

Early overcounting in otoliths: a case study of age and growth for gindai (*Pristipomoides zonatus*) using bomb ^{14}C dating

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Abstract

Gindai (*Pristipomoides zonatus*) is one of six snappers in a management complex called the Deep 7 of the Hawaiian Islands. Little is known about its life history and a preliminary analysis of otolith thin sections indicated the species may exhibit moderate growth with a lifespan approaching 40 years. Preliminary age estimates from the previous study were reinvestigated using the same otolith sections in an attempt to validate those ages with bomb radiocarbon (^{14}C) dating. From the misalignment of birth years for the otolith ^{14}C measurements with regional references — the post-peak bomb ^{14}C decline period — it was concluded that previous ages were inflated from overcounting of the earliest growth zone structure in otolith sections. The oldest gindai was re-aged to 26 years once the age reading was adjusted for early overcounting, 13 years younger than the original estimate of 39 years for this fish. In general, the earliest otolith growth of gindai was massive and complicated by numerous subannual checks. The approach of lumping the early growth structures was supported by the alignment of ^{14}C measurements from otolith core material (first year of growth). The result was greater consistency of calculated birthdates with the ^{14}C decline reference, along with minor offsets that may indicate age estimation was imprecise by a few years for some individuals. The revised von Bertalanffy growth function applied to the validated age-at-length estimates revealed more rapid growth ($k = 0.378$ cf. 0.113) and a lifespan of approximately 30 years. The findings presented here are a case study of how the bomb ^{14}C decline period can be used as a tool in the refinement of age reading protocols.

Keywords: Otolith, Radiocarbon, Lifespan, Validation, Age Estimation

Introduction

Gindai (*Pristipomoides zonatus*) is one of six snappers in a management complex called the Deep 7 of the Hawaiian Islands.

This species does not comprise a large proportion (1%–2% by weight) of the Deep 7 catch in Hawaii (Langseth et al., 2018), but its importance has increased over the recorded history of this fishery (DeMartini, 2019). The age and growth of this spe-

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cies was first studied in 2013 as a summer project by a University of Hawaii student, in which both otolith sections and gonad samples were worked up as a preliminary life history study (Schofield, 2013). The findings of the study indicated the species could be moderately slow growing ($k = 0.113$) with a lifespan approaching 40 years. However, these findings were based strictly on estimates of age from growth zone counting that had not been validated. Age-validated life history parameters are essential in understanding resource resilience and in implementing proper management strategies (Cailliet & Andrews, 2008), especially in data-poor fisheries (Newman et al., 2017), like the Deep 7.

A method called bomb radiocarbon (^{14}C) dating can directly assess the accuracy of fish age estimates from otoliths and has evolved considerably over the last 28 years (Andrews et al., 2019b; Kalish, 1993). There is a long history of success with this approach where it has been used to validate or invalidate purported annual growth zones (Andrews et al., 2013; Campana, 1999; Kalish, 1995). The use of this method to age marine organisms relies on a time-specific signal — an observable increase in ^{14}C created by thermonuclear testing in the 1950s and 1960s — and its diffusion to the marine environment (Broecker & Peng, 1982; Druffel et al., 2016; Grottoli & Eakin, 2007). This approach has become an effective tool in providing an age-validated basis for the life history parameters of numerous marine fishes around the world (e.g. Allen & Andrews, 2012; Andrews & Kerr, 2015; Andrews et al., 2005, 2018b; Campana, 1997; Horn et al., 2012; Kalish 2001; Kerr et al., 2004; Vitale et al., 2016) and has been especially effective for species that live in tropical waters (e.g. Andrews et al., 2011a, 2011b, 2013, 2016a, 2020a; Baker & Wilson, 2001; Barnett et al., 2018; Cook et al., 2009; Passerotti et al., 2014) because of increased exposure of the ocean-surface mixed layer to the atmosphere (Andrews et al., 2016b; Druffel et al., 2016). A case study of the Hawaiian pink snapper or opakapaka (*P. filamentosus*) — also a member of the Deep 7 bottomfish complex and a congener of gindai — was the foundational application of bomb ^{14}C dating to fishes of the Hawaiian Islands (Andrews et al., 2012). This age validation work has continued with other fishes of Hawaii (Andrews et al., 2016a, 2019a, 2020a; DeMartini et al., 2018; Nichols 2019), and has most recently been expanded successfully to use of the post-peak bomb ^{14}C decline period — typically more recent than the 1980s (Andrews et al., 2013, 2018a, 2020; Barnett et al., 2018; Ishihara et al., 2017).

