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Opakapaka (*Pristipomoides filamentosus*)

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ABSTRACT

Age estimation for opakapaka or pink snapper (*Pristipomoides filamentosus*) from the Hawaiian Archipelago has been an ongoing problem because otoliths of this species lack well-developed annual growth zones. Early growth was well documented and validation of otolith growth was successful for the first few years of life using daily increments, but determination of age for the largest and oldest adults was still in question. A 1983 paper by Ralston and Miyamoto developed a model for age prediction by calculating otolith dimensions which resulted in a maximum observed age of 18 years; however, the largest fish used in that study were less than the maximum length for this species in the region. This age has been subsequently and uncritically assumed as the maximum age for this species, but the 18-year estimate was based on clearly stated assumptions and the authors cautioned against unjustified estimates of longevity using their findings. Two methods that can provide independent estimates of age using adult otoliths are lead-radium and bomb radiocarbon dating. In this study, longevity estimates of opakapaka more than doubled using these methods, thus supporting the cautionary statements of the original paper.

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INTRODUCTION

Age and Growth Estimation

The opakapaka or pink snapper (*Pristipomoides filamentosus*) is an important commercial fish species found in tropical and subtropical waters, yet many of its life history characteristics remain unknown or are incompletely described (Fig. 1). Its geographical range spans from the Hawaiian Islands and central western Pacific Ocean, throughout the Indo-Pacific region, to the western Indian Ocean (Fig. 2). Despite its wide-ranging distribution, age and growth information is incomplete and results are highly variable across its range. To date, age and growth for this species has been studied from the Seychelles, Papua New Guinea, Mariana Islands, and the Hawaiian Islands using numerous age estimation techniques with a few limited forms of age validation.

One of the earliest age and growth works on *P. filamentosus* was performed on otoliths from fish collected in the Northwestern Hawaiian Islands (NWHI). This investigation identified daily growth increments apparently correlated to perceived annual growth zones (Uchiyama and Tagami, 1984). The authors concluded the first few years were validated from daily increment counting, but the relationship beyond 3 years was in question. A von Bertalanffy growth function (VBGF) was fitted to these limited data and resultant growth parameters indicated opakapaka were a fast growing and short-lived species with a maximum estimated age of 5 years. Uchiyama and Tagami (1984) were also careful to compare their preliminary findings to two other studies in progress at the time, each of which had estimates of maximum age greater than their findings (Ralston and Miyamoto, 1983; Radtke, 1987).

Ralston and Miyamoto (1983) developed a method that uses numerical integration of daily increment widths as a model for age prediction by calculating otolith dimension. The method addressed problems that were observed by Uchiyama and Tagami (1984) by providing measures of otolith growth from readable segments of the sectioned otolith axis. The method also accounted for changes in otolith growth with age; especially significant was the reduced growth rate with increasing age and the onset of maturity. A slowing of otolith growth past maturity and perceived limits to the application for the largest and oldest fish were documented. The oldest age determined in the study was 16.6 years, but the size of this fish (685 mm FL) was considerably less than the maximum size reported for opakapaka from the Hawaiian Islands (800 mm FL; Uchiyama and Kazama, 2003).

Radtke (1987) took a different position on the interpretation of daily growth increments than was described by Ralston and Miyamoto (1983). In that study, several novel techniques were applied to elucidate daily increments in the otoliths of *P. filamentosus*. Otoliths from 10 fish, selected to cover most of the length range of *P. filamentosus*, were examined for daily increments using scanning electron microscopy (SEM). To differentiate from Ralston and Miyamoto's position (1983), Radtke (1987) applied sequential surface etchings to enumerate a presumably complete count of all daily increments in each of the otolith samples. Ralston and Miyamoto (1983) argued that daily increments could not and should not be resolved past a certain size or age (apparently related to maturity), while Radtke (1987) deemed all daily increments were resolvable with the method used, even for the largest fish. However, even though abrupt changes

in increment width were observed, cessation or slowing of otolith growth after maturity was not acknowledged and no validation was performed. Fish age was ultimately determined by all daily increments for a maximum age of *ca.* 6.1 years for a 720 mm FL fish (Radtke, 1987).

Each of these early studies provided very different interpretations of age for adult *P. filamentosus*, all of which were collected from the NWHI at a similar time period, yet there was near consensus on the rate of growth in the first few years (Fig. 3). A more detailed study of the earliest growth further supported these findings by validating daily increment counts for 0+ and 1+ juvenile fish (DeMartini et al., 1994). These data, coupled with the length-at-age determined by Ralston and Miyamoto (1983), provided an opportunity for more comprehensive growth modeling, albeit length-at-age was still not available for the largest fish (Fig. 4). Similar to these findings was the resultant growth rate from a length frequency analysis of juveniles collected from off Kaneohe Bay, Oahu (Moffitt and Parrish, 1996).

The results from other age and growth studies removed geographically from the Hawaiian Islands have also been complicated by methodological limitations. Ralston and Williams (1988) continued the application of daily increment integration to *P. filamentosus* collected from the Mariana Islands. The study provided estimates of growth up to approximately 6 years using both otoliths and length frequency analysis, each providing only rough estimates as a result of low sample size. In addition, maximum size reported in the study was considerably smaller than elsewhere at 640 mm FL. In a study of *P. filamentosus* from Papua New Guinea, annual growth zones were observed and quantified for a maximum observed age of 12 years (Fry et al., 2006). The estimates in the study could not be validated with otolith edge analysis, and age estimates based on growth zone counts were not well defined (G.C. Fry, CSIRO, Australia, pers. comm.).

Age and growth studies on the Seychelles fishery are the next most extensive relative to the Hawaiian Islands, and results are once again highly variable (Fig. 5). Two management-related studies focusing on stock assessment and potential fishery yield reported estimated growth parameters for *P. filamentosus*, based on length-frequency analyses (Mees, 1993; Mees and Rousseau, 1997). These analyses indicated growth was more rapid than most other age and growth studies; however, adult age structure and maximum age could not be determined because results from such an analysis are limited to the earliest growth—once asymptotic length is reached or even approached, age classes related to changes in fish length are lost. In an assessment of otolith sections for lunar cycle influences, age and growth were estimated in a report lacking important details (Hardman-Mountford et al., 1997). Assumptions were made with respect to the periodicity of zone formation with no investigation of daily increment formation to validate lunar periodicity. It is uncertain what the range of fish lengths were for the study; however, results from a study using lunar increments must be qualified as limited to the earliest growth and juvenile fish (e.g., Campana, 1984). In a thorough investigation of otolith sections from *P. filamentosus*, age was estimated from putative annual growth zones up to 30 years (Pilling et al., 2000). An attempt to validate the annual periodicity of the growth zones using marginal increment and edge analysis was unsuccessful. This study was the first to report age from otolith sections using presumed annual growth zone counts through maximum fish length, although the counting of zones was deemed very difficult (G.M. Pilling, CEFAS, UK, pers. comm.).

