Environ Biol Fish
https://doi.org/10.1007/s10641-024-01659-3

Validation and otolith-mass prediction of age and growth for cardinal snapper *Pristipomoides macrophthalmus* of the Caribbean Sea

Ivy E. Baremore · Allen H. Andrews · Simon J. B. Gulak · Rachel T. Graham · Matthew J. Witt · Virginia R. Shervette

Received: 29 August 2024 / Accepted: 18 December 2024

Abstract Cardinal snapper *Pristipomoides macrophthalmus* is a commercially important, but commonly misidentified, deepwater species in artisanal and semi-industrial fisheries throughout the Caribbean Sea. As with many tropical deepwater fishes, little is known about the biology or ecology of the species. Bomb radiocarbon (^{14}C) dating was applied to cardinal snapper sagittal otoliths collected from the waters of Belize and Honduras during 2015–2019 to investigate the lifespan of the species from thin-sectioned otoliths with an evaluation of otolith mass as a proxy for age. Ages estimated from 28 thin-sectioned otoliths ranged from 7 to 68 years for fish that covered the range lengths and otolith masses available. Radiocarbon values were measured for each cardinal snapper otolith core, and two fish (one each from Belize and Honduras) had ^{14}C signatures consistent with pre-bomb values, effectively validating a lifespan of at least 60 years. A curvilinear relationship between otolith mass and estimated age was robust ($r^2 = 0.95$) and is likely to produce age estimates with similar margins of error to traditional, more labor-intensive methods, such as counting increments from thin-sectioned otoliths. The otolith mass-to-age relationship is a well-supported method that provides a simple, low-cost approach that can be used by fishers, managers, and other stakeholders to assess the age composition of the cardinal snapper stock in the western Caribbean Sea for present and long-term monitoring.

Keywords Belize · Honduras · Longevity · Small scale fisheries · Deepwater · Benthic · Bomb radiocarbon

Introduction

Snappers (Lutjanidae) of the genus *Pristipomoides* are generally understudied throughout their ranges, likely due to their relatively deep distributions in tropical and subtropical waters. Many of the *Pristipomoides* species are commercially and culturally important, especially in Pacific deepwater fisheries, due to their pink to red coloration, and delicate, white

I. E. Baremore (✉)
MarAlliance, Roatán, Islas de la Bahía, Honduras
e-mail: ivy@maralliance.org

I. E. Baremore · M. J. Witt
Faculty of Health and Life Sciences, University of Exeter, Exeter EX4 4PS, UK

A. H. Andrews
Pacific Community (SPC), Oceanic Fisheries Programme, FAME, 98848 Noumea, New Caledonia

S. J. B. Gulak
Sea Leucas LLC, Seacrest, FL, USA

R. T. Graham
MarAlliance, Ciudad del Saber, Panama City, Panamá

V. R. Shervette
Fish/Fisheries Conservation Lab, University of South Carolina Aiken, Aiken, SC, USA

meat that is well-suited for raw and cooked meals (Newman et al. 2016). Like other Eteline snappers, many *Pristipomoides* snappers are relatively long-lived, although there is wide variation in growth characteristics among species with lifespan estimates covering 14 to 40 + years (Anderson et al. 2009; Andrews et al. 2012; Andrews and Scofield 2021; Schemmel et al. 2021).

Two *Pristipomoides* species from tropical waters of the western Atlantic Ocean are commonly targeted by commercial fishing efforts: cardinal snapper *P. macrophlathmus* and wenchman *P. aquilonaris*. Similarities in appearance and overlap in horizontal and vertical distributions between the two species have led to confusion in the identification of cardinal snapper and wenchman (Baremore et al. 2023). Current species descriptions indicate that both species inhabit waters in the Caribbean Sea at depths ranging from 100 to 650 m and attain similar maximum sizes (cardinal snapper = 50 cm TL, wenchman = 56 cm TL; Anderson 1966; Robertson and Van Tassell 2023). Wenchman was reported to have a broader spatial distribution across the continental shelf and throughout the Caribbean Sea, while cardinal snapper was noted as absent from the Mesoamerican region in the western Caribbean (Anderson et al. 2015; Robertson and Van Tassell 2023). A recent investigation of deepwater fisheries in waters of Belize and Honduras indicated that cardinal snapper was a common component of the deepwater fish assemblages surveyed in the region and that wenchman was smaller and caught at shallower depths than cardinal snapper (Baremore et al. 2021, 2023). Cardinal snapper is captured in some Caribbean deepwater fisheries (Brownell 1972; Luckhurst et al. 2003; Baremore et al. 2021, 2023), but it has likely been misidentified and reported as wenchman or southern red snapper (*Lutjanus purpureus*) in other regions (Rosario et al. 2006; Quinn 2007; Grant 2019). This is a problem that needs to be addressed if snapper fisheries in this region are to be properly assessed for life-history characteristics and in long-term age-structured population demographics monitoring.

Deepwater fishes tend to exhibit a combination of life-history characteristics that make them inherently vulnerable to overexploitation, such as slow growth, late maturity, and typically greater lifespan (Koslow 2000; Norse et al. 2012; Newman et al. 2016; Andrews et al. 2020). Traditional age-estimation techniques using growth zone enumeration in thin-sectioned otoliths can be difficult for tropical and deepwater species due to several factors that affect otolith microstructure, such as differing seasonal variations in temperature, food availability, and water quality (Morales-Nin and Panfili 2005; Widdrington et al. 2024). Validation of age-estimation methods is necessary for accurate age analyses and yet it is rarely performed for species of low economic value, or those that occur in tropical low- and middle-income countries, or both. Caution should be exercised when life-history parameters, like growth rates, longevity, and natural mortality, are inferred from the same or similar species from regions with different fishing and mortality rates (Babcock et al. 2013; Stevens et al. 2019). Over and under estimation of age can lead to a misunderstanding of the biology and ecology of a species, and as a result, inappropriate management strategies can be implemented, with negative fishery impacts (Reeves 2003). While reliable proxies for age estimation using otolith morphometrics or mass have been assessed for deepwater species (Cook et al. 2009; Williams et al. 2015; Sanchez et al. 2019; Andrews et al. 2020; Andrews and Scofield 2021), the approaches have not been widely adopted.

Bomb radiocarbon (^{14}C) dating is a well-established method for validating estimates of age for fishes throughout the world and across a variety of marine habitats (Campana 1997; Andrews et al. 2011b; Passerotti et al. 2014; Horn et al. 2019). It is especially useful for long-lived teleost fishes for which traditional mark-recapture techniques are difficult or impossible, and in tropical species that may be difficult to age using otolith sections (Cailliet and Andrews 2008; Cook et al. 2009; Andrews et al. 2012, 2013, 2020; Andrews and Scofield 2021; Shervette et al. 2021; Overly and Shervette 2023). The method relies on a time-specific signal of ^{14}C that was created by atmospheric thermonuclear testing in the 1950s and 1960s. This signal diffused into the marine environment and was sequestered by calcified structures of marine organisms, thereby creating synchronous reference chronologies in corals, bivalves, and fishes worldwide that are useful in age validation studies (Druffel 1980; Campana 1997). Age validation for teleost fishes can be accomplished by analyzing this ^{14}C signature in the core of an otolith, representing the hatch year of the fish, in comparison to a regionally appropriate ^{14}C reference chronology.

The objectives of this study were to determine the age and growth characteristics of cardinal snapper using otoliths by (1) estimating the age from growth zone or annuli enumeration in thin-sectioned otoliths; (2) testing the validity of estimated age and lifespan with bomb ^{14}C dating; (3) establishing a basis for the low-cost method of using otolith mass as a proxy for cardinal snapper age in the study region; and (4) establishing the identification protocol for the species.

