0 is estimated
 175 age at zero length, and k is the growth coefficient representing the rate at which asymptotic
 176 length is attained. In order to resolve curvature of the ascending limb of the growth curve in *C.*
 177 *perspicillatus* and to facilitate comparisons with other length-at-age characterizations of
 178 parrotfishes elsewhere (Choat et al. 1996; Choat and Robertson 2002), a 2-parameter version of
 179 the VBGF, with t_0 constrained to zero, was used:

$$L_t = L_{\text{INF}} \cdot (1 - [e^{-k \cdot (t)}]).$$

182 Length-at-age did not asymptote in *C. carolinus*; a 2-parameter power curve of the form:

$$L_t = a \cdot t^b,$$

184 where L_t is length (FL, in cm) at age t (in yr), and a and b are constants, was therefore used to
 185 describe the growth of this species, as was done for *Scarus rivulatus* by Choat et al. (1996). All
 186 curves were fit using maximum likelihood (Marquardt's Algorithm) in nonlinear regression
 187 (Proc NLIN in PC SAS v. 9.1.3; SAS Institute 2006), using fish of all sexes and color phases
 188 pooled within each species and also for adult Terminal Phase (TP) males separately from
 189 immature and mature Initial Phase (IP) males and IP females. The latter was done because other
 190 studies have shown that growth rates can differ between initial and terminal phase fish in some
 191 parrotfish species (Choat et al. 1996; Munday et al. 2004). The corresponding VBGF curves
 192 were used to describe species- and phase-specific length-at-age.

193 The fitted species-specific curves enabled estimation of median age-at-maturity (A_{M50}) for
 194 females and median age at female-to-male sex change ($A_{\Delta 50}$) by referencing prior published
 195 values of median length at female maturity (L_{M50}) and median length at sex change ($L_{\Delta 50}$),
 196 respectively (DeMartini and Howard 2016). A_{M50} and $A_{\Delta 50}$ also were estimated by fitting a 2-

197 parameter logistic function (DeMartini and Howard 2016) between percent maturity and percent
198 sex-change, respectively, versus observed age:

$$199 \quad P_x = 1 / (1 + \exp^{[ax + b]}),$$

200 where P_x = percent mature (or sex-changed) at age x , and a and b are fitted constants.

201 Spearman's nonparametric rank correlation was used to compare each of these age-specific
202 metrics to estimated maximum age (A_{MAX}), defined as the mean of the oldest quartile of observed
203 ages (Choat and Robertson 2002; Taylor and Choat 2014). These comparisons of A_{M50} and $A_{\Delta 50}$
204 with A_{MAX} thus are analogous to DeMartini and Howard's (2016) comparisons of L_{M50} and $L_{\Delta 50}$
205 to L_{MAX} .

206 The relationship between estimated age and otolith mass (OM) was evaluated for each species
207 using non-linear regression in SAS Proc NLIN (SAS Institute Inc. 2006), in order to assess the
208 potential ability to predict the ages of these parrotfishes from their otoliths. The relationships
209 between OM and fish length (FL) and between OM and gonad-free body mass (GFBM, as RM –
210 GM) also were explored using non-linear regression. These latter regressions served to help
211 interpret species differences in the nonlinearities of otolith-to-fish body size relations, and also to
212 assist in the selection of specimens for bomb radiocarbon analyses, as described above. Other
213 conventional statistics like Spearman's rank correlation also were implemented using PC SAS
214 version 9.1.3 (SAS Institute Inc. 2006) and are described by Quinn and Keough (2002).

215

216 **Results**

217 **Age verification and precision**

218 Descriptions of growth require verification and evaluation of the precision (repeatability) of
219 the estimates (Campana 2001). In this study, precision of the age readings was evaluated for each

220 of the five species using visual counts of annuli and additionally for one species (*C. carolinus*)
221 based on the estimated number of daily growth increments (DGI). The latter DGI counts were
222 made for 22 yearling individuals and are indicated by the dark gray squares with black cross-
223 hairs on Fig. 1a. The distribution of ages of yearling *C. carolinus* estimated using DGIs fell
224 centrally within the distribution of ages estimated using counts of annuli (Fig. 1a); hence DGI
225 counts verified ages estimated using annuli for yearlings of this species. Location of the first
226 annulus in *S. rubroviolaceus* and *C. perspicillatus* was identified based on matched annulus and
227 DGI counts for three and four, older juvenile-sized specimens, respectively, and used to anchor
228 the size-at-age trajectory during early growth in these two species. Reader precision was
229 generally high (Coefficient of Variation: 2.8–10.1 %) for the five species (Table S5).

230 **Age validation**

231 Contemporary estimates of fish growth further require an evaluation of age reading accuracy
232 or bias (Campana 2001). Only a single otolith specimen was deemed unreadable, but this does
233 not necessarily imply that readings were accurate for the other 866 readable specimens (of all
234 five species). Estimates of age from growth zone counting in thin transverse otolith sections were
235 generally well defined (Fig 2a,b), although assigning ages based on visual counts of annuli alone
236 required care to avoid over-counting false checks that formed near the time of sexual maturation.
237 Over-counting during early growth was a potential pitfall for both LARGE species, and
238 convoluted growth patterns were especially apparent through the latter years of growth for *C.*
239 *perspicillatus* (Fig. 2b). Use of the bomb ^{14}C decline period validated length-at-age estimates
240 through ontogeny for *S. rubroviolaceus* as well as *C. perspicillatus* (Fig 3; Fig S2). The three
241 sets of regression relationships (for *S. rubroviolaceus*, *C. perspicillatus*, and for the reference
242 chronology spanning the relevant [1990 and more recent] portion of the bomb ^{14}C decline

243 period) did not differ in their slopes (ANCOVA; $F_{2,61} = 2.37$, $P = 0.10$). Using a common
244 (pooled) slope ($b = -3.09045$), intercepts of the three regressions were indistinguishable
245 (ANCOVA; $F_{2,63} = 1.64$, $P = 0.20$; Fig 3). Use of the post-peak decline period as a temporal
246 reference was validated with the $\Delta^{14}\text{C}$ values measured in whole lapillus otoliths (Table S4, Fig.
247 S3).

248 **Size-at-age and growth rate**

249 Ages based on counts of annuli were generally relatable to observed body lengths. For *C.*
250 *carolinus* only, ages based on annuli, including the first annulus verified by DGIs, were easily
251 relatable to observed body lengths using a 2-parameter power equation. For *C. carolinus*, growth
252 in length was highly predictable ($r^2 = 0.98$) and very rapid, with the exponent of the equation
253 (0.42) indicating a decelerating increase in length at greater ages (Table 1a). Growth was
254 adequately described by 3-parameter VBGF curves (Table 1b) for the other two SMALL species
255 ($r^2 = 0.82\text{--}0.85$; Fig. 1b,c) and for the two LARGE species ($r^2 = 0.64\text{--}0.75$; Fig. 1d,e). Although
256 values of k estimated by the 3-parameter VBGF were 0.4 yr^{-1} or greater for *C. spilurus* and *S.*
257 *psittacus* and for *S. rubroviolaceus*, k was appreciably less (0.225 yr^{-1}) for *C. perspicillatus*
258 (Table 1b). Using a 2-parameter VBGF (i.e., curves forced through the origin with t_0 constrained
259 to zero), the estimate of k for *C. perspicillatus* approached, but was still less than, the k values
260 estimated for the other species (Table 1c).

