

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

Edward E. DeMartini, Allen H. Andrews, Kathrine G. Howard, Brett M. Taylor, Dong-Chun Lou, and Mary K. Donovan

**Abstract:** Growth rates and longevity were estimated for five major fishery species of parrotfishes (“uhu”) at Oahu, Hawai’i. All species grew rapidly with von Bertalanffy growth formula  $k$  values  $\geq 0.4 \text{ year}^{-1}$ . Longevity were found to range broadly among the three small species, 4 years in *Calotomus carolinus* and 6 and 11 years in *Scarus psittacus* and *Chlorurus spilurus*, and to 15–20 years in *Scarus rubroviolaceus* and *Chlorurus perspicillatus* for the two large species. Age reading and growth curves for the latter two large species were validated using bomb radiocarbon dating. Median ages at sexual maturity as females ( $A_{M50}$ ) and at sex change (from female to terminal phase male,  $A_{\Delta 50}$ ) were estimated using logistic models. Sexual maturation occurred at 1–2 years for the small species and at 3–3.5 years in the large species.  $A_{\Delta 50}$  estimates ranged from 2 to 4 years in the small species and were about 5 and 7 years in *S. rubroviolaceus* and *C. perspicillatus*, respectively. Estimated milestones poorly corresponded to the current minimum legal size for uhu in Hawai’i (12 in. or 30.5 cm fork length). Pooling these parrotfishes for management seems generally inappropriate, especially for the two large species. Age-based metrics are more informative than size-based metrics for these fishes.

**Résumé :** Les taux de croissance et la longévité ont été estimés pour cinq espèces de poissons-perroquets (« uhu ») importantes pour la pêche à Oahu (Hawaïi). Toutes les espèces présentaient une croissance rapide caractérisée par des valeurs  $k$  de l’équation de croissance de von Bertalanffy  $\geq 0,4 \text{ an}^{-1}$ . La longévité variait considérablement entre les trois petites espèces, 4 ans chez *Calotomus carolinus* et 6 et 11 ans chez *Scarus psittacus* et *Chlorurus spilurus*, et jusqu’à 15–20 ans chez *Scarus rubroviolaceus* et *Chlorurus perspicillatus*, les deux grandes espèces. La lecture de l’âge et les courbes de croissance pour ces deux dernières grandes espèces ont été validées en utilisation la datation par le carbone bombe. Les âges médians à la maturité sexuelle comme femelles ( $A_{M50}$ ) et au moment du changement de sexe (de femelle à mâle de phase terminale,  $A_{\Delta 50}$ ) ont été estimés en utilisant des modèles logistiques. La maturation sexuelle se produisait à 1–2 ans pour les petites espèces et à 3–3,5 ans pour les grandes espèces. Les estimations de  $A_{\Delta 50}$  allaient de 2 à 4 ans pour les petites espèces et étaient d’environ 5 et 7 ans pour *S. rubroviolaceus* et *C. perspicillatus*, respectivement. Les jalons estimés présentaient une faible correspondance avec la taille légale minimum actuelle pour les uhu à Hawaïi (longueur à la fourche de 30,5 cm). Le regroupement de ces poissons-perroquets pour les fins de la gestion semble généralement contre-indiqué, en particulier pour les deux grandes espèces. Les mesures basées sur l’âge fournissent plus d’information que les mesures reposant sur la taille pour ces poissons. [Traduit par la Rédaction]

## Introduction

Parrotfishes (Labridae, tribe Scarinae: Choat et al. 2012) are of major ecological and economic importance throughout the tropical central and western Pacific, including the Hawaiian Archipelago, and at many other tropical reef areas worldwide (Bellwood and Choat 1990; Houk et al. 2012; Bonaldo et al. 2014). As esteemed food fish and preferred fishery targets, parrotfishes are often highly if not overexploited in many regions (Bellwood et al. 2012; Edwards et al. 2013; DeMartini and Smith 2015). Despite the importance of parrotfish in tropical reef fisheries, little information exists on their growth rates, ages at sexual maturity and sex

change, and longevity. Estimates of these parameters plus body sizes at maturity and sex change (DeMartini and Howard 2016) are needed for providing comprehensive demographic input to accurate, modern stock assessments. Age-based assessments are increasingly recognized as important for managing stocks of tropical reef species like parrotfishes in which demographics often vary appreciably over small (regional, local: Pinca et al. 2012; Taylor 2014; Taylor and Choat 2014) and basin-wide (Heenan et al. 2016) spatial scales.

Prior to a recent paper by DeMartini and Howard (2016), little published information on vital rates existed for the parrotfishes of Hawai’i. DeMartini and Howard (2016) estimated body sizes at

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sexual maturity and at female-to-male sex change for five major parrotfish species (three small-bodied or “small” species, palenose *Scarus psittacus* (henceforth *S. psittacus*), stareye *Calotomus carolinus* (henceforth either *Calotomus* or *C. carolinus*), and Pacific bullethead *Chlorurus spilurus* (henceforth *C. spilurus*), and two large-bodied or “large” species, redlip or ember *Scarus rubroviolaceus* (henceforth *S. rubroviolaceus*) and spectacled *Chlorurus perspicillatus* (henceforth *C. perspicillatus*), among the seven parrotfish species that occur in the Hawaiian Archipelago (Randall 2007). Six of these species are generally reported on and managed as a single unit taxon (classified by its local name “uhu”) with a single minimum legal body length for extraction in all Hawaiian fisheries comprising commercial, recreational, and artisanal. One species (*C. carolinus*) has no minimum legal size at present in Hawai‘i (DeMartini and Howard 2016).