Methods

Sample selection

Cardinal snapper specimens ($n = 388$) were collected in Belize and Honduras from 2015 to 2022 using fishery-independent vertical longlines (Baremore et al. 2023; Fig. 1). All fish specimens were weighed (±0.1 kg wet weight) and measured for standard (SL), fork (FL), and total lengths (TL, ±0.1 cm). Sagittal otolith pairs were extracted, cleaned, cataloged, and stored dry until processing. All whole otoliths were photographed, weighed (±0.0001 g), and measured for height, width, and thickness (±0.1 mm). Because of the strong decoupling of length from age exhibited by numerous tropical snappers, a sampling design using otolith mass was developed to select a likely series of the youngest to oldest fish (least to most massive otoliths) ($n = 28$; Table 1). One otolith from each pair was selected for sectioning and the other was conserved for bomb ^{14}C analysis.

Species identification

Due to known problems with identification of cardinal snapper and wenchman, several methods were applied to ensure that all samples in this study

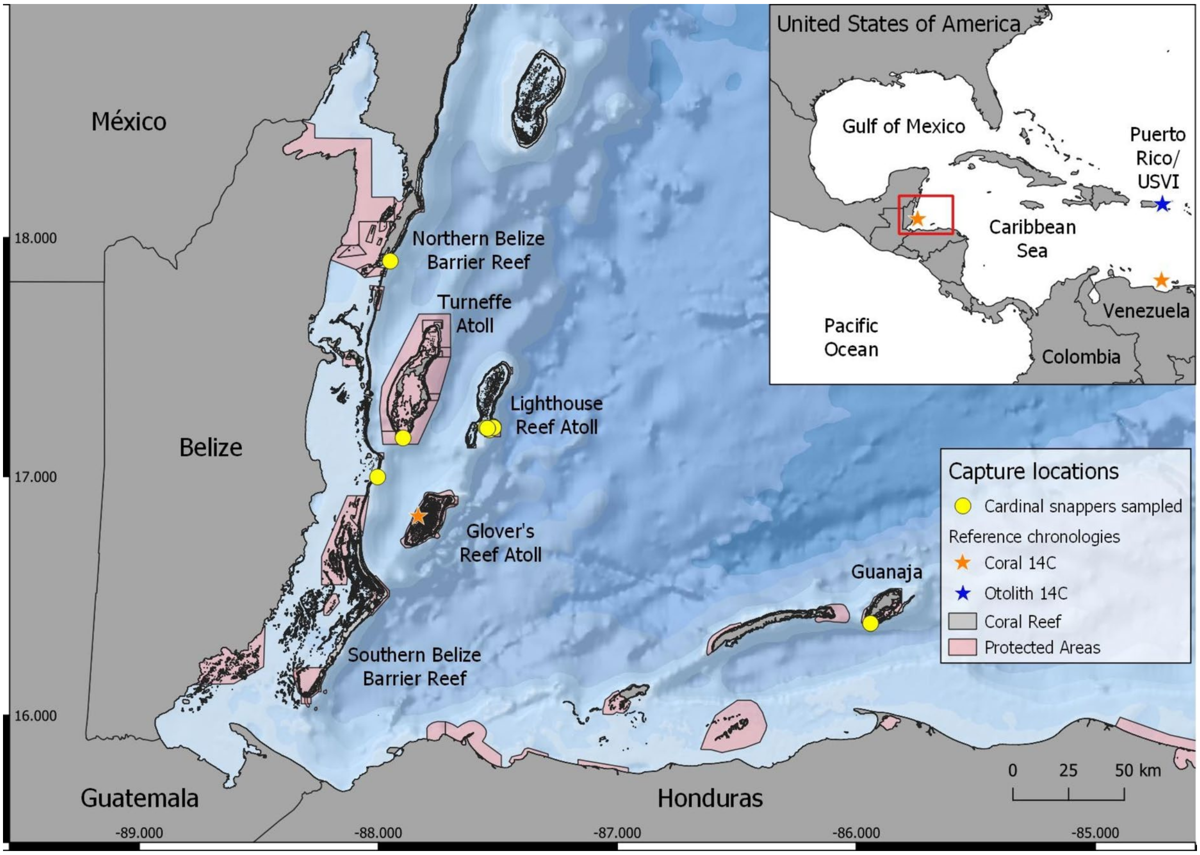


Fig. 1 Sampling locations for cardinal snapper used in age estimation and bomb ^{14}C dating from Belize and Honduras (collection years 2015–2022; Baremore et al. 2023). The ocean map layer was made with the ESRI Ocean plugin in QGIS

Table 1 Fish and radiocarbon data for the cardinal snapper (*Pristipomoides macrophthalmus*) specimens and the otoliths used in this study to align with a regional bomb ^{14}C reference chronology. Measured radiocarbon values are listed as fraction modern (F^{14}C) with the corresponding date-corrected Δ^{14}C values. Diagnostic (Diag) Δ^{14}C values for the bomb ^{14}C rise and post-peak decline with the alignment dates were used to assess age estimate accuracy. Data are sorted in descending order by otolith mass. Locations are LRA = Lighthouse Reef Atoll, Belize; TUR = Turneffe Atoll, Belize, NBZ = Northern Belize Barrier Reef, SBZ = Southern Belize Barrier Reef; GUA = Guanaja, Honduras

Lab no	Location	Collection	Sex	FL (cm)	TL (cm)	Age	Hatch	Mean otolith mass	F14C	Δ14C	Diag
S1.7–1	GUA	10-Oct-2019	M	46.5	54.0	68	1951	1.7475	0.9400	60.2	Pre-B
S1.5–1	LRA	20-May-2015	M	44.0	50.5	64	1951	1.5300	0.9497	51.4	Pre-B
S1.3–1	LRA	5-May-2016	M	43.5	50.4	49	1967	1.3185	1.1125	110.2	Rise
S1.2–1	LRA	15-May-2017	M	41.2	47.8	49	1968	1.2725	1.0835	79.9	Rise
S1.2–2	LRA	20-May-2015	M	46.0	54.5	48	1967	1.2570	1.0982	95.2	Rise
S1.2–3	GUA	10-Oct-2019	M	47.0	54.3	47	1972	1.2145	1.1138	110.8	Rise
S1.2–4	LRA	15-May-2017	M	41.9	49.5	45	1972	1.2045	1.1216	119.3	Rise
S1.1–2	LRA	18-May-2017	M	44.1	50.3	44	1973	1.1565	1.1144	111.1	Rise
S1.0–1	LRA	15-May-2017	F	41.2	47.6	37	1980	1.0920	1.1229	118.4	Peak
S1.0–2	LRA	15-May-2017	F	41.2	47.3	37	1980	1.0080	1.1043	99.6	Peak
S0.9–1	LRA	15-May-2017	M	42.0	47.0	35	1982	0.9910	1.1148	109.8	Peak
S0.9–2	LRA	15-May-2017	F	45.2	52.0	37	1980	0.9580	1.1048	100.6	Peak
S0.9–3	LRA	15-May-2017	F	40.5	46.8	40	1977	0.9520	1.1271	123.4	Peak
S0.9–4	LRA	15-May-2017	F	43.5	50.5	34	1983	0.9255	1.1166	112.1	Peak
S0.8–1	LRA	15-May-2017	M	41.0	46.9	27	1990	0.8930	1.1048	99.4	Decline
S0.8–2	LRA	15-May-2017	M	44.0	50.4	32	1985	0.8820	1.1003	95.3	Decline
S0.8–3	LRA	15-May-2017	F	43.0	49.4	28	1989	0.8700	1.1013	95.7	Decline
S0.7–1	LRA	15-May-2017	M	44.0	50.5	25	1992	0.7990	1.0932	87.3	Decline
S0.7–2	LRA	15-May-2017	F	39.3	45.4	18	1999	0.7940	1.0823	75.4	Decline
S0.7–3	LRA	15-May-2017	F	41.4	48.4	26	1991	0.7520	1.1051	99.4	Decline
S0.7–4	LRA	15-May-2017	M	39.1	44.7	16	2001	0.7370	1.0809	74.1	Decline
S0.7–5	LRA	15-May-2017	F	40.8	46.8	18	1999	0.7045	1.0841	77.4	Decline
S0.6–1	LRA	15-May-2017	M	40.0	46.3	18	1999	0.6285	1.0895	82.5	Decline
S0.5–1	LRA	15-May-2017	F	41.0	46.9	25	1992	0.5925	1.0928	85.7	Decline
S0.5–2	LRA	18-May-2017	M	38.7	45.0	18	1999	0.5040	1.0800	72.7	Decline
S0.4–1	TUR	20-Mar-2017	F	37.0	42.0	11	2006	0.4505	1.0785	71.2	Decline
S0.4–2	SBZ	19-Oct-2017	M	32.5	37.6	10	2007	0.4320	1.0706	63.0	Decline
S0.3–1	NBZ	13-Dec-2017	F	30.8	35.9	7	2010	0.3220	1.0501	42.1	Decline