261 If the length-at-age data are parsed by gonad type and color phase, some interesting additional
262 growth patterns emerge among the five species (Fig. 1a-e). Within each of the three SMALL
263 species (Fig. 1a-c), growth rates of TP males were generally faster than IP fish (all IP fish were
264 females in *C. carolinus*: DeMartini and Howard 2016). Small sample numbers required pooling
265 all IP females and IP males together for analysis in *S. psittacus* (Fig. 1b) and *C. spilurus* (Fig.

266 1c). Data were sufficient to separately evaluate growth rates of female and male IP fish in the
267 two LARGE species but there was no shared pattern. Growth rates were generally faster for TP
268 males (versus IP males or IP females) in each of the LARGE species (Fig. 1d,e).

269 **Longevity**

270 The five species differed appreciably in observed maximum ages, based on visual band counts of
271 annuli, and ranged from about 4 yr in *C. carolinus* (the largest of the three SMALL species, Fig.
272 1a) to 15–20 yr in both LARGE species (Fig. 1d,e). Observed maximum ages were 6 and 11 in *S.*
273 *psittacus* and *C. spilurus*, respectively, the two smaller of the SMALL species (Fig. 1b,c). For *C.*
274 *carolinus*, the estimated lifespan of IP fish was appreciably shorter than that of TP fish (Fig. 1a).
275 Lifespans of IP females of *C. spilurus* (Fig. 1c) and *S. rubroviolaceus* (Fig. 1e) were longer than
276 those of IP males. Maximum estimated ages for the two LARGE species were validated with
277 bomb radiocarbon dating of the largest individuals with the heaviest otoliths (Fig. 2; Tables S1,
278 S2).

279 **Age at female maturation**

280 Ages at female sexual maturation differed among the five species, ranging from 1–2 yr old in
281 the three SMALL species to 3–3½ yr old in the two LARGE species (Table 1; Figs. 1a-e). Values
282 of A_{M50} estimated by interpolation from length-at-maturity plotted on the length-at-age curve for
283 the respective species (illustrated by arrows on Figs. 1a-e) were similar to those estimated
284 directly by fitting a logistic curve to percent maturity-at-age (Table 2). A_{M50} values were
285 positively but insignificantly related (Spearman's rank correlation coefficient $\rho = 0.70$, $n = 5$, $P =$
286 0.19) to estimates of A_{MAX} for the respective species (Fig. 4).

287 **Age at sex change**

288 Ages at sex change varied considerably among the five species, and were least (2 to 4 yr old)
289 in the three SMALL species (Table 2; Fig. 1a-c). $A_{\Delta 50}$ differed most greatly between the two
290 LARGE species: about 5 yr old in *S. rubroviolaceus* versus 7 yr old in *C. perspicillatus* (Table 2;
291 Fig. 1d,e). Values of $A_{\Delta 50}$ also were positively but weakly related (Spearman's $\rho = 0.60$, $n = 5$, P
292 = 0.28) to corresponding estimates of A_{MAX} (Fig. 4).

293 **Age versus otolith mass**

294 Age was predictably related to OM for each of the five species (Table 3; Fig. 5). The relation
295 was negatively allometric (i.e., age was a positive but decelerating function of OM) in two of the
296 SMALL species (Fig. 5a) but was positively allometric—an accelerating function of OM—in both
297 LARGE species (Fig. 5b). Age was linearly related to OM (slope indistinguishable from one) in
298 the third SMALL species, *C. spilurus* (Table 3; Fig. 5a).

299 **Discussion**

300 **Age validation and longevity**

301 Until recently, age validation of marine organisms using bomb ^{14}C dating was limited to the
302 period of rapid ^{14}C increase (typically between 1958 and 1970). But for tropical regions of the
303 northern hemisphere the post peak decline period provides a slope that can be used to age
304 younger and more recently collected fish (e.g., Andrews et al. 2013; 2016a). The current study
305 confirms that both LARGE parrotfish species have a longevity near 20 yr and that counting
306 growth zone structure in sagittal otolith cross sections is accurate provided that over-counting
307 ages of young adults is avoided. The comparison of ^{14}C levels in otolith core material for the
308 LARGE parrotfish species with the regional coral and otolith ^{14}C reference records validated the
309 age and growth estimates. In addition, the slope of the ^{14}C reference decline period clearly

310 indicates that the longevity of neither of the two LARGE species could be younger or older by
311 more than ~3–4 yr because of the temporal specificity of the measured ^{14}C levels (see Fig. S1,
312 S2). Furthermore, the use of whole lapillus ^{14}C levels to confirm the alignment of measured
313 otolith core $\Delta^{14}\text{C}$ values with the decline period (Fig. S3) is an innovative tool that can be used to
314 differentiate age scenarios (old versus young) in other fishes. For the old age scenario, the
315 lapillus would integrate ^{14}C uptake from a birth year in the 1950s or 1960s, through the elevated
316 peak period, and into the decline period—the measured whole lapillus ^{14}C would exceed
317 measured core ^{14}C levels in the sagitta (see Figs. S1–S3).

318 **General growth patterns**

319 First of all, it is important to note that all five species in Hawai'i conform to prior observations
320 that parrotfishes are a group of generally fast-growing coral reef fishes with high turnover rates
321 (Hawai'i Cooperative Fishery Research Unit 2008; Howard 2008; Taylor et al. 2017). Secondly,
322 in Hawai'i as elsewhere such as on the Great Barrier Reef (GBR), Australia (Choat et al. 1996;
323 Munday et al. 2004), TP fish of all five major parrotfishes grow faster than IP fish. Additionally,
324 the IP females of *S. rubroviolaceus* and *C. spilurus* live longer than TP males, as previously
325 observed for many parrotfish species (Choat et al. 1996). Also important is that the k parameter
326 first estimated for *C. perspicillatus* using the 3-parameter VBGF was biased low because few
327 specimens less than 2 yr old were available for ageing and the fitted curve had less resolved
328 curvature in its ascending limb (Hirschhorn 1974; Ferreira and Russ 1994; Choat and Robertson
329 2002). This bias was remedied in this study by constraining the curve through the origin using
330 the 2-parameter VBGF. After doing this, the re-estimated value of k for *C. perspicillatus* derived
331 here approached the values estimated for the other study species, although length-at-age for adult

332 *C. perspicillatus* was still generally smaller, hence growth was slower, than for *S.*
333 *rubroviolaceus*, the other LARGE species.

