

A long-lived life history for onaga (*Etelis coruscans*) in the Hawaiian Islands

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HIGHLIGHTS

Etelis coruscans is a member of the commercial deep-water handline fishery of the Hawaiian Islands.

Bomb radiocarbon dating validates the otolith age-reading criteria for *Etelis coruscans*.

The longevity of *Etelis coruscans* is at least 50 years and exceeds previous estimates by 3–5 times.

Etelis coruscans appears to mature at a greater proportion of asymptotic length and age than most other deep-water snappers.

ABSTRACT

Onaga (*Etelis coruscans*) is an important component of the commercial deep-water handline fishery in Hawaii and is one of the more valuable species because of its local popularity. This species is part of a management unit called the Deep 7, a data-poor fishery comprising six snapper and one grouper species for which information about age, growth, longevity, and maturity is incomplete. Opakapaka (*Pristipomoides filamentosus*) is one of the snappers in this group and was shown to be underaged by more than 20–30 years with longevity exceeding 40 years. While some life history information is available for onaga, prior estimates of maximum age (~10–20 years) have suffered from the same problems as opakapaka. In this study, a refined age reading protocol revealed age estimates up to 55 years for an onaga near maximum size — this maximum age estimate and the age reading protocol was validated using bomb radiocarbon dating. Using an otolith reference-image, age reading protocol that relied on the validated otolith sections, almost all onaga otoliths covering nearly the full body size range

were used to generate valid growth parameters. An empirical estimate of age-at-maturity (L_{50}) is 11 years and fish near minimum retention size in Hawaii (1 pound or ~30 cm FL) may be just 2–3 years old.

Keywords: Lutjanidae; Etelinae; bomb radiocarbon; carbon-14; otolith; age and growth; deep-water handline fishery

1. Introduction

Onaga (*Etelis coruscans*) is an Indo-Pacific deep-water snapper (Lutjanidae, Etelinae) that is known by its Japanese name in Hawaii and is an important component of the regional fishery. This species is very popular in Hawaii and has high value because of its culinary appeal, bright red color, and use in local celebratory events (Pooley, 1987; Mitake and Tei, 2013; Anonymous, 2016), yet little is known about its life history and the growth characteristics that are necessary for resource sustainability. Onaga is managed as a member of the Deep 7 bottomfish complex — a data-poor fishery comprising six snapper and one grouper species (Langseth et al., 2018). Age, growth, longevity, and reproductive maturity is incomplete for most members of this management group and onaga is no exception. Opakapaka (*Pristipomoides filamentosus*) — one of the snappers of this group — has set the stage for life history studies of other Deep 7 members. The opakapaka was once thought to be short-lived with longevity that did not exceed 20 years but use of several age estimation and validation techniques indicated that the species can live more than 40 years (Andrews et al., 2012). This information, when combined with an assessment of its reproduction (Luers et al., 2018), make its life history the most well understood of the Deep 7 members.

While validated life history information is lacking for onaga, some studies have provided estimates of age and growth and descriptions of reproductive characteristics throughout its distribution (Brouard and Grandperrin, 1985; Ralston and Kawamoto, 1987; Ralston and Williams, 1988; Everson et al., 1989; Fry et al., 2006; Williams et al., 2013, 2015; Uehara et al., 2018). Most studies of this species, however, may have suffered from the same problems as opakapaka with low estimates of maximum age (~10–20 years) and unsubstantiated growth rates that are likely an artifact of the method used, limited sample size, or both (i.e., Brouard and Grandperrin, 1985; Ralston and Kawamoto, 1987; Ralston and Williams, 1988; Williams and Lowe, 1997; Fry et al., 2006). A recent study of this species stands in contrast to previous studies with an evaluation of fine growth zone structure that is visible in thin sectioned otoliths — this study revealed what may be a more realistic growth scenario with ages up to 40 years (Williams et al., 2015). Due to conflicting and incomplete information on onaga and its importance in Hawaii fisheries, it is of paramount importance to provide valid life history information for reliable assessment advice to management of its fishery (Cailliet and Andrews, 2008; Piddock et al., 2015).

The focus of this study was to determine valid growth parameter estimates for onaga using thin sectioned otoliths and bomb radiocarbon (^{14}C) dating — a method that has become very successful with validating age and growth of tropical fishes of the Indo-Pacific (e.g., Andrews et al., 2011; 2012; 2015; Andrews 2020) — and to apply this information to existing maturity information for a better understanding of its life history. Specifically, the growth zone structure of otoliths covering the available size range of onaga from the Deep 7 bottomfish fishery was examined for a consistent age reading protocol, which was then subsampled for validation using bomb ^{14}C dating. Validated otolith sections were used as a reference image to provide guidance on difficult to read otolith sections and to increase consistency in age reading interpretation (Wakefield et al., 2017). In addition, otolith mass was used as a discriminating factor to minimize potential problems with early overestimation of age from overcounting within the first few years of growth caused by check formation. These valid estimates of growth for onaga in Hawaii would then be used to provide plausible estimates of age-at-maturity with reference to a previous onaga length-at-maturity study (Everson et al., 1989) along with reasonable deductions from literature sources for other eteline snappers.

2. Methods

Onaga otoliths sampled for age estimation and validation were from fish provided by local fishers and auction sources during the years 2008–2015 ($n = 194$; Table S1). These samples were restricted to fish from the MHI fishery because the Northwestern Hawaiian Islands (NWHI) fishery is now closed (Brodziak et al., 2014; Fig. 1). Otoliths were randomly selected to cover the available size range for age reading but were also selected within 5-cm fish length classes to a number that adequately sampled age-classes (Lai, 1993; Coggins et al., 2013). In particular, we note that, under the long lifespan scenario of Coggins et al. (2013) which approximates the life history of onaga, that the ratio of length bin size ($6 \frac{2}{3}$ cm) to longevity (40 years) was $1/6$. Applying this ratio to the longevity estimate for onaga (~ 50 years) gives a length bin size of about 8.3 cm, which is the length bin size for onaga that would support the sample size results of Coggins et al. (2013). Thus, the sampling length bin size used in this study was about 40% narrower than that for the long life span scenario indicating that our sampling was more intensive with respect to the age-length relationship than that recommended by Coggins et al. (2013). Otolith mass was included as a discriminating factor for the largest and presumably oldest fish — otolith mass can function as a proxy for age because fish length is decoupled from age for species with asymptotic growth. The selected otoliths were transversely sectioned with a Buehler Isomet saw using diamond blades and mounted in the standard manner to glass slides for age reading (e.g., Andrews et al., 2002).

Initial estimates of age from preliminary surveys of the otolith sections revealed that the otoliths from some fish had consistently readable growth zone structure (see otolith section image details in Fig. 2). Seven of these well-defined otoliths were chosen for bomb ^{14}C analyses to test the validity of the age estimates from growth zone counting in the otolith sections (Table 1). The subsample of otoliths was also selected to provide purported birth years across the regional bomb ^{14}C reference record (1950s to recent years). The regional bomb ^{14}C reference record for the MHI is limited in its timespan and ends in the collection year of 1992 (Roark et al., 2006). Because of this limitation, estimated ages for the onaga otolith specimens collected in 2008 can be validated using this record beginning at 16 years of age for the MHI (Fig. 3). The coral ^{14}C record was fitted with a Loess smoothing function (spline interpolation smoothing parameter = 0.2, 2-parameter polynomial; Sigma Plot 11.2) to provide a central tendency that could be used as a temporal reference for otolith ^{14}C measurements.

Cross-sectioned adult otoliths indicated that the core region of an adult otolith was at the distal whole otolith margin (Fig. 2) and required no surface preparations prior to extraction by the micromilling machine used — some species require some surface grinding to remove more recently deposited layers (e.g., opakapaka; Andrews et al., 2012). The dimensions of a 2-year-old otolith (smallest available) were used to develop two concentric core extractions that conformed to the irregular otolith shape (Fig. 2). A micromill (Elemental Scientific Lasers, LLC, Bozeman, Montana) was used to extract two successive core samples: 1) earliest otolith growth (3.4 mm L \times 1.9 mm W \times 0.40 mm Th) using a 24-point line scan; and 2) a year-2 concentric ring around the first core (bur diameter within 4.4 mm L \times 2.7 mm W \times 0.40 mm Th) using a 19-point line scan. Each extraction was made with a 500 μm Brasseler® (Savannah, GA) bur in two passes at 0.2 mm deep with a targeted extraction mass of 3–4 mg of CaCO_3 powder.

The extracted otolith samples were submitted as carbonate to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS), Woods Hole Oceanographic Institution in Woods Hole, Massachusetts. Radiocarbon measurements were reported by NOSAMS as Fraction Modern, the measured deviation of the $^{14}\text{C}/^{12}\text{C}$ ratio from Modern. Modern is defined as 95% of the ^{14}C concentration of the National Bureau of Standards Oxalic Acid I standard (SRM 4990B) normalized to $\delta^{13}\text{C}$ VPDB (–19‰) in 1950 AD (VPDB = Vienna Pee Dee Belemnite geological standard; Coplen, 1996). Radiocarbon results were corrected for isotopic fractionation using $\delta^{13}\text{C}$ measured concurrently during AMS analysis and are reported here as $F^{14}\text{C}$ (Reimer et al., 2004). Stable isotope $\delta^{13}\text{C}$ measurements were made on a split of CO_2 taken from the CO_2 generated through acid hydrolysis.