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

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

## Methods

### Fish specimen collection and metrics

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

### Otolith preparation and visual age counts

Otoliths were obtained from fresh or frozen-thawed fish by removing the brain case using either a scalpel for smaller juveniles

or a mallet plus butcher knife or hand saw for large juveniles and adult fish. The largest pair of otoliths (sagittae) was extracted and cleaned of all attached tissue under a dissecting microscope, rinsed in water, disinfected in 95% ethanol, and air dried before dry storage in labeled vials. All available otoliths were weighed on a microbalance to the nearest 0.1 mg prior to further preparation. One member of each pair of otoliths (either left or right, random choice: Choat et al. 1996) was prepared and aged using the following series of steps. The otolith was first mounted sulcus side down near one end of a standard glass microscope slide using Crystalbond® (Electron Microscopy Sciences, Hatfield, Pennsylvania). The otolith was manually sanded using a Gemmasta Faceting Machine (Shelley’s Lapidary Supplies, South Australia) to expose the nucleus. The slide was then heated to melt the Crystalbond® and free the specimen and the section flipped over and remounted with the flat sanded side against the slide. The otolith was then further sanded to produce a thin (~200–300 µm), transverse cross section. The cross section was then covered again in Crystalbond® for viewing and enumeration of either or both daily and annual age features. Annuli, defined as an alternating pair of opaque and translucent zones (Lou 1992), were counted under a dissecting microscope using transmitted light at an average magnification of 20×. An equal number (three) of independent and nonconsecutive age readings for annuli were made for each specimen by a single reader without reference to any prior reading and the mean of these three reads used as the best estimate of age, expressed in decimal-years.

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

### Bomb radiocarbon dating

Age estimates were validated for a series of specimens of the large species (*S. rubroviolaceus* and *C. perspicillatus*). These specimens were randomly selected for bomb <sup>14</sup>C dating from across the length distribution of collected fish and spanned the estimated age range (Tables S1 and S2<sup>1</sup> in the supplemental data). To apply bomb <sup>14</sup>C dating to the otoliths of each species, the dimensions and mass of whole juvenile otoliths were used to delineate a targeted core or earliest growth within adult otolith specimens. Extraction dimensions and masses for even the smallest otoliths and youngest specimens of each species (*S. rubroviolaceus*: 3.4 mg at 1 year; *C. perspicillatus*: 22.6 mg at 2 years) exceeded the threshold values required for bomb radiocarbon analysis. Cross-sectioned adult otoliths indicated that the first few years of growth were at the distal otolith margin and required no surface preparations prior to extraction. A New Wave Research® (ESI-NWR Division, Fremont, California) micromilling machine was used to extract the earliest otolith growth of adult otoliths: *S. rubroviolaceus* cores were 1.8 mm long × 1.4 mm wide × 0.20 mm thick and were achieved using a 13-point line scan and *C. perspicillatus* cores were 2.0 mm long × 1.6 mm wide × 0.30 mm thick and were achieved using a 20-point line scan. Each extraction was made with a 500 µm Brasseler® (Savannah, Georgia) bur in a single pass; the targeted extraction mass was near 0.8 and 1.2 mg of CaCO<sub>3</sub> for each species, respectively. The extracted otolith samples were sub-

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0523>.

mitted as carbonate to the National Ocean Sciences Accelerator Mass Spectrometry Facility, Woods Hole Oceanographic Institution in Woods Hole, Massachusetts, for small sample  $^{14}\text{C}$  analysis using accelerator mass spectrometry. Radiocarbon measurements were reported by the National Ocean Sciences Accelerator Mass Spectrometry Facility as fraction modern, the measured deviation of the  $^{14}\text{C}/^{12}\text{C}$  ratio from a “modern” sample. This reference is defined as 95% of the  $^{14}\text{C}$  concentration of the NBS Oxalic Acid I standard (SRM 4990B) normalized to  $\delta^{13}\text{C}_{\text{VPDB}}$  (−19‰) in 1950 AD (VPDB, Vienna Pee Dee Belemnite geological standard; Coplen 1996). Fractionation correction was online during accelerator mass spectrometry processing and corrected values were reported here as  $F^{14}\text{C}$  (Reimer et al. 2004), with date-corrected  $\Delta^{14}\text{C}$  values also reported here (Tables S1 and S2).

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

### Data processing and statistical analyses

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

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

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

$$L_t = L_{\text{INF}}(1 - [e^{-kt}])$$

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

$$L_t = at^b$$

where  $L_t$  is length (FL) (cm) at age  $t$  (years) and  $a$  and  $b$  are constants was therefore used to describe the growth of this species, as was

done for *Scarus rivulatus* by Choat et al. (1996). All curves were fit using maximum likelihood (Marquardt's algorithm) in nonlinear regression (Proc NLIN in PC SAS v. 9.1.3; SAS Institute, Inc. 2006) using fish of all sexes and color phases pooled within each species and also for adult TP males separately from immature and mature IP males and IP females. The latter was done because other studies have shown that growth rates can differ between IP and TP fish in some parrotfish species (Choat et al. 1996; Munday et al. 2004). The corresponding VBGF curves were used to describe species- and phase-specific length-at-age.