The aim of the current study was to assess the validity of

a preliminary life history study of gindai by reinvestigating the age reading to improve the estimates with bomb ^{14}C dating. To do this, a series of youngest to oldest individuals from the original study by Schofield (2013) were selected for bomb ^{14}C analyses. Age estimates from the original study were coupled with measured ^{14}C values from otolith core material (birth year) for a direct comparison of calculated birth years to a coral and otolith ^{14}C reference chronology (Andrews et al., 2016b). This approach can provide a validated basis for estimating the age and growth for gindai — similar to what has now been established for other members of the Deep 7 (Andrews et al., 2012, 2019a, 2020a; Nadon et al., 2020; Nichols, 2019) — with guidance on making adjustments to the age reading of otoliths.

Methods

A set of specimens from the Schofield (2013) study were used in the current study to reassess estimated age using bomb ^{14}C dating (Supplementary Material 1). These otoliths were previously sectioned and investigated for estimates of age using transmitted light (Table 1). The otoliths were from collections made throughout the Hawaiian Archipelago during the years 2007 to 2011. Otoliths were selected across sizes for the ^{14}C analyses for ages and otolith masses that progressed from the youngest and least massive to the oldest and most massive specimens ($n = 39$; Table 1).

Bomb radiocarbon dating

Each of the selected otoliths was analyzed for ^{14}C by extracting core material (within the first year of growth), measuring ^{14}C levels in the carbonate sample via accelerator mass spectrometry (AMS), and comparing the measured ^{14}C values and calculated birthdates to regional ^{14}C references. Otolith extractions were performed using a New Wave micromilling machine (Elemental Scientific Lasers, LLC, Bozeman, MT, USA) and a 0.5 mm bur (Brasseler, Savannah, GA, USA). Because the otolith sections were thick (~0.5–0.7 mm), coupled with a massive first year of growth, enough material was available for ^{14}C analysis by extracting the carbonate sample directly from the mounted, thin-sectioned specimen. The mounted glass slide was secured to the milling baseplate with warmed parafilm. The extraction was performed on the micromill using a path length of 2.5 mm at a depth of 0.2 mm in two consecutive passes for a total extraction mass of 0.7–0.8 mg (see Fig. 1 for an example of the core extraction on specimen PZ 90).

Table 1. Age estimates for all gindai (*Pristipomoides zonatus*) otoliths that were selected from the original Scofield (2013) study with region (main and Northwestern Hawaiian Islands [MHI, NWHI]), fish length (fork length), sex, and mean otolith mass. Original age is unvalidated from Scofield (2013) and revised age was from reinvestigation of otolith sections from birthdate misalignments to the regional ^{14}C references