The validity of the growth-zone derived ages was evaluated using $F^{14}\text{C}$ values reported from the AMS analyses by plotting their respective birth year estimate relative to the coral ^{14}C reference. Alignment or misalignment was used to determine the validity of the age reading criteria used on the selected fish. Age-validated otoliths were used in turn to guide age estimation of other otolith sections, effectively

functioning as a "Rosetta Stone" in the age reading of otoliths that were more difficult to interpret or were obviously offset from an age-to-otolith mass relationship.

Ages were estimated by counting opaque growth zones using a Leica S8 APO stereomicroscope under transmitted light and 40X magnification by an experienced reader (AHA). Opaque zones were counted along a consistent growth axis along the ventral portion of the otolith section. Final age estimates were determined from the three separate otolith age reading sessions (after preliminary age reading surveys) during a fourth otolith reading (deemed best or most consistent age of the three reads from a fourth reading). The final ages were plotted as age vs. otolith mass to further refine age estimates. An otolith mass-to-age relationship is usually linear or slightly curvilinear (positive) with a tight fit at low to middle ages and typically progresses to greater variability for the largest and oldest fish (e.g., Boehlert, 1985, Andrews et al., 2016). This relationship was used to identify overestimates of age in young fish where growth is most rapid and to minimize the potential for counting false annuli (checks). Outliers from the otolith mass-to-age pattern were reexamined using otolith reference images from well-defined and age-validated sections to identify potential sources of over-counting. To measure between reader precision, a subset of otoliths was read independently by a second reader (RSN) to determine the level of precision for this species. Specimens included otolith sections that varied in section quality and contained both $F^{14}C$ validated ages and non-validated ages across the age distribution. The average percent error (APE) and coefficient of variation (CV) were used to describe age estimate precision within and between the readers (Chang, 1982), although it was anticipated that reference-image age readings (Wakefield et al., 2017) would increase precision relative to what was estimated based on initial (memory-based) readings.

The age estimates of the more experienced reader, which were supported by the seven age validated otoliths, were used to generate age-at-length estimates for the remainder of the onaga specimens. All reliable age-at-length estimates were fitted using nonlinear least-squares regression by gender and for pooled sexes using a modified version of the 3-parameter von Bertalanffy growth function (VBGF; SAS Institute Inc., 2006) for better curve fitting.

The modified von Bertalanffy growth function (VBGF; Schnute and Fournier, 1980) was used to characterize the expected relationship between length (L) and age (t). Here it is important to note that the modified VBGF has been shown to exhibit better statistical properties than the standard form of the von Bertalanffy curve (Ratkowsky, 1983). The modified VBGF expresses expected length at age t as,

$$(1) \quad L(t) = L_{\min} + (L_{\max} - L_{\min}) \cdot \frac{1 - \exp(\log(c)(t - t_{\min}))}{1 - \exp(\log(c)(t_{\max} - t_{\min}))}$$

where c , L_{\min} , and L_{\max} are parameters, L_{\min} is the length at the juvenile reference age of t_{\min} , L_{\max} is the length at the adult reference age of t_{\max} , and c determines the amount of curvature in the growth curve.

For the onaga growth analyses the juvenile and adult reference ages were set to be $t_{\min} = 2$ years and $t_{\max} = 51$ – 55 years (the youngest and oldest ages available for both sexes, respectively). The parameters of the standard von Bertalanffy curve $L(t) = L_{\infty}(1 - \exp(-k(t-t_0)))$ are directly related to the parameters of the modified von Bertalanffy curve via,

$$(2) \quad \begin{aligned} L_{\infty} &= \frac{L_{\max} - L_{\min} \cdot s}{1 - s} \\ k &= -\log(c) \\ t_0 &= t_{\min} - \frac{\log\left(\frac{L_{\max} - L_{\min}}{L_{\max} - L_{\min} \cdot s}\right)}{\log(c)} \end{aligned}$$

where $s = \exp((t_{\max} - t_{\min}) \cdot \log(c))$.

Parameters of the modified von Bertalanffy growth curve were estimated using the method of maximum likelihood (Kimura, 1980). Growth curves were fit to three data sets: the female and unsexed samples, the male and unsexed samples, and the female, male, and unsexed samples. Here the unsexed samples were included in the estimation of growth curves for both female and male samples because they represented the best available information on size at age for the smallest juvenile onaga. Growth curves were fit using both an additive normal error structure with zero mean and constant variance and a multiplicative lognormal error structure with mean of one and constant variance (e.g., Brodziak and Macy, 1996). Use of the additive error structure implied that expected variation in size-at-age was invariant with respect to age. In contrast, use of the multiplicative error structure implied that variability in size-at-age scaled with age to account for expected increasing variability in size-at-age with increasing age. The relative goodness of fit for the additive and multiplicative error structures were compared using model diagnostic tests on residuals for fitted length at age. In particular, we tested whether model residuals from the nonlinear regression fits were normally distributed under the normal error analyses or lognormally distributed under the lognormal error analyses. We also tested whether the fitted residuals exhibited constant variance. Last we tested whether the fitted residuals exhibited any trend with respect to age. The goodness of fit of the modified VBGF under the additive normal and multiplicative lognormal error structures were also evaluated with pseudo- R^2 values which provided a measure of the amount of variation explained under the alternative error structures (pseudo- R^2 is $\text{pseudo-}R^2 = 1 - SSE/CSS$, with

SSE being the variance of the full model and *CSS* being the variance of the mean model). The nonparametric bootstrap was applied to estimate the standard error and bias of each growth parameter (Efron, 1979). In particular, for each model error structure the fitted residuals were randomly resampled and the nonlinear regressions were re-estimated 1,000 times to produce 1,000 bootstrap replicate data sets of parameter estimates from which estimates of standard error and bias were derived. Last, the sets of female and male growth parameters were tested for differences under the best fitting error structure using the associated likelihood ratio test (Kimura, 1980).

An alignment of a previously estimated length-at-maturity for onaga in the Hawaiian Islands (Everson et al., 1989) was used in relation to the growth function derived here through time to provide an empirical estimate of age-at-maturity. References to relative lengths-at-maturity (as proportions of maximum length) for other eteline species (Grimes, 1987; Luers et al., 2018) were used to consider another reasonable alternative estimate of age-at-maturity for onaga. Both estimates of age-at-maturity were then related to current fishing regulations for size-at-retention of the species in Hawaii.

3. Results

3.1. Growth and longevity

The seven fish selected for bomb ^{14}C dating (Table 1) included the oldest fish, which provided one of the best reference images and was consistently aged to 55 years (Fig. 2). The growth zone derived age of this specimen (ETCO-001) was nearly in agreement with the coral ^{14}C reference (Table 1, Fig. 3). Its core ^{14}C values indicated a pre-bomb birth year that could be a few years older than was estimated from zone counts. The second oldest fish (ETCO-004) also appeared to be under-counted by ~1–2 years based on the ^{14}C reference. The birth years determined from growth zone counting for the smaller fish agreed with the ^{14}C reference at the upper bomb ^{14}C rise and through the decline period (after ~1976). The year of formation for the year-2 core extractions was adjusted in time by 1.5 years to account for the formation period and temporal dilution. Each ^{14}C measurement for year-2 cores was consistent with the corresponding year-1 core in terms of the expected difference in ^{14}C levels relative to the rise or decline of the reference ^{14}C record (Fig. 3). The series of 7 specimens (some with 2 successive cores) provided validation of age reading from 23 to 55 years for fish that were 74.4 to 86.9 cm FL with otolith masses differing by nearly a factor of 2 (Table 1).

Of the 194 otoliths selected for age reading, 188 could be aged using the growth zone counting criteria defined by the age-validated otolith sections. These reference-image otoliths provided guidance that led to an age reading precision of 7.0% (APE) and 9.2% (CV) for the experienced reader and were used to represent the uncertainty associated with ages and birth years (rounded to nearest year; Table 1). This estimate of precision, however, was influenced by the concurrent viewing of reference otolith

sections and the iterative re-reading of sections where the age substantially deviated from the age-to-otolith mass relationship (SM Fig. 1). As a result, precision is overestimated relative to memory-based age reading. Hence, the final age-at-length estimates used to develop growth parameters were the best and most consistent available for all of the specimens used in this study. An evaluation of inter-reader precision revealed an APE of 7.9% and CV of 11.2% ($n = 50$). This is consistent with what is considered satisfactory for tropical deep-water species due to growth structure that is more difficult to read (APE = ~10%; Newman et al., 2016). Age estimate agreement between readers was 34%, with 65% of the estimates within one year and 95% within two years.

The results for the growth curves estimated under the additive normal and multiplicative lognormal error structures were similar (Tables 2.1 and 2.2). The nonlinear regression models generally explained a substantial amount of the variation in the length at age data with pseudo- $R^2 > 0.94$ for the normal error structure models (Table 2.1) and pseudo- $R^2 > 0.92$ for the lognormal error structure models (Table 2.2). The additive normal error structure explained more of the variability in the female, male, and pooled-sex data sets (Tables 2.1 and 2.2). The model diagnostic tests of whether the growth curve residuals were normally distributed indicated that this assumption could not be rejected under the normal error structure ($P \geq 0.51$) or under the multiplicative lognormal error structure ($P \geq 0.55$). Overall, the fitted growth curves conformed to the normality assumption. The model diagnostic tests of whether the growth curves exhibited constant variance across age also indicated that the growth models conformed to this assumption under the normal ($P \geq 0.25$) and lognormal ($P \geq 0.06$) error structures. Similarly, the tests of whether residuals had no trend with age indicated that each of the models conformed to this assumption under the normal ($P \geq 0.81$) and lognormal ($P \geq 0.13$) error structures. Bootstrap estimates of standard errors for the modified von Bertalanffy curve ranged produced coefficients of variation ranging from 1% to 3% across all models (Tables 2.1 and 2.2) In comparison, estimates of the k and t_0 parameters of the standard von Bertalanffy curve were less precise with CVs ranging from 2%–9% and 13%–21%, respectively. Bootstrap estimates of parameter bias were 0%–1% under both the normal and lognormal error structures. This showed that for all of the estimated growth function parameters that bias was negligible in comparison to variance regardless of the assumed error structure for length at age. Overall, the VBGF results under the additive normal error structure explained more variation in the data and exhibited better model diagnostics than under the lognormal multiplicative error structure. As a result, the VBGF results with the additive normal error structure were judged to provide the best available estimates for female, male, and pooled-sex onaga.