334 **Geographic comparisons of growth**

335 Sparse published data on growth and age-related milestones exist for Indo-Pacific parrotfishes
336 (DeMartini and Howard 2016)—the present study represents the first major contribution for the
337 central Pacific region. The extent of growth data outside of Hawai'i also varies greatly among the
338 five species, from moderate in *C. spilurus*, to few in *S. psittacus*, *S. rubroviolaceus*, and *C.*
339 *carolinus*, to non-existent in *C. perspicillatus*, and is specified as follows. Appreciable growth-
340 related data exist for *C. spilurus* on the GBR (Choat et al. 1996; Choat and Robertson 2002), at
341 Guam in the western North Pacific (Taylor and Choat 2014), and across Micronesia (Taylor
342 2014). In general, this species has faster growth on the GBR (Choat et al. 1996) than in Hawai'i,
343 although fish grew differently (faster), matured and changed sex earlier, and attained larger sizes
344 on mid-shelf versus outer-shelf reefs of the GBR (Gust et al. 2002; Gust 2004). At Guam and
345 across Micronesia, k and A_{MAX} averaged $0.95 \cdot \text{yr}^{-1}$ and < 6 yr, but L_{M50} and $L_{\Delta 50}$ as well as A_{M50}
346 and $A_{\Delta 50}$ ranged broadly depending on environment (habitat productivity), conspecific density,
347 and fishing pressure (Taylor and Choat 2014; Taylor 2014; Taylor et al. 2014). Clearly, tropical
348 populations of *C. spilurus* in the western Pacific grow faster and mature and change sex at
349 younger ages and smaller sizes (DeMartini and Howard 2016) than do those in the subtropical
350 Oahu, Hawai'i, population. Hawai'i lies at the easternmost range limit in the central North Pacific
351 of this and all other study species except *S. rubroviolaceus* (DeMartini and Howard 2016). Water
352 temperatures in Hawai'i are cooler and slower growth likely delays age-related life-history
353 milestones (Atkinson and Sibley 1997).

354 *Scarus psittacus* is a relatively SMALL (to ~20 cm FL), fast-growing (VBGF $k > 1.0 \cdot \text{yr}^{-1}$),
355 and short-lived (to 5 yr) species on the GBR (Choat et al. 1996; Choat & Robertson 2002).
356 Growth, maturation, and sex change are comparably rapid at Guam, where average maximum
357 age (3.3 to 4.2 yr) and age at female maturity (~1.4 yr; Taylor and Choat 2014) range from
358 younger than to similar to respective estimates for the species in Hawai'i.

359 Age at sexual maturity of *C. carolinus* at Guam has been estimated as 1.1 yr, where its
360 maximum observed age was only 3 yr (Taylor and Choat 2014). The Guam estimates generally
361 confirm the extremely rapid growth rates of *C. carolinus*. Its congener *C. japonicus* has been
362 aged at several locations in Japan, where growth, although quite fast, is slower than *C. carolinus*
363 and appears to vary spatially (Kume et al. 2010, and Kawajiri et al. 1975 cited therein).

364 Sparisomatines are typically shorter-lived relative to body size (i.e., grow faster) than scarine
365 labrids (Choat and Robertson 2002).

366 Howard (2008) provided a preliminary estimate of A_{M50} (4 yr) for *S. rubroviolaceus* at Oahu.
367 Taylor and Pardee (2017 in press) recently estimated an A_{M50} of 2.6 yr, with a maximum
368 observed age of 14 yr, for *S. rubroviolaceus* at American Samoa in the central South Pacific. The
369 A_{M50} of this species is 1.9 yr at Guam, where its maximum observed age is only 6 yr (Taylor and
370 Choat 2014). Sparse data exist for locations farther west than Guam: the oldest *S. rubroviolaceus*
371 aged by Grandcourt (2002) in the Seychelles was nearly 20 yr and the youngest sex-changed
372 male was 12 yr (but only four TP males were aged). The estimates of Taylor and Choat (2014)
373 and the present study indicate that *S. rubroviolaceus* is fast growing but moderately long-lived
374 for a parrotfish and initially matures and changes sex at older ages and lives longer at Hawai'i
375 than in Guam and American Samoa. No prior estimates of age at sexual maturity or at sex
376 change exist for *C. perspicillatus*, the major endemic species of Hawaiian parrotfish.

377 **Comparisons of age milestones among species**

378 Even though both A_{M50} and $A_{\Delta 50}$ are proportional to A_{MAX} across the five species studied
379 herein, the strength of these relationships are less than those of the corresponding proportionality
380 between L_{M50} or $L_{\Delta 50}$ versus L_{MAX} (DeMartini and Howard 2016). Parrotfishes in Hawai'i are less
381 predictably age-structured than size-structured, in part because of the overall very rapid growth
382 rate of *C. carolinus*, the largest of the three SMALL species, and also because of the disparate
383 post-maturational growth rates of the two LARGE species. Our observations support the
384 contention made by Taylor and Choat (2014) that age-based metrics provide more informative
385 input to parrotfish stock assessment and management than do length-based metrics, despite the
386 apparent attractiveness and simplicity of basing regulations just on body length (Valles and
387 Oxenford 2014; Valles et al. 2015).

388 **Age-otolith mass relation**

389 Among the five species, the age-to-OM relations of the two LARGE species uniquely differ
390 from each other in a manner that is consistent with their differences in somatic growth rates.
391 *Chlorurus perspicillatus*, the slower growing of the two species, has a larger otolith at a given
392 body size (in both length and mass) than *S. rubroviolaceus*. This might simply reflect
393 phylogeny—that otoliths of species within the genus *Chlorurus* are generally more robust than
394 those of the genus *Scarus*, despite within-genus differences exemplified by *S. rubroviolaceus* and
395 *S. psittacus* (Fig. S4, S5). More importantly, there is a strong positive relation between OM and
396 fish body length and somatic mass within each of the five species (Table S6, Fig. S4-S6). The
397 strong positive relations between OM and fish age (Table 3, Fig. 6) suggest promise for using
398 OM as a proxy for age—for the capability of predicting fish age from OM, as first suggested for
399 parrotfishes by Taylor and Choat (2014)—given the caveats listed by Andrews et al. (2016a).

