

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

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Abstract: Growth characteristics of *Pristipomoides filamentosus*, a deepwater eteline snapper of major economic importance, are incomplete and inconsistent across its geographical range. Early growth rates have been validated using daily increment and length–frequency analyses, but historical estimates of adult growth rates are variable and longevity is unknown. Studies of *P. filamentosus* in the Hawaiian Islands have cautioned against unjustified estimates of longevity, but 18 years has at times been uncritically assumed as the maximum age. The present study addresses these age, growth, and longevity issues using lead–radium and bomb radiocarbon dating by providing valid age estimates for adult *P. filamentosus*. Valid length-at-age estimates ranged from approximately 10 years to more than 40 years. These data, together with robust daily increment data, were used to model a fully validated, long-lived life history for *P. filamentosus*. This study adds to the few existing studies supporting a view that many tropical fishes, particularly deepwater species, can be longer lived than previously surmised.

Résumé : Les connaissances sur les caractéristiques de la croissance de *Pristipomoides filamentosus*, un vivaneau d'eau profonde de grande importance économique, sont incomplètes et incohérentes à l'échelle de l'aire de répartition de l'espèce. Alors que les taux de croissance précoce ont été validés par l'analyse des incréments journaliers et de la fréquence des longueurs, les estimations passées des taux de croissance des adultes sont variables et la longévité est inconnue. Si des études de *P. filamentosus* dans les îles hawaïennes ont mis en relief le risque posé par les estimations injustifiées de la longévité, un âge maximum de 18 ans a par moments été pris pour acquis sans évaluation critique préalable. L'étude se penche sur ces questions touchant à l'âge, la croissance et la longévité en faisant appel à la datation au plomb–radium et au radiocarbone post-bombe pour obtenir des estimations valides de l'âge de *P. filamentosus* adultes. Des estimations valides de la longueur selon l'âge couvrent une fourchette d'âges allant d'environ 10 ans à plus de 40 ans. Ces données, combinées à des données robustes sur les incréments journaliers, ont été utilisées pour modéliser un cycle biologique de longue durée entièrement validé pour *P. filamentosus*. L'étude vient s'ajouter aux quelques rares études qui appuient la notion selon laquelle de nombreux poissons tropicaux, particulièrement des espèces d'eau profonde, pourraient vivre plus longtemps que les estimations antérieures ne le laissaient croire.

[Traduit par la Rédaction]

Introduction

Throughout the tropical and subtropical Indo-Pacific, deep-water snappers (family Lutjanidae, subfamily Etelinae) are increasingly fished, yet knowledge of their ecology is limited. This group consists of common inhabitants of steep coral and rock reefs, residing at depths usually exceeding 100 m, and these fishes can attain lengths exceeding 100 cm (Parrish

1987). *Pristipomoides filamentosus* is an eteline snapper of major fishery importance. Its geographic range extends throughout the tropical and subtropical Indo-Pacific from the Hawaiian Archipelago and the central western Pacific Ocean to the western Indian Ocean and south along northwestern and northeastern Australia (Allen 1985; Kramer et al. 1994; Newman 2006). It is known most commonly as the crimson or rosy jobfish throughout much of its range, but in Hawaii it is

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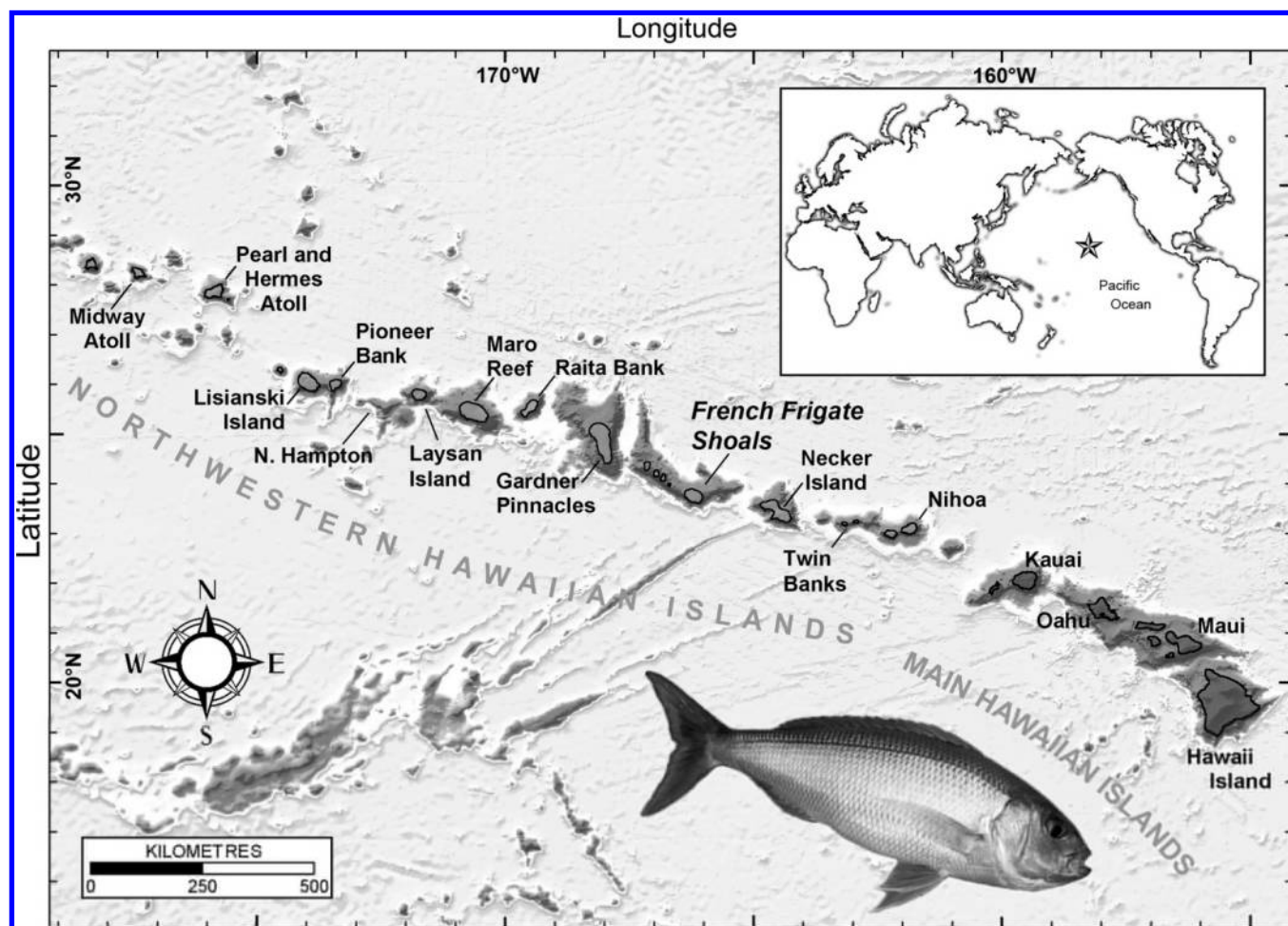
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Fig. 1. Map of Hawaiian Archipelago with its central Pacific Ocean location, main Hawaiian Islands (MHI), and Northwestern Hawaiian Islands (NWHI) designated. Collection locations are labeled, with the primary $\Delta^{14}\text{C}$ coral reference record location at French Frigate Shoals (FFS) emphasized. A photograph of a *Pristipomoides filamentosus* from the MHI is also provided out of interest. Base bathymetric map was modified from Pacific Islands Benthic Habitat Mapping Center, School of Ocean and Earth Science and Technology, University of Hawaii at Manoa.



known as pink snapper or by its Hawaiian name, opakapaka. As is usually the case with eteline snappers, many of the life history characteristics of *P. filamentosus* are unknown or incompletely described (Moffitt 2006). Of particular concern is the variability of estimated age and growth parameters across its geographical range. To date, age and growth for *P. filamentosus* has been studied in the Seychelles, Papua New Guinea, Mariana Islands, and the Hawaiian Archipelago using numerous techniques, with a few limited forms of age validation.

Fish collections in the Northwestern Hawaiian Islands (NWHI) led to the earliest age and growth studies for *P. filamentosus* (Fig. 1). Uchiyama and Tagami (1984) investigated daily growth increments and validated the first few years of growth, but annual growth zones beyond 3 years was uncertain with a maximum estimated age of 5 years. Ralston and Miyamoto (1983) developed a numerical integration model that addressed problems observed by Uchiyama and Tagami (1984). The greatest age determined was 16.6 years, but the size of this fish (685 mm fork length, FL) was less than the largest fish in the Hawaiian Islands (800 mm FL; Uchiyama and Kazama

2003). Ralston and Miyamoto (1983) argued that daily increments could not be resolved past a certain size or age and that their results should not be extrapolated to larger fish. In contrast, Radtke (1987) claimed that all daily increments were resolvable, even for the largest fish. Using sequential surface etchings and scanning electron microscopy, a maximum calculated age of 6.1 years was estimated for a 720 mm FL fish (Radtke 1987). These early studies provided different age interpretations for adult *P. filamentosus*, yet there was near consensus on the first few years. More detailed studies of the earliest growth further supported the findings (DeMartini et al. 1994; Moffitt and Parrish 1996), but length-at-age was still in question for the largest fish.

The results from other age and growth studies, distant from the Hawaiian Islands, were also complicated by methodological limitations. Ralston and Williams (1988) applied daily increment integration to *P. filamentosus* collected from the Mariana Islands, but low sample size and truncated fish lengths limited the study. In a study of *P. filamentosus* from Papua New Guinea, putative annual growth zones suggested a maximum estimated age of 12 years (Fry et al. 2006). Age and

Table 1. Synopsis of growth parameters from fitted von Bertalanffy functions to various forms of estimated age data for *Pristipomoides filamentosus*.

| Region | Study | Length (FL, mm) | von Bertalanffy parameter | | |
|--------------------|-------------------------------|----------------------|---------------------------|---------------------------|---------------|
| | | | L_{∞} (mm FL) | K (year ⁻¹) | t_0 (years) |
| Hawaii | Ralston and Miyamoto 1983 | 185–687 | 780 (fixed) | 0.146 | -1.67 |
| | | | 664 | 0.235 | -0.81 |
| | Uchiyama and Tagami 1984 | NR | 971 | 0.31 | 0.02 |
| | Radtke 1987 | 200–720 | 698* | 0.534* | 0.18* |
| | DeMartini et al. 1994 | 84–687 | 704 | 0.25 | 0.22 |
| Mariana Islands | Moffitt and Parrish 1996 | 70–250 | 780 (fixed) | 0.21 | 0 |
| | Ralston and Williams 1988 | 250–640 | 670 (LFA) | 0.203 | 0.52 |
| PNG | Fry et al. 2006 | 271–552 [†] | 551 | 0.118 | -4.0 |
| | | | 584 | 0.289 | -0.54 |
| Seychelles | Mees 1993 | 250–770 | 817 (LFA) | 0.288 | 0.0 |
| | Mees and Rousseau 1997 | NR | 758 (LFA) | 0.244 | -0.3 |
| | Hardman-Mountford et al. 1997 | NR | 780–860 [‡] | 0.33–0.36 | -0.16–0.06 |
| | Pilling et al. 2000 | 260–800 | 780 [§] | 0.111 | -1.44 |

Note: Modified from Andrews et al. (2011a). FL, fork length; LFA, length frequency analysis; NR, not reported; PNG, Papua New Guinea.

*Curve fit using IGOR (Cope 2000) because reported function was unconventional.

[†]Length reported as standard length was converted to FL based using a conversion factor (Uchida et al. 1982).

[‡]Parameters reported for separate sexes.

[§]Reanalysis of von Bertalanffy growth function (VBGF) fit to age–length data provided different parameters than reported (623 cf. 780 mm FL).