The likelihood ratio tests for differences in sets of growth curve parameters between genders for adult fish indicated that there were significant differences at the 99% confidence level between females and males under both normal ($X^2 = 18.45 > X^2_{[0.01],3} = 11.35$, $P < 0.01$) and lognormal ($X^2 = 16.94 > X^2_{[0.01],3}$

= 11.35, $P < 0.01$) error structures. Similarly, pairwise comparisons of the point estimates and associated standard errors of the female and male growth curve parameters indicated that there were substantial differences between the female and male size-at-age parameters of L_{\min} , L_{\max} , and L_{∞} (Tables 2.1 and 2.2). Based on this evidence, we concluded that onaga likely exhibit sexually dimorphic growth in the Hawaiian archipelago.

3.2. Length-at-age and maturity

Length-at-maturity was previously estimated as between 67.5–72.5 cm FL (Everson et al., 1989), which corresponds to an estimated age-at-maturity of ~11–14 years based on the length-at-age relationships presented in this study. Everson et al., (1989) further reported a median length at 50% maturity (L_{50}) of 66.3 cm FL, which translates to an age of 9–11 years using the growth data presented here (Fig. 4). Additional information in Everson et al., (1989) along with data provided in other studies calls into question whether these estimates of length-at-maturity (hence, age-at-maturity) for onaga in the MHI are accurate. Further evaluation and implications follow in the Discussion.

4. Discussion

4.1. Factors influencing growth and longevity

The longevity of onaga in the MHI is greater than reported in the literature and from other locations across its Indo-Pacific distribution. The maximum age of 55 years estimated and validated in this study was greater by a factor of ~3–5 relative to many previous studies (Table 3). It is important to note, however, that most other studies mention that the greatest age estimate was unlikely to represent longevity and should be considered with caution. These salient observations were related to recognition of either inadequate sampling near maximum reported sizes for the region, the methodological limitations (i.e., various daily increment counting methods), or some of both. The greatest age reported for this species in a previous study was from Vanuatu at 40 years (Williams et al., 2015). The age reading method was similar to what was used in the current study which quantified fine increment structure for the oldest fish. Both studies used thin sections for age reading, but transmitted light on thicker sections (~0.5–0.6 mm) — in contrast to low-angle reflected light on very thin sections (~0.15–0.20 mm; Williams et al., 2015) — was used in the present study to make use of the crystalline structure and layered matrix of the otolith (Fig. 2). Each method has its merits: the use of very thin sections viewed using reflected light reveal increment structure that is uncomplicated by overlapping or slanting growth layers; the use of thicker sections utilizes the light diffraction qualities of the otolith matrix while conserving increment structure that would be lost with thinner preparations. In selecting one method over the other it is important to consider that the thin sectioning technique utilized by Williams et al., (2015) is best achieved

with a polishing machine that ensures a uniform viewing thickness. Achieving a uniform thickness of 0.15 to 0.20 mm is difficult when sections are prepared by hand because there is a high risk of compromising the section readability by removing too much material from some or all of the otolith section (Corey Wakefield, Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia; pers. comm. 2018). One or the other method might provide better results but this is often dependent on the species and how the otolith grows through time (e.g., regular vs. irregular growth zone formation). While the longevity estimate determined here is considerably greater than those reported by other studies, the growth coefficient estimate was similar to most previously reported values. This may be an artifact of truncated age-at-length data that is reflected in some studies by an unrealistic L_{∞} trajectory (Table 3). Compared to other large-bodied marine teleosts that are commercially important, including many other Lutjanids, onaga is a moderately slow growing and long-lived species; nonetheless, the findings of this study call into question prior Lutjanid findings where methodological limitations may not have been fully considered (e.g., Manooch, 1987).

Age reading of onaga otoliths was moderately difficult because the otolith growth structure was well-defined in only 10–20% of the specimens; age reading was greatly improved, however, using age-validated otolith sections. Use of the counting criteria defined in these otoliths functioned as a reference-image that is analogous to the Rosetta Stone — a key to deciphering readable but difficult to interpret markings. Direct and simultaneous comparison of the age validated reference-image otolith sections with other sections that were difficult to read provided an opportunity to improve the ability of the age reader to identify and quantify annual growth zones. While this is not typical of age and growth studies, this study should be considered as one that provides validated and fundamental life history input to management of a data-poor fishery — reducing age estimate error was seen as more important than identifying potential problems associated with establishing a memory-based age reading protocol. The overall precision for the experienced age reader was improved from the initial age reading precision due to the influence of the reference image otoliths and the iterative age reading of outliers from the otolith mass-to-age relation. Such is was consistent with other tropical deep-water studies. Further, both otolith mass and thickness were recently shown to be the most important predictors of age in several snappers of the South Pacific, including *E. coruscans* (Williams et al., 2015). Hence, the use of concurrent viewing of reference-image otoliths provided a perspective for identifying and quantifying growth structure that was as consistent as possible for each otolith section. As a result, almost all otoliths provided age-at-length estimates with high confidence in conformity to the validated age reading protocol.

4.2. Factors influencing size and age at maturity

Everson et al. (1989) reported length-at-maturity as between 67.5–72.5 cm FL and made a preliminarily estimated age-at-maturity for onaga captured primarily in the MHI. The 67.5–72.5 length class corresponds to an age range of 11–14 years from the validated length-at-age estimates presented in our paper; however, this length class represented a range at which 77% of the females were mature. Of greater significance is the length of 66.3 cm FL reported by Everson et al. (1989) as the median length at 50% maturity (L_{50}), which equates to an age of 11 years (Fig. 4). Further, the smallest mature female onaga (52.2 cm FL) and first encountered ripe female onaga (60.5 cm FL) reported by Everson et al. (1989) would have been 6–7 years and 8–10 years old, respectively. Everson et al. (1989) also calculated an age-at-first maturity for the smallest observed female as 5–6 years using previously reported growth parameters (Ralston and Kawamoto 1987) that resemble those estimated in the current study. Furthermore, these prior estimates suggest that the species matures at a disproportionately large body size — at ~75% of L_{∞} and 71% of maximum reported length in the Hawaiian Islands (94 cm FL: Sundberg and Underkoffler, 2011) — when compared to median values of ~50% for deep-dwelling eteline lutjanids at oceanic islands (Grimes 1987). The estimated proportions for onaga in Hawaii are unusual and considerably greater than what was recently estimated for the opakapaka in Hawaii, which sexually matures at a length of 40.7 cm FL (3–4 years) and just 53% of maximum length (Luers et al., 2018). It is possible that the number of onaga used by Everson et al. (1989) was insufficient to properly describe length-at-maturity. Reported sizes-at-maturity in other locations across the Indo-Pacific for this species are typically smaller than the estimates of Everson et al., (1989) and may be attributed to interregional differences in growth (e.g., Brouard and Grandperrin, 1985). A recent study of *E. coruscans* from Okinawa, Japan, however, estimated an L_{50} of 67.1 cm FL at 76% of maximum observed length (Uehara et al., 2018), values similar to those of Everson et al. (1989).

Regardless of whether onaga mature at 50% or 75% of maximum length, the current minimum legal size for possession in Hawaii of 1 lb. (Division of Aquatic Resources, 2019), equivalent to ~30 cm FL or 32% of maximum length (Fig. S2), is questionably appropriate because a fish this size would be 2–3 years old and certainly immature (Fig. 4). This might elicit rightful concern by fishers over management practices that could fail to allow sufficient fish to mature and spawn, thereby ensuring stock replenishment (Madge et al., 2016). Hence, the current minimum retention size for onaga caught in the Hawaiian Islands might be reconsidered in terms of its length- and age-at-maturity.

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Table 1. Fish and otolith data, estimated age and birth year, and corresponding radiocarbon and age data determined for onaga (*Etelis coruscans*) in the MHI. All otoliths were sampled twice in the otolith core at (A) within the first year of growth, and (B) at the second-year band. Estimated age was the finalized otolith growth zone count. Measured F¹⁴C was correlated with the regional coral reference record to provide the years of formation and the associated birth year period that reflects attributes of ¹⁴C levels through time.