Region	Specimen ID	Length (FL cm)	Sex	Otolith mass (g)	Original age (yr)	Revised age (yr)	$\text{F}^{14}\text{C} \pm 1\text{SD}$	Revised birthdate
NWHI	PZ 02	20.7	M	0.149	2	1	1.0634 ± 0.0028	2007.46
	PZ 16	30.7	M	0.195	8	2	1.0667 ± 0.0039	2006.47
	PZ 21	32.8	F	0.298	9	3	1.0676 ± 0.0039	2005.47
	PZ 80	35.8	F	0.427	17	12	1.1054 ± 0.0030	1995.47
	PZ 81	36.5	F	0.389	14	7	1.0898 ± 0.0032	2000.47
	PZ 82	36.7	F	0.515	27	10	1.1221 ± 0.0034	1997.47
	PZ 62	39.5	M	0.391	15	8	1.0830 ± 0.0032	2000.47
	PZ 87	41.2	F	0.609	19	15	1.1245 ± 0.0025	1992.47
	PZ 66	41.4	F	0.523	19	7	1.0834 ± 0.0033	2000.70
	PZ 89	41.6	M	0.502	17	12	1.1013 ± 0.0044	1995.49
	PZ 68	42.0	M	0.575	19	11	1.1124 ± 0.0035	1997.47
	PZ 90	43.2	F	0.785	39	26	1.1572 ± 0.0030	1980.47
	PZ 35	43.4	F	0.741	26	17	1.1298 ± 0.0036	1990.70
	PZ 72	43.8	F	0.591	21	12	1.1043 ± 0.0037	1995.70
	PZ 74	44.2	M	0.674	20	16	1.1182 ± 0.0037	1991.80
	PZ 38	44.6	F	0.866	28	23	1.1442 ± 0.0035	1984.70
	PZ 39	46.5	M	0.679	19	12	1.0990 ± 0.0032	1995.80
	PZ 40	48.2	F	0.815	32	22	1.1404 ± 0.0029	1985.49
MHI	PZ 01	15.9	F	0.091	1	0.5	1.0579 ± 0.0028	2008.41
	PZ 03	21.0	F	0.138	3	1	1.0673 ± 0.0024	2007.90
	PZ 05	23.8	F	0.152	3	1	1.0650 ± 0.0024	2008.32
	PZ 11	29.0	M	0.206	5	1	1.0617 ± 0.0029	2008.32
	PZ 12	29.7	F	0.241	7	2	1.0621 ± 0.0025	2009.69
	PZ 14	30.4	F	0.199	6	1	1.0626 ± 0.0023	2008.32
	PZ 20	32.5	M	0.242	7	3	1.0574 ± 0.0040	2008.68
	PZ 48	34.0	M	0.283	7	3	1.0638 ± 0.0028	2006.32
	PZ 50	34.0	F	0.305	12	3	1.0707 ± 0.0029	2006.33
	PZ 22	34.0	F	0.317	9	3	1.0669 ± 0.0038	2006.33
	PZ 52	34.5	F	0.278	9	3	1.0737 ± 0.0027	2006.31
	PZ 47	34.5	M	0.297	12	3	1.0645 ± 0.0025	2006.33
	PZ 55	36.0	M	0.309	11	3	1.0624 ± 0.0027	2006.33
	PZ 59	37.2	F	0.313	11	4	1.0647 ± 0.0026	2005.32
	PZ 60	38.2	F	0.383	16	8	1.0760 ± 0.0030	2001.31
	PZ 65	41.2	F	0.650	21	16	1.1204 ± 0.0031	1993.31
	PZ 88	41.6	M	0.490	17	8	1.0835 ± 0.0027	2003.69
	PZ 32	42.0	F	0.503	18	9	1.1016 ± 0.0032	1999.91
	PZ 69	42.5	M	0.479	16	8	1.0720 ± 0.0027	2001.31
	PZ 71	43.0	F	0.500	22	15	1.1167 ± 0.0031	1995.64
	PZ 36	43.5	M	0.503	15	9	1.0884 ± 0.0035	2002.69

NWHI, Northwestern Hawaiian Islands; MHI, Main and Northwestern Hawaiian Islands.