Age estimation for the largest *P. filamentosus* has been an ongoing problem for the development of reliable and consistent growth parameters (Table 1). As a result of the wide range of questionable age and growth results, potential growth trajectories for this species are numerous (Fig. 6). Aside from rough estimates of age from the Seychelles based on putative annual growth zones, no age estimates are available for the largest fish. Because Ralston and Miyamoto (1983) provided some of the most rigorous evidence for proper growth modeling of *P. filamentosus*, a maximum estimated age was determined anonymously from the published growth function. Based on fish length attaining 90% of the asymptotic length, an estimate of 18 years was derived and has been reported as the maximum age for this species (e.g., Manooch III, 1987). However, this estimate was based on a method that: 1) made assumptions about otolith growth during adult stages; 2) was not applied to the largest fish sizes; and 3) should be independently tested based on limitations of the method at great ages (Morales-Nin, 1988; Stevenson and Campana, 1992). In addition, Ralston and Miyamoto (1983) 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 PIFSC laboratory observations, it is evident that opakapaka otoliths from the Hawaiian Islands lack well-developed, annual growth zones. Hence, it is important to apply age validation techniques that can address the issue of adult age, growth and longevity in order to develop accurate life history parameters that can be used in stock assessments and effective management plans.

Age Validation

Age validation techniques for fishes range widely in efficacy and precision (Campana, 2001). Techniques that rely on establishing a temporal context to early growth by measuring changes in otolith growth zones or fish length require an extrapolation of the early growth findings to larger and older fish for which growth increment or length mode resolution has been lost (e.g., Mace et al., 1990; Mees and Rousseau, 1997). In addition, daily increment and marginal increment analyses (MIA) and length frequency analysis are graphical and subjective; the techniques cannot test the accuracy of age data directly because they do not generate an independent measure of age. Alternatively, known age of fish of captive rearing can be compared with ages estimated independently by otolith readers, or the marking and recapturing of older fish can be conducted. Both methods generate known measures of time (a period that is usually only a portion of the lifespan) and allow the use of probability-based statistical techniques to test and measure accuracy; however, marking, tagging, and laboratory conditions can modify growth and survival, generating error with respect to the population. Moreover, both techniques are logistically complex for large fishes, often do not cover early life, and involve long delays in the acquisition of late-life data (e.g., shark tag data from 1962 to 1993; Kohler et al., 1998). Hence, methods to measure age of the largest and oldest fish directly are of great importance. Advances in the use of radiochemical proxies for age have provided opportunities for independent age determination of fishes, and the primary techniques currently in use are bomb radiocarbon (^{14}C) and lead-radium dating. These methods of age validation can function as independent measures of age, but the applicability of each technique is limited by a number of considerations. An application of both age validation methods to a single species, however, can provide

complementary findings, both of which can provide age estimates that do not rely on previous estimates of age, assuming that the specific requirements of each method can be met.

Lead-radium Dating

Lead-radium dating is a geochronological technique that has been used to date recent geological formations, such as accretionary carbonates (e.g., Condomines and Rihs, 2006). Use of this system as a chronometer relies on the decay of the relatively long-lived radioisotope radium-226 (^{226}Ra), a naturally occurring product of the uranium-238 (^{238}U) decay series (Fig. 7), to the relatively short-lived granddaughter product lead-210 (^{210}Pb). Because the half-life of radium-226 is much greater (~ 1600 years) than lead-210 (22.26 years), the disequilibrium of the lead-radium system can function as a natural chronometer as lead-210 builds into equilibrium with radium-226. Once radium-226 is incorporated and isolated by some kind of structure (e.g., the crystalline lattice of a fish otolith), it is the ingrowth of lead-210 activity relative to radium-226 activity that provides a measure of time. In an ideal system there would be no exogenous source of lead-210, and the lead-radium ratio would increase purely from ingrowth. This ingrowth would exponentially approach a ratio of 1, at which time the rate of lead-210 decay would be equal to the rate of lead-210 ingrowth from radium-226 (Fig. 8). In this line of research, it is the radioactivity (often expressed simply as "activity") of each isotope that is measured in decays per minute (dpm) per unit mass (g), expressed as $\text{dpm}\cdot\text{g}^{-1}$. This dynamic equilibrium is called secular equilibrium and is achieved to within 1% in a period of 156 years or seven lead-210 half-lives.

For fish, lead-radium dating depends on the incorporation of radium-226 from the aquatic environment, where it is naturally sequestered into the otolith carbonate matrix. Radium-226 subsequently decays to lead-210 over time at a well-defined rate and is conserved with time (Andrews et al., 2009). The otolith lead-radium system can be used to provide a radiometric estimate of age, based on the disequilibrium within the first year or few years of growth (i.e., within the otolith core). This tool is unique because any processes other than the passage of time do not regulate it. Given a measured lead-radium activity ratio from otolith core material, an age can be estimated within the margin of uncertainty from the measured quantities (Smith et al., 1991; Panfili et al., 2002). This kind of information can serve as a form of age validation for other age estimation methods (e.g., growth zone counting), but it can also provide age estimates where no other information is available.

The feasibility of lead-radium dating otolith material depends heavily on the levels of radium-226 uptake and the mass of the otolith core. For a successful application to work on small quantities of otolith material radium-226 levels need to be either relatively high, or otolith material of sufficient sample mass must be available (typically pooled otolith cores). Measured levels of radium-226 from otoliths of marine fishes can vary by approximately two orders of magnitude (~ 0.01 to 1.0 $\text{dpm}\cdot\text{g}^{-1}$; see Andrews, 2009 for a chapter dedicated to radium-226 in otoliths). The range of applicability can be demonstrated with two age and growth papers: bocaccio rockfish (*Sebastes paucispinis*; Andrews et al., 2005) and Atlantic tarpon (*Megalops atlanticus*; Andrews et al., 2001). The bocaccio rockfish study exemplified the limits of detection and applicability by providing only rough estimates of age; the levels for radium-226

(consequently lead-210) were too low to provide a reasonable margin of error associated with the calculated activities and radiometric age. Conversely, the Atlantic tarpon study exemplified use of low sample mass for meaningful lead-radium dating because radium-226 levels were some of the highest reported from otoliths; as a result of this and a large otolith core, ages were estimated for individual tarpon using lead-radium dating.