Sample # (WHOI #)	Collection Date	Length	Otolith mass	Estimated age	Birth year	F ¹⁴ C ± 2SD	δ ¹³ C (‰)	F ¹⁴ C years	Birth year period
ETCO-001A (OS-107552)	2008.18	86.9	0.2881	55 ± 2	1953	0.9390 ± 0.0021	-6.39	<1953	Pre-bomb
ETCO-001B (OS-110513)					1954	0.9447 ± 0.0025	-4.89	<1953	Pre-bomb
ETCO-002B* (OS-110514)	2008.15	78.6	0.2610	43 ± 2	1965	1.0995 ± 0.0028	-4.82	1964–66	Rise
ETCO-003B* (OS-107693)	2008.19	85.0	0.2404	40 ± 2	1968	1.1325 ± 0.0042	-5.37	1966–68	Rise
ETCO-004A (OS-107490)	2008.47	79.0	0.2309	48 ± 2	1960	0.9701 ± 0.0028	-5.51	1957–59	Rise
ETCO-004B (OS-110516)					1961	0.9759 ± 0.0031	-5.57	1958–60	Rise
ETCO-005A (OS-110517)	2008.19	79.6	0.1821	23 ± 1	1985	1.1305 ± 0.0028	-5.89	1984–88	Decline
ETCO-005B (OS-110518)					1986	1.1203 ± 0.0031	-5.49	1986–90	Decline
ETCO-006A (OS-110527)	2008.14	74.4	0.1666	26 ± 1	1981	1.1395 ± 0.0024	-6.38	1978–83†	Decline
ETCO-006B (OS-110528)					1982	1.1373 ± 0.0024	-5.95	1982–86	Decline
ETCO-007A (OS-110529)	2007.81	84.0	0.1689	30 ± 1	1978	1.1446 ± 0.0030	-6.05	1977–82†	Decline
ETCO-007B (OS-110530)					1979	1.1461 ± 0.0025	-5.56	1977–82†	Decline

* First core from each sample lost during sample handling.

† Inflection in the record provides a wider range of dates.

Table 2.1. Model diagnostics and parameter estimates for onaga (*Etelis coruscans*) length at age fitted with the modified von Bertalanffy growth function (VBGF) under the best-fitting additive normal error structure. All groups included the unsexed (immature) individuals for each model fit. P-values are listed for each model diagnostic test. Standard errors are reported beneath parameter estimates. The modified VBGF parameters L_{max} and L_{min} are the predicted lengths at ages $t_{max}=55$ and $t_{min}=2$ years, respectively.

P-Values for Model Diagnostic Tests

Sex	Normality	Constant Variance	Residual Trend	R^2
Female	0.71	0.52	0.81	0.96
Male	0.51	0.70	0.92	0.94
Pooled	0.85	0.25	0.98	0.94

Parameter Estimates

Sex	L_{∞}	k	t_0	L_{min}	L_{max}	c	n
Female	87.6 ±	0.121 ±	-1.02 ±	26.7 ±	87.4 ±	0.886 ±	114
	1.2	0.007	0.21	0.8	1.2	0.006	
Male	82.7 ±	0.126 ±	-1.37 ±	28.6 ±	82.6 ±	0.882 ±	102
	1.4	0.008	0.26	0.8	1.4	0.007	
Pooled	85.3 ±	0.124 ±	-1.10 ±	27.3 ±	85.2 ±	0.883 ±	187
	1.0	0.006	0.19	0.7	0.9	0.005	

Table 2.2. Model diagnostics and parameter estimates for onaga (*Etelis coruscans*) length at age fitted with the modified von Bertalanffy growth curve under the alternative multiplicative lognormal error structure by gender. All groups included the unsexed (immature) individuals for each model. P-values are listed for each model diagnostic test. Standard errors are reported beneath parameter estimates. The modified VBGF parameters L_{max} and L_{min} are the predicted lengths at ages $t_{max}=55$ and $t_{min}=2$ years, respectively.

P-Values for Model Diagnostic Tests

Sex	Normality	Constant Variance	Residual Trend	R ²
Female	0.86	0.45	0.13	0.93
Male	0.55	0.21	0.42	0.92
Pooled	0.59	0.06	0.22	0.92

Parameter Estimates

Sex	L_{∞}	k	t_0	L_{min}	L_{max}	c	n
Female	89.9 ±	0.105 ±	-1.45 ±	27.3 ±	89.5 ±	0.900 ±	114
	2.8	0.008	0.21	0.5	2.7	0.008	
Male	84.0 ±	0.116 ±	-1.58 ±	28.6 ±	83.9 ±	0.890 ±	102
	2.8	0.011	0.25	0.6	2.7	0.010	
Pooled	86.8 ±	0.113 ±	-1.38 ±	27.6 ±	86.5 ±	0.893 ±	187
	1.9	0.007	0.18	0.5	1.8	0.006	

Table 3. Summary of von Bertalanffy growth function (VBGF) parameters for this study (sexes separate and pooled (P) and two curve fitting scenarios) compared with parameters estimated by other studies of onaga (*Etelis coruscans*) in the Hawaiian Islands and other regions of the Pacific Ocean. The MHI and NWHI have been separated in some cases because growth may differ between subregions. Early studies may have suffered from assumptions that were necessary at the time due to inadequate sample sizes and limited technologies.

Region	Sex	L_{∞}	k	t_0	Ages	Method	Study
Hawaii (MHI)	F	87.6	0.121	-0.120	1-55	Section age	Current study (additive normal)
	M	82.7	0.126	-1.37			
	P	85.3	0.124	-1.10			
	F	89.9	0.105	-1.45	1-55	Section age	Current study (lognormal)
	M	84.0	0.116	-1.58			
	P	86.8	0.113	-1.38			
Hawaii (MHI)	-	89.4	0.143	n.r.	n.r.	LFA & growth	Ralston and Kawamoto (1987)
Hawaii (NWHI)	-	95.7	0.137	n.r.	n.r.	performance ¹	"
Hawaii (Archipelago)	-	117.5	0.106	-0.36	1-13	Daily integration ²	Williams and Lowe (1997)
	-	92.1	0.273	+1.6	2-9		
Mariana Islands	-	109.1	0.123	-1.19	1-9	Daily integration	Ralston and Williams (1988)
Papua New Guinea	-	79.5 ³	0.27	n.r.	2-20	Section age	Fry <i>et al.</i> (2006)
New Caledonia	-	99.4	0.14	-0.93	2-17 ⁴	Section age	Williams <i>et al.</i> (2013)
Vanuatu	-	82	0.128	n.r.	10 ⁵	Daily increments	Brouard and Grandperrin (1985) ⁶

1. Length frequency analysis (LFA) used for L_{∞} estimate with k from growth performance relationship for snapper and grouper (Manooch 1987).

2. Used 2 forms of the daily increment integration method (Ralston and Williams 1988, Smith and Kostlan 1991).

3. Standard length was used in this study and was converted from 72.9 cm SL to 79.5 cm FL using Uchida *et al.*, (1982).

4. Parameters reported for this age range but observed section age for onaga reported to 40 years in Williams *et al.*, (2015).

5. Unknown age estimate range, but plotted age of just under 4000 days implies maximum age of ~10 years from daily counts.

6. Brouard *et al.*, (1983) is cited, but life history parameters appear to have been revised in this publication.

n.r. Not reported: 2-parameter VBGF likely with t_0 forced through the origin.

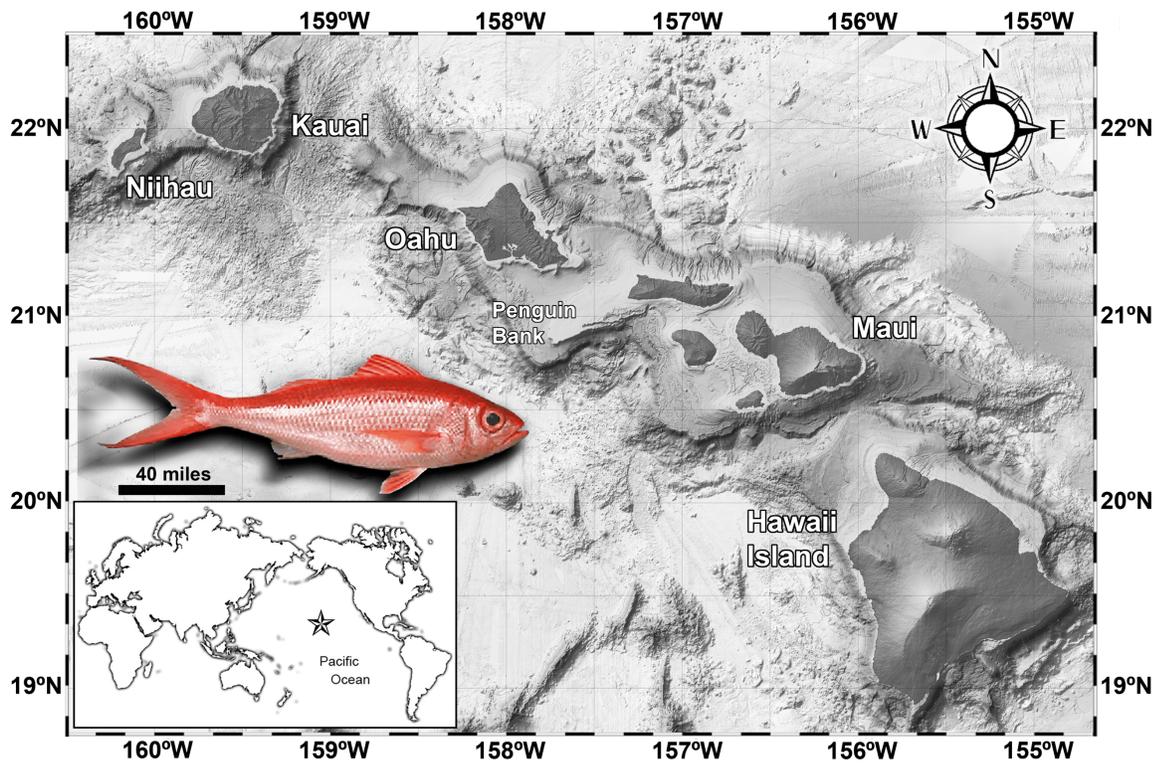


Fig. 1. The fish used in this study were collected from the MHI fishery in areas associated with the labeled locations. Onaga (*Etelis coruscans*; inset photograph) living in the ocean mixed layer of this region are thought to have experienced a common timeline for the bomb radiocarbon signal based on oceanographic observations (Andrews et al., 2016). Base map of Hawaiian Islands was sourced and modified with permission from the School of Ocean and Earth Science and Technology (SOEST) and the Hawaii Institute of Geophysics and Planetology (HIGP) at University of Hawaii, Manoa.