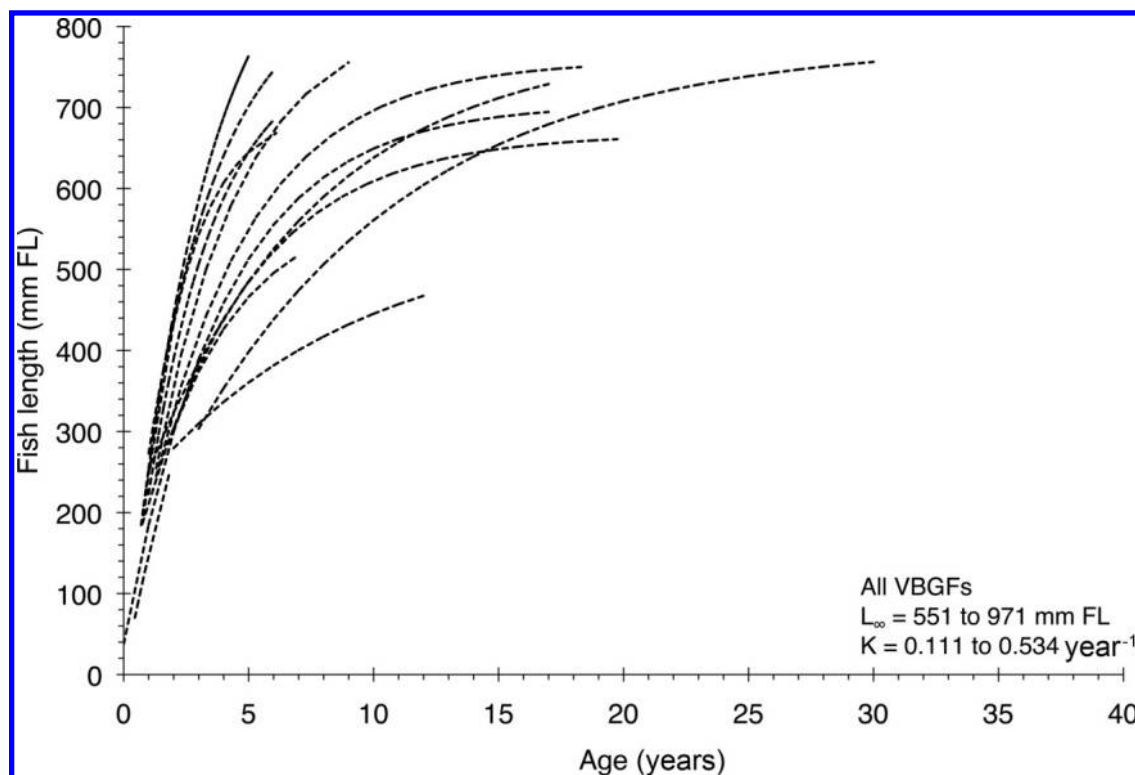
growth studies of *P. filamentosus* from the Seychelles fishery have also been extensive. Two management-related studies used length–frequency analysis to derive a rapid growth rate (Mees 1993; Mees and Rousseau 1997); however, length analyses are limited to the earliest growth where length changes can be observed and are inappropriate for long-lived fishes that attain an asymptotic length. Another article evaluated otolith sections for lunar cycle increments, but lacked important details (Hardman-Mountford et al. 1997). A more thorough investigation of otolith sections for *P. filamentosus* in the Seychelles revealed putative annual growth zones up to 30 years, but zone counts were dubious at best, and validation using marginal increment analysis was unsuccessful (Pilling et al. 2000).

Age estimation for the largest *P. filamentosus* has been an ongoing problem in the development of reliable growth parameters (Table 1). As a result of the wide range of questionable age and growth results, there are numerous potential growth trajectories for this species (Fig. 2). Aside from approximations of age for fish from the Seychelles based on putative annual growth zones, age estimates for the largest *P. filamentosus* do not exist. Because Ralston and Miyamoto (1983) provided some of the most rigorous evidence for proper growth modeling of *P. filamentosus*, a maximum age has sometimes been extrapolated using Ralston and Miyamoto's (1983) growth function. For example, assuming that maximum observed length is 90% of asymptotic length, an estimate of 18 years was derived and reported as the maximum age for this species (Manooch 1987). However, this estimate was based on a method that (i) made assumptions about otolith growth during adult stages; (ii) was not applied to the largest fish sizes; and (iii) should be independently tested because ages estimated for the largest fish are typically biased low (Stevenson and Campana 1992). In addition, Ralston and Miyamoto (1983,

p. 532) warned against using the information for estimating maximum age by stating, "extrapolation [. . .] may be an unrealistic exercise and growth rates of large fish may in fact be overestimated." Based on the previously mentioned studies and recent laboratory observations of otolith sections, it is evident that *P. filamentosus* otoliths from the Hawaiian Islands lack well-developed annual growth zones. Hence, it is vital that validated estimates of age be made to address the unresolved issue of adult growth and longevity and to develop accurate life history parameters for use in stock assessments and effective management plans.

Recent advances in the use of radiochemical proxies and environmental markers for age have provided opportunities for age validation. The primary techniques currently in use are lead–radium and bomb radiocarbon (¹⁴C) dating. Lead–radium dating is a geochronological technique that relies on the decay of radium-226 (²²⁶Ra) to lead-210 (²¹⁰Pb), the disequilibrium of which functions as a natural chronometer within the otolith (Smith et al. 1991; Panfili et al. 2002). This kind of information can serve to validate other age estimation methods, such as growth zone counting (Andrews et al. 2009), or can be used to generate age estimates when no other age data are available. Bomb radiocarbon dating is a technique that relies on a conserved record of the rapid increase in radiocarbon from atmospheric testing of thermonuclear devices (Broecker and Peng 1982). The initial uptake of bomb-produced radiocarbon by the marine environment, reported as delta carbon-14 ($\Delta^{14}\text{C}$) in reference to an established pre-nuclear radiocarbon record (Stuiver and Polach 1977), was virtually synchronous in the mixed layer of mid-latitude oceans (Grottoli and Eakin 2007). This time-specific signal provides a reference period that can be used to determine fish age and can corroborate age estimates from growth zone counting in otoliths (e.g., Kalish 1993; Campana 1997; Andrews et al. 2011b), but the method

Fig. 2. Plot of all known von Bertalanffy growth functions for *P. filamentosus* throughout its geographic range. Metrics for growth characteristics were from studies based on otolith or fish growth observations (daily, lunar, or annual increments or zones; length–frequency analysis; and tag–recapture observations). Age estimation procedures and results vary considerably, and prior to the present study, age of the largest fish had not been validated. See Table 1 for growth function parameters for studies considered here. Modified from Andrews et al. (2011a).



can also provide age estimates where little or no other information was available (Andrews et al. 2005). An application of both age validation methods to a single species can provide complementary findings (Andrews et al. 2007).

In this study, lead–radium and bomb radiocarbon dating were used to answer questions about the age, growth, and potential life span of *P. filamentosus*. Both methods were used to determine the age of large adults to determine if the purported maximum age of 18 years is correct. In addition, medium-sized *P. filamentosus* were aged using these methods, and length-at-age was determined for fish toward the upper limit of the numerical integration method used by Ralston and Miyamoto (1983). Given these successful age determinations, a revised von Bertalanffy growth function (VBGF) was developed for *P. filamentosus* across all size classes, incorporating the best available age-at-length estimates from other studies. Based on the validated age and growth for *P. filamentosus* in the Hawaiian Islands, other regional studies were investigated for potential differences. As a corollary to the project, otoliths from juvenile fish provided an opportunity to test the closed system assumption required in lead–radium dating — an issue that was partially addressed by Andrews et al. (2009).

Materials and methods

Age estimation

Age estimation from counting assumed annual growth zones in *P. filamentosus* otoliths was unsuccessful. Specimens from the

Hawaiian Islands were particularly ill-defined in annual growth structure. Investigators at both NOAA Fisheries, Honolulu, Hawaii (A. Andrews, personal observation), and at the Western Australian Fisheries and Marine Research Laboratories (S. Newman, WAFMRL, Department of Fisheries, Government of Western Australia, P.O. Box 20, North Beach, WA 6920, Australia, personal communication, 2011) found *P. filamentosus* otoliths were difficult to read or unreadable using several different preparation techniques and viewing methods. A lack of well-developed annual growth zones for *P. filamentosus* appears to be a common problem, although there are reports of limited success (Pilling et al. 2000; Fry et al. 2006). Hence, our approach was to apply bomb radiocarbon and lead–radium dating to otoliths, independent of growth zone counting methods.

Lead–radium dating feasibility

Developing an effective sampling design is reliant upon estimating the limitations of lead–radium dating specifically for *P. filamentosus* otoliths. Important considerations were (i) individual and collective sample mass availability for whole juvenile otoliths and otolith cores of adults; (ii) the radium-226 activity for otoliths from the region; and (iii) the sample age (estimated age plus time since capture). In most cases, the second member of the pair of sagittae (hereafter otoliths) from each fish was conserved for bomb radiocarbon dating. The baseline assessment of lead–radium levels used whole juvenile otoliths of known age.

Table 2. Summary of characteristics for *P. filamentosus* fish and otoliths processed for lead–radium dating.

| Sample | Age group (sample age, years) | Length (mm FL, range) | No. of otoliths | Sample mass (g) | Mean core mass (g) |
|------------|-------------------------------|-----------------------|-----------------|-----------------|--------------------|
| OP 1997 | 1+ (11.3)* | 167 (106–208) | 19 [†] | 0.5791 | 0.031 |
| OP 1987 | 2+ (20.5)* | 334 (322–347) | 14 [†] | 1.1654 | 0.087 |
| OP 600–620 | Unknown (1.9) [‡] | 609 (602–616) | 16 [§] | 1.1508 | 0.072 |
| OP 660–680 | Unknown (1.9) [‡] | 670 (661–676) | 16 [§] | 1.2436 | 0.078 |
| OP 700+ | Unknown (0.7) [‡] | 720 (700–746) | 16 [§] | 1.5538 | 0.097 |

Note: Estimated age composition, mean time since capture, and pooled otolith number and mass is listed. Age was unknown for the adult groups (fish length based). Sample mass was for the combined otolith sample, consisting of whole otoliths for the juvenile groups and otolith cores for the adult groups. Modified from Andrews et al. (2011a).

*Time since collection plus one-half the estimated average fish age for each sample.

[†]Whole otoliths.

[‡]Time between collection and analysis.

[§]Extracted otolith cores.

Two groups of juvenile otoliths were pooled from collections made 10 years apart. The intent of this portion of the study was to determine baseline levels of radium-226 and to test the closed system assumption (no loss of lead–radium series radioisotopes over time; Andrews et al. 2009) for otolith material by measuring the lead–radium ratio from otoliths of known age (collected 11 and 21 years prior to analysis; Table 2). Radium-226 activity in otolith material is typically 0.03–0.05 disintegrations per minute per gram (dpm·g⁻¹) (Andrews 2009). Based on this estimate, approximately 1.0 g of otolith material was targeted for sufficient activity. Age was known for small fish based on validated early growth studies (Ralston and Miyamoto 1983; DeMartini et al. 1994). These sample groups were processed first and provided information necessary for lead–radium dating of adult-sized fish.

The composition of otolith groups for adult fish was based on the lead–radium dating of the juvenile otolith groups and the availability of otoliths from similar sized fish. Dimensions and the mass of juvenile otoliths, with measured radium-226 activity (provided later), were considered relative to what could be extracted as an otolith core from adult fish. The mean dimensions and mass from 14 juvenile otoliths (OP 1987: 11.4 mm length × 7.0 mm width × 1.2 mm thickness and 0.088 g) was the target size for adult otolith cores. This sample size was chosen as a balance between (i) a required sample mass exceeding 1 g (based on radium-226 activity) and (ii) the number of samples available in the size class for the collection period. The first set of otoliths represented the largest fish available ($n = 16$) from specimens collected in 2007–2008 for which age was neither known nor estimated (OP 700+; Table 2). All were collected within a year of each other with similar fish length used as a criterion for grouping, resulting in slightly more than 1 g of total core material. Each core was extracted by (i) grinding the whole adult otoliths on a lapidary wheel to the shape of a juvenile otolith and (ii) microscopic comparison of the core with two reference 2+ year otoliths collected in 2008. Growth zones and the nuclear region visible within the otolith were used to verify cores with the first few years of growth. Subsequent to the findings from the first adult otolith age group (OP 700+), two additional adult otolith groups of smaller size classes were cored to determine age (OP 600–620 and OP 660–680; Table 2).