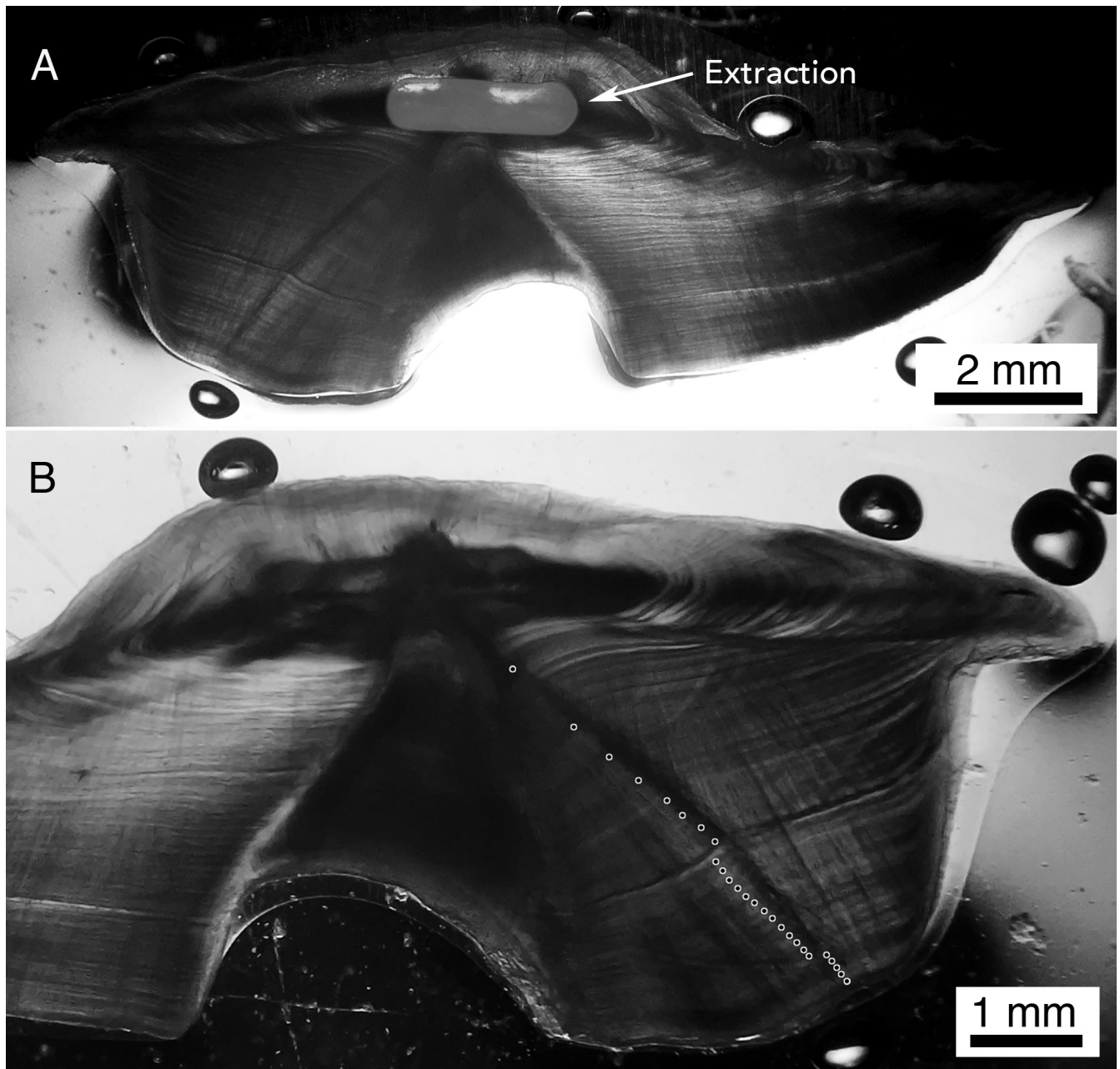


Fig. 1. Otolith section images from gindai (*Pristipomoides zonatus*) specimen PZ 90 showing the core extraction (grey shaded area) from the micromill (A) and the revised age-reading scenario (B). The milled extraction is a trough cut into the original aged otolith section at the core region (2.5 mm long x 0.5 mm wide x 0.4 mm deep) within the first year of growth. The marked section image is the obverse of the same otolith section where lumping of fine growth structure was used for the first 8 years and splitting was used for the remaining growth zones out to 26 years (aged to 25–27 years depending on interpretation). Note that there are numerous ways to count this otolith and that it is possible to attain the original age of 39 years by splitting the earliest growth zones (see Fig. 5 of Scofield (2013) ; Supplementary Material 1). In addition, some growth zone structure that was counted to 26 years is difficult to see because it requires a change in the angle of transmitted light, and may also require panning the eye across the concentric zone structure to either unify or split the area of interest. This age reading protocol was used to age all otoliths that were reinterpreted with support from bomb ^{14}C dating in this study.

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 analyzed via routine AMS analyses and 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; Stuiver & Polach, 1977).