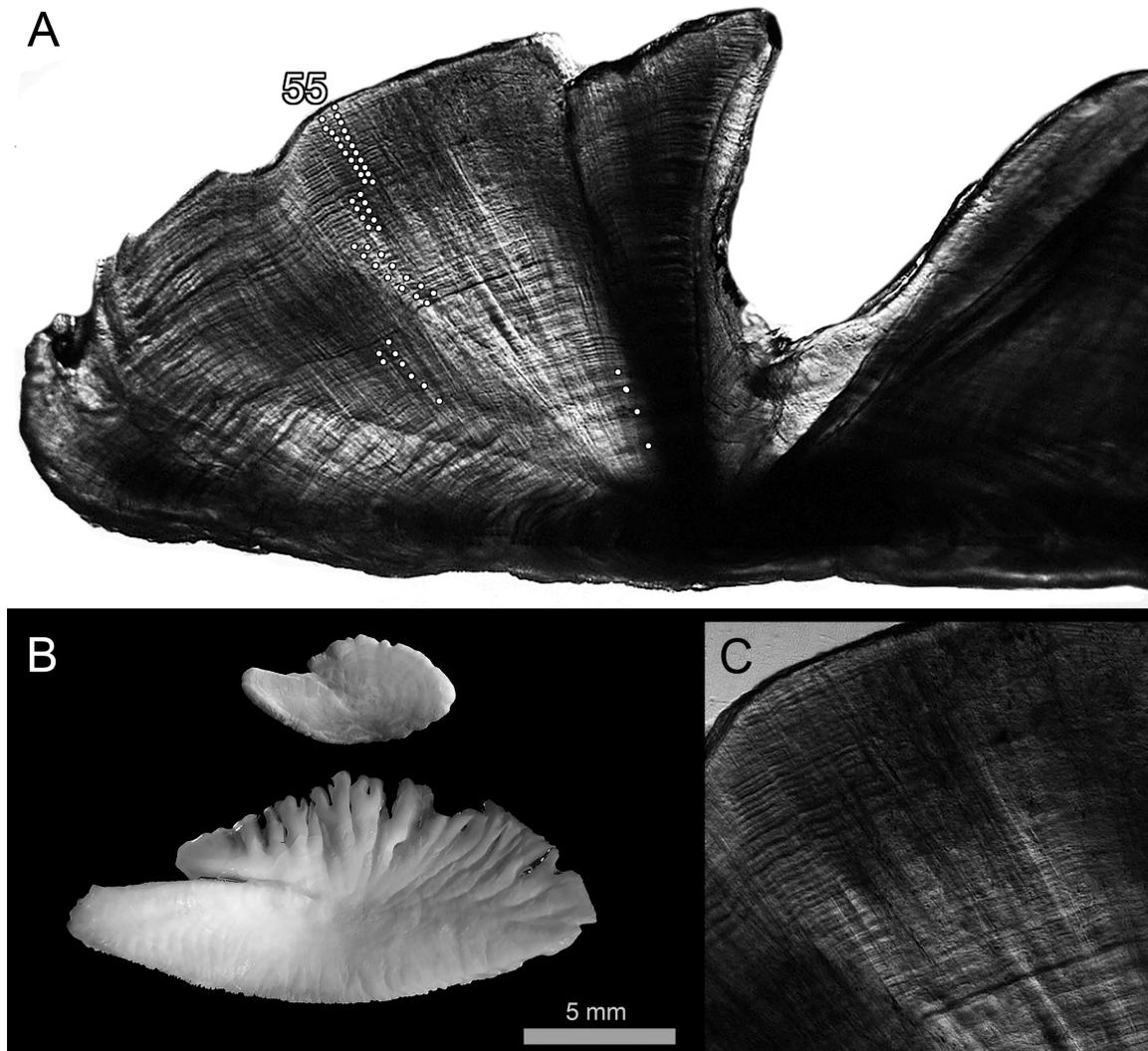


Fig. 2. Onaga (*Etelis coruscans*) otolith images of (A) a transverse section of an adult viewed under transmitted light, (B) lateral views (distal side) of the original whole otolith of the section shown (A) with the smallest juvenile otolith available, and (C) a zoomed detail of the fine increment structure counted toward the outer edge. The adult section (A) was aged to 55 years (growth zone counts are marked by small white dots) — a Rosetta Stone in the age estimation of other sections that were not as well defined. The juvenile otolith (B) was aged to 2 years and was used as a template in determining core extraction protocol on the micromilling machine, coupled with observations for the surface location and dimension of the second-year sample in sectioned otoliths (A). The growth structure identified and counted for estimates of age was similar to that shown for *E. coruscans* in the South Pacific (Williams et al., 2015).

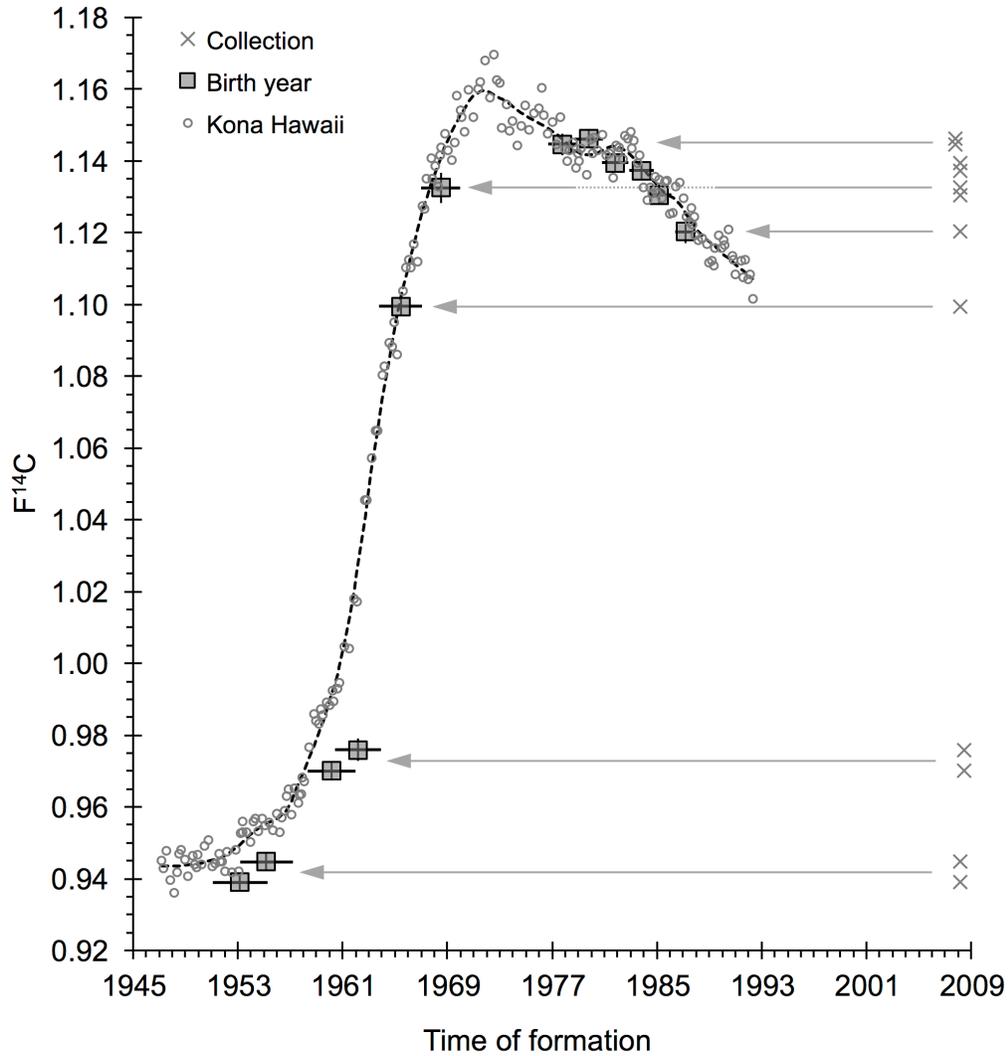


Fig. 3. Plot of the coral bomb ¹⁴C reference record (Kona, Hawaii Island; Andrews et al., 2016) that is relevant for the region with measured ¹⁴C values from the extraction of 12 otolith core samples from 7 fish (5 fish with both year-1 and year-2 cores; Table 1). The age of onaga (*Etelis coruscans*) was determined by counting growth zones in otolith sections for an estimated birth year (arrows project from collection date back to calculated birth year). The validity of age reading was determined from the alignment or misalignment of the measured F¹⁴C value with the reference record. Horizontal and vertical error bars represent the final estimate of age reading precision (D = 5.3%) and instrument precision (1 SD).