Radiochemical protocol

The radiochemical protocol used in this study is described elsewhere. The details of chromatographic separation of radium-226 from barium and calcium and analysis of radium-226 using mass spectrometry are provided in Andrews et al. (1999b, 2009), and the details on measuring lead-210 activity are described in Andrews et al. (1999a).

Lead–radium dating

Radiometric age was estimated using the measured lead-210 and radium-226 activities from the otolith samples using the following equation:

$$(1) \quad t_{\text{age}} = \frac{\ln \left(1 - \frac{A_{210}}{A_{226}} \right)}{-\lambda}$$

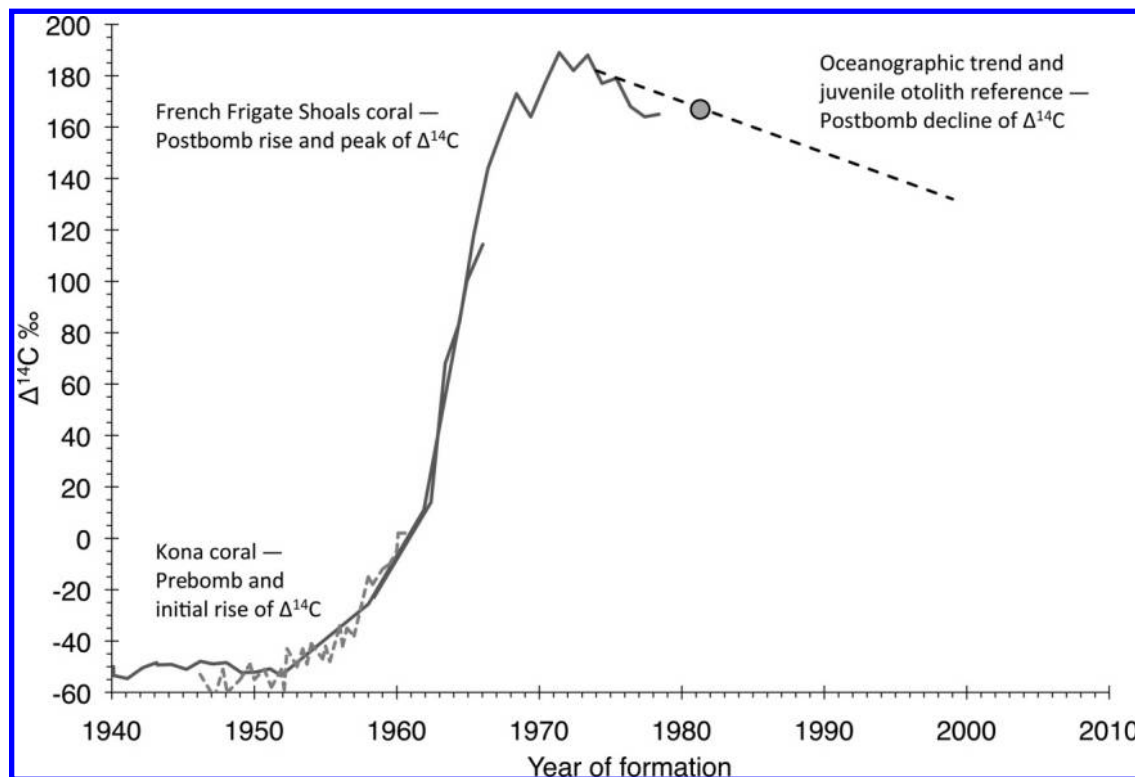
where t_{age} is the radiometric age at time of analysis, A_{210} is the lead-210 activity at time of analysis, A_{226} is the radium-226 activity measured using inductively coupled plasma mass spectrometry (ICP–MS), and λ is the decay constant for lead-210 (Smith et al. 1991). The age of adult samples were determined considering the core age gradient (Smith et al. 1991). A radiometric age range, based on the analytical uncertainty, was calculated for each sample by using error propagation through the final age determinations (2 standard errors, SE). Calculated error included the standard sources of error (e.g., pipetting, spike and calibration uncertainties), α -counting statistics for lead-210 (Wang et al. 1975), and the ICP–MS analysis routine.

To provide a tangible representation of how radiometric age compared with the expected lead–radium ratios from different age estimates, length-at-age was estimated from the DeMartini et al. (1994) VBGF. These hypothetical age estimates were used to reveal potential differences between estimated age and radiometric age. (Note that no age estimates from growth zone counting were available for the fish used in lead–radium dating.)

Bomb radiocarbon dating feasibility

Reference $\Delta^{14}\text{C}$ records from previous studies were compiled to prepare for bomb radiocarbon dating of *P. filamentosus* in the

Fig. 3. Bomb radiocarbon references used in correlating measured $\Delta^{14}\text{C}$ values from otolith cores of fish collected in the NWHI. The most informative period (rise in $\Delta^{14}\text{C}$) was primarily the French Frigate Shoals record, which was supplemented with prebomb and rise data from the main Hawaiian Islands Kona coral record because no other records exist (solid and dashed lines in the 1940s to 1960s; Druffel 1987, Roark et al. 2006). In addition, the decline rate for the postbomb period (dashed line beyond 1970) was estimated based on a single juvenile otolith (shaded circle) collected in 1981 and regional oceanographic data (Druffel et al. 2008). The trend was a decrease of $\Delta^{14}\text{C}$ in seawater at a rate of approximately 2‰ per year. Modified from Andrews et al. (2011a).



Hawaiian Islands. These reference records provided a temporal basis for comparing measured $\Delta^{14}\text{C}$ levels in otoliths of *P. filamentosus* specimens. The applicable bomb radiocarbon records in the Hawaiian Islands were from hermatypic coral cores collected at Kahe Point, Oahu, and Kona, Hawaii Island, in the main Hawaiian Islands (MHI) and at French Frigate Shoals (FFS) in the central portion of the NWHI (Fig. 1). Because there were differences in the postbomb $\Delta^{14}\text{C}$ records from the MHI and the NWHI, and the best *P. filamentosus* otolith archive was from the NWHI, we used FFS as the primary reference. The coral $\Delta^{14}\text{C}$ record at FFS almost completely documented the rise in $\Delta^{14}\text{C}$ and spanned a period of 1958 to 1978 (Druffel 1987). While the record was instrumental for age determination using $\Delta^{14}\text{C}$ values during the rise of $\Delta^{14}\text{C}$, it was necessary to establish a regional lower limit for $\Delta^{14}\text{C}$ levels prior to the affects of atmospheric testing. Because it is reasonable to assume that prebomb $\Delta^{14}\text{C}$ levels were similar across a much broader region, as opposed to the postbomb peak of $\Delta^{14}\text{C}$ (Druffel 2002; Grottoli and Eakin 2007), the record from Kona, Hawaii Island, was added from two sources; these records provided ample representation of regional prebomb levels to approximately midway through the rise of $\Delta^{14}\text{C}$ in 1966 (Druffel et al. 2001; Roark et al. 2006; Fig. 3). In addition to the rise of $\Delta^{14}\text{C}$, it was important to consider the decline in the $\Delta^{14}\text{C}$ record past 1978, which was not known from coral records. To supplement the regional

reference, a monotonic decline of $\Delta^{14}\text{C}$ in regional surface seawater was documented at a rate of approximately 2‰ per year (Druffel et al. 2008). This rate of decline was used as a reference for discriminating between early or late $\Delta^{14}\text{C}$ values from otoliths that may approach FFS peak values. In support of this notion, a single juvenile *P. filamentosus* otolith from a 174 mm FL fish, collected in 1981 from FFS, was tested for $\Delta^{14}\text{C}$. This sample provided a reference value (166.9‰) and was similar to the value predicted by the hypothesized decline in $\Delta^{14}\text{C}$ (Fig. 3). This rate of decline was considered conservative and could be more rapid based on the decline observed in the Kona record (Roark et al. 2006).

Age estimation from measured $\Delta^{14}\text{C}$ levels in otoliths of *P. filamentosus* specimens, by comparison with the regionally specific $\Delta^{14}\text{C}$ reference records, was initially deemed feasible from the results of lead–radium dating (no prior age estimates were available). The lead–radium dating results indicated that fish in the first adult group (OP 700+) were old enough to have birth years in the informative region of the $\Delta^{14}\text{C}$ reference records (between 1955 and 1970). In most cases, one otolith was used for each fish in the lead–radium dating, leaving the second otolith available for bomb radiocarbon dating. Otoliths from the NWHI in 2007–2008 were selected from this group for bomb radiocarbon dating (appendix E in Andrews et al. 2011a). In addition, otoliths from an archival series of specimens spanning a collection period of 10 years

were selected for bomb radiocarbon dating of smaller and younger fish (appendices F–H in Andrews et al. 2011a). These archived samples were collected from the NWHI from Necker Island to Laysan Island ($n = 35$) and from the Mariana Islands ($n = 4$). The Mariana Island samples were also compared with a coral $\Delta^{14}\text{C}$ record from Okinawa, Japan, because of its more westerly position and likely oceanographic similarity to the Mariana Islands (Konishi et al. 1981). Otoliths were selected from the archival series using approximations of age based on fish length and otolith mass and the potential for the otolith to provide a birth year within the informative period of the rise in $\Delta^{14}\text{C}$.

Radiocarbon analysis protocol

Core material from the selected otoliths was extracted using a micromilling machine. Because otoliths had been stored for several decades in various manners, individual otoliths were cleaned using a succession of 70% ethanol, mild detergent, weak acid, and deionized water. The detergent, acid, and water cleaning steps included sonication for several minutes, with repetition dependent on otolith appearance. Otoliths that appeared satisfactorily cleaned were air-dried overnight prior to mounting for milling. Uncleanable otoliths were not used. Whole otoliths were mounted on glass slides with the sulcus side down, making the distal surface accessible for core extraction by micromilling. Cytoseal was used as an adhesive and was allowed to cure for several days prior to further preparation. Because the adult otoliths accrete a small amount of otolith material onto the distal side of the otolith, wet hand grinding using 320- to 1000-grit, carbide wet-dry sandpaper was performed to expose the earliest otolith growth. The first few years of growth were clearly visible as grinding proceeded, and the concentric growth zone structure was used as a guide in exposing the core. Milling proceeded as an extraction of the smallest core structure visible, using as a template a small crenulated otolith outline that was slightly more opaque than the additional otolith growth layers.

Extraction of the otolith core utilized the computer automated capabilities of a New Wave Research (ESI–NWR Division; Fremont, California, USA) micromilling machine. A 0.5 mm diameter Brassler (Savannah, Georgia, USA) bit was used to drill an overlapping surface scan within the oval dimensions of 2.8 mm long \times 1.8 mm wide. The surface scan was a guided extraction that conformed to the uneven surface structure of each otolith. Otolith material was extracted to a depth of 400 μm with two passes of the scan at 200 μm each. These dimensions were well within the 1-year-old otolith dimensions and liberated a sample mass near 3 mg (appendices E–H in Andrews et al. 2011a). The extracted samples were submitted to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at Woods Hole Oceanographic Institution (WHOI) in Woods Hole, Massachusetts, for routine radiocarbon analyses.

Radiocarbon measurements were reported from NOSAMS as the Fraction Modern (Fm), which was used to calculate $\Delta^{14}\text{C}$ with a correction for natural isotopic fractionation. Fraction Modern is the measured deviation of the $^{14}\text{C}/^{12}\text{C}$ ratio from a “modern” sample. This internationally agreed upon reference is defined as 95% of the radiocarbon concentration of the NBS Oxalic Acid I standard (SRM 4990B) normalized to $\delta^{13}\text{C}_{\text{VPDB}}$ (-19‰) in 1950 AD (VPDB = Vienna Pee Dee

Belemnite geological standard; Olsson 1970). Sample Fm values were initially normalized to -25 per mil (‰) using the $\delta^{13}\text{C}_{\text{VPDB}}$ and were later adjusted for biological fractionation using the mean $\delta^{13}\text{C}$ value from 11 *P. filamentosus* otoliths (mean $\delta^{13}\text{C} = -4.9\text{‰}$). Sample-specific $\delta^{13}\text{C}$ values were used for Fm determination of the 11 reference $\delta^{13}\text{C}$ samples (appendices E–H in Andrews et al. 2011a).