Comparison of measured ^{14}C values at their respective birthdates, and relative to the regional ^{14}C references, provided a baseline for interpreting the validity of age estimates from the Scofield (2013) study (Supplementary Material 1). Alignment or misalignment of the calculated birthdate — determined as the date of collection minus the age estimate — with the years and ^{14}C levels of the post-peak ^{14}C decline (more recent than ~1980) can validate or invalidate the age estimates (See Andrews et al. (2020b) for an example of age scenario elimination using the post-peak bomb ^{14}C decline period). The reference records used in this study were two coral and otolith ^{14}C data sets: 1) Kure Atoll of the Northwestern Hawaiian Islands (NWHI), and 2) Kona of Hawaii Island of the main Hawaiian Islands (MHI; Andrews et al., 2016b; Fig. 2).

Age estimation and reassessment

Otoliths were initially prepared and read for estimates of age in a manner that was described in Scofield (2013) and a subset was selected from this study (Table 1; Supplementary Material 1). Because original age estimates led to birth years that were offset from the expected years of formation on the coral reference curves, the ages were recounted using an age reading protocol that is illustrated and enumerated for sample PZ 90 (aged 26 years; Fig. 1). Revised birthdates were calculated from ages counted with the new protocol and were plotted for alignment with the regional bomb ^{14}C decline records. The revised information for age was also correlated with otolith mass because the relation is typically linear or slightly curvilinear and can be used as a tool in the iterative selection of outliers to reassess estimates of age (Fig. 3). The age-at-length estimates, once verified with alignment to the reference records, were used to generate