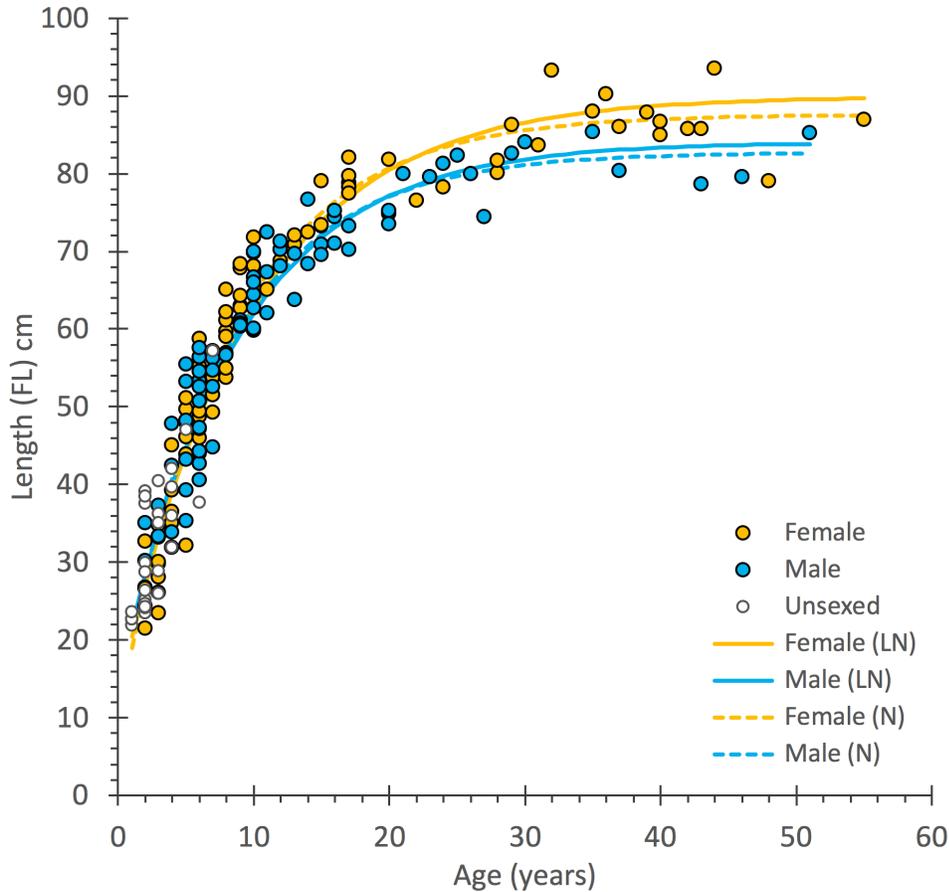


Fig. 4. Scatterplots of age-at-length data with von Bertalanffy growth curves for onaga (*Etelis coruscans*) of the Hawaiian Islands (sexes separate, lognormal (LN) and normal (N) parameters; Table 3). Empirical estimates of age-at-maturity from these curves for females using an L_{50} of 66.3 cm FL from Everson et al., (1989) corresponds with an age of 11 years, and an alternate L_{50} near length-at-maturity for similar deep-dwelling eteline lutjanids ($\sim 50\% L_{max}$; Grimes 1987) corresponds to an age of 5–6 years. The age of a minimum retention sized onaga (1-pound, 0.45 kg) in Hawaii would be immature and 2–3 years old.

Supplementary Material

Table S1. Fish data from specimens used in this study. Fish length was fork length (FL) and mean otolith mass included both whole sagittal otoliths for most fish. Final age in years was the accepted age estimate from 3 age readings. Final age was the final count (deemed best read of three reads during the fourth reading by an experienced age reader) and using the validated reference-image otolith sections when necessary (i.e., the iterative age reading of outliers from the otolith mass-to-age relationship).

Lab number	Fish specimen number	Fish length FL (cm)	Fish mass (kg)	Gonad mass (g)	Sex	Otolith mass (g)	Final age (years)
OH-001	M12-2-5-427	86.9	9.62	104.2	F	0.289	55
OH-002	M9-1-2-321	78.6	6.54	76.0	M	0.249	43
OH-003	M14-3-5-520	85.0	8.69	101.2	F	0.240	40
OH-004	IM7-6-10-445	79.0	7.69	122.4	F	0.237	48
OH-005	M14-2-8-512	79.6	7.30	325.7	M	0.181	23
OH-006	M8-2-6-338	74.4	5.64	46.2	M	0.166	27
OH-007a	CK2-1-2-2	84.0	7.80	176.7	M	0.165	30
OH-007b	M8-2-5-320	72.5	5.72	56.8	F	0.153	14
OH-008	M8-1-2-301	70.8	5.40	24.9	M	0.146	15
OH-009	CK5-1-4-4	79.8	7.72	109.6	U	n.a.	16
OH-010	M8-1-7-311	71.0	5.34	37.0	M	0.126	16
OH-011	M14-2-7-511	72.4	5.44	48.0	M	0.122	11
OH-012	CK1-1-7-7	61.1	3.72	31.5	M	0.098	9
OH-013	M4-1-10-290	60.7	3.48	20.6	M	0.075	9
OH-014	M8-1-5-308	56.3	2.94	4.3	M	0.078	7
OH-015	LW3-1-7-57	48.7	1.68	1.9	F	0.067	6
OH-016	M7-2-8-174	53.3	2.18	3.8	M	0.088	6
OH-017	JA6-1-3-81	46.1	1.36	1.7	F	0.051	5
OH-018	JA1-1-3-2	39.7	0.98	0.9	U	0.044	4
OH-019	CK3-1-3-3	31.9	0.52	0.3	U	0.031	4
OH-020	JA9-2-7-151	28.8	0.40	0.2	U	0.028	3
OH-021	JA10-2-5-162	23.5	0.23	0.2	U	0.024	2
OH-022	JA14-3-5-297	21.9	0.18	0.1	U	0.018	1
OH-023	NT4-1-9-26	26.1	0.34	0.3	F	0.034	3
OH-024	NT4-2-3-30	28.0	0.41	0.3	F	0.034	3
OH-025	NT4-1-6-23	26.8	0.39	0.2	F	0.029	2
OH-026	NT4-1-4-21	21.5	0.18	0.1	F	0.021	2
OH-027	NT3-1-6-20	26.6	0.32	0.2	F	0.029	2
OH-028	NT3-1-2-16	23.5	0.25	0.2	F	0.026	3
OH-029	NT2-1-10-9	32.2	0.59	0.7	F	0.038	5
OH-030	M14-3-1-515	52.5	2.20	1.7	M	0.055	6

OH-031	M14-2-10-514	68.3	4.79	35.4	M	0.130	14
OH-032	M14-2-6-510	70.2	4.83	62.5	M	0.102	12
OH-033	M14-1-9-503	74.8	5.53	72.9	M	0.181	20
OH-034	M14-1-8-502	69.5	4.81	61.7	M	0.138	15
OH-035	M14-1-5-465	74.4	5.62	83.4	M	0.131	16
OH-036	M14-1-4-457	68.7	4.85	34.3	F	0.109	12
OH-037	M14-1-1-423	60.5	3.33	7.0	M	0.090	9
OH-038	M1-2-9-257	75.2	6.60	113.7	M	n.a.	20
OH-039	M12-2-7-480	87.9	9.60	139.7	F	0.267	39
OH-040	M12-2-6-419	81.8	7.60	80.7	F	0.145	20
OH-041	M12-2-3-492	85.7	9.58	116.7	F	0.278	43
OH-042	M12-1-8-458	85.7	9.42	99.8	F	0.237	42
OH-043	M12-1-6-463	44.8	1.38	1.0	M	0.050	7
OH-044	M12-1-5-475	80.0	6.78	47.4	M	0.178	21
OH-045	M10-2-6-364	78.7	7.06	66.4	F	0.164	17
OH-046	M10-2-5-363	85.2	8.68	51.1	M	0.258	51
OH-047	M10-2-4-362	73.2	5.74	51.1	M	0.155	17
OH-048	M10-2-3-361	79.9	6.78	115.2	M	0.207	26
OH-049	M10-2-2-299	70.0	5.02	19.3	M	0.108	10
OH-050	M9-2-4-385	54.7	2.66	3.0	M	0.069	7
OH-051	M9-2-2-382	51.5	2.04	2.9	F	0.069	7
OH-052	M9-2-1-358	46.0	1.48	2.5	F	0.053	6
OH-053	M9-1-10-344	64.4	3.96	9.0	M	0.081	10
OH-054	M9-1-8-340	67.3	4.45	21.6	M	0.115	11
OH-055	M9-1-6-336	79.7	6.56	60.9	F	0.129	17
OH-056	M9-1-5-335	49.4	1.48	2.1	F	0.064	6
OH-057	M9-1-4-334	60.3	3.20	21.0	F	0.075	9
OH-058	M9-1-3-330	47.1	1.68	1.7	F	0.062	6
OH-059	M8-2-2-317	70.2	5.28	53.0	M	0.142	17
OH-060	M8-2-1-315	72.5	5.68	28.0	M	0.123	11
OH-061	M8-1-4-305	85.4	8.22	146.2	M	0.182	35
OH-062	M7-3-8-262	69.7	4.94	30.9	M	0.120	13
OH-063	M7-3-7-250	59.6	3.36	8.9	F	0.074	8
OH-064	M7-3-5-232	71.2	5.78	32.2	M	0.117	12
OH-065	M7-3-4-230	78.3	7.00	53.8	F	0.137	17
OH-066	M7-3-3-225	81.3	7.28	72.0	M	0.204	24
OH-067	M7-3-1-216	42.7	1.28	1.1	M	0.046	6
OH-068	M7-2-10-180	56.6	2.80	7.8	M	0.075	8
OH-069	M2-1-6-136	71.8	5.72	21.2	F	0.104	10
OH-070							skipped