400 **Management implications of species differences**

401 The parrotfish component of the shallow-water reef fish fisheries at Oahu is dominated
402 numerically by *S. rubroviolaceus* and *C. carolinus* and in biomass by *S. rubroviolaceus* and *C.*
403 *perspicillatus* (DeMartini and Howard 2016). These three and the two other fishery species of
404 parrotfishes differ substantially in A_{M50} and $A_{\Delta50}$, in addition to L_{M50} and $L_{\Delta50}$. The latter values
405 range below and above the current minimum size limit (12 inches or 30.5 cm) set for all species
406 of parrotfishes in Hawai'i (except *C. carolinus*, for which no minimum size limit presently exists:
407 DeMartini and Howard 2016). A_{M50} values for *S. rubroviolaceus* and *C. perspicillatus* in Hawai'i
408 are about 3 to 3½ yr, corresponding to a shared L_{M50} of about 35 cm FL. $A_{\Delta50}$ values for these
409 two species, however, differ greatly (about 5 yr for *S. rubroviolaceus* and 7 yr for *C.*
410 *perspicillatus*), even though both species change sex at about 47 cm FL. Growth rates of the two
411 species diverge greatly after the sexual maturation of females, with adult female *C. perspicillatus*
412 growing much more slowly than adult female *S. rubroviolaceus*, even though growth rates of TP
413 males are relatively faster than those of IP fish in both species. The inherently different growth
414 rates of these two LARGE species suggests that they should not be managed as a pooled taxon.

415 The endemic species *C. perspicillatus* increases markedly in abundance with latitude across
416 the unfished (and nearly human-depopulate) Northwestern Hawaiian Islands (NWHI)—a pattern
417 typical of Hawaiian endemics (DeMartini and Friedlander 2004). In contrast, the broadly
418 distributed Indo-Pacific *S. rubroviolaceus* is relatively uncommon throughout the NWHI (Nadon
419 et al. 2015) and is rare to absent at latitudes north of French Frigate Shoals (Hobson 1984). Mean
420 biomass densities of *C. perspicillatus* are historically much lower than those of *S. rubroviolaceus*
421 at Oahu (Howard et al. 2009). The relatively lower abundances of *C. perspicillatus* in the MHI
422 could reflect this latitudinal gradient, but could also be related to a greater susceptibility to

423 extraction or other environmental influences including both the anthropogenic (e.g.,
424 sedimentation resulting from coastal development) and the non-anthropogenic (wave exposure
425 and related benthic composition and structural heterogeneity: Taylor et al. 2014). The
426 confounding of human influence with biogeographic distributions precludes definitive attribution
427 of observed patterns exclusively to any environmental factor and further research is needed to
428 investigate possible fishing effects on demography and population structure. Our study used
429 specimens collected from Oahu, where parrotfish catches average 3-31 % greater compared to
430 other islands within the MHI (McCoy 2015). Comparisons with vital rates estimated using
431 specimens collected from other MHI with lower fishing pressure could elucidate how
432 demography and population structure might be related to fishing, given expectations of sized-
433 based fishing effects on sex-changing fishes (Hamilton et al. 2007).

434 This study, together with DeMartini and Howard (2016), demonstrates the general necessity
435 of incorporating empirically derived vital rates, cross-referencing size and age, when establishing
436 fisheries regulations like minimum size limits for multi-species taxa. DeMartini and Howard
437 (2016) concluded that minimum size for both LARGE species (*S. rubroviolaceus* and *C.*
438 *perspicillatus*) of Hawaiian parrotfishes should be 14 inches (35.6 cm) FL in order to better
439 protect female spawning stocks and safeguard against recruitment overfishing, given that the
440 present minimum size of 12 inches protects fewer than 20% of the spawning females of these
441 two species. DeMartini and Howard (2016) further concluded that prohibiting the take of blue
442 and green-colored TP parrotfishes might be used to protect sex-changed males. In *S.*
443 *rubroviolaceus*, moreover, the per capita impact of large IP females on habitat (substratum) as
444 ecological engineers is equally as important as the impact of TP males (Ong and Holland 2010).
445 This suggests that additional protection might be needed for all large-bodied individuals,

446 regardless of sex and color-phase. The ecosystem benefits of protecting all large parrotfishes
447 from harvest in the Caribbean have recently been modeled by Bozec et al. (2016), although the
448 influences of parrotfishes on the ecosystem might differ in the Caribbean where parrotfishes
449 differ phylogenetically, functionally, and demographically from related species in the tropical
450 Pacific (Bonaldo et al. 2014; Taylor et al. 2017). Benefits might nonetheless be provided by
451 protecting fish of both sexes and color-phases of these two species above a threshold body size
452 (e.g., 50 cm [20 inches] FL), as well as fish at sizes below the 35.6 cm (14-inch) FL median
453 length at female sexual maturity (DeMartini and Howard 2016). Thus, sizes of 35-50 cm (14-20
454 inches) FL might represent a reasonable slot size for take. Regardless of whether or not
455 minimum size limits are changed or slot sizes are implemented, the different growth rates and
456 lifespans among parrotfishes in Hawai'i support the general recommendation of DeMartini and
457 Howard (2016) that they not be managed as a single unit taxon. Future research should address
458 the need for collection of comprehensive and accurate, species-, sex-, and size-specific catch and
459 abundance data in order to estimate optimal harvest strategies for these economically and
460 ecologically important species.

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602 **FIGURE CAPTIONS**

603 **Fig. 1.** Scatterplots and fitted curves of fork length FL (cm) versus age (yr) for each tractable sex and
604 color phase of (a) *Calotomus carolinus* (Initial Phase IP: $n = 118$; Terminal Phase TP: $n = 30$); (b) *Scarus*
605 *psittacus* (IP: $n = 72$; TP: $n = 30$); (c) *Chlorurus spilurus* (IP: $n = 80$; TP: $n = 53$); (d) *Chlorurus*
606 *perspicillatus* (IP male: $n = 48$; IP female: $n = 95$; TP: $n = 38$); and (e) *Scarus rubroviolaceus* (IP male: n
607 $= 52$; IP female: $n = 150$; TP: $n = 60$), among the five major species of Hawaiian parrotfishes examined.
608 Scatterplots represent the complete data (all phases pooled) for each species. For *C. carolinus* only,
609 length-at-age estimates for 22 yearling fish are illustrated as dark gray squares with white cross-hairs.
610 Growth of *C. carolinus* was modeled as a decelerating power curve of the form, $FL = a \cdot Age^b$ because
611 length-at-age failed to asymptote using the von Bertalanffy growth formula (VBGF). A 3-parameter
612 VBGF curve was used to describe growth of each of the other four species. Male and female IP fish were
613 pooled for *C. spilurus* and for *S. psittacus* because data were otherwise too few; all IP *C. carolinus* are
614 females (DeMartini and Howard 2016). All curves were fit by maximum likelihood using SAS Proc
615 NLIN (SAS Institute Inc. 2006); specific parameter values are listed in Table 1a,b. The black and dark
616 grey arrows depict length- and age-at-maturity (L_{M50} and A_{M50}) and length- and age-at-sex change ($L_{\Delta 50}$
617 and $A_{\Delta 50}$), respectively. Note variable x- and y-axes among panels.