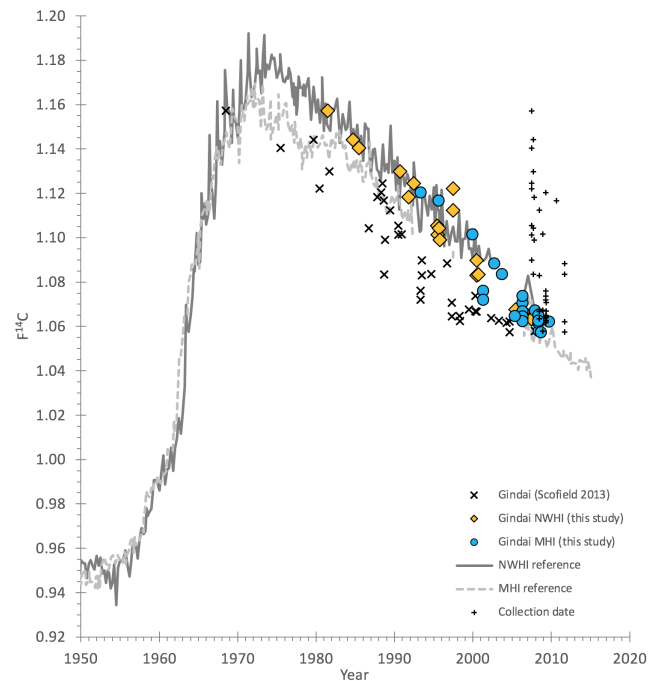


Fig. 2. Bomb ^{14}C plot of the selected series of gindai (*Pristipomoides zonatus*) otoliths from the early study by Scofield (2013) with revised dates from a reinvestigation section age. The original estimates of age (X symbol) were used to calculate birth years that are typically well-removed from the expected birth year determined by the regional ^{14}C reference records. Revised age estimates from a combination of ^{14}C alignment and reference-image otolith age-reading led to a stronger alignment of the calculated birth dates with the ^{14}C reference records. Reference records plotted here are from two coral and otolith ^{14}C data sets (Kure Atoll coral and otoliths of the Northwestern Hawaiian Islands (NWHI reference) and Kona of Hawaii Island with otoliths of the main Hawaiian Islands (MHI reference); see Andrews et al. (2016b) for details).

a revised von Bertalanffy growth function with parameters that can be compared to the Scofield (2013) results.

Results and Discussion

Bomb ^{14}C dating revealed that the original age interpretations for gindai from otolith sections were not accurate and that the age reading overcounted growth zones in the earliest otolith growth. The offset observed from the birthdates — calculated from the original age estimates in Scofield (2013) — indicated age was being overestimated and that the overcounting began with the youngest fish. This was evident by the early and con-

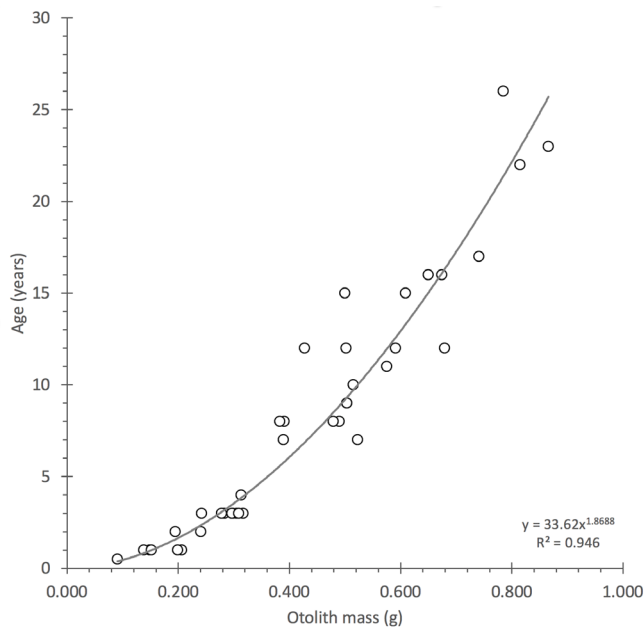


Fig. 3. Plot of the validated age estimates with mean otolith mass for gindai (*Pristipomoides zonatus*) of the Hawaiian Islands indicating a strongly curvilinear relation. The observation of mass growth indicated half the otolith mass can be accreted in the first 5–10 years of life with the latter otolith growth accreted in the following 15–20 years for this series of specimens.

sistent offset of the ^{14}C data from the reference chronologies (Fig. 2). Hence, the age reading was restructured from counting of fine increment structure in the earliest otolith growth (See otolith figure in Supplementary Material 1), to grouping or lumping of this fine structure into broader bands of growth (Fig. 1), resulting in reduced age estimates for youngest to oldest fish (Table 1). The grouping of finer growth structure was accomplished by reducing the magnification, and in some instances defocusing the microscope, to allow the eye to see broader more diffuse zones that could be counted (take note of the first 8 years that are marked for specimen PZ 90; Fig. 1). Ultimately, a common early growth structure that could be used to describe more rapid growth was visible among the otolith sections, but it was difficult to quantify. Reference-image otolith age reading — use of what appear to be the best sections for the otolith age reading protocol (Fig. 1; Andrews et al., 2020a; Wakefield et al., 2017) — was employed for sections that needed clarification on how the earliest growth should be counted.