OH-071	M2-1-2-142	79.5	6.78	61.2	M	0.211	46
OH-072	M1-2-10-287	82.3	7.20	73.6	M	0.209	25
OH-073	M1-1-1-268	76.6	7.06	45.6	M	0.118	14
OH-074	LW4-1-10-128	33.9	0.64	0.4	M	0.036	4
OH-075	LW3-1-9-59	44.0	1.38	2.1	F	0.052	6
OH-076	LW3-1-8-58	44.2	1.29	1.6	M	0.058	6
OH-077	LW2-2-5-95	43.9	1.29	1.1	F	0.055	5
OH-078	LW2-2-3-93	47.3	1.59	1.3	M	0.067	6
OH-079	LW2-2-2-92	33.3	0.61	0.5	M	0.036	3
OH-080	LW2-2-1-91	45.0	1.36	1.8	F	0.055	4
OH-081	LW2-1-9-89	43.2	1.27	1.2	M	0.055	5
OH-082	LW2-1-8-88	34.8	0.68	0.5	F	0.042	3
OH-083	LW2-1-4-82	29.8	0.41	0.2	F	0.033	3
OH-084	JA15-1-3-283	33.2	0.64	0.5	F	0.042	3
OH-085	JA14-3-4-295	42.4	1.25	1.1	M	0.049	4
OH-086	JA14-3-3-293	35.0	0.70	0.5	F	0.037	4
OH-087	JA14-2-9-277	36.5	0.79	1.1	F	0.041	4
OH-088	JA14-2-1-268	30.2	0.43	0.3	M	0.029	2
OH-089	JA14-1-9-266	32.7	0.64	0.6	F	0.033	2
OH-090	JA14-1-7-263	25.9	0.29	0.1	U	0.023	3
OH-091	JA14-1-4-255	39.3	1.00	1.0	F	0.048	4
OH-092	JA10-2-8-178	30.0	0.45	0.4	F	0.031	3
OH-093	JA9-2-10-154	24.8	0.26	0.2	U	0.025	2
OH-094	JA9-3-4-159	23.4	0.22	0.1	U	0.022	2
OH-095	JA9-2-5-149	36.0	0.86	0.9	U	0.040	4
OH-096	JA9-2-4-148	29.9	0.42	0.2	U	0.030	2
OH-097	JA9-1-5-129	28.7	0.40	0.1	U	0.030	2
OH-098	JA8-3-8-135	36.2	0.74	0.4	U	0.040	3
OH-099	JA8-3-5-132	40.4	0.96	1.1	U	0.042	3
OH-100	JA8-3-4-131	37.7	0.88	0.84	U	0.066	6
OH-101	JA8-3-3-128	35.3	0.72	0.51	M	0.036	5
OH-102	JA8-3-2-127	39.2	0.92	0.59	M	0.036	5
OH-103	JA8-3-1-126	25.2	0.26	0.15	U	0.025	2
OH-104	JA8-2-7-121	37.3	0.86	0.64	M	0.042	3
OH-105	JA8-2-6-118	37.6	0.9	0.98	U	0.036	2
OH-106	JA8-2-4-116	35.1	0.72	0.57	M	0.036	2
OH-107	JA8-2-1-111	35.1	0.78	0.65	U	0.033	3
OH-108	JA8-1-10-107	39.1	1.02	0.59	U	0.043	2
OH-109	JA6-1-4-93	49.7	1.7	2.85	F	0.069	5
OH-110	JA6-1-2-79	53.2	2.38	4.33	M	0.077	5

OH-111	JA5-1-5-65	42.0	1.14	0.49	U	0.055	4
OH-112	JA3-1-8-7	22.6	0.16	0.08	U	0.020	1
OH-113	JA1-1-5-16	38.4	0.9	0.47	U	0.039	2
OH-114	IM3-4-8-281	62.7	3.78	45.8	M	0.103	10
OH-115	IM4-1-7-314	69.8	4.68	44.9	F	0.122	10
OH-116	HM2-1-1-4	26.3	0.3	0.10	U	0.028	2
OH-117	CK11-1-3-3	66.6	4.74	27.9	M	0.145	10
OH-118	CK8-1-10-10	63.8	4.36	16.0	M	0.128	13
OH-119	CK8-1-7-7	73.5	5.9	68.6	M	0.201	20
OH-120	CK8-1-6-6	65.0	4.32	15.2	F	0.099	11
OH-121	CK8-1-5-5	59.8	3.18	8.2	M	0.091	10
OH-122	CK8-1-2-2	60.0	3.26	4.0	M	0.083	10
OH-123	CK7-1-2-2	40.6	0.98	1.1	M	0.045	6
OH-124	CK6-2-10-20	79.0	6.56	62.4	F	0.168	15
OH-125	CK6-2-3-13	61.1	3.32	6.5	F	0.093	8
OH-126	CK6-1-8-8	49.2	1.88	7.9	F	0.067	7
OH-127	CK6-1-7-7	68.1	4.42	31.0	M	0.127	12
OH-128	CK6-1-6-6	55.2	2.52	15.9	F	0.073	6
OH-129	CK5-1-8-8	47.0	1.54	2.0	U	0.052	5
OH-130	CK5-1-7-7	62.7	3.56	13.9	U	0.078	unreadable
OH-131	CK5-1-6-6	63.0	4.24	45.4	F	0.107	9
OH-132	CK4-1-9-9	57.1	2.92	n.a.	U	0.080	7
OH-133	CK4-1-7-7	56.4	2.84	4.9	M	0.065	6
OH-134	CK4-1-6-6	58.4	3.00	18.3	M	0.083	unreadable
OH-135	CK4-1-5-5	57.5	2.96	8.9	M	0.087	6
OH-136	CK1-1-8-8	54.5	2.52	27.6	M	0.074	6
OH-137	CK1-1-5-5	66.0	4.28	43.7	M	0.091	10
OH-138	CK1-1-4-4	62.0	3.5	11.5	M	0.082	11
OH-139	CK1-1-1-1	75.2	6.38	119.4	M	0.177	16
OH-140	AK1-1-9-9	24.6	0.25	0.16	U	0.027	2
OH-141	AK1-1-6-6	31.9	0.52	0.42	F	0.035	4
OH-142	M12-1-10-498	55.5	2.56	2.77	M	0.071	5
OH-143	CTAM1-4	22.7	0.40	n.a.	U	0.021	1
OH-144	SAITO1-3	23.6	0.22	n.a.	U	0.024	1
OH-145	CTAM1-5	24.1	0.24	n.a.	U	0.024	2
OH-146	KK3-4	24.3	0.24	n.a.	U	0.024	2
OH-147	NT4-1-5-22	24.4	0.27	0.10	F	0.027	2
OH-148	M8-1-10-314	47.8	1.84	3.12	M	0.056	4
OH-149	M12-1-2-454	48.0	1.80	1.45	M	0.060	5
OH-150	CK6-2-2-12	48.2	1.68	4.62	M	0.062	5

OH-151	ROYM9-1	51.1	2.16	17.3	F	0.065	5
OH-152	LAYNE22-2	50.7	2.06	n.a.	M	0.072	6
OH-153	M7-3-9-265	52.5	2.26	3.57	M	0.068	7
OH-154	GVI3-8	53.3	2.5.0	27.4	F	0.077	6
OH-155	M7-2-6-158	53.8	2.36	3.95	F	0.061	8
OH-156	20140831ROY-04	53.8	2.6.0	41.0	F	0.071	7
OH-157	GVI10-6	54.9	3.18	13.2	F	0.093	8
OH-158	GVI6-17	56.9	2.95	n.a.	F	0.078	8
OH-159	ROYM9-3	57.1	2.94	35.0	F	0.069	7
OH-160	ROYM9-2	58.7	3.34	68.3	F	0.080	6
OH-161	GVI10-1	59.0	3.64	34.8	F	0.088	8
OH-162	GVI3-9						no otolith
OH-163	GVI3-17	60.4	3.64	31.2	F	0.084	9
OH-164	GVI3-13	62.2	4.09	40.7	F	0.095	8
OH-165	GVI3-14	62.7	4.09	87.9	F	0.092	9
OH-166	GVI3-10	64.3	4.55	114.4	F	0.104	9
OH-167	GVI15-11	64.4	4.55	44.2	F	0.118	10
OH-168	GVI4-1	65.0	4.32	60.5	F	0.133	8
OH-169	GVI6-5	67.8	5.00	22.9	F	0.116	9
OH-170	GVI6-5	67.8	5.00	22.9	F	n.a.	unreadable
OH-171	GVI4-6	68.1	5.23	35.6	F	0.114	10
OH-172	GVI6-22	68.3	5.68	51.1	F	0.115	9
OH-173	GVI7-5	70.8	5.45	69.5	F	0.138	13
OH-174	M11-4-5-447	72.1	5.74	48.0	F	0.111	13
OH-175	GVI18-18	73.2	6.82	75.6	F	0.168	15
OH-176	M12-1-1-417	73.3	6.14	72.5	F	0.160	15
OH-177	GVI22-1	76.5	6.4	123.2	F	0.166	22
OH-178	GVI22-3	77.5	7.48	234.1	F	0.155	17
OH-179	GVI13-2	78.3	9.55	164.4	F	0.219	24
OH-180	GVI3-7	80.1	7.73	237.8	F	0.193	28
OH-181	M14-3-4-519	80.4	7.64	144.7	M	0.194	37
OH-182	M10-2-9-367	81.7	7.48	107.7	F	0.216	28
OH-183	LAYNE13-2	82.0	7.62	n.a.	F	0.153	17
OH-184	M13-1-5-415	82.6	7.78	120.7	M	0.206	29
OH-185	CK10-1-3-3	83.6	4.56	97.0	F	0.237	31
OH-186	SE13-02-28						replicate #
OH-187	SE13-02-28	86.0	8.62	n.a.	F	0.243	37
OH-188	SE13-02-27	86.25	9.16	75.3	F	0.207	29
OH-189	M14-2-5-509	86.6	8.87	93.8	F	0.211	40
OH-190	IM4-1-9-320						no otolith

OH-191	LAYNE13-9	87.0	8.71	n.a.	F	0.150	low mass†
OH-192	KK2-1	87.1	9.30	313.4	F	0.160	low mass†
OH-193	SE13-02-22	88.0	9.43	n.a.	F	0.239	35
OH-194	GVI17-2						no otolith
OH-195	SE13-02-26	90.25	9.25	n.a.	F	0.230	36
OH-196	SE13-02-25	93.25	9.71	135.2	F	0.225	32
OH-197	LAYNE13-7	93.5	10.89	n.a.	F	0.257	44

n.a. Otolith mass not available because the otolith was broken with missing pieces.