The calculated $\Delta^{14}\text{C}$ values reported in this study were corrected for age, or time of formation, based on an approximate birth year. Because age was not known or estimated prior to the radiocarbon analysis, a retrospective estimate was generated based on the initial $\Delta^{14}\text{C}$ value and its known proximity in time relative to the reference $\Delta^{14}\text{C}$ records. This kind of adjustment provides a $\Delta^{14}\text{C}$ value that is more comparable to the $\Delta^{14}\text{C}$ reference time series. The year used in the corrections was based on a $\Delta^{14}\text{C}$ criterion as follows:

Birth year $\Delta^{14}\text{C}$ adjustment criteria:

- 1950 for $\Delta^{14}\text{C} < -46\text{‰}$ (prebomb)
- 1963 for $\Delta^{14}\text{C} -46\text{‰}$ to 165‰ (rise)
- 1972 for $\Delta^{14}\text{C} > 165\text{‰}$ (near peak)

The reason for such corrections is to provide a $\Delta^{14}\text{C}$ value that takes into account the decay that has taken place between the approximate time of birth and the time of measurement, as is the case with all regional $\Delta^{14}\text{C}$ reference records.

Bomb radiocarbon dating

Estimates of age were determined by projecting the measured $\Delta^{14}\text{C}$ values back in time from the measurement date to the regional $\Delta^{14}\text{C}$ reference series. First, a birth year was estimated based on the correlation of the measured $\Delta^{14}\text{C}$ value with the regional $\Delta^{14}\text{C}$ reference curves, which were initially attributed to a general region of the curve (prebomb, bomb rise, peak, or postbomb decline). For prebomb levels, a minimum birth year and age was estimated based on the last year the level was measured, plus an approximated uncertainty of 1–2 years. Levels measured near the regional peak in $\Delta^{14}\text{C}$ were assigned an age range that could be attributed to time the region held those levels of $\Delta^{14}\text{C}$. For samples between the peak and upper part of the rise in $\Delta^{14}\text{C}$, there were complications with birth year classification because of the similar levels measured later in time. Samples could be classified as either on the upper rise or on the postbomb decline with a nominal uncertainty of ± 1 to ± 2 years, depending on the proximity to peak levels. Because the postbomb decline was not measured, other proxies were used to estimate the decline rate (see Bomb radiocarbon dating feasibility section above for details). Based on this estimated rate of decline, birth years and ages were calculated with a nominal uncertainty of 3 years earlier in time. This was chosen because the decline rate was likely to be a conservative upper limit. Furthermore, some archived samples were collected either prior to or too close to the postbomb decline period for age estimation. Therefore, these samples were assigned a birth year and estimated age using only the upper rise portion of the $\Delta^{14}\text{C}$ reference record. Samples that could be placed on the bomb rise period were considered diagnostic and were assigned an age with a narrow uncertainty of ± 1 year. These data, coupled with the archived samples classified as upper rise, were used later to generate length-at-age estimates for developing a revised VBGF.

von Bertalanffy growth function

Parameters of a VBGF for *P. filamentosus* in the Hawaiian Archipelago were estimated using a Bayesian hierarchical approach (e.g., Cope and Punt 2007; Zhang et al. 2009) with age reading method treated as a random effect. Each of the age reading methods was treated separately because it was expected that each would produce different amounts of observation error in length-at-age data. We initially modeled the VBGF parameters L_∞ , K , and t_0 with random effects, but found that the t_0 parameter was very imprecisely estimated (coefficient of variation, $CV > 300\%$) for both the bomb radiocarbon and the lead-radium data sets. This imprecision was due to a lack of size-at-age measurements for fish younger than 10 years in both the bomb radiocarbon and the lead-radium data sets. To address this lack of data, we simplified the model structure and estimated a common t_0 parameter for each of the age reading methods. This was the base case model in which L_∞ and K were estimated for each age reading method. Two alternative VBGFs were also examined to determine whether simpler assumptions about the observation errors were more appropriate.

The VBGFs were estimated using the most reliable age data, which included the collections of length-at-age data from Ralston and Miyamoto (1983, $n = 65$), DeMartini et al. (1994, $n = 35$), and the length-at-age data developed in this study. This combined data set consisted of a total of 136 length-at-age samples with lengths ranging from 84 to 768 mm and ages ranging from 0.35 years to approximately 46 years (mean maximum age from lead-radium dating).

The expected length of the i th fish aged with the j th ageing method under the von Bertalanffy growth curve ($E[L_{i,j}]$) was modeled as

$$(2) \quad E[L_{i,j}] = L_{\infty,j} \{1 - \exp(-K_j(t_{i,j} - t_0))\}$$

where fish age was $t_{i,j}$, and $L_{\infty,j}$ and K_j were the asymptotic length and Brody growth rate parameters, respectively, measured by the j th age reading method. The observation model for length of the i th fish aged with the j th age reading method ($L_{i,j}$) as a function of expected length under the von Bertalanffy growth curve and observation error ε_j for the j th age reading method was

$$(3) \quad L_{i,j} = E[L_{i,j}] + \varepsilon_j \quad \text{where} \quad \varepsilon_j \sim N(0, \sigma_j^2)$$

In eq. 3, the observation errors are normally distributed with zero mean and a method-specific length-at-age variance. As a result, any potential heterogeneity in the variance of length-at-age estimates among the age reading methods was directly incorporated into the sample likelihood for each method.

Prior distributions for the $L_{\infty,j}$ and K_j parameters were normally distributed with hyperparameters equal to the population mean and variance of asymptotic length and growth rate, respectively, while the prior for the t_0 parameter was a diffuse normal distribution centered at zero, for example

$$(4) \quad L_{\infty,j} \sim N(\mu_\infty, \sigma_\infty^2) \quad \text{and} \\ K_j \sim N(\mu_K, \sigma_K^2) \quad \text{and} \quad t_0 \sim N(0, 100)$$

We did not use any auxiliary information on the likely values of the population parameters of the VBGF from previous studies of *P. filamentosus* growth. As a result, uninformative priors were used for both the population hyperparameters and the observation error variances. In particular, the prior for the population mean asymptotic length was set to be a diffuse normal distribution, and the prior for the mean Brody growth rate parameter was set to be a diffuse beta distribution (as parameterized in WinBUGS; <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>):

$$(5) \quad \mu_\infty \sim N(100, 10000) \quad \text{and} \quad \mu_K \sim \text{Beta}(1, 1)$$

The priors for the parameter variances and the observation error variances were all set to be diffuse inverse gamma distributions (as parameterized in WinBUGS; <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>), because this distribution is the conjugate prior for the unknown variance of a normally distributed mean (e.g., Ntzoufras 2009).

$$(6) \quad \frac{1}{\sigma_\infty^2} \sim \text{Gamma}(10^{-4}, 10^{-4}) \quad \text{and} \\ \frac{1}{\sigma_K^2} \sim \text{Gamma}(10^{-4}, 10^{-4}) \quad \text{and} \\ \frac{1}{\sigma_j^2} \sim \text{Gamma}(10^{-4}, 10^{-4})$$

In summary, the observation likelihood of the base case VBGF model was described by eqs. 2 and 3, while the prior distributions of the model parameters were described by eqs. 4, 5, and 6.

In addition to the base case model, we also evaluated two alternative VBGF models. The first alternative model was identical to the base case hierarchical model but assumed a single common error variance σ^2 for all age reading methods. This homogeneous variance (HV) model was included to evaluate whether the assumption of unequal variances among age reading methods was justifiable given the observed length-at-age data. The second alternative was a simple Bayes (SB) model with no hierarchical structure for age reading method and a common observation error variance among age reading methods. In this approach, there was a single prior for the asymptotic length L_∞ given by eq. 5, a single prior for the growth parameter K also given by eq. 5, and a single common error variance σ^2 for all age reading methods. The SB model was included to evaluate whether the hierarchical model improved the fit to the heterogeneous length-at-age data. The goodness of fit of the alternative and base case models to the observed data were evaluated using the deviance information criterion (DIC; Spiegelhalter et al. 2002), a Bayesian analog of the Akaike information criterion. In this context, the VBGF model with the minimum DIC value would be judged to provide the best predictive model fit to the data with the caveat that differences of less than two units of deviance indicated that there was no substantial difference between model fits and that differences of more than seven units were substantial (e.g., Spiegelhalter et al. 2002).

Posterior distributions of the parameters of the VBGF models were estimated by Markov chain Monte Carlo (MCMC)

Table 3. Radiometric results for juvenile whole otolith groups and the cored adult otolith group of *P. filamentosus*.

| Sample | ^{210}Pb (dpm·g ⁻¹) ± % error* | ^{226}Ra (dpm·g ⁻¹) ± % error* | $^{210}\text{Pb};^{226}\text{Ra}$ (2 SE) | Radiometric age (years, range) | Corrected age (years, range) |
|------------|---|---|--|--------------------------------|------------------------------|
| OP 1997 | 0.0117±9.2 | 0.0394±22 | 0.298 (0.071) | 11.9 (8.8–15.3) | 0.6 (–2.5–4.0) |
| OP 1987 | 0.0125±6.9 | 0.0258±13 | 0.486 (0.072) | 22.3 (18.1–27.0) | 1.8 (–2.4–6.5) |
| OP 600–620 | 0.0174±5.7 | 0.0324±16 | 0.537 (0.090) | 25.8 (20.0–32.7) | 23.9 (18.2–30.9) |
| OP 660–680 | 0.0192±5.1 | 0.0258±14 | 0.742 (0.108) | 44.5 (33.3–61.9) | 42.6 (31.4–60.1) |
| OP 700+ | 0.0223±4.3 | 0.0294±13 | 0.759 (0.104) | 46.6 (33.1–64.7) | 45.6 (34.4–64.0) |

Note: Listed are the measured lead-210 and radium-226 activities (disintegrations per minute per gram, dpm·g⁻¹) for the samples (±2 standard errors, SE). Calculated activity ratios and their corresponding margin of error were used to calculate sample age and uncertainty, with a final age for each group corrected for time since capture.

*Calculation based on propagation of 2 SE using the delta method (Knoll 1989) and the ICP-MS analysis routine (±2 SE).

simulation using the WinBUGS software (Lunn et al. 2000; WinBUGs version 1.4 available at <http://www.mrc-bsu.cam.ac.uk/bugs/>). Two chains were simulated for each model run. Each chain consisted of 275 000 iterations sampled with a thinning rate of 1/25 and a burn-in period of 25 000 iterations for a total of 20 000 MCMC samples. Convergence of the MCMC samples to the posterior distribution was checked using the Gelman and Rubin (1992), Geweke (1992), and Heidelberger and Welch (1983) diagnostics as implemented in the R language (R Development Core Team 2008) and the CODA package (Plummer et al. 2006). Autocorrelations were also monitored to assess whether the MCMC samples were serially correlated. Lastly, distributions of the mean standardized residuals, grouped by age reading method for the base case model and combined for the HV and SB models, were tested for normality using the Shapiro–Wilk *W* statistic. Overall, the convergence diagnostics were used to confirm that the burn-in period and the thinning rate were adequate for generating independent chains of samples from the posterior distribution of model parameters, and the autocorrelation and residual diagnostics were used to test whether modeling assumptions were valid.

Results

Lead–radium dating

Both juvenile sample groups provided baseline information on radium-226 and provided reliable data for testing the closed system assumption. The juvenile sample group from 1987 provided a sample mass exceeding 1 g and was the most promising in terms of measuring radium-226 across the range of potential activities (Table 2). The more recent sample group from 1997 to 1998 was younger in terms of fish age (1+ vs. 2+ years) and provided less mass, despite having more otoliths, because otoliths were smaller. As expected, the activity of radium-226 was near 0.03 dpm·g⁻¹ and OP 1987 provided greater relative precision than OP 1997 because sample mass was greater. Meaningful lead-210 and radium-226 activities were acquired from both samples (Table 3). Because the logistics of sample processing for lead–radium dating led to measurement of lead-210 (polonium-210 by proxy) before radium-226 determinations, it was determined early in the study that sample activities were at viable counting levels on the alpha-spectrometer with four to six counts per day. Radiometric age closely agreed with the known age of each juvenile age group (Table 3). The total sample age was calculated based on the mean time since collection for each group, plus one-half of the

mean age of these whole juvenile otoliths to compensate for the lead-210:radium-226 ingrowth gradient formed in the first 1–2 years of growth. Comparison of the known age of each sample with the expected ingrowth model provided evidence to support (i) the conservation of the lead–radium system isotopes during long storage times and the closed system assumption and (ii) the accurate determination of age for core material extracted from adult otoliths (Fig. 4). From this information, an application of lead–radium dating to cored otoliths from adults was considered feasible.