Bomb Radiocarbon Dating

Bomb radiocarbon dating is a technique that has evolved as a unique application in the age validation of fishes and invertebrates. The approach relies on a conserved record of the rapid increase in radiocarbon that occurred in the oceans of the world as a result of atmospheric testing of thermonuclear devices in the 1950s and 1960s (Broecker and Peng 1982). The 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 and this signal was first recorded from marine carbonates in hermatypic corals (Druffel and Linick, 1978). This time-specific signal provides a reference period that can be used to determine age. Applications to fishes began with an innovative comparison of $\Delta^{14}\text{C}$ values recorded in otolith carbonate relative to regional $\Delta^{14}\text{C}$ records from hermatypic corals (Kalish, 1993). In this and other studies, measured $\Delta^{14}\text{C}$ levels provided an independent determination of age for corroboration of ages estimated from counts of growth zones in otoliths (Campana, 1997; Kalish et al., 2001). Bomb radiocarbon dating has since been applied successfully as an age validation tool in numerous teleost ageing studies using otoliths (e.g., Andrews et al., 2007; Ewing et al., 2007; Neilson and Campana, 2008) and has expanded to other calcified hard parts in marine organisms ranging from calcareous algae and invertebrates to toothed whales (e.g., Frantz et al., 2005; Roark et al., 2006; Stewart et al., 2006; Kilada et al., 2007).

Bomb radiocarbon dating has limitations in terms of application and resultant age resolution. Use of bomb radiocarbon dating in the marine environment is limited to the period of rapid increase in $\Delta^{14}\text{C}$, typically between approximately 1955 and 1967. It is the agreement of the measured $\Delta^{14}\text{C}$ values from the species with age in question with a reference $\Delta^{14}\text{C}$ time-series that becomes a form of age validation. Hence, the utility of this approach for determining age or lifespan is limited to the difference between the collection year and informative period of the rise in $\Delta^{14}\text{C}$. In addition, an appropriate regional reference time series is necessary for calibration of measured $\Delta^{14}\text{C}$ values because regional uptake of radiocarbon can vary considerably (e.g., Druffel, 2002).

Study Objectives

In this study, lead-radium and bomb radiocarbon dating were used to address questions about the age, growth and potential lifespan of *P. filamentosus*. Can the age of *P. filamentosus* adults be determined using lead-radium and bomb radiocarbon dating and does longevity exceed the maximum estimated age of 18 years? In addition, can age be determined for smaller *P. filamentosus* using these methods and will length-at-age be similar to ages

determined toward the upper limit of the numerical integration method used by Ralston and Miyamoto (1983)? Given successful age estimations from these methods, can a revised VBGF be determined for *P. filamentosus* across all size classes utilizing the best available length-at-age data? As a corollary to the project, otoliths from juvenile fish collected one to two decades prior to processing provided a unique opportunity to test the closed system assumption required in lead-radium dating, an issue that is addressed by Andrews et al. (2009).

MATERIALS AND METHODS

Lead-radium Dating Feasibility

Developing an effective sample design is reliant upon estimating the limitations of lead-radium dating with application to *P. filamentosus* otoliths. The most important considerations were: 1) individual and collective sample mass availability for juvenile whole otoliths and adult otolith cores; 2) the potential radium-226 activity for otoliths from the region; and 3) the total sample age (estimated age plus time since capture). In most cases, a second otolith from each fish was left for other research opportunities (i.e., bomb radiocarbon dating). To make an initial assessment of lead-radium levels, a preliminary analysis of whole otolith material from juvenile opakapaka otoliths of known age was used to provide a baseline for the study.

Two juvenile groups of otoliths were pooled from collection years that differed by 10 years (Appendix A). The aim of this portion of the study was to not only determine baseline levels of radium-226 but also to test the closed system assumption for otolith material by measuring the lead-radium ratio from otoliths of known age (collected 11 years and 21 years prior to analysis; Table 2). Initial sample masses were chosen to provide a good indication of lead-210 and radium-226 activity, given a best guess at the lowest case scenario. Radium-226 activity in otolith material is typically 0.03 to 0.05 dpm·g⁻¹ (Andrews, 2009). Based on this estimate, a minimum of 0.5 grams of core material was targeted for each group to collect sufficient activity. Otolith readers at the Pacific Islands Fisheries Science Center made age estimates for the juvenile groups previously. It was well supported that age was less in question for the smallest fish based on validated length-at-age data for early growth studies (i.e., Ralston and Miyamoto, 1983; DeMartini et al., 1994). These sample groups were processed first to provide information necessary for the application of lead-radium dating to adult otoliths.

The composition of adult otolith groups was determined based on the lead-radium dating of the juvenile otolith groups and the availability of otoliths from fish of similar sizes (Appendices B-D). 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 otoliths. The mean dimensions and weight from the 14 juvenile otoliths (OP 1987), 11.4 mm L × 7.0 mm W × 1.2 mm T and 0.088 g, were used as a target for coring the adult otoliths. This sample size was chosen as a balance between: 1) a required sample mass exceeding 1 g (based on radium-226 activity); and 2) the number of samples available in the size class for the collection period. The first set of otoliths was from the largest fish available ($n = 16$) from collections made in 2007-2008, and age was not known or estimated in any manner (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: 1) grinding on a lapidary wheel to the shape of a juvenile otolith; and 2) microscopic comparison of the core to two reference 2+ otoliths collected in 2008. Growth zones and the nuclear region visible within the otolith in hand were used to verify the concentric structure of each core to the first few years of growth. Subsequent to the findings from the first adult otolith age group (OP 700+), two additional adult otolith groups were selected from the same collection years in smaller size classes to determine the age (OP 600-610 and OP 660-680; Table 2). Coring of the otoliths followed the same protocol stated above and each resulted in slightly more than 1 g of cored otolith material.

Radiochemical Protocol

A detailed protocol describing sample preparation, chromatographic separation of radium-226 from barium and calcium, and analysis of radium-226 using mass spectrometry has been described elsewhere (Andrews et al., 1999b). These procedures have not changed for this study, except for two aspects of the analysis: 1) radium recovery was improved by shifting the collection interval on the final chromatography column to begin at 200 μL (as opposed to 250 μL); and 2) purified radium samples were analyzed using an improved ICP-MS (Inductively Coupled Plasma Mass Spectrometry) technique. Other than these details, only an overview of the radium-226 procedures is given here together with details on the determination of lead-210 activity. Because the levels of radium-226 and lead-210 typically found in otoliths are extremely low (femtograms [10^{-15} g] for radium-226 and attograms [10^{-18} g] for lead-210) and the great potential for contamination from various sources were possible, trace-metal clean procedures and equipment were used throughout sample preparation, separation, and analysis. All acids used were ultra-pure, double distilled (GFS Chemicals®) and dilutions were made using Millipore® filtered Milli-Q water ($18 \text{ M}\Omega \text{ cm}^{-1}$).