† Otolith mass was inordinate relative to fish length and indicated that the data for the specimen were unreliable.

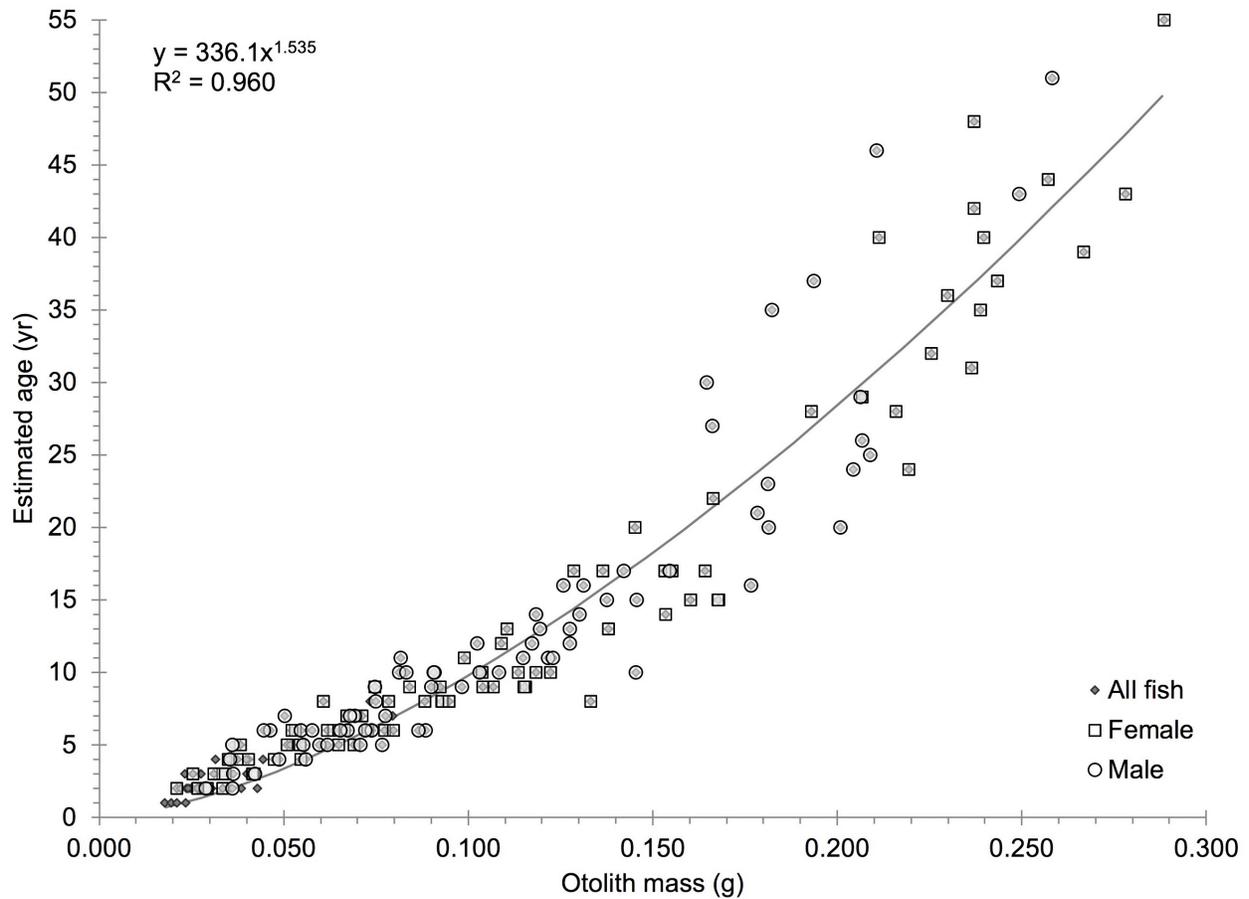


Figure S1. Otolith mass relative to the estimated age from growth zone counting was used as a tool to refine outlying age estimates associated with the first 2 decades of growth, the region of the curve that is most diagnostic for age. Outlying ages that were visible as an inordinate separation from the slightly curvilinear relationship were reevaluated based on the reference-image otolith sections that had been age validated with bomb ^{14}C dating. This approach was iterative in that repeated reads were necessary to resolve the most consistent age reading estimate. This tool is often overlooked in age and growth studies and should be employed to avoid the introduction of spurious age estimates.

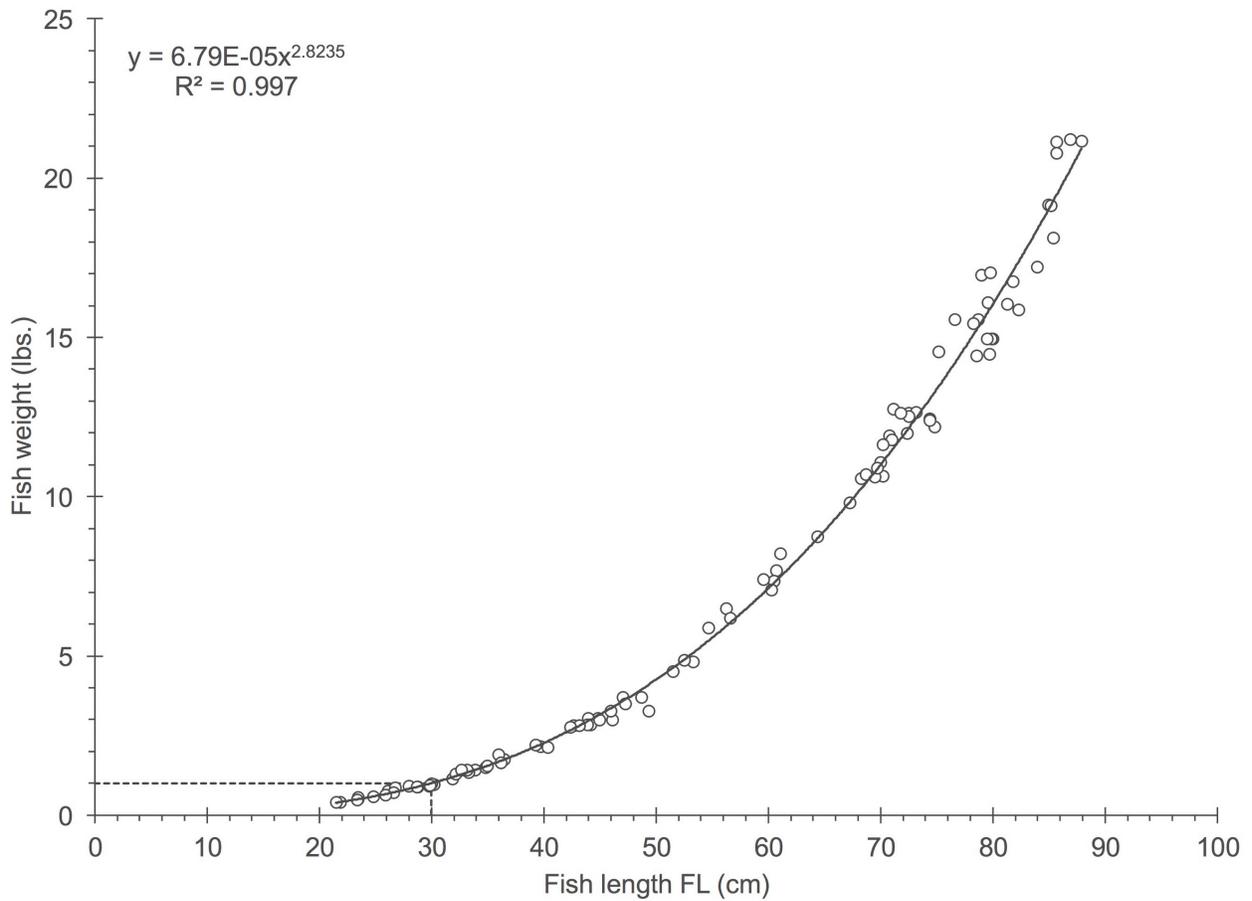


Figure S2. The relationship between round (whole fish weight) and body length for some of the onaga (*Etelis coruscans*) specimens used in this study (Table S1). This relationship was used to provide an age estimate for fish of minimum retention size (confer intersection of the two dashed lines). Specifically, current fishing regulations in Hawaii limit retention to onaga ≥ 1 pound (~ 30 cm) and this equates to an age of 2–3 years (Fig. 4). The findings are similar to a length-to-weight relationship described for onaga in the NWHI (Uchiyama and Kazama 2003).

SM Reference

Uchiyama, J.H., Kazama, T.K. 2003. Updated weight-on-length relationships for pelagic fishes caught in the central North Pacific Ocean and bottomfishes from the Northwestern Hawaiian Islands. NOAA Fisheries, PIFSC Admin. Rep. H-03-01.