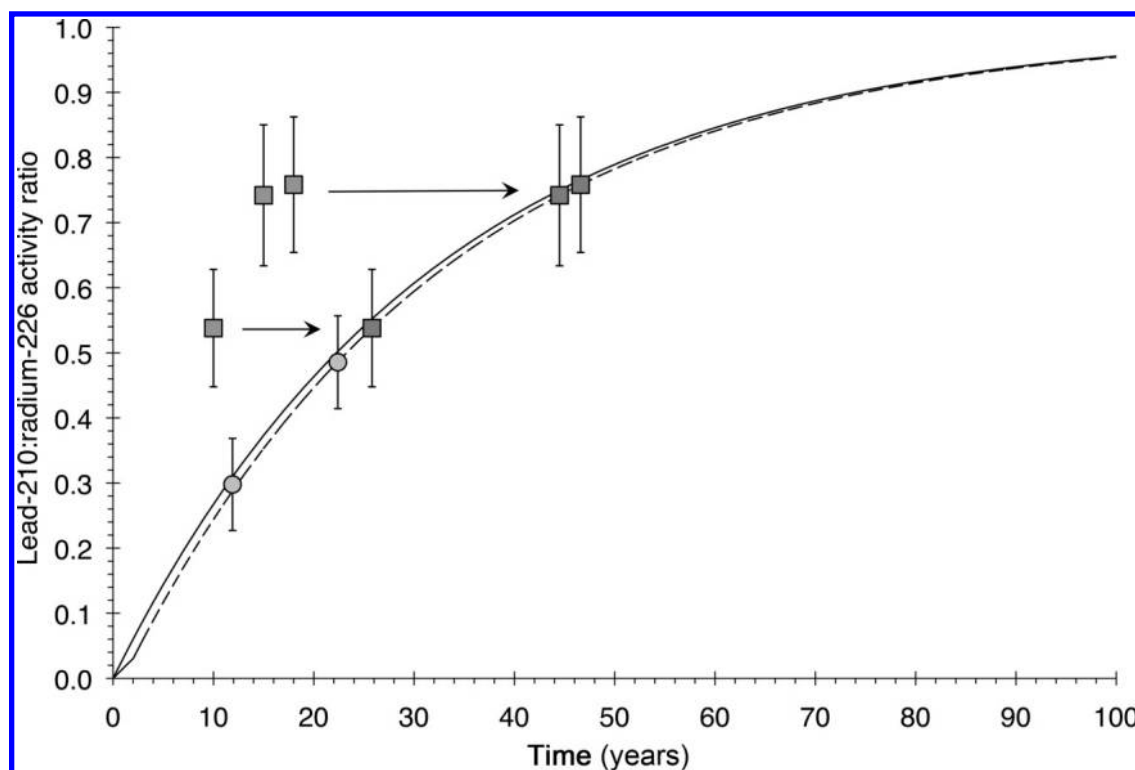
Adult otoliths selected from fish in three length groups collected in 2007–2008 were cored and analyzed for lead-210 and radium-226 activity. The resultant otolith core groups weighed from 1.1508 to 1.5538 g and consisted of 16 otoliths each (Table 2). Mean otolith core mass was slightly greater than the target mass in the first group analyzed (OP 700+). The following groups (OP 600–620 and OP 660–680) more closely approximated the target core mass. After a count period of 61.7 to 89.0 days on the alpha-spectrometer for the adult samples, the counts acquired were sufficient for the determination of lead-210 activity. These groups provided greater lead-210 activity than the juvenile samples, as would be expected for fish older than 20 years. Radium-226 activity was measured for all samples and was similar to the results from the juvenile sample groups (Table 3). The mean activity among the otolith samples was 0.0306 ± 0.0056 dpm·g⁻¹ (±1 SD, *n* = 5). Each adult group provided a unique lead–radium ratio that was used to determine radiometric age. To compare the estimated age-at-length (approximated from the DeMartini et al. (1994) VBGF) with radiometric age in the lead–radium ingrowth plot, ages of 10, 16, and 18 years were used for the three adult groups (smallest to largest). The age discrepancy exemplified by an inaccurate fit of those age estimates to the lead–radium ingrowth curve indicated that the age of these large fish was greater (Fig. 4).

Lead–radium dating of the adult otolith groups provided a mean age for each group. The age of fish in the groups, corrected for the time since capture (0.7 to 1.9 years), increased as expected with increasing mean fish length. The age of the group of smallest fish was more than 18 years old, and the age of the group of largest fish was more than 34 years old. Projecting the vertical error bars (2 SE) horizontally to the ingrowth curve provided the range of radiometric age uncertainty.

Bomb radiocarbon dating

A total of 43 otolith samples from fish collected in the NWHI were analyzed for radiocarbon. Calculated $\Delta^{14}\text{C}$ values

Fig. 4. Total sample age for each juvenile group (time since collection plus one-half of the average fish age) plotted (circles) relative to measured lead–radium activity for each sample. Comparison with the ingrowth model for lead–radium ingrowth provided a baseline assessment of the radium-226 daughter product conservation within the otolith over time spent in storage. Placement of the measured ratios for the adult age groups (squares) at an estimated 10 to 18 years demonstrated the wide divergence from the ingrowth curve. The measured lead–radium ratio from the cored adult otolith samples meets the ingrowth curve at ages 24 to 46 years, indicating age was underestimated. The solid ingrowth curve line represents straight ingrowth of lead-210 from radium-226, and the dashed line represents the core compensated (2 years) ingrowth curve. Vertical error bars represent 2 standard errors (SE) for the measured ratio from the measurement of lead-210 and radium-226 activities. Modified from Andrews et al. (2011a).



ranged from a low value of -52.9‰ (prebomb) to a high value of 186.2‰ (peak), a range similar to the regional coral $\Delta^{14}\text{C}$ reference series. In addition, four otolith samples from fish collected in the Mariana Islands were analyzed and provided a first look at regional differences in length-at-age. Fish and sample-specific details, other than are necessary for understanding the findings of the present study, were reported elsewhere (Andrews et al. 2011a).

Bomb radiocarbon dating was feasible for recently collected fish (2007–2008) based on lead–radium dating. Because the mean age of 16 large adult *P. filamentosus* exceeded 34 years (OP 700+), birth years for some fish should have been during the rise in $\Delta^{14}\text{C}$. Otolith samples from the NWHI, collected at Twin Banks, Gardner Pinnacles, North Hampton Seamounts, and Pioneer Bank (Fig. 1), were selected from this group for comparison with the bomb radiocarbon reference series (Fig. 3). These samples provided core material with $\Delta^{14}\text{C}$ values ranging from 96.2‰ to 186.2‰ ($n = 8$; Table 4a). Based on a projection of the measured $\Delta^{14}\text{C}$ levels from the year of collection back to the reference $\Delta^{14}\text{C}$ records for the region, age could be determined from both the decline (decline-age) and rise (rise-age) in $\Delta^{14}\text{C}$ for the region (Fig. 5a). Between these scenarios, age estimates were approximately 3 to 28 years for decline-age and approximately 35 to 43 years for rise-age. Age for two of

the samples was diagnostic based on rise and peak $\Delta^{14}\text{C}$ values; Gardner-1 ($96.2\text{‰} \pm 5.6\text{‰}$) was precisely aged as 43.1 ± 1 years old and North Hampton-1 ($186.2\text{‰} \pm 4.8\text{‰}$) was narrowly assigned to 35.4 ± 2 years old. The North Hampton-1 sample provided the greatest $\Delta^{14}\text{C}$ value of the study. For the remaining six of eight samples, it was not possible to determine which age scenario was accurate without unsupported assumptions; however, lead–radium dating indicated the group comprised mostly older individuals (rise-age values).

The archival otoliths that were collected between 1978 and 1988 from the NWHI provided a wide-ranging age series from bomb radiocarbon dating ($n = 35$). Sample locations ranged from Necker Island to Laysan Island (Fig. 1). For clarity of presentation, these samples were labeled by collection location and are organized from east to west in the NWHI (Table 4b). Projected $\Delta^{14}\text{C}$ values, from the year of collection back to the reference $\Delta^{14}\text{C}$ records, typically provided either a pair of age scenarios or a single diagnostic age. Two age estimates were possible when projection of the $\Delta^{14}\text{C}$ value crossed both the decline and the rise of $\Delta^{14}\text{C}$ (decline-age and rise-age, respectively). Diagnostic age estimates (rise-age only) were based on a collection year exclusion from the decline period (Fig. 5a). In some cases age could not be assigned because the possible date of formation was either ambiguous or poorly defined.

Table 4. (a) Bomb radiocarbon dating results for *P. filamentosus* otoliths collected in 2007–2008 from NWHI. (b) Bomb radiocarbon dating results for archived *P. filamentosus* otoliths, collected in 1978–1988 from NWHI. (c) Bomb radiocarbon dating results for archived *P. filamentosus* otoliths, collected in 1982 from the Mariana Islands.

| Sample No. | $\Delta^{14}\text{C}$ (‰) | Collection year | Decline-age (years) | Rise-age (years) | Fish length (mm FL) |
|---|---------------------------|-----------------|-----------------------|------------------|---------------------|
| (a) Otoliths collected in 2007–2008 from NWHI. | | | | | |
| Twin-1 | 129.1±10.1 | 2007.9 | 7.5 + 3 | 41.9±1* | 718* |
| Twin-2 | 143.6±5.0 | 2008.2 | 15.0 + 3 | 41.7±1 | 706 |
| Gardner-1 | 96.2±5.6 | 2007.9 | NA | 43.1±1* | 730* |
| Gardner-2 | 121.3±5.2 | 2007.6 | 3.3 + 3 | 41.9±1* | 718* |
| Gardner-3 | 137.3±5.0 | 2007.6 | 11.3+3 | 41.3±1 | 745 |
| Gardner-4 | 144.9±10.6 | 2007.5 | 15.0+3 | 41.0±1 | 718 |
| North Hampton-1 | 186.2±4.8 | 2007.8 | NA | 35.4±2* | 719* |
| Pioneer-1 | 170.9±4.9 | 2007.4 | 27.8+4 | 38.1±2 | 746 |
| (b) Otoliths collected in 1978–1988 from NWHI. | | | | | |
| Necker-1 | -17.9±3.6 | 1981.1 | NA | 22.6±1* | 600* |
| Necker-2 | 135.3±4.4 | 1981.1 | NA | 15.1±1* | 604* |
| Necker-3 | 171.7±4.5 | 1984.5 | 5.3 + 3 | 15.2±2 | 622 |
| Necker-4 | 174.9±4.2 | 1980.2 | 2.7 + 3 | 10.6±1 | 603 |
| FFS-1 | -31.6±4.1 | 1978.6 | NA | 21.6±1* | 672* |
| FFS-2 | -1.6±3.6 | 1988.2 | NA | 27.7±1* | 642* |
| FFS-3 | 61.6±4.0 | 1978.6 | NA | 15.1±1* | 662* |
| FFS-4 | 117.7±4.9 | 1978.6 | NA | 13.1±1* | 631* |
| FFS-5 | 136.6±4.8 | 1988.2 | NA | 22.2±1* | 627* |
| FFS-6 | 143.8±5.5 | 1988.2 | NA | 21.7±1* | 603* |
| FFS-7 | 158.2±4.3 | 1978.6 | 0.3 + 3 | 11.1±2* | 576* |
| Gardner-5 [†] | 148.3±4.3 | 1981.6 | NA | 21.6±1* | 577* |
| Gardner-6 | 170.6±4.4 | 1981.6 | 1.9 + 3 | 27.7±1 | 507 |
| Gardner-7 | 174.4±4.6 | 1981.6 | 3.8 + 3 | 15.1±1 | 564 |
| Raita-1 | 102.7±8.8 | 1981.6 | NA | 13.1±1* | 656* |
| Raita-2 | 160.7±5.2 | 1980.3 | NA | 22.2±1* | 649* |
| Raita-3 | 169.1±5.5 | 1981.6 | 1.2 + 3 | 21.7±1* | 665* |
| Raita-4 | 170.5±4.5 | 1980.3 | 0.5 + 3 | 11.1±2* | 614* |
| Maro-1 | -52.9±4.4 | 1980.8 | NA | ≥28.8 | 645 |
| Maro-2 | -52.3±4.5 | 1980.8 | NA | ≥28.8 | 728 |
| Maro-3 | -45.5±4.8 | 1981.1 | NA | 27.1±2* | 673* |
| Maro-4 | -45.5±3.8 | 1981.6 | NA | 27.6±2* | 682* |
| Maro-5 | -42.3±4.2 | 1981.6 | NA | 26.6±2* | 742* |
| Maro-6 | -38.2±3.9 | 1980.8 | NA | 24.8±2* | 716* |
| Maro-7 | 150.0±4.1 | 1980.8 | NA | 13.9±1* | 655* |
| Maro-8 | 150.2±7.6 | 1980.8 | NA | 13.9±1* | 626* |
| Maro-9 | 171.0±5.0 | 1978.6 | -0.9 + 3 [‡] | 9.3±2* | 577* |
| Laysan-1 | -45.1±4.0 | 1988.2 | NA | 34.4±2* | 768* |
| Laysan-2 | -38.6±3.9 | 1988.2 | NA | 32.2±2* | 723* |
| Laysan-3 | 111.4±4.8 | 1988.2 | NA | 22.8±1* | 702* |
| Laysan-4 | 145.4±5.6 | 1988.2 | NA | 21.6±1* | 738* |
| Laysan-5 | 152.8±4.4 | 1988.2 | -0.4 + 3 [‡] | 21.1±1* | 660* |
| Laysan-6 | 155.6±4.9 | 1988.2 | 1.0 + 3 | 21.0±1* | 665* |
| Laysan-7 | 158.3±4.3 | 1988.2 | 2.3 + 3 | 20.8±1* | 721* |
| Laysan-8 | 159.6±4.8 | 1988.2 | 3.0 + 3 | 20.7±1* | 729* |