Dried and weighed samples were dissolved in TFE beakers on hot plates at 90°C by adding 8N HNO_3 in 1-2 mL aliquots. Several alternations between 8N HNO_3 and 6N HCl , with an *aqua regia* transition, resulted in complete sample dissolution. The dried sample, after dissolution, formed a yellowish precipitate. To reduce remaining organics (otolin), *aqua regia* transitions were continued until sample color became nearly white when dry. To put the residue into the chloride form required for the lead-210 activity determination procedure, the samples were redissolved in 1 mL 6N HCl and taken to dryness five times at $90\text{-}120^\circ\text{C}$. A whitish residue indicated that sufficient amounts of the organics had been removed. Lead-210 activity was determined from these samples prior to ICP-MS analysis for radium-226.

To determine lead-210 activity in the otolith samples, the α -decay (alpha-decay) of polonium-210 (^{210}Po) was used as a daughter proxy for lead-210. To ensure that activity of polonium-210 was solely a result of ingrowth from lead-210, the time elapsed from fish capture to polonium-210 determination was greater than 2 years, with the exception of the adult age group; because the adult age group consisted of otolith cores, the 2-year waiting period was not necessary. Samples prepared for polonium-210 analysis were spiked with polonium-208, a yield tracer. The amount of polonium-208 added was estimated based on observed radium-226 levels present in other species of deepwater fishes (Andrews, 2009) or in previously analyzed opakapaka

specimens of this study. This amount was adjusted to approximately 5 times the expected polonium-210 activity in the otolith sample to reduce error in the lead-210 activity determination. The spiked samples were redissolved in approximately 50 mL of 0.5N HCl on a hot plate at 90°C covered with a watch glass. The sample polonium-210 and polonium-208-tracer were extracted proportionally through an auto-deposition process for 4 hours using a silver planchet. The activities of these isotopes were determined using α -spectrometry on the plated samples. Additional procedural and system details are described elsewhere (Andrews et al., 1999a). The solution remaining after polonium plating was dried and saved for radium-226 analyses.

To prepare the samples for radium-226 activity determination, each sample was spiked with radium-228, a yield tracer, and an ion-exchange separation technique was used to separate radium from calcium and barium (Andrews et al., 1999b). The purified samples were processed using ICP-MS, and the measured ratios of radium-226:radium-228 were used to calculate radium-226 activity in the samples.

Lead-radium Dating

Age was estimated from the measured lead-210 and radium-226 activities (Equation 1). Because the activities were measured using the same sample, the calculation was independent of sample mass. Radiometric age was calculated for whole juvenile otoliths using the following equation,

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

where t_{age} was the radiometric age at the time of analysis, A_{210} was the lead-210 activity at time of analysis, A_{226} was the radium-226 activity measured using ICP-MS, and λ was the decay constant for lead-210 (Smith et al., 1991). The age of the adult sample was determined taking into consideration 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 SE). Calculated error included the standard sources of error (i.e., pipetting, spike and calibration uncertainties, etc.), α -counting statistics for lead-210 (Wang et al., 1975), and the ICP-MS analysis routine.

In order to provide a tangible representation of how radiometric age determinations compare with expected lead-radium ratios from different age scenarios, each age group was given a rough estimate of length-at-age from Ralston and Miyamoto (1983). These hypothetical age estimates were used in a lead-radium ingrowth plot to better differentiate measures of age (Fig. 8). Proper alignment of the measured ratios with the ingrowth curve was used to estimate age with a precision based on the propagated error and analytical uncertainty of numerous factors in the radiochemical processing (e.g., radioisotope tracer, weighing, instrument error, etc.) using the delta method (Wang et al. 1975).

Bomb Radiocarbon Dating Feasibility

To prepare for the bomb radiocarbon dating of *P. filamentosus* in the Hawaiian Islands, appropriate reference $\Delta^{14}\text{C}$ records were documented for a potential comparison with measured levels in otoliths of *P. filamentosus* specimens. The applicable bomb radiocarbon records in the Hawaiian Islands were from hermatypic coral cores taken from Kahe Point, Oahu and Keauhou Bay, Kona, Hawaii in the main Hawaiian Islands to French Frigate Shoals in the central-eastern portion of the Northwestern Hawaiian Islands (Fig. 9). The Kahe Point coral is a fragmentary $\Delta^{14}\text{C}$ time series that only documented the peak and post-bomb decline from 1970 to 1979 and it is of little use in the age determination of fish in this study, but can provide a regional reference for peak $\Delta^{14}\text{C}$ values (Druffel, 1987). The coral from Kona was initially an incomplete record for the bomb radiocarbon signal and ranged from 1893 to 1966, nearly midway through the rise in $\Delta^{14}\text{C}$ (Druffel et al., 2001). This record was recently supplemented with a more thorough sample series spanning approximately from 1946 to 1992; these data have not yet been formally published, however, and were gleaned from a study of Hawaiian deep-sea corals (Fig. 8 of Roark et al., 2006). For the purpose of this study, these data were roughly digitized from the Figure 8 plot of Roark et al. (2006) to provide a more complete time series for the MHI. The coral $\Delta^{14}\text{C}$ record from French Frigate Shoals (FFS) is nearly complete in terms of the rise in $\Delta^{14}\text{C}$ and spans the period from 1958 to 1978 (Druffel, 1987). However, for the record to be complete, the earliest portion should include a few years of pre-bomb $\Delta^{14}\text{C}$ levels to provide a regional baseline. Because each of these $\Delta^{14}\text{C}$ records was incomplete, reasonable assumptions were made to develop comprehensive records for the Hawaiian Islands.

The records for peak $\Delta^{14}\text{C}$ levels were greater for FFS by 15–20‰ (ppt) when compared to the MHI records and needed to be considered separately in this study, assuming that *P. filamentosus* specimens from the MHI and NWHI remained in those regions through ontogeny (Fig. 10). Hence, the $\Delta^{14}\text{C}$ reference record for the MHI was a combination of both Kona records and the fragmentary Kahe Point record. For the NWHI, the record was a combination of two additional resources that required some assumptions. First, the pre-bomb $\Delta^{14}\text{C}$ levels that were not measured for FFS were assumed to be similar to the Kona record. This is likely a valid assumption based on the similarity of other mid-latitude, subtropical $\Delta^{14}\text{C}$ records (Druffel, 2002), but this assumption should be tested using a future reference time series from the region. Second, the decline in the $\Delta^{14}\text{C}$ record past 1978 for the region was also not known; Druffel et al. (2008), however, documented a monotonic decline of $\Delta^{14}\text{C}$ record past 1978 for the region was also not known; however, Druffel et al. (2008) documented a monotonic decline of $\Delta^{14}\text{C}$ in regional seawater at a rate of approximately 2‰ per year. This rate of decline was used as a potential 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 opakapaka 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‰) that was similar to the value predicted by the hypothesized decline in $\Delta^{14}\text{C}$ (Fig. 10). This rate of decline was considered conservative and could be more rapid based on the decline in the Kona record. Hence, the calculated rate of decline (2‰ per year) was used as a reference in calibrating age from measured $\Delta^{14}\text{C}$ levels in otoliths of *P. filamentosus* from the NWHI.