The fitted species-specific curves enabled estimation of median age at maturity ( $A_{\text{M50}}$ ) for females and median age at female-to-male sex change ( $A_{\Delta 50}$ ) by referencing prior published values of median length at female maturity ( $L_{\text{M50}}$ ) and median length at sex change ( $L_{\Delta 50}$ ), respectively (DeMartini and Howard 2016).  $A_{\text{M50}}$  and  $A_{\Delta 50}$  also were estimated by fitting a two-parameter logistic function (DeMartini and Howard 2016) between percent maturity and percent sex change, respectively, versus observed age:

$$P_x = 1/(1 + \exp[ax + b])$$

where  $P_x$  is the percent mature (or sex changed) at age  $x$  and  $a$  and  $b$  are fitted constants. Spearman's nonparametric rank correlation was used to compare each of these age-specific metrics with estimated maximum age ( $A_{\text{MAX}}$ ), defined as the mean of the oldest quartile of observed ages (Choat and Robertson 2002; Taylor and Choat 2014). These comparisons of  $A_{\text{M50}}$  and  $A_{\Delta 50}$  with  $A_{\text{MAX}}$  thus are analogous to DeMartini and Howard's (2016) comparisons of  $L_{\text{M50}}$  and  $L_{\Delta 50}$  with  $L_{\text{MAX}}$ .

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

## Results

### Age verification and precision

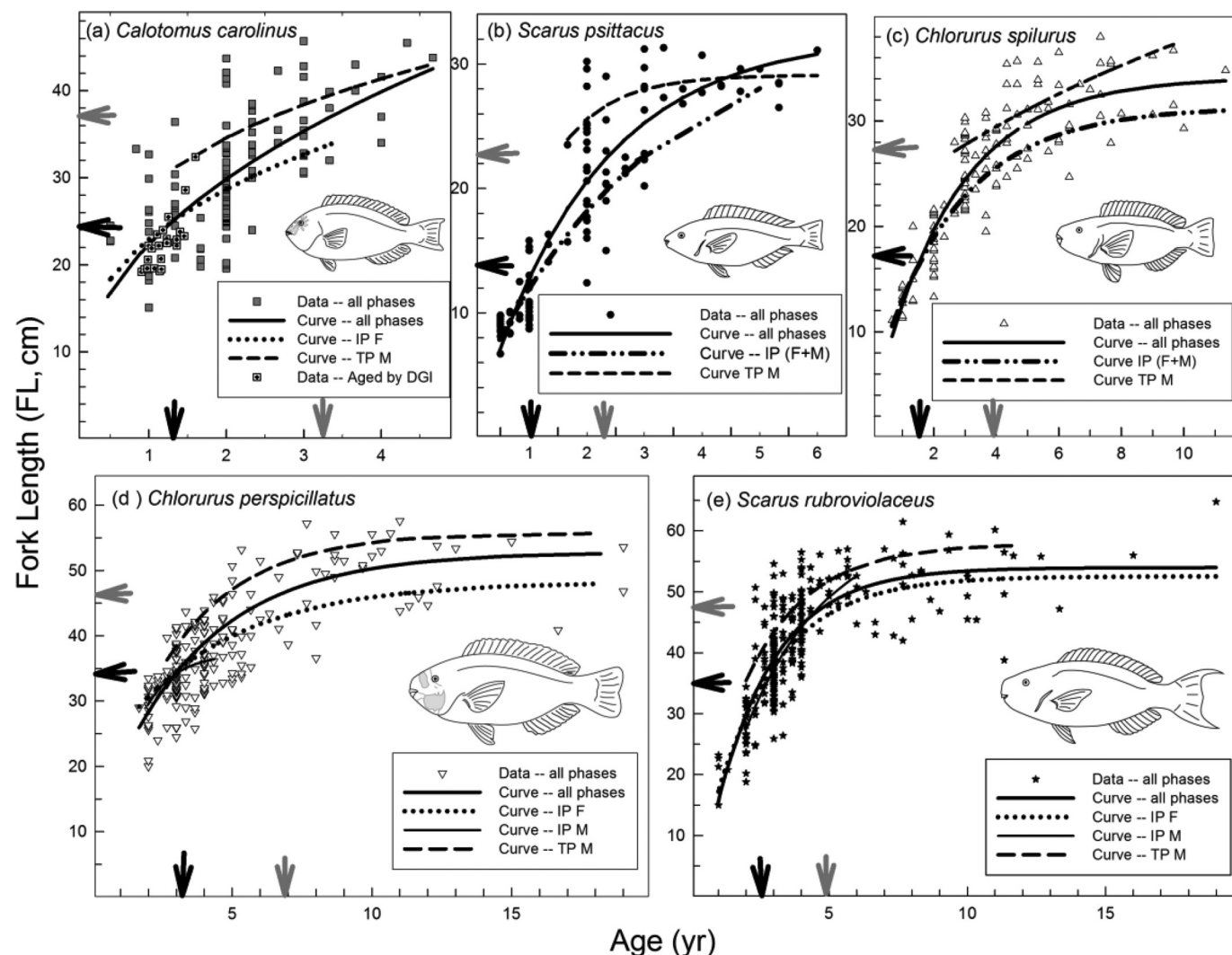
Descriptions of growth require verification and evaluation of the precision (repeatability) of the estimates (Campana 2001). In this study, precision of the age readings was evaluated for each of the five species using visual counts of annuli and additionally for one species (*C. carolinus*) based on the estimated number of DGIs. The latter DGI counts were made for 22 yearling individuals and are indicated by the dark gray squares with black cross-hairs on Fig. 1a. The distribution of ages of yearling *C. carolinus* estimated using DGIs fell centrally within the distribution of ages estimated using counts of annuli (Fig. 1a); hence, DGI counts verified ages estimated using annuli for yearlings of this species. Location of the first annulus in *S. rubroviolaceus* and *C. perspicillatus* was identified based on matched annulus and DGI counts for three and four older juvenile-sized specimens, respectively, and used to anchor the size-at-age trajectory during early growth in these two species. Reader precision was generally high (coefficient of variation 2.8%–10.1%) for the five species (Table S5).