Table 4 (concluded).

| Sample No. | $\Delta^{14}\text{C}$ (‰) | Collection year | Age-FFS (years) | Age-Okinawa (years) | Fish length (mm FL) |
|---|---------------------------|-----------------|---------------------------|----------------------------|---------------------|
| (c) Otoliths collected in 1982 from the Mariana Islands. | | | | | |
| Mariana-1 | 144.0 \pm 4.4 | 1982.4 | 15.9 \pm 1 [§] | 13.9 \pm 1 [§] | 453 |
| Mariana-2 | 138.1 \pm 4.3 | 1982.3 | 16.3 \pm 1 [§] | 14.3 \pm 1 [§] | 491 |
| Mariana-3 | 11.9 \pm 5.2 | 1982.4 | 20.4 \pm 1 | 20.4 \pm 1 | 512 |
| Mariana-4 | -24.8 \pm 4.0 | 1982.4 | 24.4 \pm 1 | 26.9 \pm 1 | 521 |

Note: Data modified from Andrews et al. (2011a). For parts (a) and (b), age determination was from a projection of the measured $\Delta^{14}\text{C}$ value to either the rise or decline in $\Delta^{14}\text{C}$ (Decline-age and Rise-age; Fig. 5a). Sample numbering differs from original report, and an error of transposed data was corrected in data from Mariana Islands. For part (c), age determination was from a projection of the measured $\Delta^{14}\text{C}$ value to either the NWHI or Okinawa $\Delta^{14}\text{C}$ references (Age-FFS (French Frigate Shoals) and Age-Okinawa; Fig. 5b). NA, not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

*Diagnostic age and length values used to develop the VBGF (Fig. 6).

†Sequence continued from Table 4a.

‡Estimate for decline in $\Delta^{14}\text{C}$ leads to a lowest age of zero based on collection year.

§Range of uncertainty overlaps and a mean age ± 2 years was used in VBGF plot.

||Incorporation of small peak in Okinawa $\Delta^{14}\text{C}$ record at ~ 1956 with duration of < 8 months was possible.

The archival otolith samples from Necker Island and FFS were collected between 1978 and 1988 from fish whose lengths ranged 576–672 mm FL ($n = 11$). These samples provided $\Delta^{14}\text{C}$ values that ranged from near prebomb levels at -31.6‰ to near peak levels at 174.9‰ (Fig. 5a). Three samples could not be assigned a single age estimate because both decline-age and rise-age correlations provided viable age estimates of up to 3 to 8 years and approximately 11 to 15 years, respectively. However, length-at-age data from other studies indicated 3 years was too low for FFS-7, and an age of approximately 11 years was assigned. The remaining eight samples could only be assigned rise-age estimates of approximately 13 to 28 years (Table 4b).

The archival otolith samples from Gardner Pinnacles and Raita Bank were collected between 1980 and 1982 from fish ranging 507–665 mm FL ($n = 7$). These samples provided $\Delta^{14}\text{C}$ values that ranged from mid-rise levels at 102.7‰ to near peak levels at 174.4‰ (Fig. 5a). Measured $\Delta^{14}\text{C}$ levels for four of the seven samples provided both decline-age and rise-age estimates of up to 3 to 7 years and approximately 11 to 28 years, respectively. However, length-at-age data from other studies indicated decline-age was too low for Raita-3 and Raita-4, and a rise-age estimate was assigned to each fish. The remaining three samples were diagnostic at approximately 13 to 22 years (Table 4b).

The archival otolith samples from Maro Reef were collected between 1978 and 1982 from fish ranging 577–742 mm FL ($n = 9$). These samples provided $\Delta^{14}\text{C}$ values that ranged from pre-bomb levels at -52.9‰ to near peak levels at 171.0‰ (Fig. 5a). For these fish, both decline-age and rise-age could be determined for only one of the nine samples, with the remaining eight samples being either diagnostic (rise-age only) or limited to a minimum age from prebomb $\Delta^{14}\text{C}$ levels. The decline-age estimated for Maro-9 was up to 2 years; however, length-at-age data from previous studies make this estimate unlikely, and a rise-age of approximately 9 years was assigned (Table 4b). Rise-age estimates were diagnostic for six fish at approximately 14 to 28 years. Two fish could only be assigned a birth year prior to the rise of $\Delta^{14}\text{C}$ and were assigned a minimum age of approximately 29 years, but these fish could have been older. Hence, these latter samples could not be used in length-at-age analyses.

The archival otolith samples from Laysan Island were all collected in 1988 from some of the largest fish of this study ranging 660–768 mm FL ($n = 8$). These samples provided $\Delta^{14}\text{C}$ values that ranged from near prebomb levels at -45.1‰ to near peak levels at 159.6‰ (Fig. 5a). Either decline-age or rise-age classification was possible for four of the eight samples. In all four cases the decline-age was too low to be considered viable relative to pre-existing length-at-age data, and each was assigned an age of approximately 21 years. The remaining samples could only be attributed to either prebomb or rise-age. Rise-age estimates from the upper part of the slope were approximately 22–23 years. Two samples near prebomb levels were considered elevated enough to be assigned to birth years at the early rise in $\Delta^{14}\text{C}$. Hence, these samples were assigned ages of approximately 32 to 34 years old. Four of the eight samples in this group were considered diagnostic (Table 4b).

In summary, there were 33 length-at-age estimates from bomb radiocarbon dating of *P. filamentosus* from the NWHI, of which 23 of 33 were aged with high confidence and deemed diagnostic. The lengths of fish ranged from 576 to 768 mm FL, with age estimates ranging from approximately 9 to 43 years (Tables 4a and 4b). The 10 samples that were not considered diagnostic had decline-age estimates that were regarded as too low to be realistic based on other early growth studies. As a result, all 33 fish were assigned validated age estimates for use in growth modeling.

The archival otolith samples also provided an opportunity to apply bomb radiocarbon dating to otoliths from the Mariana Islands. All of these samples were collected in 1982 and were from fish with lengths of 453 to 512 mm FL ($n = 4$). These samples provided $\Delta^{14}\text{C}$ values that ranged from lower slope at -24.8‰ to upper slope at 144.0‰ for the rise in $\Delta^{14}\text{C}$ (Table 4c). Age estimation was specific to the rise of $\Delta^{14}\text{C}$ (rise-age only); however, an additional consideration for this sample set was its remote location relative to the coral $\Delta^{14}\text{C}$ reference series of the Hawaiian Islands. To more fully encompass the region, a coral $\Delta^{14}\text{C}$ record from Okinawa, Japan, provided an additional reference (Konishi et al. 1981). The rise-age correlation for upper slope $\Delta^{14}\text{C}$ values was less specific because of an offset by approximately 2 years later for Okinawa (Fig. 5b). As a result, the age

Fig. 5. (a) Measured $\Delta^{14}\text{C}$ levels in *P. filamentosus* otolith cores from the NWHI plotted at both the collection year and the correlated year of formation on the NWHI $\Delta^{14}\text{C}$ reference records. A birth year was estimated for the archived otoliths, collected between 1978 and 1988 (\times symbols), and the recently collected otoliths, collected in 2007–2008 (open circles), by projecting the $\Delta^{14}\text{C}$ values back to the $\Delta^{14}\text{C}$ reference record (diamonds and solid circles, respectively). Age was calculated from correlated birth years at the $\Delta^{14}\text{C}$ rise. In some cases, a possible birth year was estimated at the $\Delta^{14}\text{C}$ peak and decline. Reference $\Delta^{14}\text{C}$ records were described in Fig. 3. (b) Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from Mariana Islands plotted both at the collection year (\times symbols) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamonds). Age was determined from correlated birth years at the rise in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the records for the associated reference time period, with an added consideration for a hermatypic coral record from Okinawa, Japan (dotted line with open circles; Konishi et al. 1981). Modified from Andrews et al. (2011a).