A comparison of measured $\Delta^{14}\text{C}$ levels in otoliths of *P. filamentosus* specimens with the regionally specific $\Delta^{14}\text{C}$ reference records for age determination was deemed feasible, based on the findings of the 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 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 for possible bomb radiocarbon dating. Otoliths were selected from this group for bomb radiocarbon dating in order to avoid between-fish variation (Appendix E). These samples were collected from the MHI and the NWHI in 2007-2008. In addition, otoliths from an archival series spanning a collection period of 10 years were selected for bomb radiocarbon dating of smaller and younger fish (Appendices E-H). These latter samples were collected from the NWHI (Necker Island to Laysan Island; $n = 35$) and from the Mariana Islands ($n = 4$). The Mariana Island samples were also compared to a $\Delta^{14}\text{C}$ record from Okinawa, Japan because of its more westerly position and potential oceanographic similarity (Konishi et al., 1981). Otoliths were selected from the archival series using rough estimates of age, based on fish length and otolith weight and the potential for the otolith to provide a birth year in 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 DI-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. 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 CA 94538 USA) micromilling machine (Fig. 11). A 0.5 mm diameter Brassler® (Savannah, GA 31419 USA) bit was used to drill an overlapping surface scan within the oval dimensions of 2.8 mm long by 1.8 mm wide. The surface scan was a guided extraction that conformed to the uneven surface structure of each otolith. A depth of 400 μm was extracted 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). 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 definition is defined as 95% of the radiocarbon concentration of the NBS Oxalic Acid I standard (SRM 4990B) normalized to $\delta^{13}\text{C}$ (VPDB = -19‰) in 1950 AD (Olsson 1970). Samples were initially normalized to -25 per mil using the $\delta^{13}\text{C}_{\text{VPDB}}$ and later adjusted to the mean $\delta^{13}\text{C}$ value from nine *P. filamentosus* otoliths (mean $\delta^{13}\text{C}$ = -4.9‰); the nine samples that were used to generate $\delta^{13}\text{C}$ values used the sample specific $\delta^{13}\text{C}$ values (Appendices E-H).

The calculated $\Delta^{14}\text{C}$ values reported in this study were also corrected for age, or time of formation, based on a roughly estimated 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 has been deemed better than no correction (pers. comm., E.R.M. Druffel, University of California, Irvine). Each region (MHI and NWHI) had slightly different criteria for the age correction because of differences in the amplitude of the rise in $\Delta^{14}\text{C}$. The year used in the corrections were based on a $\Delta^{14}\text{C}$ criterion as follows (Appendices E-H):

MHI birth year adjustment criteria:
1950 for $\Delta^{14}\text{C} < -46\text{‰}$ (pre-bomb)
1961 for $\Delta^{14}\text{C} -46$ to 110‰ (rise)
1978 for $\Delta^{14}\text{C} >110$ to <135‰ (widely defined)
1974 for $\Delta^{14}\text{C} 135$ to 167‰ (near peak)

NWHI birth year adjustment criteria:
1950 for $\Delta^{14}\text{C} < -46\text{‰}$ (pre-bomb)
1963 for $\Delta^{14}\text{C} -46$ 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 death and the time of measurement; hence, the same calculated $\Delta^{14}\text{C}$ would result for any given measurement time.

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 (pre-bomb, bomb rise, peak, or post-bomb decline). For pre-bomb levels, a minimum birth year and age were estimated based on the last year the level was measured, plus a nominal uncertainty of approximately 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 $\Delta^{14}\text{C}$, complications with birth year classification developed because of the similar levels

measured later in time. For the MHI, samples could be classified as either on the upper rise or the post-bomb decline based largely on the roughly digitized Kona coral record from Roark et al. (2006). Age determined from the rise in $\Delta^{14}\text{C}$ had a nominal uncertainty of ± 1 to ± 2 years, depending on the proximity to peak levels. The same samples were also given a Kona record decline-age with a nominal uncertainty of ± 3 years because the Kona decline rate was more gradual. For the NWHI, samples were treated in a similar manner relative to the greater amplitude of the FFS record. The post-bomb decline was not measured, however, and 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 estimated post-bomb decline for useful age estimation. Therefore, these samples were only assigned a birth year and estimated age from the upper rise portion of the $\Delta^{14}\text{C}$ reference record. Samples that could be placed on the bomb rise period were diagnostic and were assigned an age with a narrow uncertainty of ± 1 year. These data, coupled with the archive samples classified as upper rise, were used later to generate length-at-age estimates for developing a revised VBGF.

Modified Growth Function

Parameters of a VBGF for opakapaka in the Hawaiian Archipelago were estimated for this report. The VBGF was estimated using the most reliable age data, which included the collections of length-at-age data from Ralston and Miyamoto (1983), DeMartini et al. (1994), 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 mm to 768 mm and ages ranging from 0.35 years to approximately 46 years (mean lead-radium maximum age). Variability in length-at-age estimates among the age reading methods for the combined data set was assumed to be similar for fitting the VBGF.

Maximum likelihood estimates of the parameters of the VBGF were estimated using nonlinear regression under two alternative assumptions about the variability in the observed length-at-age data (e.g., Brodziak and Macy, 1996). The first assumption was that the observation error about the VBGF was additive and normally distributed with zero mean and constant variance across ages. The second assumption was that the observation error about the VBGF was multiplicative and lognormally distributed with mean equal to 1 and constant variance across ages, along with an approximate bias correction multiplier of $\exp(\sigma^2/2)$ for L_∞ where σ^2 is the residual variance of the regression fit.

The two error assumptions differed in how individual fish length-at-age varied about the mean growth curve. Under the additive error term, the error in predicting individual fish length-at-age was invariant with respect to age. In contrast, under the multiplicative error term, the prediction error in size at age scaled with fish age, which implied that there was more variability in predicted size at age for older fish. We compared the fits of the VBGF under the two assumptions using the pseudo- R^2 for nonlinear regression where the pseudo- R^2 was calculated as

one minus the ratio of the residual sum of squares to the corrected total sum of squares for the model.

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 possibilities (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 $0.03 \text{ dpm}\cdot\text{g}^{-1}$ (Table 3). Sample group OP 1987 provided the greater precision relative to OP 1997 because sample mass was greater. Nonetheless, 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 4). The total sample age was calculated based on the average time since collection for each group plus half the average estimated age for the otoliths within each group to compensate for the ingrowth gradient for lead-210:radium-226 that would form for the first 1-2 years of growth. Comparison of the known age of each sample with the expected ingrowth model provided evidence to support: 1) the conservation of the lead-radium system isotopes during long storage times and the closed system assumption; and 2) the accurate determination of age for core material extracted from adult otoliths (Fig. 12). From this information, an application of lead-radium dating to adult cored otoliths was deemed feasible.