### Age validation

Contemporary estimates of fish growth further require an evaluation of age reading accuracy or bias (Campana 2001). Only a single otolith specimen was deemed unreadable, but this does not



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



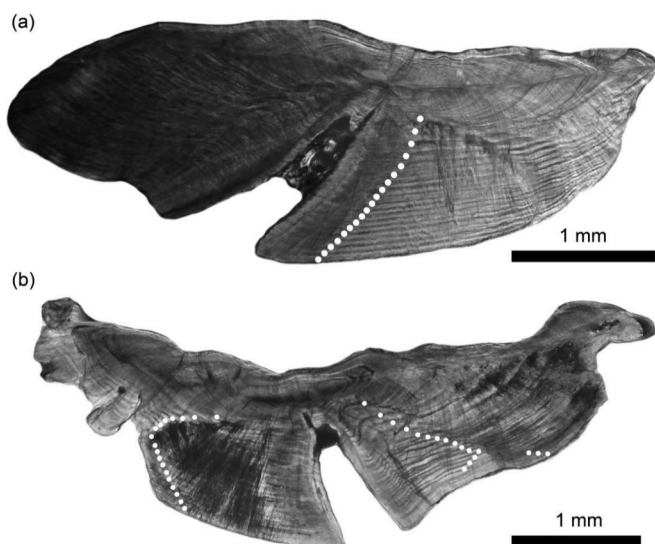
necessarily imply that readings were accurate for the other 866 readable specimens (of all five species). Estimates of age from growth zone counting in thin transverse otolith sections were generally well defined (Fig. 2), although assigning ages based on visual counts of annuli alone required care to avoid overcounting false checks that formed near the time of sexual maturation. Overcounting during early growth was a potential pitfall for both large species, and convoluted growth patterns were especially apparent through the latter years of growth for *C. perspicillatus* (Fig. 2b). Use of the bomb  $^{14}\text{C}$  decline period validated length-at-age estimates through ontogeny for *S. rubroviolaceus* as well as *C. perspicillatus* (Fig. 3; Fig. S2). The three sets of regression relationships (for *S. rubroviolaceus* and *C. perspicillatus* and for the reference chronology spanning the relevant (1990 and more recent) portion of the bomb  $^{14}\text{C}$  decline period) did not differ in their slopes (ANCOVA:

$F_{[2,61]} = 2.37$ ,  $P = 0.10$ ). Using a common (pooled) slope ( $b = -3.09045$ ), intercepts of the three regressions were indistinguishable (ANCOVA:  $F_{[2,63]} = 1.64$ ,  $P = 0.20$ ) (Fig. 3). Use of the post-peak decline period as a temporal reference was validated with the  $\Delta^{14}\text{C}$  values measured in whole lapillus otoliths (Table S4; Fig. S3).

#### Size-at-age and growth rate

Ages based on counts of annuli were generally relatable to observed body lengths. For *C. carolinus* only, ages based on annuli, including the first annulus verified by DGIs, were easily relatable to observed body lengths using a two-parameter power equation. For *C. carolinus*, growth in length was highly predictable ( $r^2 = 0.98$ ) and very rapid, with the exponent of the equation (0.42) indicating a decelerating increase in length at greater ages (Table 1a). Growth was adequately described by three-parameter VBGF curves