were *P. macrophthalmus* (cardinal snapper). Lateral line scale counts were made for captured *Pristipomoides* individuals or from photographs when possible. Those with scale counts ≥ 54 were identified as cardinal snapper (Anderson 1966; Robertson and Van Tassell 2023; Fig. 2). Relationships among otolith morphometrics, including length, width, depth, and weight, were examined for outliers, as were the horizontal plane shape and extent of otolith curvature as otolith morphometrics are different between the two species.

Otolith processing and bomb radiocarbon dating

Sagittal otoliths selected for sectioning and refinement of the age-reading protocol were embedded in resin and cut into three transverse sections (0.5 mm thick) with a low-speed saw using diamond-edged blades. Sections were mounted to slides using a clear mounting medium and viewed under a stereomicroscope at 20–60 × magnification. Digital images were taken of the otolith sections for each fish and were evaluated for growth zone structure.

Fig. 2 Mature female cardinal snapper (42.3 cm FL) with 54–55 lateral line scales, pink-colored pectoral fin base, and golden eye. Photo by Samuel RD Owen

The second sagittal otolith of each pair was prepared for core material extraction by embedding it whole in resin. Each was cut with a low-speed saw with a diamond-edged blade to obtain a thick sections (3 mm) containing the otolith core and was mounted to a microscope slide. The mounted sections were thinned to ~1 mm thick to the point where the core could be milled as a well-centered extraction (Fig. 3). The carbonate sample was extracted directly from the section using a New Wave micromilling machine (Elemental Scientific Lasers, Bozeman, MT, USA) with a 0.5 mm carbide bur (Brasseler, Savannah, GA, USA). The extraction scan path length was 2.5 mm (end-to-end) at a depth of 0.15 mm in three consecutive passes for a total sample mass of approximately 0.5 to 1.0 mg (Fig. 3). Otolith core material for each sample was transferred to pre-cleaned vials for ^{14}C analysis.

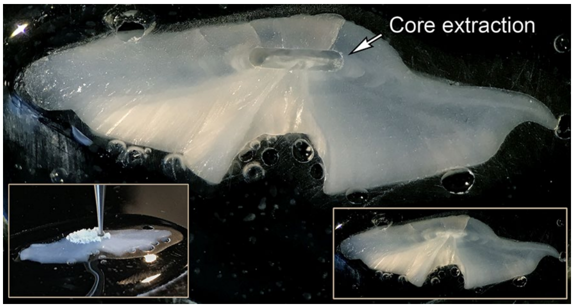


Fig. 3 Thick-cut cardinal snapper otolith with the core extracted using the micromill for.^{14}C analysis with AMS. The extraction was in the form of powder that was collected from the surface of the slide (inset image left) after removal with a 0.5-mm carbide cutting bur (Brasseler, USA). Scale can be observed from the core extraction path of 2.5 mm (end-to-end) in the nuclear region of the cored otolith section. Note the clearly specific removal of otolith core material from the original section (inset image lower right)

Radiocarbon measurements — accelerator mass spectrometry

The extracted otolith samples were analyzed by gas-accelerator mass spectrometry (AMS) for carbon isotopes using the Mini Carbon Dating System (MICADAS; (Synal et al. 2007) in the Laboratory of Ion Beam Physics at ETH Zürich, Switzerland (Wacker et al. 2013). Samples were processed in septum-sealed vials (Labco, Exetainer 4.5 mL vials) purged with helium. Sample CO_2 was subsequently generated with 80% phosphoric acid. Fossil and modern reference materials (IAEA-C1) (Rozanski 1991) and an in-house coral standard (CSTD, nominal F^{14}C value 0.9447 ± 0.0002, G. Dos Santos, pers. comm.) were analyzed in parallel with the otolith samples. Data evaluation was performed with the “Beautiful AMS Tool of Switzerland” software (BATS), an analysis routine that functions as a reliable data reduction tool (Wacker et al. 2013). All ^{14}C results were reported as fraction modern (F^{14}C), which corresponds to the fractionation-corrected sample activity (Reimer et al. 2004).

Reference ^{14}C time series

Coral and otolith ^{14}C records from the Gulf of Mexico and Caribbean Sea were assembled to illustrate the consistency of the bomb-produced ^{14}C time series across this large area and to provide a baseline for comparison of the measured ^{14}C values from the cardinal snapper samples, consisting of records from validated coral cores (Druffel 1980, 1996; Kilbourne et al. 2007; Wagner et al. 2009; Moyer and Grottoli 2011; Toggweiler et al. 2019; Paterne et al. 2023), known-age juvenile fish otoliths (Baker and Wilson 2001; Cook et al. 2009; Andrews et al. 2013, 2020; Shervette et al. 2021), and edge material extracted from older fish otoliths with known collection dates (Shervette et al. 2021). Each of the ^{14}C reference samples as a time series covered some or all of the bomb ^{14}C signal within the mixed surface layer (<100 m depth). The combined ^{14}C reference time series was fitted with a Loess curve (2 parameter, 0.3 spline interpolation) to show the central tendency and to provide a basis for the alignment of otolith core ^{14}C values. Two additional records were fitted with the same Loess curve to illustrate slight regional differences and the potential influence of different water sources: (1) Glover's Reef Atoll, Belize (Druffel 1980); and (2) coral reefs off Venezuela (Wagner et al. 2009; Fig. 1). The Belize record was the closest coral record to the study area and represented a more timely ^{14}C response record for the ^{14}C rise period, depicting waters with greater residence time in the mixed layer; however, this chronology does not extend into the post-peak decline period due to its early collection date (Druffel 1980). The reference time series from Venezuela is a slightly ^{14}C-deficient record that represents the expected influence of mixed equatorial waters via the North Equatorial and North Brazil currents (Toggweiler et al. 2019).