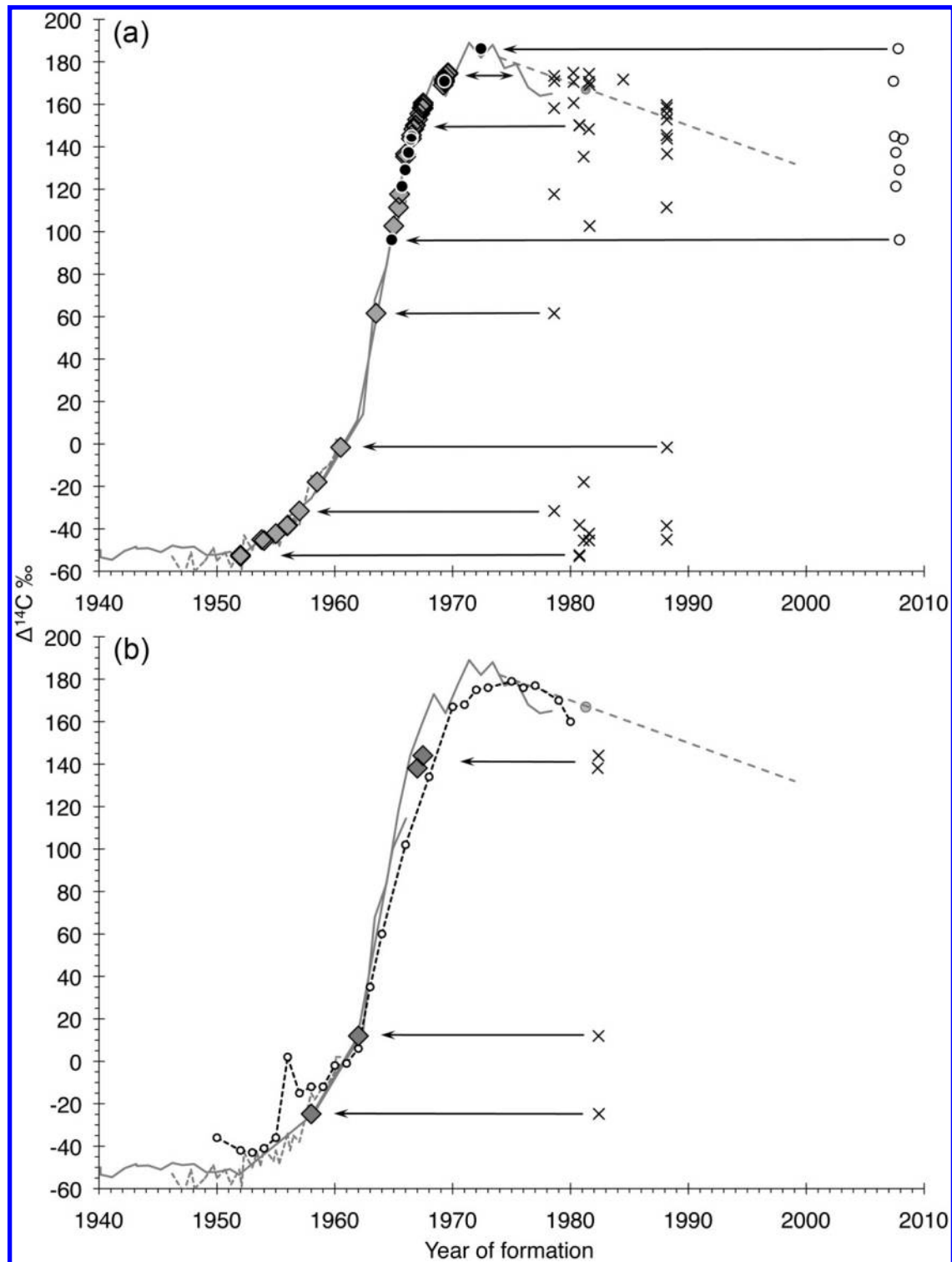
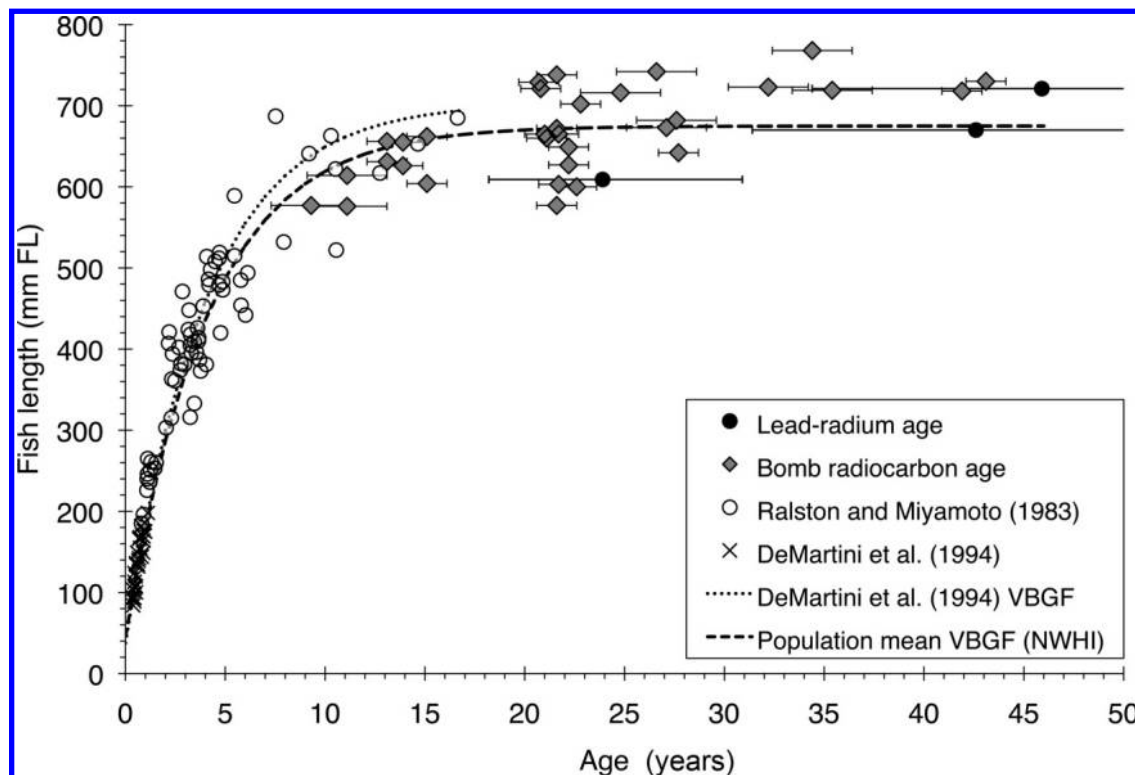


Fig. 6. Revised von Bertalanffy growth curve plotted with all otolith-based age data considered reliable for *P. filamentosus* in the NWHI. VBGF parameter estimates for the population mean were $L_{\infty} = 675$, $K = 0.242$, and $t_0 = -0.29$. Plotted for comparison is the curve fit from DeMartini et al. (1994) that also used the age data from Ralston and Miyamoto (1983), with parameters similar to the comprehensive curve fit ($L_{\infty} = 704$, $K = 0.25$, $t_0 = 0.22$). Note that breaks in the age-at-length bomb radiocarbon data (i.e., near the 15- to 20-year range) are an artifact of the collection year availability for *P. filamentosus* specimens relative to the informative or diagnostic rise in $\Delta^{14}\text{C}$ period. Modified from Andrews et al. (2011a).



assigned to two fish near the upper slope was given a wider range of approximately 14 to 16 years for each fish (Mariana-1 and Mariana-2). For the lower portion of the rise in $\Delta^{14}\text{C}$, the regional records were similar, with the exception of a minor peak at 1956. The $\Delta^{14}\text{C}$ value for Mariana-3 exceeds this peak value and was assigned an age of approximately 24 years. The $\Delta^{14}\text{C}$ value for Mariana-4 was assigned an age of approximately 27 years, but a narrow possibility of incorporating the peak at 1956 could mean the fish was approximately 24 years old. These data were not used in the development of a VBGF because they were too far removed from the NWHI population.

von Bertalanffy growth function

The three convergence diagnostics each indicated that the MCMC simulations produced independent samples from the posterior distribution of parameter estimates of the VBGF for base case, homogeneous variance, and simple Bayes models. There were no significant autocorrelations for lags of 1 to 50 observed in the MCMC chains for any of the parameters for each model. Similarly, the assumption that the standardized residuals from the fitted length-at-age data were normally distributed could not be rejected based on the Shapiro–Wilk test for each model. Overall, these diagnostics indicated that the posterior distribution of the model parameters was adequately sampled with the MCMC simulations.

The goodness of fit comparison of the base case hierarchical model and the two alternative models indicated that there was a substantial difference in the quality of model fits. The DIC value for the base case hierarchical model was $\text{DIC}_{\text{BASE}} = 728.8$. In comparison, the respective DIC values for the homogeneous variance and simple Bayes models were $\text{DIC}_{\text{HV}} = 763.8$ and $\text{DIC}_{\text{SB}} = 779.7$ and the DIC differences (ΔDIC) for the alternative models relative to the base case model were substantial with $\Delta\text{DIC}_{\text{HV}} = 35.0$ and $\Delta\text{DIC}_{\text{SB}} = 50.9$. As a result, the base case hierarchical model with heterogeneous variances for the age reading methods was judged to provide the best fit to the *P. filamentosus* length-at-age data.

The posterior means of the VBGF parameters estimated with the base case hierarchical model were used to describe expected length-at-age for the *P. filamentosus* population in Hawaii (Fig. 6). The population estimates of the VBGF parameters and their standard errors ($\pm\sigma$) were $L_{\infty} = 675$ mm FL (± 18 mm), $K = 0.242$ (± 0.057), and $t_0 = -0.29$ years (± 0.09 years). Correlations among the VBGF parameters were $\rho(L_{\infty}, K) = -0.21$, $\rho(L_{\infty}, t_0) = -0.14$, and $\rho(t_0, K) = 0.30$. Overall, the fitted growth curve indicated that *P. filamentosus* growth in Hawaii is rapid for juvenile fish but slows considerably by the time fish reach about 10 years of age at an expected length of roughly 90% of the estimated asymptotic length (Fig. 6).

Estimates of the VBGF parameters from the individual age reading methods were generally similar to the population estimates. Estimates of asymptotic length for the bomb radiocarbon ($n = 33$), lead–radium ($n = 3$), Ralston and Miyamoto (1983; $n = 65$), and DeMartini et al. (1994; $n = 35$) data sets were $L_{\infty} = 682, 675, 666,$ and 676 mm FL, respectively, and these estimates ranged from -1% to $+1\%$ of the population estimate of L_{∞} . Similarly, estimates of the Brody growth rate coefficient K for the bomb radiocarbon, lead–radium, Ralston and Miyamoto (1983), and DeMartini et al. (1994) data sets were $K = 0.214, 0.238, 0.269,$ and 0.246 , respectively, ranging from -12% to $+11\%$ of the population estimate of K . Thus, the age reading method had a stronger effect on the estimate of the Brody growth coefficient than on the estimate of the asymptotic length. The estimated standard deviations of observed length-at-age (mm FL) for the bomb radiocarbon, lead–radium, Ralston and Miyamoto (1983), and DeMartini et al. (1994) data sets were $\sigma = 45.6, 64.2, 48.2,$ and 13.5 mm. Overall, the most precise measurements of length at age appeared to be the DeMartini et al. (1994) data set, while the bomb radiocarbon and the Ralston and Miyamoto (1983) data sets had similar precisions.

Discussion

Lead–radium dating

The lead–radium dating of otolith groups from adult *P. filamentosus* provided a first look at an independent estimate of age for some of the largest specimens collected from the Hawaiian Islands. The mean age of the largest-sized group was 45.6 years (range: 34.4–64.0 years, 2 SE) and was considerably older than the previously attributed maximum age of 18 years. Lead–radium dating of smaller-sized fish reinforced the greater length-at-age scenario with two additional age estimates exceeding 18 years (23.9 and 42.6 years). Hence, the caution expressed by Ralston and Miyamoto (1983) against extrapolating daily growth increment age data to the largest fish was correct. Previous studies made inaccurate assumptions for the age and growth of adult fish (Uchiyama and Tagami 1984; Radtke 1987).

The findings from the juvenile *P. filamentosus* samples supported an application of lead–radium dating to extracted otolith core material from adult fish. Radiometric age determined from cores of adult fish is analogous to the storage time for the juvenile otoliths; hence, the measured ratio from cored otoliths would provide a measure of adult fish age. The test for potential loss of isotopes during storage time was successful by showing that no measureable loss of radium-226 daughter products occurred during either of two lengthy storage times (11.3 and 20.5 years). Studies have voiced concerns about the possible violation of the closed otolith system because of large losses of radon-222 (Gauldie and Cremer 2000), but no rigorous studies to date have documented losses that were considered significant relative to the determination of age from lead–radium dating, and such losses have been considered a surface emanation process that is temporary (e.g., Whitehead and Ditchburn 1995; Baker et al. 2001; Kastle and Forsberg 2002). The findings of the current study provide further evidence that no significant loss of lead–radium series isotopes occurs from otoliths, whether in vivo or stored dry, and that lead–radium dating continues to be a viable and accurate option for age estimation using otoliths.

Radium-226 levels were at the low end of what was expected ($0.3\text{--}0.5$ dpm-g⁻¹), but this was understandable in the broader context of radium-226 fluxes within the marine environment. The flux of radium-226 is typically greatest near continental margins and sea floors with low sedimentation rates (Broeker and Peng 1982; Fanning et al. 1982); the location of Hawaii as a central Pacific Ocean archipelago provides a reasonable explanation for the relatively low radium-226 values, as has been recorded for the surface waters of the Pacific (Broeker and Peng 1982). Although activity was low in otolith material, radiometric age determination was possible given a collective sample mass of more than 1 g of otolith cores.