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



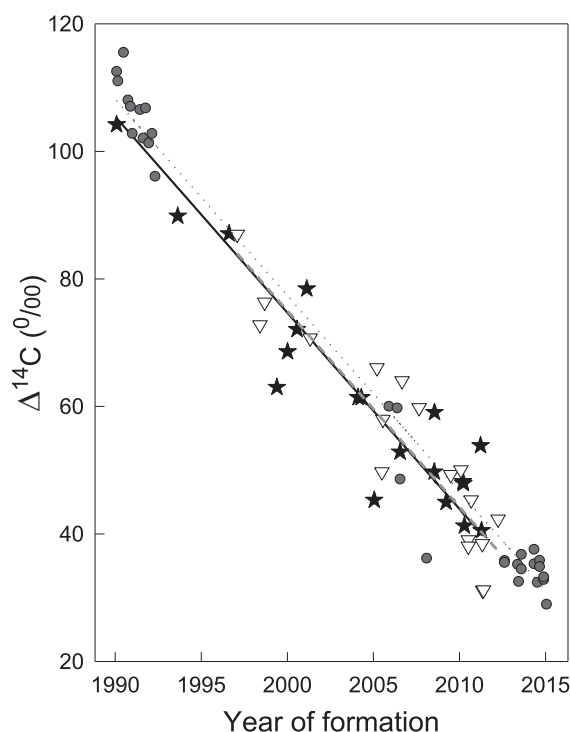
(Table 1b) for the other two small species ( $r^2 = 0.82\text{--}0.85$ ) (Figs. 1b and 1c) and for the two large species ( $r^2 = 0.64\text{--}0.75$ ) (Figs. 1d and 1e). Although values of  $k$  estimated by the three-parameter VBGF were  $0.4\text{--}1\text{ year}^{-1}$  or greater for *C. spilurus* and *S. psittacus* and for *S. rubroviolaceus*,  $k$  was appreciably less ( $0.225\text{ year}^{-1}$ ) for *C. perspicillatus* (Table 1b). Using a two-parameter VBGF (i.e., curves forced through the origin with  $t_0$  constrained to zero), the estimate of  $k$  for *C. perspicillatus* approached, but was still less than, the  $k$  values estimated for the other species (Table 1c).

If the length-at-age data are parsed by gonad type and color phase, some interesting additional growth patterns emerge among the five species (Fig. 1). Within each of the three small species (Figs. 1a–1c), growth rates of TP males were generally faster than for IP fish (all IP fish were females in *C. carolinus*; DeMartini and Howard 2016). Small sample numbers required pooling all IP females and IP males together for analysis in *S. psittacus* (Fig. 1b) and *C. spilurus* (Fig. 1c). Data were sufficient to separately evaluate growth rates of female and male IP fish in the two large species but there was no shared pattern. Growth rates were generally faster for TP males (versus IP males or IP females) in each of the large species (Figs. 1d and 1e).

### Longevity

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

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



### Age at female maturation

Ages at female sexual maturation differed among the five species, ranging from 1–2 years old in the three small species to 3–3.5 years old in the two large species (Table 1; Fig. 1). Values of  $A_{M50}$  estimated by interpolation from length-at-maturity plotted on the length-at-age curve for the respective species (illustrated by arrows on Fig. 1) were similar to those estimated directly by fitting a logistic curve to percent maturity-at-age (Table 2).  $A_{M50}$  values were positively but insignificantly related (Spearman's rank correlation coefficient:  $\rho = 0.70$ ,  $n = 5$ ,  $P = 0.19$ ) to estimates of  $A_{MAX}$  for the respective species (Fig. 4).

### Age at sex change

Ages at sex change varied considerably among the five species and were least (2–4 years old) in the three small species (Table 2; Figs. 1a–1c).  $A_{\Delta50}$  differed most greatly between the two large species: about 5 years old in *S. rubroviolaceus* versus 7 years old in *C. perspicillatus* (Table 2; Figs. 1d and 1e). Values of  $A_{\Delta50}$  also were positively but weakly related (Spearman's rank correlation coefficient:  $\rho = 0.60$ ,  $n = 5$ ,  $P = 0.28$ ) to corresponding estimates of  $A_{MAX}$  (Fig. 4).

**Table 1.** Summary statistics of (a) a two-parameter power equation (*Calotomus carolinus* (CCAR) only, model as specified below), (b) a standard three-parameter von Bertalanffy growth formula (VBGF) (also as specified below for *Chlorurus perspicillatus* (CPER), *Chlorurus spilurus* (CSPI), *Scarus psittacus* (SPSI), and *Scarus rubroviolaceus* (SRUB) only), and (c) a two-parameter VBGF with  $t_0$  constrained to zero (model fit through the origin) for the latter four species relating fork length (FL) (cm) to age (years).

| (a) Power equation: $FL = a \times \text{age}^b$ |              |                   |       |        |       |              |     |
|--|--------------|-------------------|-------|--------|-------|--------------|-----|
| 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  | $L_{\infty}$ | $SE_{L_{\infty}}$ | $k$   | $SE_k$ | $t_0$ | $SE_{t_0}$   | $n$ |
| CPER   | 53.2         | 1.93              | 0.225 | 0.038  | -1.48 | 0.54         | 206 |
| CSPI   | 34.4         | 1.00              | 0.400 | 0.045  | -0.13 | 0.16         | 133 |
| SPSI   | 32.7         | 1.96              | 0.486 | 0.079  | -0.01 | 0.10         | 101 |
| SRUB   | 53.5         | 0.80              | 0.410 | 0.032  | 0.12  | 0.15         | 272 |
| (c) VBGF: $FL = L_{\infty}(1 - [e^{-k(t)}])$     |              |                   |       |        |       |              |     |
| Acronym  | $L_{\infty}$ | $SE_{L_{\infty}}$ | $k$   | $SE_k$ | $r^2$ | 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 |

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

**Table 2.** Summary statistics for the relation between (a) median percent maturity of initial phase female and age (years) and (b) median percent sex-changed terminal phase male and age (years), as described by the two-parameter logistic model shown, for each of the five species of Hawaiian parrotfishes studied.