618 **Fig. 2.** Transverse cross sections of sagittal otoliths from the oldest individuals used in this study, with
619 annuli indicated by white dots. *Scarus rubroviolaceus* (a) were aged to 19 yr (specimen SR-16) using the
620 regular annuli pattern denoted with white dots, with the potential for over counting seen in the earliest
621 growth. *Chlorurus perspicillatus* (b) was aged to 18 yr (specimen CP-21) in sections with annuli that
622 were more irregular and subjectively identified through ontogeny. The first annulus for each species was
623 verified by counts of daily increments; counting false annuli (the accessory checks present) would have
624 led to a temporal offset in the decline fit from bomb radiocarbon dating (Fig. 3).

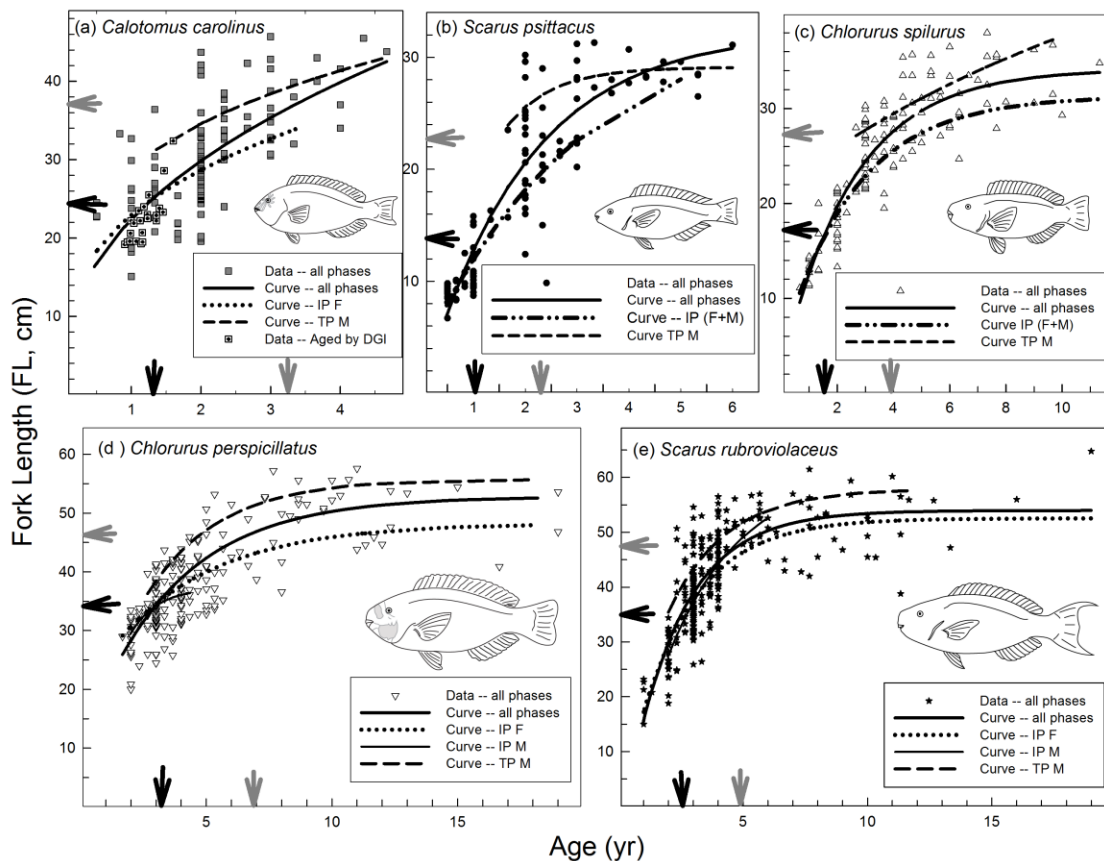
625 **Fig. 3.** Scatterplots and fitted curves depicting the relations between $\Delta^{14}\text{C}$ and year of formation for select
626 sagittal otolith specimens of *Scarus rubroviolaceus* (black stars, solid black line) and *Chlorurus*
627 *perspicillatus* (open triangles-inverted, dashed gray line), and for the 1990 and more recent portion of the
628 decline period of a reference time series (Andrews et al. 2016b) of Kona corals augmented by juvenile
629 otoliths (gray circles, dotted gray line) that temporally overlaps the birth-year of formation of the
630 parrotfish specimens. Note near congruence of the curves for the two species. The full bomb radiocarbon
631 reference curve, including the entire decline period back to about 1982, as well as the rise and peak
632 periods, is provided in Fig. S1. Further differentiation of the reference juvenile parrotfish otoliths is
633 provided in Fig. S2 where innovative work on ^{14}C uptake by the lapillus otolith, used as a tool to
634 differentiate formation period (rise versus decline), is presented (Table S4, Fig. S3).

635 **Fig. 4.** Plots of A_{M50} (hollow symbols) and $A_{\Delta50}$ (filled symbols) estimates for each of the five parrotfish
636 (Labridae) species (coded by the species-specific acronyms listed in Table 1) versus the A_{MAX} estimate of
637 the respective species. A_{M50} and $A_{\Delta50}$ values were estimated using 2-parameter logistic fits of proportion
638 mature Initial Phase (IP) females among all IP female fish and proportion Terminal Phase (TP) males
639 among all fish, respectively. Values of A_{MAX} were calculated as the mean of the oldest quartile of
640 specimens that were aged for the respective species. Vertical bars represent 2 SE or approximate 95% CI.

641 **Fig. 5.** Scatterplots and fitted curves predicting age (yr) from otolith mass (OM)(in g) for (a) the three
642 SMALL species: *Calotomus carolinus* (dark gray squares and dark gray line; $n = 149$), *Chlorurus spilurus*
643 (open triangles-up and gray line; $n = 134$), *Scarus psittacus* (black circles and line; $n = 101$), and (b) the
644 two LARGE species: *Chlorurus perspicillatus* (open triangles-inverted and gray line; $n = 204$) and *Scarus*
645 *rubroviolaceus* (black stars and line; $n = 273$), among the five major species of Hawaiian parrotfishes
646 examined. Note different scales of the x-axis in (a) and (b).