Age estimation

Ages were estimated by counting growth zones of the thin-sectioned otoliths, with opaque zones counted using an area along the ventral growth axis and the ventral side of the otolith sulcus (Fig. 4). Initial estimates were made independently by three age readers (two experienced and one novice) with a consensus age determination from a consultation among the three readers. When age estimates differed among readers for the initial reads, final ages were determined by consensus of three readers viewing the otolith images concurrently. Age estimates from otolith sections were used to compute the estimated hatch year of the fish based on the year of sample collection. Hatch year from the otolith core ^{14}C for each specimen was overlaid on the reference time series described above.

To refine the age-reading protocol, minor offsets on the post-peak decline were used to adjust ages that were more difficult to derive without consultation of well-defined otolith. Otoliths that were offset in time were slightly over- or underestimated for age based on the side that the data point fell out relative to the decline relationship. Otoliths that were well-defined were used as a visual reference (Rosetta Stone otoliths) to adjust the counting scenario for the over- or underaged fish. Age estimate precision among readers was determined prior to and after the age reading protocol was refined using average percent error (APE) and coefficient of variation (CV) (Beamish and Fournier 1981; Chang 1982); however, a consistent age reading protocol was difficult to derive due to the growth zone structure in the earliest part of the otolith section. Hence, it was deemed that otolith mass may be the most consistent indicator of age.

The otolith mass-to-age relationship was investigated with linear and non-linear regressions and the final model was chosen based on the highest correlation coefficient (r^2) and an examination of the residuals. To further investigate the otolith mass-to-age relationship, age estimates were determined for the remaining set of cardinal snapper otoliths ($n=360$) by applying the final mass-to-age regression model (derived from the bomb ^{14}C validated otoliths) to the measured mean otolith mass of the sagittal pair. Length-at-age estimates were plotted, and a three-parameter von Bertalanffy growth function (VBGF) (von Bertalanffy 1938) was fitted to the predicted and validated ages ($n=388$):

$$L_t = L_\infty \left(1 - e^{-k(t-t0)}\right),$$

where L_∞ was the asymptotic length (FL), k was the growth coefficient, and t_0 was the x-intercept of the curve.

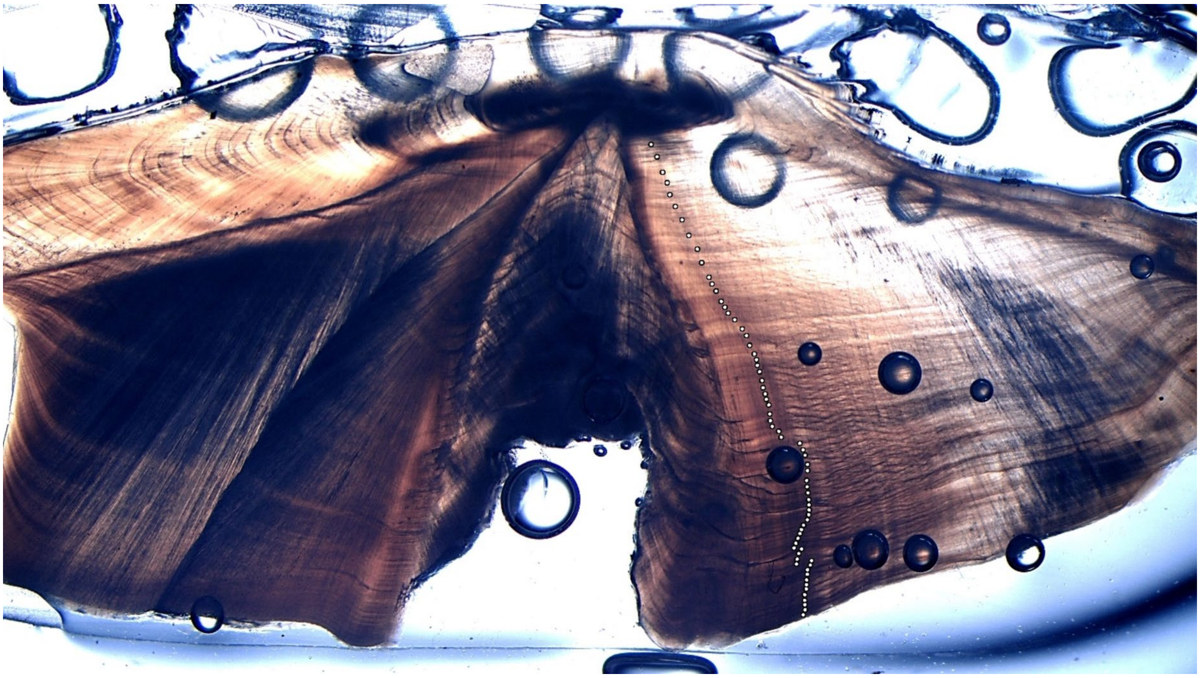


Fig. 4 Photograph of a sagittal otolith transverse section from a cardinal snapper *Pristipomoides macrophthalmus* aged to 68 years with fairly well-defined growth zone structure that was validated with bomb ^{14}C dating (sample number S1.7–1). Note that counting early is wider and more encompassing of smaller increments based on counting and alignment of smaller and younger individuals. This section is an example of a Rosetta Stone otolith that was used in the refinement of otolith age reading when considering minor misalignments of measured ^{14}C values from the collective bomb ^{14}C reference chronology. Hence, the final age reading protocol is based on validated age estimates, similar to the approach used for its congener, *P. zonatus* of the Hawaiian Islands and Guam (Andrews and Scofield 2021; Schemmel et al. 2021), but mass was ultimately deemed most reliable in terms of age estimation

Results

Two fish specimens initially identified visually as cardinal snapper were determined to be wenchman and removed from further analyses. One wenchman was identified based on its small size at maturity (female, 15.0 cm FL) and subsequent lateral line scale count of 52. The second was identified from otolith morphometrics (small otolith mass in relation to body size) and subsequent lateral line scale count of <54 from a photo.

Otoliths from the selected 28 cardinal snapper (30.8 – 47.0 cm FL, 0.32 – 1.75 g mean otolith mass) were used in initial assessments of age from the thin-sectioned otoliths, in combination with extraction of otolith core material for bomb ^{14}C dating (Table 1). Of the fish selected for the analyses, 26 were collected in Belize ($n=23$ from Lighthouse Reef Atoll, $n=2$ from the Belize Barrier Reef, and $n=1$ from Turneffe Atoll) and two in Guanaja, Bay Islands, Honduras (Table 1; Fig. 1). Depth of capture ranged from 212 to 363 m.

Radiocarbon values were successfully obtained for otolith cores from all 28 cardinal snapper age validation samples. Pre-bomb ^{14}C values from two otoliths ($n=1$ from Belize, $n=1$ from Honduras) were consistent with the range of pre-bomb levels from the ^{14}C reference time series based on the estimated hatch years (Table 1; Fig. 5). These two samples were males between 44.0 and 46.5 cm FL and had the two heaviest otoliths (>1.5 g) of all cardinal snapper samples processed in the current study. Individuals with lower sagittal otolith masses had hatch year estimates and ^{14}C values that occurred within the upper rise and peak periods, and through the recent decline period, of the combined ^{14}C reference chronology (Fig. 5). The youngest fish (estimated age of 7 years) had the lowest otolith mass and the oldest fish (estimated age