| Acronym  | $a$   | $SE_a$ | $b$    | $SE_b$ | $r^2$ | Prob > $ r $ | $n$ |
|--|-------|--------|--------|--------|-------|--------------|-----|
| (a) Model: $Pct_{\text{maturity}} = 100/(1 + \exp^{-a(\text{age}-b)})$   |       |        |        |        |       |              |     |
| 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: $Pct_{\text{sex change}} = 100/(1 + \exp^{-a(\text{age}-b)})$ |       |        |        |        |       |              |     |
| 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   |

**Note:** Species are listed by acronym defined in Table 1. Standard errors (SE) are indicated for all parameter estimates. Sample sizes are the number of age-classes used in the analysis. In Table 2b, the value 75 was used as the asymptotic percentage value in the numerator instead of 100 for SRUB to avoid the influence of old initial phase females; also, the oldest age-class was truncated at 10+ years for CPER, 8+ years for CSPI, and 6+ years for SRUB to avoid the influence of old initial phase females.

### Age versus OM

Age was predictably related to OM for each of the five species (Table 3; Fig. 5). The relation was negatively allometric (i.e., age was a positive but decelerating function of OM) in two of the small species (Fig. 5a) but was positively allometric, an accelerating function of OM, in both large species (Fig. 5b). Age was linearly related to OM (slope indistinguishable from 1) in the third small species, *C. spilurus* (Table 3; Fig. 5a).

### Discussion

#### Age validation and longevity

Until recently, age validation of marine organisms using bomb  $^{14}\text{C}$  dating was limited to the period of rapid  $^{14}\text{C}$  increase (typically between 1958 and 1970). But for tropical regions of the Northern Hemisphere, the post-peak decline period provides a slope that

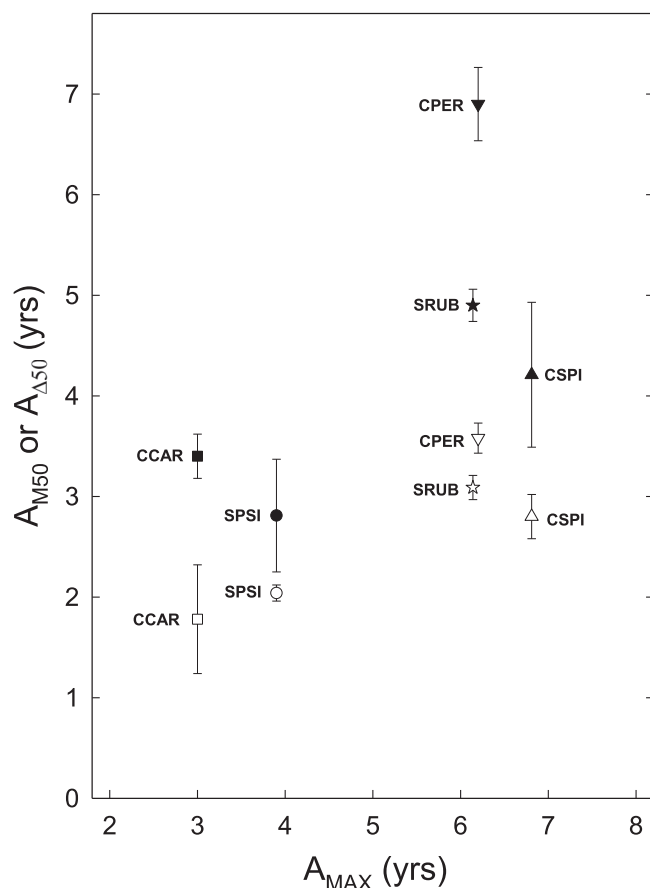
can be used to age younger and more recently collected fish (e.g., Andrews et al. 2013, 2016a). The current study confirms that both large parrotfish species have a longevity near 20 years and that counting growth zone structure in sagittal otolith cross sections is accurate provided that overcounting ages of young adults is avoided. The comparison of  $^{14}\text{C}$  levels in otolith core material for the large parrotfish species with the regional coral and otolith  $^{14}\text{C}$  reference records validated the age and growth estimates. In addition, the slope of the  $^{14}\text{C}$  reference decline period clearly indicates that the longevity of neither of the two large species could be younger or older by more than ~3–4 years because of the temporal specificity of the measured  $^{14}\text{C}$  levels (see Figs. S1 and S2). Furthermore, the use of whole lapillus  $^{14}\text{C}$  levels to confirm the alignment of measured otolith core  $\Delta^{14}\text{C}$  values with the decline period (Fig. S3) is an innovative tool that can be used to differentiate age scenarios (old versus young) in other fishes. For the old age scenario, the lapillus would integrate  $^{14}\text{C}$  uptake from a birth year in the 1950s or 1960s through the elevated peak period and into the decline period; the measured whole lapillus  $^{14}\text{C}$  would exceed measured core  $^{14}\text{C}$  levels in the sagitta (see Figs. S1–S3).