647

648 Fig. 1



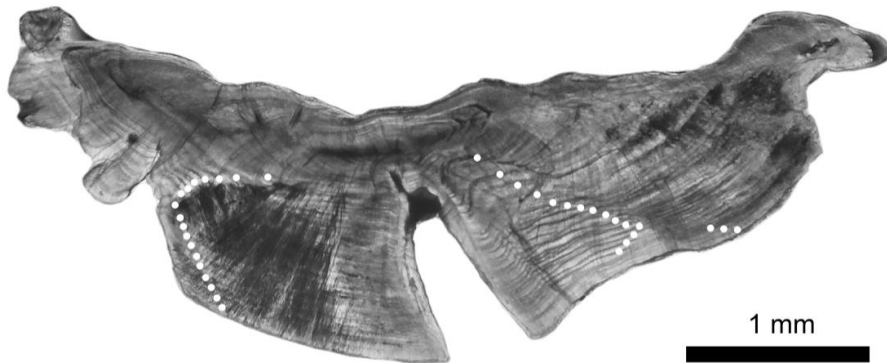
649
 650 **Fig. 1.** Scatterplots and fitted curves of fork length FL (cm) versus age (yr) for each tractable sex and
 651 color phase of (a) *Calotomus carolinus* (Initial Phase IP: $n = 118$; Terminal Phase TP: $n = 30$); (b) *Scarus*
 652 *psittacus* (IP: $n = 72$; TP: $n = 30$); (c) *Chlorurus spilurus* (IP: $n = 80$; TP: $n = 53$); (d) *Chlorurus*
 653 *perspicillatus* (IP male: $n = 48$; IP female: $n = 95$; TP: $n = 38$); and (e) *Scarus rubroviolaceus* (IP male: n
 654 $= 52$; IP female: $n = 150$; TP: $n = 60$), among the five major species of Hawaiian parrotfishes examined.
 655 Scatterplots represent the complete data (all phases pooled) for each species. For *C. carolinus* only,
 656 length-at-age estimates for 22 yearling fish are illustrated as dark gray squares with white cross-hairs.
 657 Growth of *C. carolinus* was modeled as a decelerating power curve of the form, $FL = a \cdot Age^b$ because
 658 length-at-age failed to asymptote using the von Bertalanffy growth formula (VBGF). A 3-parameter
 659 VBGF curve was used to describe growth of each of the other four species. Male and female IP fish were
 660 pooled for *C. spilurus* and for *S. psittacus* because data were otherwise too few; all IP *C. carolinus* are
 661 females (DeMartini and Howard 2016). All curves were fit by maximum likelihood using SAS Proc
 662 NLIN (SAS Institute Inc. 2006); specific parameter values are listed in Table 1a,b. The black and dark
 663 grey arrows depict length- and age-at-maturity (L_{M50} and A_{M50}) and length- and age-at-sex change ($L_{\Delta 50}$
 664 and $A_{\Delta 50}$), respectively. Note variable x- and y-axes among panels.

665 Fig. 2

(a)



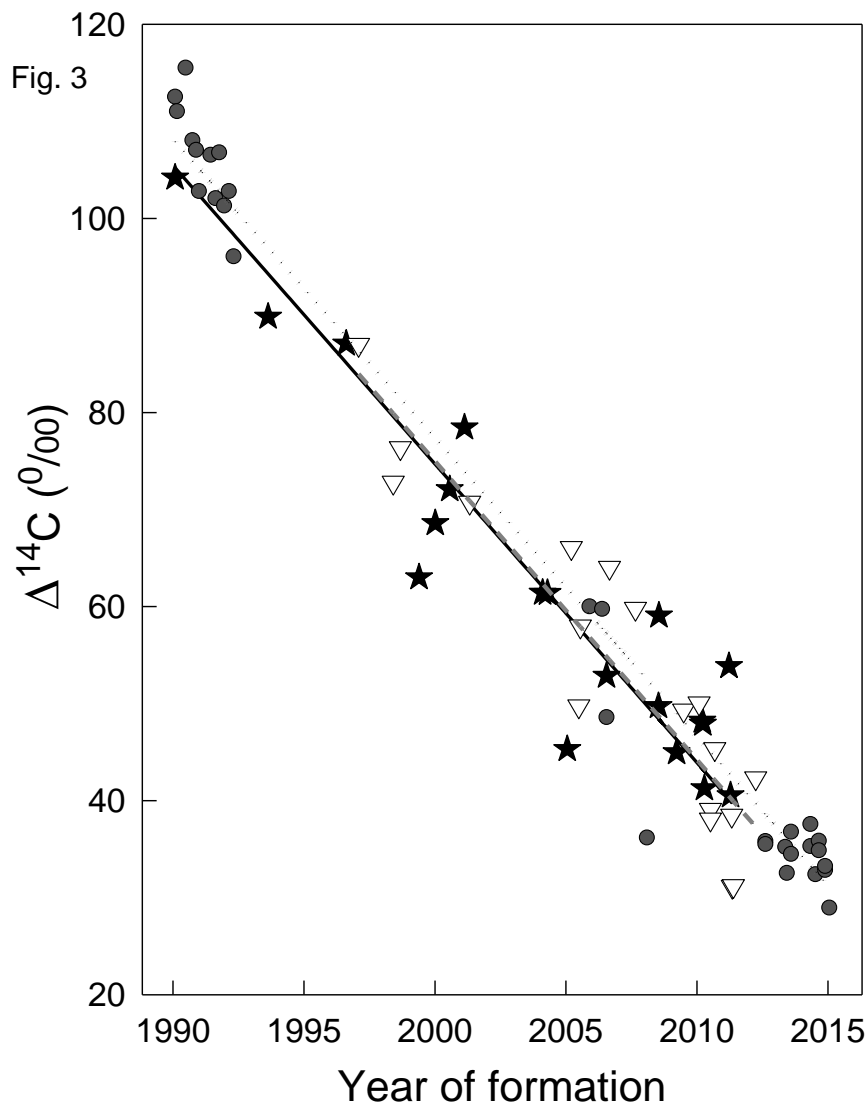
(b)