Adult otoliths selected from fish in three length-groups 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 all consisted of 16 otoliths each (Table 2). Mean otolith core weight was slightly greater than the target weight in the first group analyzed (OP 700+). The following groups (OP 600-610 and OP 660-680) more closely approximated the target core weight. After a count period of 61.7 days to 89.0 days on the alpha-spectrometer for the adult samples, the counts acquired were sufficient for 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 determined from the juvenile sample groups (Table 3). The mean activity among the otolith samples was $0.0306 \pm 0.0056 \text{ dpm}\cdot\text{g}^{-1}$ ($n = 5$, 1 SD). Each adult group provided a unique lead-radium ratio that was used to determine radiometric age. To compare the estimated age-at-length (roughly derived from the Ralston and Miyamoto (1983) 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 data to the lead-radium ingrowth curve indicated the ages of these large fish were greater than originally estimated (Fig. 12).

Lead-radium dating of the adult otolith groups provided a mean age for each group. Once corrected for the time since capture (0.7 to 1.9 years), the age of fish in the groups increased as expected with increasing mean fish length (Table 4). The smallest group was more than 18 years old and the largest fish group was greater than 34 years old. Projecting the vertical error bars (2 SE) horizontally to the ingrowth curve provided the range of age estimate uncertainty.

Bomb Radiocarbon Dating

The MHI otolith samples selected from the largest fish recently collected in 2007-2008 were primarily from Niihau and Kauai, with one from southeast of Oahu at Penguin Bank ($n = 7$, Appendix E). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from 111.0‰ to 128.1‰ (Table 5). 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-age and rise-age options in $\Delta^{14}\text{C}$ for the region (Fig. 13). Age estimates were approximately 18 to 24 years for the age-decline option and were approximately 42 to 43 years for the age-rise option. It was not possible to determine which of these two age scenarios was accurate without further assumptions. Comparisons of ages based on lead-radium dating of these fish with analogous determinations for other specimens (sample number OP 700+), however, indicated that the mean age exceeded 34 years, which would suggest a mix of decline-age and rise-age values.

The NWHI otolith samples selected from the largest fish collected in 2007-2008 were from Twin Banks, Gardner Pinnacles, North Hampton Seamounts, and Pioneer Bank ($n = 8$, Appendix E). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from 96.2‰ to 186.2‰ (Table 6). 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. 14). Age estimates were approximately 3 to 28 years for the decline-age and were approximately 35 to 43 years for the rise-age. Age for two samples was diagnostic based on measured levels at the rise and peak in $\Delta^{14}\text{C}$ for the region. A measurement of $\Delta^{14}\text{C}$ at 96.2 ± 5.6 was strictly defined as 43.1 ± 1 years old (Gardner-1). A sample that provided the greatest $\Delta^{14}\text{C}$ value of the study at 186.2 ± 4.8 was narrowly attributed to 35.4 ± 2 years old. For the remaining six of the eight samples, it was not possible to determine which age scenario was accurate without further assumptions. However, a comparison of ages of these specimens based on lead-radium dating with other specimens (sample number OP 700+) indicated that the mean age exceeded 34 years, which again suggests would indicate a mix of decline-age and rise-age values.

The archived otoliths that were collected between 1978 and 1988 from the NWHI provided the most comprehensive series of longevity determinations, based on bomb radiocarbon dating. Sample locations ranged across multiple locations in the NWHI from Necker Island (Mokumanamana) to Laysan Island ($n = 35$, Appendices F-G). For clarity of presentation, these samples have been labeled by collection location, starting in the east and progressing towards the west in the NWHI (Tables 7-10).

The archival otolith samples from Necker Island and FFS were collected between 1978 and 1988 and included fish with lengths ranging from 576 to 672 mm FL ($n = 11$, Appendix F). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from near pre-bomb levels at -31.6‰ to near peak levels at 174.9‰ (Table 7). 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, a pair of age scenarios were evident based on both the decline (decline-age) and the rise (rise-age) of $\Delta^{14}\text{C}$ for only a few samples, with the remainder being diagnostic (definitely rise-age) based on a collection year exclusion from the decline period (Fig. 15). Viable ages of 3 years (upper limit) to approximately 5 years were possible for the three samples from the decline-age correlation. The corresponding rise-age for these fish was approximately 11 to 15 years. The remaining samples could only be attributed to the rise in $\Delta^{14}\text{C}$ for the region. Rise-age estimates were approximately 13 to 28 years for the most diagnostic bomb radiocarbon dating in this group (Fig. 15).

The archival otolith samples from Gardner Pinnacles and Raita Bank were collected between 1980 and 1982 and included fish with lengths ranging from 507 to 665 mm FL ($n = 7$, Appendix F). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from mid-rise levels at 102.7‰ to near peak levels at 174.4‰ (Table 8). 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) of $\Delta^{14}\text{C}$ for four of the seven samples, with the remaining three being diagnostic (definitely rise-age), based on a collection year exclusion from the decline period (Fig. 16). Viable ages of 3 years (upper limit) to approximately 4 years were possible for four samples from the decline-age correlation. The corresponding rise-age for these fish was approximately 11 to 28 years. The remaining samples could only be attributed to the rise in $\Delta^{14}\text{C}$ for the region. Rise-age estimates were approximately 13 to 22 years for the most diagnostic bomb radiocarbon dating in this group.

The archival otolith samples from Maro Reef were collected between 1978 and 1982 and included from fish with lengths ranging from 577 to 742 mm FL ($n = 9$, Appendix G). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from pre-bomb levels at -52.9‰ to near peak levels at 171.0‰ (Table 9). 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) of $\Delta^{14}\text{C}$ for only one of the nine samples, with the remaining eight being either diagnostic (definitely rise-age) based on a collection year exclusion from the decline period or limited to a minimum age from pre-bomb levels (Fig. 17). A viable age of 2 years (upper limit) for the smallest fish in this group was near the limit of fish length-at-age from previous early growth studies; hence, it could be attributed to the rise-age of approximately 9 years. The remaining samples could only be attributed to pre-bomb and the rise in $\Delta^{14}\text{C}$ for the region. Rise-age estimates were approximately 14 to 28 years for the most diagnostic bomb radiocarbon dating in this group. Pre-bomb samples were given a minimum age of approximately 29 years, and these samples could be older.