Bomb radiocarbon dating

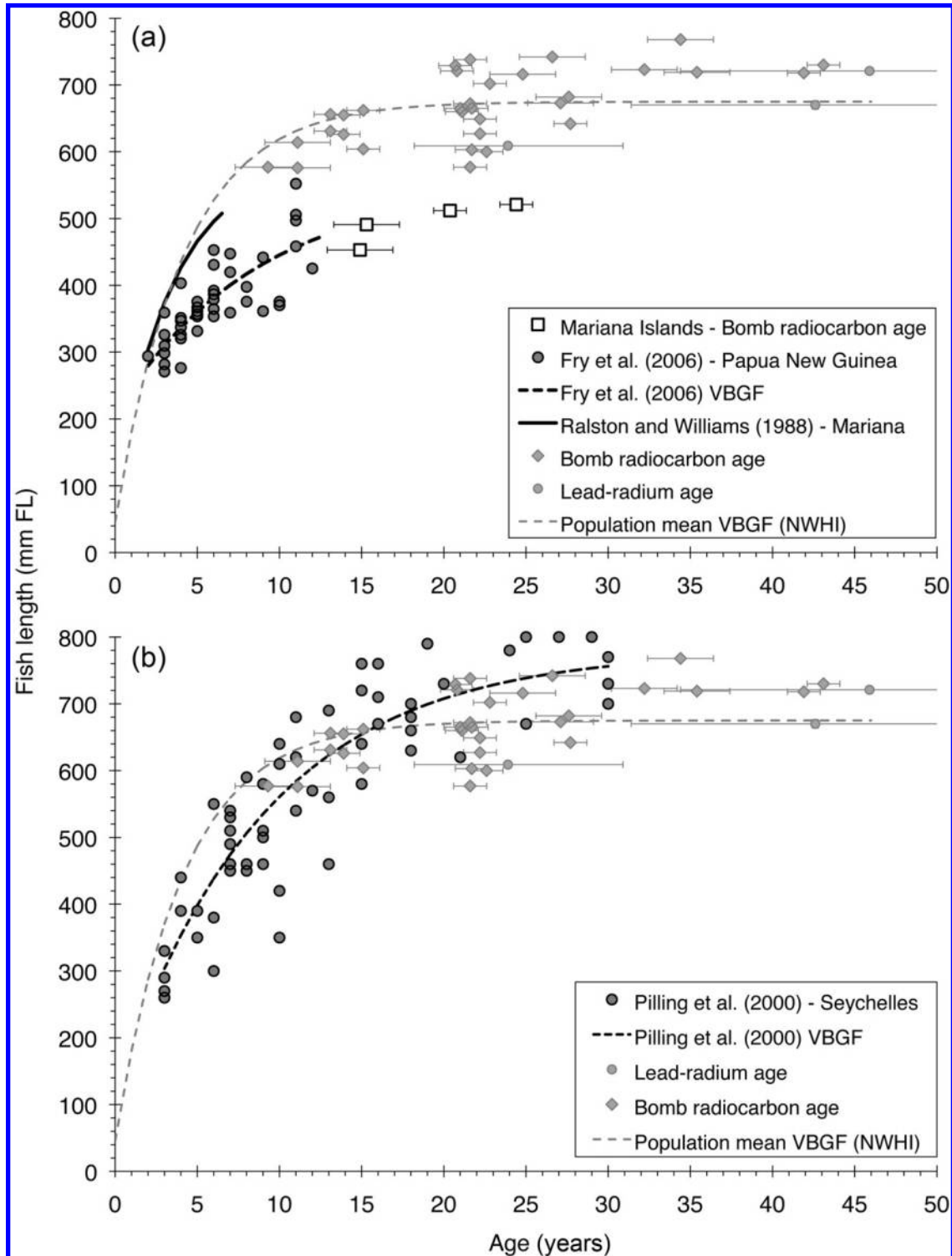
Bomb radiocarbon dating requires birth year otolith material to have formed between approximately 1955 and 1970 for age determination, and recently collected fish would need to be between 40 to 55 years old for the method to be applicable. Prior to our use of lead–radium dating to age the otoliths of *P. filamentosus*, there was no evidence to indicate that bomb radiocarbon dating might be feasible for recently collected otoliths. Lead–radium dating provided the necessary information to explore bomb radiocarbon dating of the largest fish group (OP 700+). Some of the oldest fish aged in this study (up to 43 years) were in this group; however, some of these fish provided $\Delta^{14}\text{C}$ levels that could not be dated accurately. For the recent collections from the NWHI, there were numerous fish that were diagnostic and could be aged accurately to more than 30 or 40 years. In general, none of the fish in this group could have been older than 44 years based on the limits of measured $\Delta^{14}\text{C}$ levels and the reference $\Delta^{14}\text{C}$ records. Hence, the mean age of the group from lead–radium dating can be refined further to between the mid 30s and early 40s (lower 2 SE limit = 34.4 years from lead–radium dating).

When investigating the age and growth of *P. filamentosus* using bomb radiocarbon dating, it was evident that otolith collections were needed from archives to age fish in smaller size classes. A search of the available samples revealed valuable collections that were made between 1978 and 1988. By utilizing fish length and otolith mass as gross proxies for fish age, otoliths were selected from these archives that had a potential birth year during the informative period. The result was a very successful application for 33 of the 35 selected samples from the NWHI. In some cases, a retrospective judgment needed to be made to exclude younger age scenarios based on previous early growth studies where length-at-age was validated (Ralston and Miyamoto 1983). As a result of these $\Delta^{14}\text{C}$ assays, the age data begins to overlap with the upper limits of the age data from Ralston and Miyamoto (1983), effectively filling in the missing information for the largest *P. filamentosus* and allowing a comprehensive reassessment of growth characteristics of the species over its entire size range in the NWHI.

Growth and life history characteristics

The comprehensive nature of age validation for *P. filamentosus* from this study and previous reliable studies has provided a unique opportunity to describe the growth characteristics of this species in Hawaii. It is important to have a reliable growth curve for estimating the number of fish captured at age in commercial

Fig. 7. (a) Bomb radiocarbon age data for *P. filamentosus* from the Mariana Islands, plotted with the results from the NWHI, indicate that growth characteristics differed for *P. filamentosus* between the two regions. For comparison, the VBGF determined from early growth interpretations by Ralston and Williams (1988) is plotted with age estimates and growth function from Fry et al. (2006) from Papua New Guinea. Ralston and Williams (1988) provided a curve fit to numerical integration of daily increment widths ($L_{\infty} = 584$, $K = 0.289$, $t_0 = -0.5$), whereas the growth curve of Fry et al. (2006) was based on visual counts of presumed annual growth zones ($L_{\infty} = 551$, $K = 0.118$, $t_0 = -4.0$). (b) Age data and growth function for *P. filamentosus* from the Seychelles (Pilling et al. 2000), based on visual counts of presumed annual growth zones ($L_{\infty} = 780$, $K = 0.111$, $t_0 = -1.4$), plotted with the results from the NWHI. This comparison indicates growth characteristics might be similar for the two regions.



fisheries based on observed length–frequency data. The *P. filamentosus* population in Hawaii is part of the Hawaiian bottomfish complex that was considered to have experienced overfishing in the early 2000s (Moffitt et al. 2006). The improved understanding of growth and expected life span estimated to be on the order of 40 years from this study provides a better understanding of the life history characteristics and a credible range of intrinsic growth rates for the bottomfish complex. This, in turn, provides a more reliable set of life history information for conducting stock assessments (Brodziak et al. 2011).

The hierarchical Bayes approach to estimating the VBGF parameters allowed us the flexibility to investigate and compare models with heterogeneous and homogeneous variances for the four ageing data sets. The heterogeneous variance model provided a substantially better fit to the observed data, as might be expected given the intrinsic differences in the ageing methods. However, we also observed that the empirical differences between the hierarchical Bayes estimates and some previous maximum likelihood estimates (MLEs), assuming additive normal errors for the Hawaii data set were not substantial. In particular, Andrews et al. (2011a) reported that the MLEs of the L_{∞} , K , and t_0 parameters estimated using the same data set with a constant variance, zero mean, and additive normal error term were $L_{\infty} = 674$ mm FL, $K = 0.252$, and $t_0 = -0.33$, which differed from the mean hierarchical Bayes estimates by -0.1% , 4.1% , and 13.8% , respectively. Thus, the practical differences between the classical frequentist and Bayesian estimation approaches were minor, which reinforces the compatibility of both approaches (e.g., Clark 2005), especially when uninformative prior distributions are employed, as was done in this study.

The results from bomb radiocarbon dating for the specimens collected in the Mariana Islands were unique in terms of age-at-length relative to the NWHI. Estimated length-at-age from bomb radiocarbon dating of the four *P. filamentosus* specimens from the Mariana Islands differed greatly from those collected in the Hawaiian Islands. The four specimens suggest that *P. filamentosus* grow more slowly and probably do not attain as great a size in the Mariana Islands compared with *P. filamentosus* in the NWHI (Fig. 7a). Other studies from the region and another region farther south provide additional information about regional differences in growth rates and possible longevity. Ralston and Williams (1988) and Fry et al. (2006) each estimated a smaller maximum length relative to the Hawaiian Islands, although these studies suffered from low sample size, a narrow range of fish lengths, or both. When these data were considered in concert with the bomb radiocarbon dates, there was collective evidence that *P. filamentosus* in the far western Pacific Ocean grow more slowly and may not grow as large. The greatest bomb radiocarbon age from the Mariana Islands was approximately 23–28 years old at a length of 521 mm FL, considerably smaller than the largest fish collected by Ralston and Williams (1988) at 640 mm FL. The greatest age estimated by Ralston and Williams (1988) was 6 years old for fish near 500 mm FL. Putative annual growth zone counts for *P. filamentosus* from the Lihir Island group, Papua New Guinea, provided one of the more aberrant growth functions. Age estimation was limited to 2 to 12 years for up to what may or may not have been the maximum sized fish for the region (552 mm FL). Assuming

that fish in this region can attain greater sizes, perhaps similar to those in the Mariana Islands, an extension of the growth function trajectory would approximate the age-at-length determined from radiocarbon dating (Fig. 7a).

In contrast with the differences noted previously, age and growth estimates for *P. filamentosus* from the Seychelles, based on counts of purportedly annual growth zones (Pilling et al. 2000), appeared more similar to length-at-age estimates for the NWHI (Fig. 7b). The *P. filamentosus* age data for the Seychelles were estimated using growth zone counts that were thought to be annual, but growth structure was reported as poorly defined and very questionable (G. Pilling, Secretariat of the Pacific Community, BP D5, 98848 Noumea, New Caledonia, personal communication, 2011). Marginal increment analysis and even an edge type analysis were unsuccessful because the zone structure was not clear and some other form of age validation is necessary. Based on estimated age and collection dates in the 1990s, these estimates can be investigated with bomb radiocarbon dating on a select group of the largest and oldest fish from the Pilling et al. (2000) study. It is recommended that a validation of longevity for *P. filamentosus* be investigated for this important fishery.

These summary geographic comparisons indicate that further study is necessary to document regional similarities and differences in growth for *P. filamentosus* across its geographical range. When this is considered with recent observations of high genetic connectivity across the Indo-Pacific and an apparent genetic isolation of the Hawaiian Archipelago (Gaither et al. 2011), applying the growth function we have developed to other regions outside the Hawaiian Archipelago is unwarranted and should be done with reservation only. Moreover, our VBGF model was limited to otolith-based growth estimates. Recent information based on estimates of growth for MHI fish using tag–recapture data needs to be included when making further refinements to an age-based stock assessment of *P. filamentosus* in Hawaii. Although equivocal differences in the mass-at-length of *P. filamentosus* exist between the MHI and NWHI (Sundberg and Underkoffler 2011), the tag–recapture-based growth curve for MHI *P. filamentosus* closely resembles our otolith-based characterization for NWHI fish (D. Kobayashi, NOAA Fisheries, PIFSC, Honolulu, Hawaii, personal communication, 2011). Furthermore, *P. filamentosus* populations lack genetic structure across the Hawaiian Islands (Gaither et al. 2011), and there is no heritable basis for possible subregional variation in length-at-age in Hawaii. This provides strong support for the inclusion of *P. filamentosus* otolith data from the NWHI when assessing and managing its MHI stock.

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