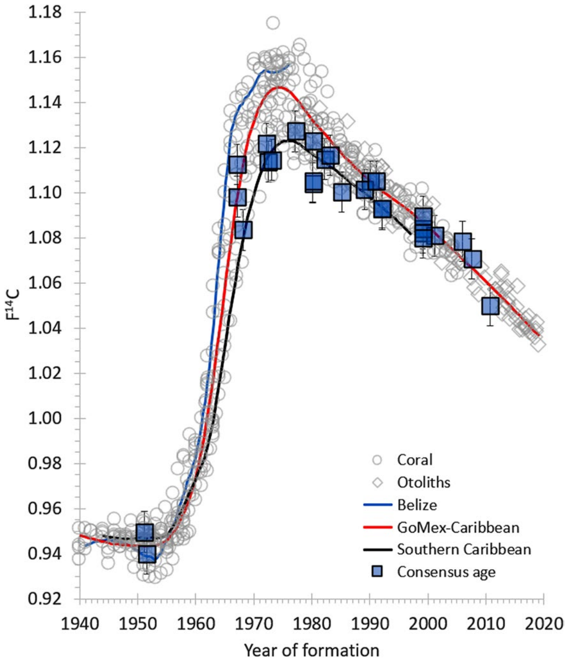


Fig. 5 All known coral and otolith ^{14}C records for the Gulf of Mexico and Caribbean Sea with Loess curve (2 parameter, 0.3 spline interpolation; Andrews et al. 2013; Shervette et al. 2021). The hatch years for cardinal snapper were calculated from the consensus ages for the measured ^{14}C values from otolith cores, which were determined in concert with Rosetta Stone reference otolith sections and the alignment to the regional reference chronologies. Included are fits to coral records from Glover's Reef off Belize (Druffel 1980) and from reefs off Venezuela (Wagner 2009) to illustrate minor differences that are associated with the oceanography of the Caribbean Sea

of 68 years) had the greatest otolith mass (Table 1). Among reader precision was 5.7% (APE) and 7.7% (CV).

An analysis of the relationship between otolith mass and age revealed a strong correlation that was supported by the alignment of ^{14}C values with the reference chronologies. A power function provided the best fit for the otolith mass-to-age relationship ($r^2 = 0.947$; Fig. 6). Although a linear relationship had a similar fit to the data ($r^2 = 0.946$), it provided underestimates for the youngest fish with otolith mass < 0.2 g. The highest residual error was found for fish between 15 and 30 years of age ($n = 10$).

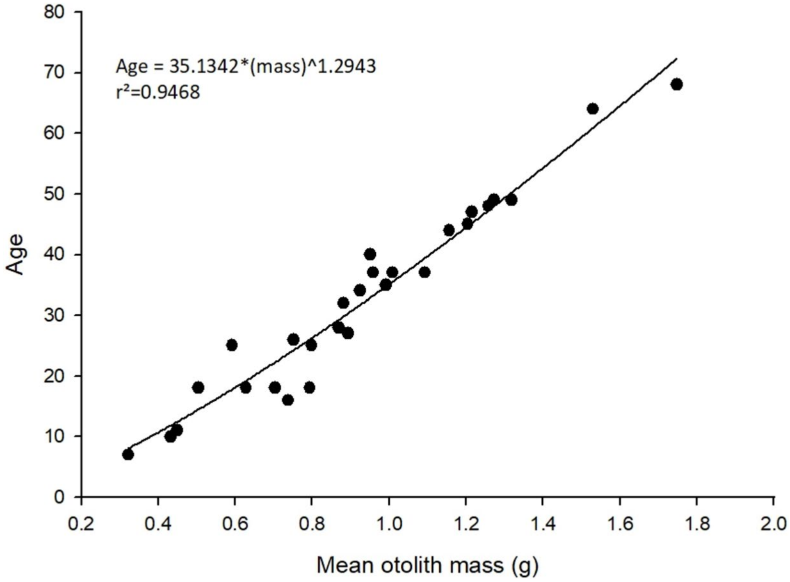
Application of the mean otolith mass-to-age predictive regression to the full dataset of cardinal snapper ($n = 360$) generated estimated ages ranging from 3 to 44 years (18.5 – 46.2 cm FL; 0.146 – 1.189 g mean otolith mass). Estimated ages provided a plausible length-at-age curve, as no negative ages were estimated for the smallest fish with the lightest otoliths (Fig. 7). The VBGF parameters estimated from the calculated and validated ages ($n = 388$) were also reasonable based on the size-at-age distribution ($L_\infty = 44.5$ cm FL, $k = 0.11$, $t_0 = -2.5$).

Discussion

Bomb ^{14}C dating successfully validated the lifespan of the deepwater cardinal snapper in the western Caribbean Sea to at least 60 years. Several tropical deepwater snappers in the Pacific Ocean have confirmed lifespans of more than 30 – 40 years using bomb ^{14}C dating (Andrews et al. 2011a, 2012, 2020; Nichols 2019; Andrews and Scofield 2021), but to date, the ages of relatively few lutjanid species have been validated (Piddocke et al. 2015). The lifespan of cardinal snapper is among the highest reported for snappers in the western Atlantic Ocean and stands in contrast to other regional species as a fish that attains a maximum size of ~ 48 cm FL (55 cm TL). In comparison, queen snapper *E. oculatus* and northern red snapper *L. campechanus* can reach respective lifespans of 45 and 60 years (Andrews et al. 2019; Overly and Shervette 2023), but their maximum reported sizes are twice the length at ~ 100 cm FL in the western Atlantic Ocean (Anderson Jr. 2001; Robertson and Van Tassell 2023).

Early overcounting of growth zones can lead to overestimated age for cardinal snapper, a common problem in the age reading of otoliths, as highlighted by a case study on gindai *P. zonatus* otoliths from Hawaiian waters (Andrews and Scofield 2021). Another study of *P. zonatus* in Guam utilized the validated age reading protocol by referring to the original otolith sections to derive similar growth characteristics (Schemmel et al. 2021). Lacking validation, studies on the age and growth of cardinal snapper would likely suffer the same fate as initially described for *P. zonatus*, in which growth was estimated to be much slower and the lifespan at least a decade greater, before the age reading protocol was refined using bomb ^{14}C dating. These studies underscore the importance of validating age and growth estimates, as well as the long-held recommendation that all age

Fig. 6 Logarithmic regression of otolith mass-to-age relationship for aged cardinal snapper showing a strong correlative relationship

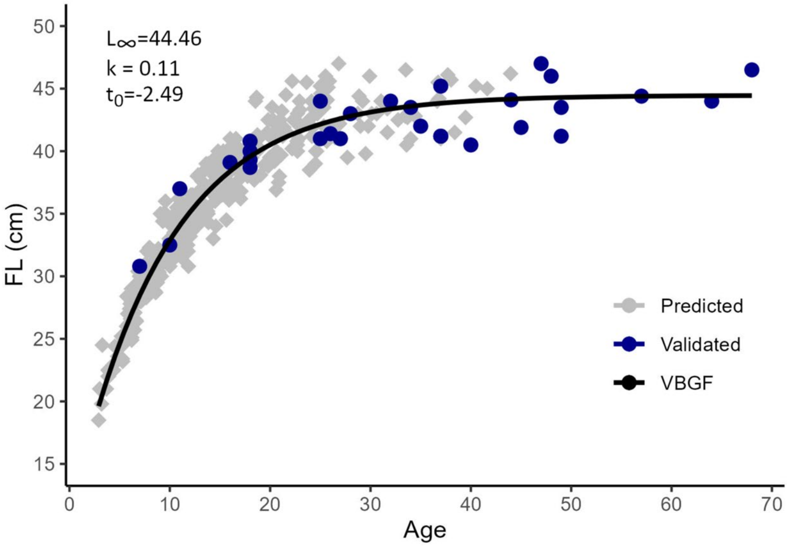


classes must be validated for age and growth studies (Campana 2001).