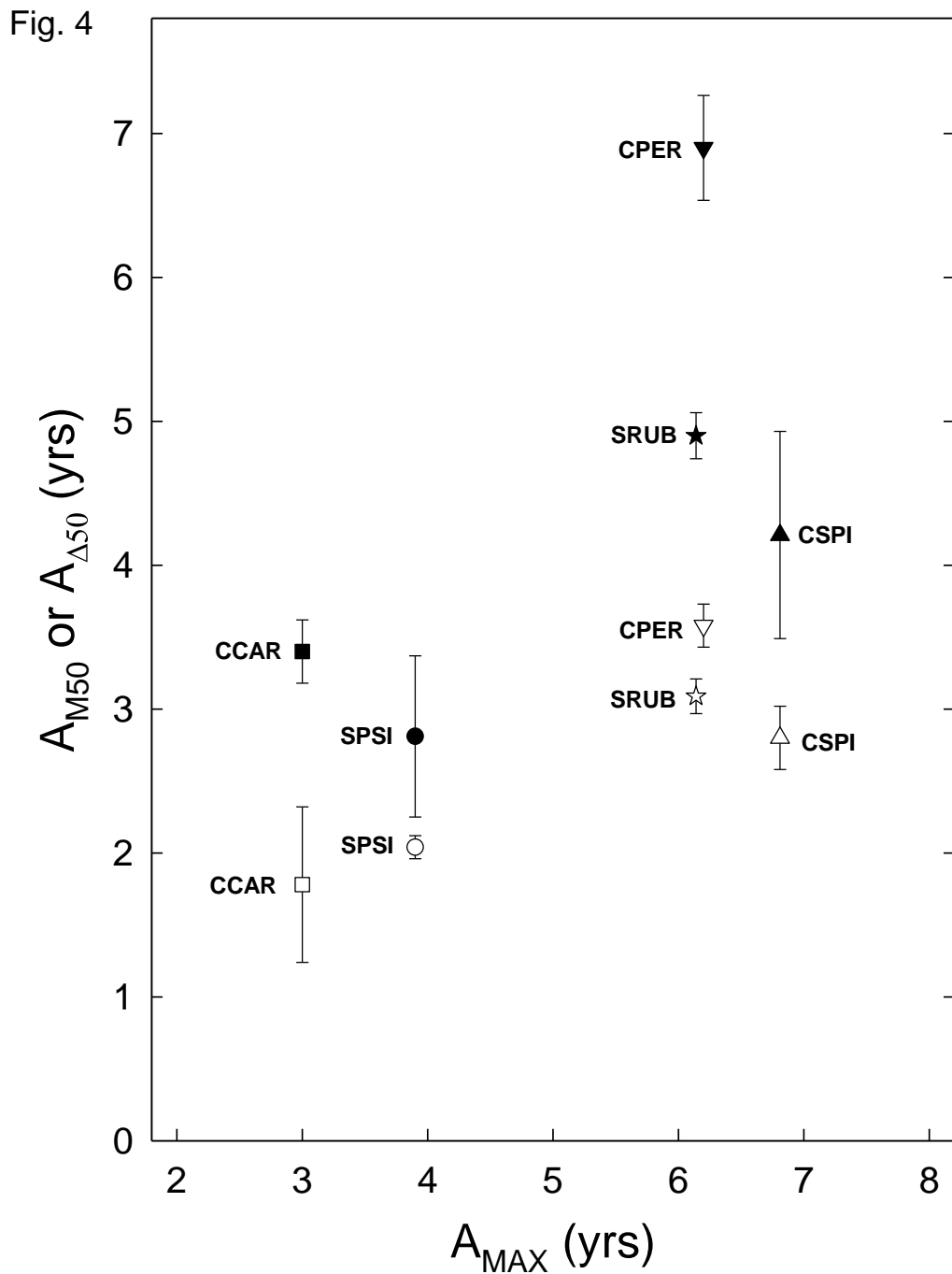
666

667 **Fig. 2.** Transverse cross sections of sagittal otoliths from the oldest individuals used in this study, with
668 annuli indicated by white dots. *Scarus rubroviolaceus* (a) were aged to 19 yr (specimen SR-16) using the
669 regular annuli pattern denoted with white dots, with the potential for over counting seen in the earliest
670 growth. *Chlorurus perspicillatus* (b) was aged to 18 yr (specimen CP-21) in sections with annuli that
671 were more irregular and subjectively identified through ontogeny. The first annulus for each species was
672 verified by counts of daily increments; counting false annuli (the accessory checks present) would have
673 led to a temporal offset in the decline fit from bomb radiocarbon dating (Fig. 4).

674

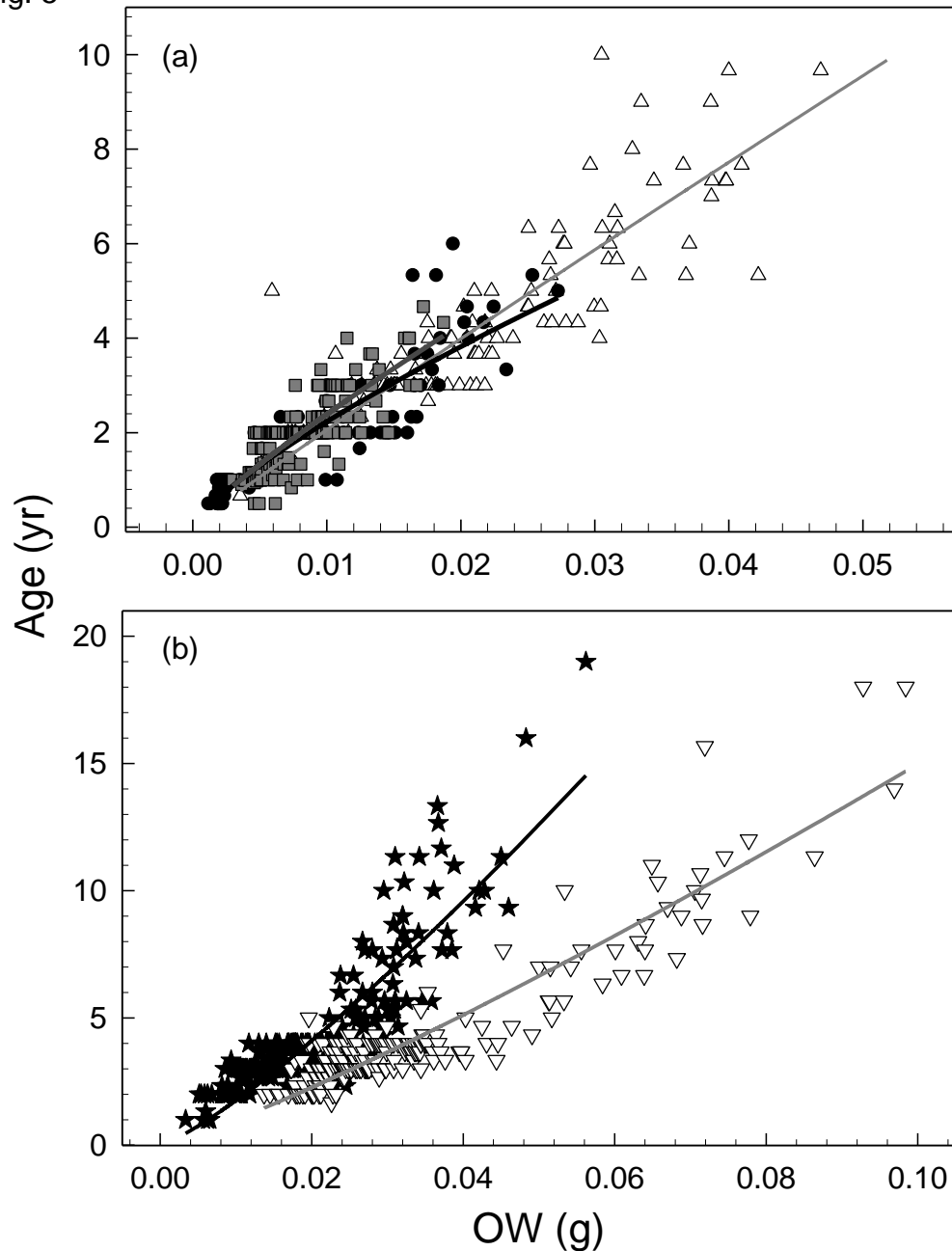


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 677 sagittal otolith specimens of *Scarus rubroviolaceus* (black stars, solid black line) and *Chlorurus*
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 679 decline period of a reference time series (Andrews et al. 2016b) of Kona corals augmented by juvenile
 680 otoliths (gray circles, dotted gray line) that temporally overlaps the birth-year of formation of the
 681 parrotfish specimens. Note near congruence of the curves for the two species. The full bomb radiocarbon
 682 reference curve, including the entire decline period back to about 1982, as well as the rise and peak
 683 periods, is provided in Fig. S1. Further differentiation of the reference juvenile parrotfish otoliths is
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 689 the respective species. A_{M50} and $A_{\Delta 50}$ values were estimated using 2-parameter logistic fits of proportion
 690 mature Initial Phase (IP) females among all IP female fish and proportion Terminal Phase (TP) males
 691 among all fish, respectively. Values of A_{MAX} were calculated as the mean of the oldest quartile of
 692 specimens that were aged for the respective species. Vertical bars represent 2 SE or approximate 95% CI.