In this study, transmitted light was used on thick sections

(~0.5–0.7 mm) where the light diffraction qualities of the otolith matrix were conserved. The reason for this approach is to use the different forms of growth structure (alternating densities due to inclusion of otolin; Campana, 1999) in which angled light transmitted through the otolith can exploit variations in diffraction indices of the otolith matrix — the Leica stereo microscope S8 APO outfitted with the Rotterman Contrast™ transmitted light base (TL4000 RC) is an optimal system for taking advantage of this otolith section artifact to view growth zone structure that is simply not visible with direct transmission (perpendicular to the otolith plane) of light through the otolith section. However, a technique used by Ong et al. (2016) described a method that used a brightfield on thin sectioned otoliths (0.15–0.19 mm) and the growth zone structure was clearly visible. While the older growth zones were fairly well defined for gindai in thicker sections, the problems with grouping early zones may not be solved with ultra-thin sections. One potential solution was with use of the crenulated and knob-like structures seen along the dorsal and ventral axes of the thin sections (Fig. 1B) — numerous smaller zones seen in the early growth structure could be lumped based on an association with these structural features. This approach was used in some cases for gindai and the approach was familiar from previous work on other fishes where there were counting problems in the earliest otolith growth (e.g., Andrews et al., 1999, 2005, 2013, 2018b; Kerr et al., 2004).

Once the ages for gindai were reevaluated relative to the bomb ^{14}C decline period and a revised counting scenario was developed, the alignment of the birthdates were in closer agreement with the expected ^{14}C decline dates (Fig. 2). Some remain offset and this may be due to either, 1) unresolved ages that are actually older or younger than estimated by a few years, or 2) greater offsets in ^{14}C due to regional variations that have not been accounted for — each ^{14}C reference record is from one end of the Hawaiian Archipelago to the other and the gyre waters of the North Pacific have been demonstrated to have a range of water sources that can be ^{14}C -depleted for various reasons (Andrews et al., 2016b; Kumamoto et al., 2013). Regardless, the revised estimates are much closer to the actual age of the gindai specimens — on the basis of clear misalignment of the preliminary study birthdates (Fig. 2) — than the original estimates provided by Scofield (2013).

Because the revised age estimates from growth zone counting are likely accurate to within a few years based on the alignment of calculated birthdates to the bomb ^{14}C decline (Fig. 2), the values were used to generate a von Bertalanffy growth

function from the age-at-length data (Fig. 4). The life history parameters differed greatly from the original study by Scofield (2013) in that growth rate was greater and lifespan was lower. The rapid early growth exhibited by the revised growth curve was considerably different ($k = 0.378$ cf. 0.113) and closer to estimates made in a preliminary study of the same species off Western Australia (WA; estimated $k = 0.26$ – 0.30 ; Corey Wakefield, Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia; pers. comm. 2019). While the k value presented here