Misidentification of cardinal snapper and wenchman is problematic for managers throughout the ranges of the species. It is likely that wenchman mature at a much smaller size (~ 13 cm FL) than cardinal snapper (~ 25–30 cm FL) and reach a slightly smaller maximum length (44 cm vs. 48 cm FL, respectively). Individual variation in coloration of the body and caudal fins has been observed in cardinal snapper; therefore, color should not be a primary tool for species identification. Although wenchman mature at a smaller size, the appearance becomes more similar to cardinal snapper when greater than 30 cm FL. Lateral line scale count appears to be the most reliable method of distinguishing the two species, as the number does not overlap (wenchman: 49 – 52 vs. cardinal: 54 – 57; Anderson 1966; Robertson and Van Tassell 2023), although it is somewhat of a burdensome technique for fisheries practitioners to use in the field and on every fish collected.

Larger, older fish can be especially important for sustaining fish populations due to numerous factors,

Fig. 7 Fork length (FL) at predicted age for all sampled cardinal snapper as determined from mean otolith mass (grey diamonds) and 28 cardinal snapper that were validated with bomb.^{14}C dating (blue circles), with a fitted von Bertalanffy Growth Function (VBGF) for the combined dataset ($L_\infty = 44.5$ cm FL, $k = 0.11$, $t_0 = -2.5$)



including reduction in lifetime productivity, loss of genetic diversity, and loss of rebound potential from overfishing (Beamish et al. 2006; Cailliet and Andrews 2008). There is also evidence that BOFFs (Big Old Fecund Females) can not only contribute exponentially more eggs than the younger females, but also produce larvae that have higher survival rates (Birkeland and Dayton 2005; Longhurst 2006; Hixon et al. 2014). Size-selective fishing can also cause evolutionary changes in the life-history traits of exploited populations, potentially leading to fishery collapse (Pukk et al. 2013). Differing exploitation rates of deepwater fishes appear to have truncated the size structure and depth-distribution of snappers in Honduras relative to Belize: cardinal snapper from the more heavily exploited Honduran waters were, on average, nearly 7 cm smaller than their counterparts in Belize where fishing effort is lower (Baremore et al. 2023). Given the potential longevity of cardinal snapper, removal of the largest and oldest fish could undermine its spawning potential in the region if the younger fish are indeed less productive than the older fish (Beamish et al. 2006).

Traditional methods used to estimate the age of fishes are typically labor intensive, require technical expertise, and are ultimately costly or unattainable in some regions. As a result, fishery managers and scientists in low- and middle-income countries rarely undertake species-specific age and growth studies due to lack of funding, climate-controlled laboratory space and specialized equipment, and other long-term capacities such as retaining trained personnel (Pita et al. 2019). The use of otolith mass as a proxy for fish age has been studied since the 1970s (e.g. Beamish 1979; Boehlert 1985; Pilling et al. 2003) and was recently revealed as a statistically supported proxy for age estimation for other fish species (Pacheco et al. 2021). Despite the great potential of this approach, there seems to be a reticence among practitioners to apply the use of otolith mass to estimate age on a broader scale (Williams et al. 2015).

The findings of this study indicate that there is a strong relationship between otolith mass and age of cardinal snapper and that it can be used to approximate age in the study area. Although the sample size was low, the regression included fish from a representative sampling of young to old fish. This approach alleviates the problem of length-based age classes that are lost with asymptotic growth due to a decoupling of age from fish length early in life (Andrews et al. 2016). Hence, low-cost digital scales can be used to study the age structure of cardinal snapper from collections made in the field in an efficient and inexpensive manner—especially considering the high otolith mass range of youngest to oldest fish—and would enable rapid feedback to stakeholders on stability or changes to the age structure, including the landings of immature fish. However, as the use of otoliths for age and growth studies is necessarily a lethal technique, caution should be applied when considering the implementation of fishery-independent studies, especially for fishes that are vulnerable to extinction.

Otolith growth is influenced by several factors, including temperature, water chemistry, photoperiod, and diet, and unlike somatic growth, otoliths continue to grow through ontogeny (Morales-Nin 2000). Because otolith mass is directly related to the proportion of aragonite and total organic matter, the chemical composition of the seawater likely affects the weight of individual fish otoliths, and therefore regional differences in water chemistry are likely to cause variation in otolith mass at age (Kalish 1989; Campana 1999; Lou et al. 2005). Analysis of otolith mass to age relationships for common coral trout *Plectropomus leopardus* across differing spatial scales indicated that otolith mass-to-age relationships generally predicted modal age within ± 1 year, with predictive accuracy highest at local scale levels and lowest at regional levels (Lou et al. 2005). Individual variation in otolith mass, as well as overlap in the range of otolith mass across ages, are likely causes of error in the predictive otolith mass to age model. Future work should focus on increasing the sample size and exploring more options for estimation of error due to the variability of the relationship between otolith mass and age of cardinal snapper.

Excluding low-cost alternative methods from study results can contribute to “parachute science” because there exists little opportunity for replication or continuation of studies by local scientists and managers in many countries. Developing simple, replicable methods for resource management and conservation should be a priority for scientists whenever possible. The use of otolith mass as a proxy for age creates an immediate opportunity for implementation in field surveys of this nature. We recommend that fisheries assessments of cardinal snapper in the western Caribbean use otolith mass as a proxy for age, and that further investigation of the life history traits, including reproductive age, size, and periodicity be pursued to complete the information necessary for proper understanding and management.

Acknowledgements Thank you to Negar Haghipour (AMS sample processing) along with Lukas Wacker, Marcus Christl, and Arno Synal (project support) from the Laboratory of Ion Beam Physics at ETH Zürich. We thank the many research officers, fishers, volunteers, and interns who helped collect samples and record data, including Cameron Rhodes, Cynthia Xiu, Thomas Meyer, Perry Fennell, Julia Shuart Fennel, Clara Sabal, Daniel Castellanos, Evaristo Muschamp, Evan Cuevas, Hilmar Salazar, Exson Flores, Mario David, Argelia Bustillo, and Martha Medrano. Matthew Craig and Jamie Stevens provided valuable suggestions for the improvement of the manuscript. Research was conducted under annual research permits from the Belize Fisheries Department (0017-15; 0009-16; 0013-17; 0003-19; 0004-20; 0003-21; 0009-22) and in Honduras from the Instituto Nacional de Conservación y Desarrollo Forestal Áreas Protegidas y Vida Silvestre (ICF) (Resolución-DE-MP-119-2015; 136-2016; 054-2018; 071-2021) and Secretaria de Agricultura y Ganadería (SAG) (Resolución-SAG-045-2021). Export permits were obtained prior to shipping samples. For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Author contribution Ivy Baremore collected all biological samples for the analysis and was the third reader of the otolith sections for age estimation. Simon Gulak catalogued, prepared, and sectioned the otoliths and performed all otolith measurements. Allen Andrews extracted the otolith core material, processed the extracted material for analysis, analyzed the bomb radiocarbon data, and was the first reader. Virginia Shervette was the second reader and digitized all otolith sections. Rachel Graham conceptualized and fundraised for the project. Project development and data analyses were supervised by Matthew Witt and Rachel Graham. Ivy Baremore wrote the first draft of the manuscript, and all authors reviewed and contributed to the final manuscript.

Funding MAR Fund, University of Exeter, MarAlliance, NOAA Saltonstall-Kennedy Grant Number: NA22NMF4270149.

Data availability Datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval Field methodology was approved through the University of Exeter's ethics review board (Application ID: 493411).

Conflict of interest The authors declare no competing interests.