Fig. 5



693
 694 **Fig. 5.** Scatterplots and fitted curves predicting age (yr) from otolith mass (OM)(in g) for (a) the three
 695 SMALL species: *Calotomus carolinus* (dark gray squares and dark gray line; $n = 149$), *Chlorurus spilurus*
 696 (open triangles-up and gray line; $n = 134$), *Scarus psittacus* (black circles and line; $n = 101$), and (b) the
 697 two LARGE species: *Chlorurus perspicillatus* (open triangles-inverted and gray line; $n = 204$) and *Scarus*
 698 *rubroviolaceus* (black stars and line; $n = 273$), among the five major species of Hawaiian parrotfishes
 699 examined. Note different scales of the x-axis in (a) and (b).

700 **Table 1.** Summary statistics of (a) a 2-parameter power equation (*C. carolinus* [CCAR] only, model as
 701 specified below); (b) a standard 3-parameter von Bertalanffy growth formula (VBGF, also as specified
 702 below, for *C. perspicillatus* [CPER], *C. spilurus* [CSPI], *S. psittacus* [SPSI], and *S. rubroviolaceus*
 703 [SRUB] only); and (c) a 2-parameter VBGF with t_0 constrained to zero (model fit through the origin), for
 704 the latter four species, relating fork length (FL, in cm) to age (in yr).
 705

(a) Power equation: $FL = a Age^b$

Acronym	a	SE_a	B	SE_b	r^2	Prob > $ r $	N
CCAR	22.3	0.64	0.42	0.03	0.975	< 0.0001	149

(b) VBGF: $FL = L_{\infty}(1 - [e^{-k(t-t_0)}])$

Acronym	L_{∞}	$SE_{L_{\infty}}$	k	SE_k	t_0	SE_{t_0}	r^2	Prob > $ r $	N
CPER	53.2	1.93	0.225	0.038	-1.48	0.54	0.636	< 0.0001	206
CSPI	34.4	1.00	0.400	0.045	-0.13	0.16	0.817	< 0.0001	133
SPSI	32.7	1.96	0.486	0.079	-0.01	0.10	0.850	< 0.0001	101
SRUB	53.5	0.80	0.410	0.032	0.12	0.15	0.751	< 0.0001	272

(c) VBGF: $FL = L_{\infty}(1 - [e^{-k(t)}])$

Acronym	L_{∞}	$SE_{L_{\infty}}$	k	SE_k	r^2	Prob > $ r $	N
CPER	49.4	0.97	0.378	0.184	0.984	< 0.0001	206
CSPI	33.9	0.74	0.434	0.024	0.987	< 0.0001	133
SPSI	32.5	1.44	0.494	0.042	0.976	< 0.0001	101
SRUB	53.8	0.71	0.389	0.014	0.989	< 0.0001	272

706

707 **Note:** The power equation and both VBGF models were fit by non-linear regression (Marquardt's algorithm) using Proc
 708 NLIN in PC SAS version 9.13 (SAS Institute, 2006). Species are ordered alphabetically by acronym. Sexes and color phases are
 709 pooled within species. Standard errors (SE) are indicated for all parameter estimates.

710

711 **Table 2.** Summary statistics for the relation between (a) median percent maturity of Initial Phase female
 712 and age (yr) and (b) median percent sex-changed Terminal Phase male and age (yr), as described by the
 713 2-parameter logistic model shown, for each of the five species of Hawaiian parrotfishes studied.

714

(a) Model: $Pct_{maturity} = 100 / (1 + \exp^{-a \{Age-b\}})$

Acronym	a	SE_a	b	SE_b	r^2	Prob > $ r $	n
CCAR	0.987	0.347	1.7794	0.2719	0.983	0.017	4
CPER	0.878	0.209	3.8097	0.2200	0.977	< 0.0001	14
CSPI	2.041	0.419	2.8026	0.1102	0.987	< 0.0001	12
SPSI	5.517	0.770	2.0445	0.0352	0.997	< 0.0001	7
SRUB	1.457	0.108	3.2592	0.0464	0.999	< 0.0001	17

(b) Model: $Pct_{sex\ change} = 100 / (1 + \exp^{-a \{Age-b\}})$

Acronym	a	SE_a	b	SE_b	r^2	Prob > $ r $	n
CCAR	1.928	0.350	3.3988	0.1097	0.987	0.0015	5
CPER	0.782	0.200	6.3274	0.3959	0.931	< 0.0001	10
CSPI	0.856	0.263	4.2063	0.3562	0.940	< 0.0001	8
SPSI	1.737	0.797	2.8091	0.2805	0.925	< 0.0001	7
SRUB	0.809	0.109	5.1341	0.1615	0.988	< 0.0001	6

715

716 **Note:** Species are listed by acronym defined in Table 1. Standard errors (SE) are indicated for all parameter estimates.

717 Sample sizes are the number of age-classes used in the analysis. In (b) the value 75 was used as the asymptotic percentage value

718 in the numerator instead of 100 for SRUB to avoid the influence of old IP females; also, the oldest age-class was truncated at 10+

719 yr for CPER, 8+ yr for CSPI, and 6+ yr for SRUB to avoid the influence of old IP females.

720

721 **Table 3.** Summary statistics for the relation between age (in yr) and sagittal otolith mass (OM, in grams)
 722 as described by the nonlinear power equation, $Y = a X^b$, for each of the five species of Hawaiian
 723 parrotfishes studied.

Model: $Age = a OM^b$

Acronym	a	SE_a	b	SE_b	r^2	Prob > $ r $	n
CCAR	115.6	27.42	0.8425	0.0510	0.952	< 0.0001	149
CPER	255.9	23.24	1.1876	0.0302	0.961	< 0.0001	204
CSPI	166.3	25.24	0.9536	0.0420	0.961	< 0.0001	134
SPSI	79.05	17.38	0.7745	0.0516	0.935	< 0.0001	100
SRUB	730.4	86.27	1.2783	0.0328	0.959	< 0.0001	273

724 **Note:** The relation was curvilinear and decelerating for CCAR and SPSI but curvilinear and accelerating for CPER and
 725 SRUB, whereas the relation was linear for CSPI. Species are ordered by acronyms defined in Table 1. Standard errors (SE) are
 726 indicated for all parameter estimates.
 727

Draft