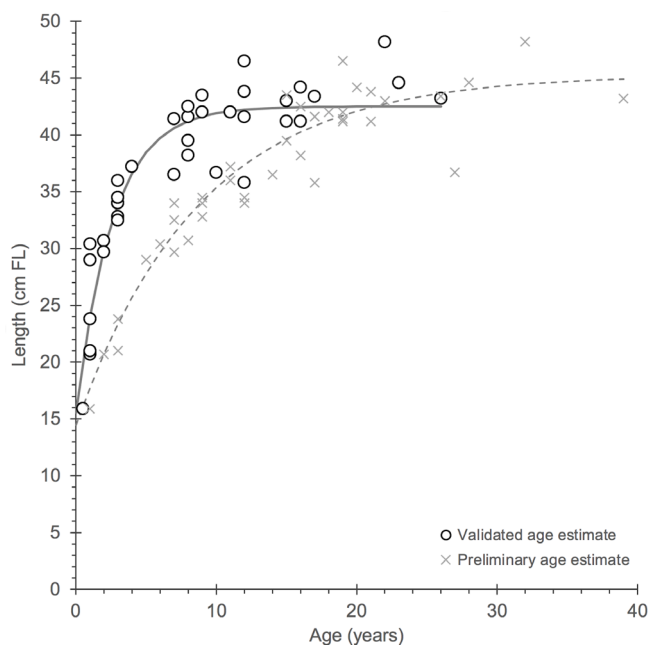


Fig. 4. Von Bertalanffy growth functions for gindai (*Pristipomoides zonatus*) in the Hawaiian Islands from the preliminary Scofield (2013) work (X symbol) and the current study (open circles) from which a considerable contrast can be observed between otolith age interpretations and growth parameters. The early work by Scofield (2013) was based on observations of purportedly annual growth zones that appeared to be well-defined, resulting in a moderate growth rate ($k = 0.113$) and maximum age approaching 40 years. Reassessed ages that were validated with bomb ^{14}C dating reveal a growth rate that is significantly greater ($k = 0.378$) with a reduced maximum age approaching 30 years. Growth function parameters for Scofield (2013): $L_{\infty} = 45.3$ cm FL, $k = 0.113$ yr $^{-1}$ and $t_0 = -3.4$ yr and the current study: $L_{\infty} = 42.5$ cm FL, $k = 0.378$ yr $^{-1}$ and $t_0 = -1.2$ yr. These findings also indicate that age at 50% maturity (A_{50}) is earlier than 6 years (the original estimate by Scofield (2013)) and is closer to 2 years ($L_{50} = 29.7$ cm FL).

is also greater than what was observed in WA, the growth function was based on few individuals and could change with the addition of more aged gindai from Hawaii using the proposed age reading protocol presented here (Fig. 1). Furthermore, the unpublished data from WA is supported with an approach similar to dendrochronology where identifiable growth events were well-correlated in time (e.g., Ong et al., 2016). Longevity is lower than originally estimated by Scofield (2013) and may be closer to 30 years in Hawaii. However, the findings from WA indicate the species may live more than 50 years from the well-defined age reading protocol (Corey Wakefield, Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia; pers. comm. 2019). It must be noted that gindai in Hawaii may not live 50 years because otoliths with a mass approaching 0.9 g (aged to early to mid-20s) were rare in collections across the Hawaiian Islands, assuming otolith mass is a reasonable proxy for age given the strongly curvilinear relationship (Table 1; Fig. 3).

Overall, the findings of this study reveal that age can be easily overestimated when validation is not attempted — studies that employ only otolith section age-reading run the risk of establishing invalid life history characteristics (e.g., O'Malley et al., 2019). Growth parameters from Scofield (2013) were believable at the time because a consistent age reading protocol was developed and other regional snapper species were longer lived than previously thought. Onaga (*Etelis coruscans*), another member of the Deep 7, has a k value of 0.105–0.126 (Andrews et al., 2021), which was consistent with the early gindai study. However, its congener opakapaka (*P. filamentosus*) — along with ehu (*E. carbunculus*) — have more rapid growth with k values on the order of 0.20–0.25 (Andrews et al., 2012; Nichols, 2019). It follows that a species often landed with the Deep 7 fishes, the uku or grey snapper (*Aprion virescens*), exhibits a rapid growth rate ($k \approx 0.3$) that is similar to gindai with a validated lifespan from bomb ^{14}C dating of 25 years (DeMartini, 2019; Nadon et al., 2020). Hence, the importance of employing age validation techniques, like the unique utility of the bomb ^{14}C decline period, to authenticate age reading protocols and the estimates of age and growth derived from otolith sections are highlighted here for deep-water snapper in Hawaii and are broadly applicable to tropical marine fishes.

Supplementary Materials

Supplementary materials are only available online from: <https://>

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Competing interests

No potential conflict of interest relevant to this article was reported.

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Availability of data and materials

Upon reasonable request, the datasets of this study can be available from the corresponding author.

Ethics approval and consent to participate

This article does not require IRB/IACUC approval because there are no human and animal participants.

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