References

Anderson Jr. WD (2001) National Audubon society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda. Alfred A. Knopf, Inc., New York

Anderson Jr William D (1966) A new species of Pristipomoides (Pisces: Lutjanidae) from the tropical western Atlantic. Bull Mar Sci 16:814–826

Anderson B, Lombardi-Carlson L, Hamilton A (2009) Age and growth of wenchman *Pristipomoides aquilonaris* from the northern Gulf of Mexico. Proc Gulf Carib Fish Inst 61:210–217

Andrews AH, Kalish JM, Newman SJ, Johnston JM (2011a) Bomb radiocarbon dating of three important reef-fish species using Indo-Pacific Δ^{14}C chronologies. Mar Freshwater Res 62:1259–1269. https://doi.org/10.1071/MF11080

Andrews AH, Kerr LA, Burgess GH, Cailliet GM (2011b) Bomb radiocarbon and tag-recapture dating of sandbar shark (*Carcharhinus plumbeus*). Fish Bull 109:454–465

Andrews AH, DeMartini EE, Brodziak J, Nichols RS, Humphreys RL (2012) A long-lived life history for a tropical, deepwater snapper (*Pristipomoides filamentosus*): bomb radiocarbon and lead–radium dating as extensions of daily increment analyses in otoliths. Can J Fish Aquat Sci 69:1850–1869. https://doi.org/10.1139/f2012-109

Andrews AH, Barnett BK, Allman RJ, Moyer RP, Trowbridge HD (2013) Great longevity of speckled hind (*Epinephelus drummondhayi*), a deep-water grouper, with novel use of postbomb radiocarbon dating in the Gulf of Mexico. Can J Fish Aquat Sci 1140:1131–1140

Anderson W, Claro R, Cowan J, Lindeman K, Padovani-Ferreira B, Rocha LA, Sedberry G (2015) *Pristipomoides macrophthalmus* (errata version published in 2017). The IUCN Red List of Threatened Species 2015: e.T190372A115315839. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T190372A1949460.en

Andrews AH, DeMartini EE, Eble JA, Taylor BM, Lou DC, Humphreys RL (2016) Age and growth of bluespine unicornfish (*Naso unicornis*): a half-century lifespan for a keystone browser, with a novel approach to bomb radiocarbon dating in the Hawaiian Islands. Can J Fish Aquat Sci 73:1575–1586. https://doi.org/10.1139/cjfas-2016-0019

Andrews AH, Yeman C, Welte C, Hattendorf B, Wacker L, Christl M (2019) Laser ablation–accelerator mass spectrometry reveals complete bomb ^{14}C signal in an otolith with confirmation of 60-year longevity for red snapper (*Lutjanus campechanus*). Mar Freshwater Res 70:1768. https://doi.org/10.1071/MF18265

Andrews AH, Brodziak J, DeMartini EE, Cruz E, Andrews AH, Brodziak J, DeMartini EE, Cruz E (2020) Long-lived life history for onaga *Etelis coruscans* in the Hawaiian Islands. Mar Freshwater Res 72:848–859. https://doi.org/10.1071/MF20243

Andrews AH, Scofield TR (2021) Early overcounting in otoliths: a case study of age and growth for gindai (*Pristipomoides zonatus*) using bomb ^{14}C dating. Fish Aquat Sci 24:53–62. https://doi.org/10.47853/FAS.2021.e6

Babcock EA, Coleman R, Karnauskas M, Gibson J (2013) Length-based indicators of fishery and ecosystem status: Glover's Reef Marine Reserve, Belize. Fish Res 147:434–445. https://doi.org/10.1016/j.fishres.2013.03.011

Baker SM, Wilson CA (2001) Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico. Limnol Oceanogr 46:1819–1824. https://doi.org/10.4319/lo.2001.46.7.1819

Baremore IE, Graham RT, Witt MJ (2021) Fishing down the reef slope: characteristics of the nearshore deepwater fisheries of MesoAmerica. Ocean Coastal Manage 211:105773. https://doi.org/10.1016/j.ocecoaman.2021.105773

Baremore IE, Graham RT, Owen SRD, Witt MJ (2023) Small-scale fishing has affected abundance and size distributions of deepwater snappers and groupers in the MesoAmerican region. Rev Fish Biol Fish. https://doi.org/10.1007/s11160-023-09796-1

Beamish RJ (1979) Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J Fish Res Bd Can 36:141–151. https://doi.org/10.1139/f79-023

Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38:982–983. https://doi.org/10.1139/f81-132

Beamish RJ, McFarlane GA, Benson A (2006) Longevity overfishing. Prog Oceanogr 68:289–302. https://doi.org/10.1016/j.pocean.2006.02.005

Birkeland C, Dayton P (2005) The importance in fishery management of leaving the big ones. Trends Ecol Evol 20:356–358. https://doi.org/10.1016/j.tree.2005.03.015

Boehlert GW (1985) Using objective criteria and multiple regression models for age determination in fishes. Fish Bull 83:103–117

Brownell WN (1972) Fisheries of the Virgin Islands. Commer Fish Rev 924:23–30

Cailliet GM, Andrews AH (2008) Age-validated longevity of fishes: its importance for sustainable fisheries. In: Fisheries for global welfare and environment. TERRAPUB, pp 103–120

Campana SE (1997) Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock *Melanogrammus aeglefinus*. Mar Ecol Prog Ser 150:49–56. https://doi.org/10.3354/meps150049

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297. https://doi.org/10.3354/meps188263

Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J Fsh Biol 59(2):197–242. https://doi.org/10.1111/j.1095-8649.2001.tb00127.x

Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. Can J Fish Aquat Sci 39:1208–1210. https://doi.org/10.1139/f82-158

Cook M, Fitzhugh GR, Franks JS (2009) Validation of yellowedge grouper, *Epinephelus flavolimbatus*, age using nuclear bomb-produced radiocarbon. Environ Biol Fish 86:461–472. https://doi.org/10.1007/s10641-009-9536-x

Druffel EM (1980) Radiocarbon in annual coral rings of Belize and Florida. Radiocarbon 22:363–371. https://doi.org/10.1017/S0033822200009656

Druffel ERM (1996) Post-bomb radiocarbon records of surface corals from the tropical Atlantic Ocean. Radiocarbon 38:563–572. https://doi.org/10.1017/S0033822200030095

Grant S (2019) MCAAP: a review of the deepslope demersal fish in Belize

Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J Mar Sci 71:2171–2185. https://doi.org/10.1093/icesjms/fst200

Horn PL, McMillan PJ, Neil HL (2019) Age and life histories of black and smooth oreos inferred using bomb radiocarbon dating and stable isotope analysis. N Z J Mar Freshwater Res 53:77–96. https://doi.org/10.1080/00288330.2018.1481436

Kalish JM (1989) Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J Exp Mar Biol Ecol 132:151–178. https://doi.org/10.1016/0022-0981(89)90126-3

Kilbourne KH, Quinn TM, Guilderson TP, Webb RS, Taylor FW (2007) Decadal- to interannual-scale source water variations in the Caribbean Sea recorded by Puerto Rican coral radiocarbon. Clim Dyn 29:51–62. https://doi.org/10.1007/s00382-007-0224-2

Koslow J (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES J Mar Sci 57:548–557. https://doi.org/10.1006/jmsc.2000.0722

Longhurst A (2006) The sustainability myth. Fish Res 81:107–112. https://doi.org/10.1016/j.fishres.2006.06.022

Lou DC, Mapstone BD, Russ GR, Davies CR, Begg GA (2005) Using otolith weight–age relationships to predict age-based metrics of coral reef fish populations at different spatial scales. Fish Res 71:279–294. https://doi.org/10.1016/j.fishres.2004.09.003