#### General growth patterns

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



**Fig. 4.** Plots of  $A_{M50}$  (open symbols) and  $A_{\Delta50}$  (solid symbols) estimates for each of the five parrotfish (Labridae) species (coded by the species-specific acronyms listed in Table 1) versus the  $A_{MAX}$  estimate of the respective species.  $A_{M50}$  and  $A_{\Delta50}$  values were estimated using two-parameter logistic fits of proportion mature initial phase females among all initial phase female fish and proportion terminal phase males among all fish, respectively. Values of  $A_{MAX}$  were calculated as the mean of the oldest quartile of specimens that were aged for the respective species. Vertical bars represent 2 SE or approximate 95% CI.



**Table 3.** Summary statistics for the relation between age (years) and sagittal otolith mass (OM) (grams) as described by the nonlinear power equation  $Y = aX^b$  for each of the five species of Hawaiian parrotfishes studied.

| Acronym                                | $a$   | $SE_a$ | $b$    | $SE_b$ | $r^2$ | Prob > $ r $ | $n$ |
|--|-------|--------|--------|--------|-------|--------------|-----|
| <b>Model: Age = <math>aOM^b</math></b> |       |        |        |        |       |              |     |
| 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 |

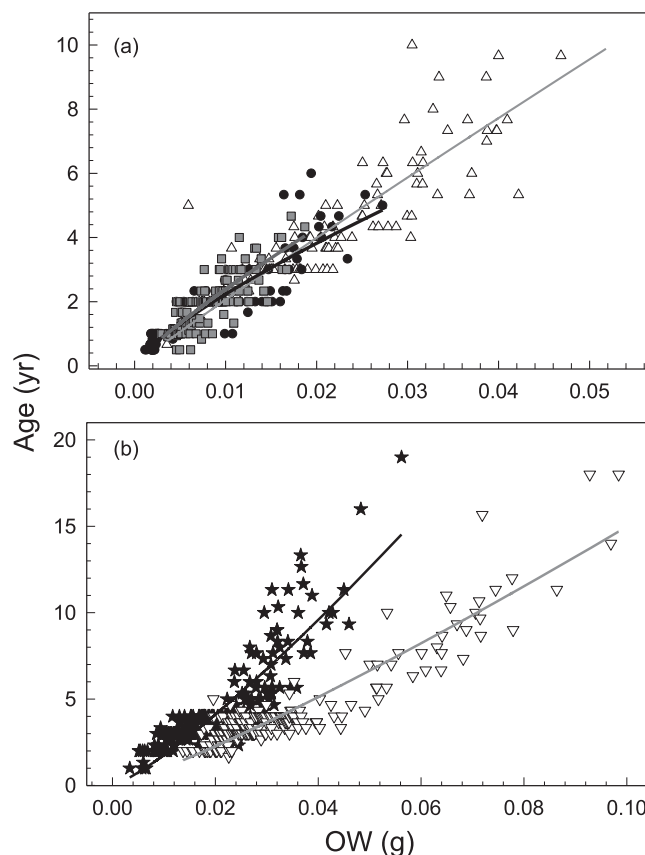
**Note:** The relation was curvilinear and decelerating for CCAR and SPSI but curvilinear and accelerating for CPER and SRUB, whereas the relation was linear for CSPI. Species are ordered by acronyms defined in Table 1. Standard errors (SE) are indicated for all parameter estimates.

age for adult *C. perspicillatus* was still generally smaller, and hence growth was slower, than for *S. rubroviolaceus*, the other large species.

### Geographic comparisons of growth

Sparse published data on growth- and age-related milestones exist for Indo-Pacific parrotfishes (DeMartini and Howard 2016); the present study represents the first major contribution for the

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



central Pacific region. The extent of growth data outside of Hawai'i also varies greatly among the five species, from moderate in *C. spilurus* to few in *S. psittacus*, *S. rubroviolaceus*, and *C. carolinus* to nonexistent in *C. perspicillatus*, and is specified as follows. Appreciable growth-related data exist for *C. spilurus* on the GBR (Choat et al. 1996; Choat and Robertson 2002), at Guam in the western North Pacific (Taylor and Choat 2014), and across Micronesia (Taylor 2014). In general, this species has faster growth on the GBR (Choat et al. 1996) than in Hawai'i, although fish grew differently (faster), matured and changed sex earlier, and attained larger sizes on midshelf versus outer-shelf reefs of the GBR (Gust et al. 2002; Gust 2004). At Guam and across Micronesia,  $k$  and  $A_{MAX}$  averaged  $0.95\text{-year}^{-1}$  and  $<6$  years, but  $L_{M50}$  and  $L_{\Delta50}$  as well as  $A_{M50}$  and  $A_{\Delta50}$  ranged broadly depending on environment (habitat productivity), conspecific density, and fishing pressure (Taylor 2014; Taylor and Choat 2014; Taylor et al. 2014). Clearly, tropical populations of *C. spilurus* in the western Pacific grow faster and mature and change sex at younger ages and smaller sizes (DeMartini and Howard 2016) than do those in the subtropical Oahu, Hawai'i, population. Hawai'i lies at the easternmost range limit in the central North Pacific of this and all other study species except *S. rubroviolaceus* (DeMartini and Howard 2016). Water temperatures in Hawai'i are cooler and slower growth likely delays age-related life-history milestones (Atkinson and Sibly 1997).