The archival otolith samples from Laysan Island were all collected in 1988 and were included fish with lengths ranging from 660 to 768 mm FL ($n = 8$, Appendix G). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from near pre-bomb levels at -45.1‰ to near peak levels at 159.6‰ (Table 10). 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) of $\Delta^{14}\text{C}$ for four of the eight samples, with the remaining four being diagnostic (definitely rise-age), based on a collection year exclusion from the decline period (Fig. 18). A viable age of approximately 3 years (upper limit) for a fish 660 mm FL seemed unlikely, but could not be eliminated from consideration. Other decline-age fish could have been 4 to 6 years old (upper limit). All four decline-aged fish in this group could have been older at approximately 21 years. The remaining samples could only be attributed to either pre-bomb or rise-age. Rise-age estimates from the upper part of the slope were approximately 22 years to 23 years. Two samples were near pre-bomb levels, but were considered elevated enough to be attributed to early rise in $\Delta^{14}\text{C}$ birth years. Hence, these samples were approximately 32 to 34 years old. Four of the eight samples in this group were most diagnostic for bomb radiocarbon dating.

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 included fish with lengths ranging from 453 to 512 mm FL ($n = 4$, Appendix H). These samples provided $\Delta^{14}\text{C}$ values from core material that ranged from lower slope at -24.8‰ to upper slope at 144.0‰ for the rise in $\Delta^{14}\text{C}$ (Table 11). 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 only the rise (rise-age) of $\Delta^{14}\text{C}$. An additional consideration for this sample set was its remote location relative to the NWHI coral $\Delta^{14}\text{C}$ record. To more fully encompass the region, a coral record from Okinawa provided an additional age reference (Konishi et al. 1981; Fig. 19). Upper slope samples were less diagnostic because the regional $\Delta^{14}\text{C}$ records differed slightly (rise of $\Delta^{14}\text{C}$ offset by approximately 2 years later for Okinawa). These samples were given a wider age determination of approximately 14 to 16 years. For the lower portion of the rise in $\Delta^{14}\text{C}$, no offset was evident between regional records and as a result, the lower slope samples correlated well with both records for ages of approximately 20 and 24 years. One potential exception is a remote possibility that the small peak at 1956 was measured in the core of Mariana-4, making the potential age of this sample older by about 2.5 years.

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 diagnostic; no samples were diagnostic from the MHI. The lengths of NWHI fish ranged from 576 to 768 mm FL, with age estimates ranging from approximately 9 to 43 years (Table 12). The 10 samples that were not considered diagnostic had a decline-age estimate that was regarded as too low to be realistic, based on other early growth studies.

Modified Growth Function

Similar fits to the *P. filamentosus* length-at-age data were obtained under both alternative assumptions about the variability in observed length at age. Maximum likelihood estimates for the VBGF using the multiplicative lognormal error were: $L_{\infty} = 662$, $k = 0.294$, $t_0 = -0.16$ (Fig. 20). In comparison, the maximum likelihood estimates for the VBGF using the additive normal error were: $L_{\infty} = 674$, $k = 0.252$, $t_0 = -0.33$. Overall, the VBGF with a multiplicative error provided a better fit to the combined length-at-age data (pseudo- $R^2 = 0.98$) than the VBGF with

an additive error (pseudo- $R^2 = 0.96$). However, it is recommended that this information be used with caution, as the details are worked out for a VBGF fit that can properly address the potential heterogeneity in the variances of length-at-age measurements between the ageing methods.

Of secondary interest but nonetheless important to note, estimated length-at-age of the four *P. filamentosus* specimens from the Mariana Islands differed greatly from those collected in the Hawaiian Islands (Fig. 21). These four specimens suggest that *P. filamentosus* grow more slowly in the Mariana Islands than those in the NWHI (Fig. 20). Ages of the Mariana Island specimens also were greater than predicted for the Mariana Islands by the preliminary length-at-age data provided by Ralston and Williams (1988).

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 opakapaka collected from the Hawaiian Islands. The mean age of the largest-sized group was 45.6 years (34.4 to 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. Hence, the caution expressed by Ralston and Miyamoto (1983) against extrapolating daily-growth-increment age data to the largest fish was correct. Our findings furthermore indicate that previous studies reporting a rapid growth rate and a short-lived life history were not accurate.

The findings from the juvenile opakapaka samples provided support for an application of lead-radium dating to extracted otolith core material from adult fish. Radiometric age determined from cores of adult fish is conceptually similar in terms of the storage time for the juvenile otoliths, and the measured ratio would provide a proxy for fish age. The test for potential loss of isotopes during storage time was successful by showing that no significant loss of radium-226 daughter products occurred during either of two lengthy (11.3 and 20.5 yr) storage times. Studies have voiced concerns about the possible violation of the closed otolith system as a result 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 temporary (e.g., Whitehead and Ditchburn, 1995; Baker et al., 2001; Kestelle and Forsberg, 2002; Andrews et al., 2009). The findings of the current study provides further support for the contention that no significant loss of lead-radium isotopes occurs in otoliths, whether *in vivo* or stored dry, and that lead-radium dating is a viable and accurate option for age estimation using otoliths.

Radium-226 levels were at the low end of what was expected (0.3 to 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 island provides a reasonable basis 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 application of lead-radium dating to the otoliths of *P. filamentosus*, no evidence was provided to hypothesize that an application of bomb radiocarbon dating was feasible for recently collected otoliths. Lead-radium dating provided the necessary information to explore bomb radiocarbon dating of the largest fish group (OP 700+). In this group were some of the oldest fish aged in this study (up to 43 years); however, many of the fish provided $\Delta^{14}\text{C}$ levels that could not be dated accurately. All of the fish from the MHI could have been near 20 years old or near 40 years old because of the ambiguous levels for the rise and decline of $\Delta^{14}\text{C}$ in the regional coral records. 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).

To further investigate 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 weight as rough 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 to 33 of the 35 selected samples from the NWHI with 4 additional investigative samples aged from the Mariana Islands. 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 reassessment of growth characteristics of the species in the NWHI.

Regional Bomb Radiocarbon Records

The four investigative samples from the Mariana Islands provide some insight on how minor changes in the regional $\Delta^{14}\text{C}$ reference records can change estimates of age. In this part of the study, the distance of the Mariana Islands from the NWHI $\Delta^{14}\text{C}$ reference record was considerable; surely there is more of an Indo-Pacific influence on regional oceanography in the Mariana Islands. Hence, the coral $\Delta^{14}\text{C}$ record from Okinawa, Japan was considered as potentially more appropriate to be a reference record. The initial rise in $\Delta^{14}\text{C}$ was similar to the record used for the NWHI, although the lower portion and pre-bomb was from Kona, Hawaii based on assumptions of similar pre-bomb levels for a wider region of the North Pacific.