Luckhurst B, Booth S (2003) Zeller D (2003) Brief history of Bermudian fisheries, and catch comparison between national sources and FAO records. Fish Cent Res Rep 11(6):163–169

Morales-Nin B (2000) Review of the growth regulation processes of otolith daily increment formation. Fish Res 46:53–67. https://doi.org/10.1016/S0165-7836(00)00133-8

Morales-Nin B, Panfili J (2005) Seasonality in the deep sea and tropics revisited: what can otoliths tell us? Mar Freshwater Res 56:585–598. https://doi.org/10.1071/MF04150

Moyer RP, Grottoli AG (2011) Coral skeletal carbon isotopes (δ13C and Δ^{14}C) record the delivery of terrestrial carbon to the coastal waters of Puerto Rico. Coral Reefs 30:791–802. https://doi.org/10.1007/s00338-011-0758-y

Newman SJ, Williams AJ, Wakefield CB, Nicol SJ, Taylor BM, O'Malley JM (2016) Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. Rev Fish Biol Fish 26:537–562. https://doi.org/10.1007/s11160-016-9442-1

Nichols RS (2019) Sex-specific growth and longevity of 'Ehu', *Etelis carbunculus* (family Lutjanidae), within the Hawaiian Archipelago. Master's Thesis, University of Hawaii

Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, Froese R, Gjerde KM, Haedrich RL, Heppell SS, Morato T et al (2012) Sustainability of deep-sea fisheries. Mar. Policy 36:307–320. https://doi.org/10.1016/j.marpol.2011.06.008

Overly KE, Shervette VR (2023) Caribbean deepwater snappers: application of the bomb radiocarbon age estimation validation in understanding aspects of ecology and life history. PLoS ONE 18:e0295650. https://doi.org/10.1371/journal.pone.0295650

Pacheco C, Bustamante C, Araya M (2021) Mass-effect: understanding the relationship between age and otolith weight in fishes. Fish Fish 22:623–633. https://doi.org/10.1111/faf.12542

Passerotti MS, Andrews AH, Carlson JK, Wintner SP, Goldman KJ, Natanson LJ (2014) Maximum age and missing time in the vertebrae of sand tiger shark (*Carcharias taurus*): validated lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans. Mar Freshwater Res 65:674–687. https://doi.org/10.1071/MF13214

Paterne M, Druffel ERM, Guilderson TP, Blamart D, Moreau C, Weil-Accardo J, Feuillet N (2023) Pulses of South Atlantic water into the tropical North Atlantic since 1825 from coral isotopes. Sci Adv 9:eadi1687. https://doi.org/10.1126/sciadv.adi1687

Piddocke TP, Butler GL, Butcher PA, Purcell SW, Bucher DJ, Christidis L (2015) Age validation in the Lutjanidae: a review. Fish Res 167:48–63. https://doi.org/10.1016/j.fishres.2015.01.016

Pilling GM, Grandcourt EM, Kirkwood GP (2003) The utility of otolith weight as a predictor of age in the emperor *Lethrinus mahsena* and other tropical fish species. Fish Res 60:493–506. https://doi.org/10.1016/S0165-7836(02)00087-5

Pita C, Villasante S, Pascual-Fernández JJ (2019) Managing small-scale fisheries under data poor scenarios: lessons from around the world. Mar Policy 101:154–157. https://doi.org/10.1016/j.marpol.2019.02.008

Pukk L, Kuparinen A, Järv L, Gross R, Vasemägi A (2013) Genetic and life-history changes associated with fisheries-induced population collapse. Evol Appl 6:749–760. https://doi.org/10.1111/eva.12060

Quinn NJ (2007) Exploring the potential for pelagic and deep water demersal fisheries on the north coast of Jamaica. In: 59th Gulf and Caribbean Fisheries Institute. pp 191–196

Reeves SA (2003) A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES J Mar Sci 60:314–328. https://doi.org/10.1016/S1054-3139(03)00011-0

Reimer PJ, Brown TA, Reimer RW (2004) Discussion: Reporting and calibration of post-bomb 14C data. Radiocarbon 46:1288–1304

Robertson DR, Van Tassell J (2023) Shorefishes of the greater Caribbean: online information system. Version 3.0. Smithsonian Tropical Research Institute, Balboa, Panamá

Rosario A, Rojas J, Piñeiro E, Peña N, Torres W (2006) Completion report to National Marine Fisheries Service on the reproductive cycle of queen snapper (*Etelis oculatus*) and the wenchman (*Pristipomoides macrophthalmus*)

Rozanski K (1991) Consultants group meeting on ^{14}C reference materials for radiocarbon laboratories. Austria, Vienna

Sanchez PJ, Pinsky JP, Rooker JR (2019) Bomb radiocarbon age validation of warsaw grouper and snowy grouper. Fisheries 44:524–533. https://doi.org/10.1002/fsh.10291

Schemmel E, Nichols R, Cruz E, Boyer JFF, Camacho FA, Schemmel E, Nichols R, Cruz E, Boyer JFF, Camacho FA (2021) Growth, mortality, and reproduction of the oblique-banded snapper (*Pristipomoides zonatus*) in Guam. Mar Freshwater Res 73:351–365. https://doi.org/10.1071/MF21094

Shervette VR, Overly KE, Rivera Hernández JM (2021) Radiocarbon in otoliths of tropical marine fishes: reference Δ^{14}C chronology for north Caribbean waters. PLoS ONE 16:e0251442. https://doi.org/10.1371/journal.pone.0251442

Stevens MH, Smith SG, Ault JS (2019) Life history demographic parameter synthesis for exploited Florida and Caribbean coral reef fishes. Fish Fish 20:1196–1217. https://doi.org/10.1111/faf.12405

Synal H-A, Stocker M, Suter M (2007) MICADAS: A new compact radiocarbon AMS system. Nucl Instrum Methods Phys Res, Sect B 259:7–13. https://doi.org/10.1016/j.nimb.2007.01.138

Toggweiler JR, Druffel ERM, Key RM, Galbraith ED (2019) Upwelling in the ocean basins north of the ACC: 1. On the upwelling exposed by the surface distribution of Δ^{14}C. J Geophys Res: Oceans 124:2591–2608. https://doi.org/10.1029/2018JC014794

von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws. II). Hum Biol 10:181–213

Wacker L, Fahrni SM, Hajdas I, Molnar M, Synal H-A, Szidat S, Zhang YL (2013) A versatile gas interface for routine radiocarbon analysis with a gas ion source. Nucl Instrum Methods Phys Res, Sect B 294:315–319. https://doi.org/10.1016/j.nimb.2012.02.009

Wagner AJ, Guilderson TP, Slowey NC, Cole JE (2009) Pre-bomb surface water radiocarbon of the Gulf of Mexico and Caribbean as recorded in hermatypic corals. Radiocarbon 51:947–954. https://doi.org/10.1017/S0033822200034020

Widdrington JB, Reis-Santos P, Morrongiello JR, Macdonald JI, Wakefield CB, Newman SJ, Nicol SJ, Gillanders BM (2024) Otolith growth chronologies reveal distinct environmental sensitivities between and within shallow- and deep-water snappers. Rev Fish Biol Fish. https://doi.org/10.1007/s11160-024-09898-4

Williams AJ, Newman SJ, Wakefield CB, Bunel M, Halafihi T, Kaltavara J, Nicol SJ (2015) Evaluating the performance of otolith morphometrics in deriving age compositions and mortality rates for assessment of data-poor tropical fisheries. ICES J Mar Sci 72:2098–2109. https://doi.org/10.1093/icesjms/fsv042