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

Age at sexual maturity of *C. carolinus* at Guam has been estimated as 1.1 years, where its maximum observed age was only 3 years (Taylor and Choat 2014). The Guam estimates generally confirm the extremely rapid growth rates of *C. carolinus*. Its congener *Calotomus japonicus* has been aged at several locations in Japan, where growth, although quite fast, is slower than for *C. carolinus* and appears to vary spatially (Kume et al. 2010 and Kawajiri 1975 cited therein). Sparisomatines are typically shorter-lived relative to body size (i.e., grow faster) than scarine labrids (Choat and Robertson 2002).

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

### Comparisons of age milestones among species

Even though both  $A_{M50}$  and  $A_{\Delta50}$  are proportional to  $A_{MAX}$  across the five species studied herein, the strength of these relationships is less than those of the corresponding proportionality between  $L_{M50}$  or  $L_{\Delta50}$  versus  $L_{MAX}$  (DeMartini and Howard 2016). Parrotfishes in Hawai'i are less predictably age structured than size structured, in part because of the overall very rapid growth rate of *C. carolinus*, the largest of the three small species, and also because of the disparate post-maturational growth rates of the two large species. Our observations support the contention made by Taylor and Choat (2014) that age-based metrics provide more informative input to parrotfish stock assessment and management than do length-based metrics, despite the apparent attractiveness and simplicity of basing regulations just on body length (Valles and Oxenford 2014; Valles et al. 2015).

### Age-OM mass relation

Among the five species, the age-to-OM relations of the two large species uniquely differ from each other in a manner that is consistent with their differences in somatic growth rates. *Chlorurus perspicillatus*, the slower growing of the two species, has a larger otolith at a given body size (in both length and mass) than *S. rubroviolaceus*. This might simply reflect phylogeny, that otoliths of species within the genus *Chlorurus* are generally more robust than those of the genus *Scarus*, despite within-genus differences exemplified by *S. rubroviolaceus* and *S. psittacus* (Figs. S4 and S5). More importantly, there is a strong positive relation between OM and fish body length and somatic mass within each of the five species (Table S6; Figs. S4–S6). The strong positive relations between OM and fish age (Table 3; Fig. 5) suggest promise for using OM as a proxy for age, for the capability of predicting fish age from OM, as first suggested for parrotfishes by Taylor and Choat (2014), given the caveats listed by Andrews et al. (2016a).

### Management implications of species differences

The parrotfish component of the shallow-water reef fish fisheries at Oahu is dominated numerically by *S. rubroviolaceus* and *C. carolinus* and in biomass by *S. rubroviolaceus* and *C. perspicillatus* (DeMartini and Howard 2016). These three and the two other fishery species of parrotfishes differ substantially in  $A_{M50}$  and  $A_{\Delta50}$ , in addition to  $L_{M50}$  and  $L_{\Delta50}$ . The latter values range below and above the current minimum size limit (12 in. or 30.5 cm) set for all species of parrotfishes in Hawai'i (except *C. carolinus*, for which no minimum size limit presently exists: DeMartini and Howard 2016).  $A_{M50}$  values for *S. rubroviolaceus* and *C. perspicillatus* in Hawai'i are about 3–3.5 years, corresponding to a shared  $L_{M50}$  of about 35 cm FL.  $A_{\Delta50}$  values for these two species, however, differ greatly (about 5 years for *S. rubroviolaceus* and 7 years for *C. perspicillatus*), even though both species change sex at about 47 cm FL. Growth rates of the two species diverge greatly after the sexual maturation of females, with adult female *C. perspicillatus* growing much more slowly than adult female *S. rubroviolaceus*, even though growth rates of TP males are relatively faster than those of IP fish in both species. The inherently different growth rates of these two large species suggest that they should not be managed as a pooled taxon.

The endemic species *C. perspicillatus* increases markedly in abundance with latitude across the unfished (and nearly human depopulated) Northwestern Hawaiian Islands, a pattern typical of Hawaiian endemics (DeMartini and Friedlander 2004). In contrast, the broadly distributed Indo-Pacific *S. rubroviolaceus* is relatively uncommon throughout the Northwestern Hawaiian Islands (Nadon et al. 2015) and is rare to absent at latitudes north of French Frigate Shoals (Hobson 1984). Mean biomass densities of *C. perspicillatus* are historically much lower than those of *S. rubroviolaceus* at Oahu (Howard et al. 2009). The relatively lower abundances of *C. perspicillatus* in the Main Hawaiian Islands could reflect this latitudinal gradient but could also be related to a greater susceptibility to extraction or other environmental influences including both the anthropogenic (e.g., sedimentation resulting from coastal development) and the nonanthropogenic (wave exposure and related benthic composition and structural heterogeneity) (Taylor et al. 2014). The confounding of human influence with biogeographic distributions precludes definitive attribution of observed patterns exclusively to any environmental factor and further research is needed to investigate possible fishing effects on demography and population structure. Our study used specimens collected from Oahu, where parrotfish catches average 3%–31% greater compared with other islands within the Main Hawaiian Islands (McCoy 2015). Comparisons with vital rates estimated using specimens collected from other Main Hawaiian Islands with lower fishing pressure could elucidate how demography and population structure might be related to fishing, given expectations of sized-based fishing effects on sex-changing fishes (Hamilton et al. 2007).

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



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

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