Assuming that the record used for the NWHI is representative of the temporal changes in marine $\Delta^{14}\text{C}$, complications arise between the reference records. First, there was a small peak in $\Delta^{14}\text{C}$ near 1955 that is characteristic of the Indo-Pacific region and has been attributed to nuclear device testing in the Marshall Islands in 1954 (Fallon and Guilderson, 2008). This signal may complicate age estimate precision for $\Delta^{14}\text{C}$ levels measured at the early rise in $\Delta^{14}\text{C}$ for fish from this vicinity. As a result, the estimated age for one of the oldest samples from the Mariana Islands was either 24 or 27 years old. Second, the scenario for the upper portion of the rise in $\Delta^{14}\text{C}$ is an offset of approximately 2 years later by the Okinawa record. Hence, the estimated age for 2 samples with measured $\Delta^{14}\text{C}$ levels in this part of the reference records have a mean age of approximately 15 years with a wider uncertainty than is usual for this period of ± 2 years.

The minor contrast between age estimation using two records for the *P. filamentosus* collected in the Mariana Islands highlights the importance of defining the temporal behavior of regional rises in $\Delta^{14}\text{C}$. For the Hawaiian Islands, some assumptions were necessary because of discontinuities in the regional $\Delta^{14}\text{C}$ records. Future publication and release of the data series used in Roark et al. (2006) would provide better documentation and could improve the precision of age determinations from this record. Pending $\Delta^{14}\text{C}$ analyses of additional coral core samples from Waikiki, Oahu and Kure Atoll (A.H. Andrews, in-house samples slated for future analysis) will provide more spatially and temporally comprehensive reference records for future age and growth studies.

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Table 1.--Synopsis of growth parameters from fitted von Bertalanffy functions to various forms of estimated age data. LFA refers to Length Frequency Analysis.

Study	Region	Length (FL mm)	von Bertalanffy parameters		
			L_{∞} (mm FL)	k (yr ⁻¹)	t_0 (yr)
Ralston and Miyamoto (1983)	Hawaii	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 ^a	0.534 ^a	0.18 ^a
DeMartini et al. (1994)		84 – 687	704	0.25	0.22
Moffitt and Parrish (1996)		70 – 250	780 (fixed)	0.21	0
Ralston and Williams (1988)	Mariana Islands	250 – 640	670 (LFA)	0.203	0.52
			584	0.289	-0.54
Fry et al. (2006)	PNG	271 – 552 ^b	551	0.118	-4.0
Mees (1993)	Seychelles	250 – 770	817 (LFA)	0.288	0.0
Mees and Rousseau (1997)		Nr	758 (LFA)	0.244	-0.3
Hardman-Mountford (1997)		Nr	780-860 ^c	0.33-0.36	-0.16-0.06
Pilling et al. (2001)		260 – 800	780 ^d	0.111	-1.44

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

b. Length reported as SL was converted to FL based using a conversion factor (Uchida et al., 1982).

c. Parameters reported for separate sexes.

d. Reanalysis of VBGF fit to age-length data provided different parameters than reported (623 *cf.* 780).

nr = not reported

Table 2.--Summary of characteristics for opakapaka otolith samples processed in this study. Estimated age composition and average capture date for each group with resultant pooled sample number and weight are given. Age was not known for the adult groups (fish-length based). Sample weight was the combined otolith sample, consisting of whole otoliths for the juvenile groups and otolith cores for the adult groups.

Sample	Age group (yr)	Average capture date	Number of otoliths	Sample weight (g)	Average core weight (g)
OP 1997	1+	8 Jan 1998	19	0.5791	0.031 ^a
OP 1987	2+	4 Nov 1987	14	1.1654	0.087 ^a
OP 600-610	Unknown	22 Nov 2007	16	1.1508	0.072 ^b
OP 660-680	Unknown	25 Nov 2007	16	1.2436	0.078 ^b
OP 700+	Unknown	11 Nov 2007	16	1.5538	0.097 ^b

a. Whole otoliths

b. Extracted otolith cores

Table 3.--Radiometric results for opakapaka juvenile whole otolith groups and the cored adult otolith group. Listed are the measured lead-210:radium-226 activities ($\text{dpm}\cdot\text{g}^{-1}$, disintegrations per minute) for the samples (± 2 SE). Calculated activity ratios and their corresponding margin of error were used to calculate sample age and uncertainty (Table 4).

Sample	Age group (yr)	^{210}Pb ($\text{dpm}\cdot\text{g}^{-1}$) \pm % error ¹	^{226}Ra ($\text{dpm}\cdot\text{g}^{-1}$) \pm % error ¹	$^{210}\text{Pb}:$ ^{226}Ra activity ratio	2 SE
OP 1997	1+	0.0117 ± 9.2	0.0394 ± 22	0.298	0.071
OP 1987	2+	0.0125 ± 6.9	0.0258 ± 13	0.486	0.072
OP 600-610	Unknown	0.0174 ± 5.7	0.0324 ± 16	0.537	0.090
OP 660-680	Unknown	0.0192 ± 5.1	0.0258 ± 14	0.742	0.108
OP 700+	Unknown	0.0223 ± 4.3	0.0294 ± 13	0.759	0.104

¹ Calculation based on propagation of 2 SE using the delta method (Knoll, 1989) and the ICPMS analysis routine (± 2 SE).

Table 4.--Estimated age and radiometric age for opakapaka. Radiometric age was calculated from the measured lead-210:radium-226 activity ratios and corrected for time since capture date. Radiometric age range was based on the analytical uncertainty and error propagation (2 SE).

Sample	Age group (yr)	Sample age (yr)	Radiometric age (yr, range)	Corrected age (yr, range)	Length (mm FL, range)
OP 1997	1+	11.8 ^a (11.3) ^b	11.9 (8.8 – 15.3)	0.6 (-2.5 – 4.0)	167 (106 – 208)
OP 1987	2+	21.5 ^a (20.5) ^b	22.3 (18.1 – 27.0)	1.8 (-2.4 – 6.5)	334 (322 – 347)
OP 600-610	Unknown	Unknown (1.9) ^b	25.8 (20.0 – 32.7)	23.9 (18.2 – 30.9)	609 (607 – 616)
OP 660-680	Unknown	Unknown (1.9) ^b	44.5 (33.3 -61.9)	42.6 (31.4 – 60.1)	670 (661 – 676)
OP 700+	Unknown	Unknown (0.7) ^b	46.6 (33.1 – 64.7)	45.6 (34.4 – 64.0)	720 (700 – 746)

a. Time since collection plus half the estimated average fish age for each sample.

b. Time between collection and analysis.

Table 5.--Bomb radiocarbon dating results for recently collected opakapaka otoliths collected from the main Hawaiian Islands in 2008. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 13). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
Niihau Kauai-1	111.0 ± 5.3	2008.2	17.8 ± 3	42.7 ± 1	725
Niihau Kauai-2	117.9 ± 5.7	2008.0	20.2 ± 3	42.1 ± 1	716
Niihau Kauai-3	118.7 ± 6.4	2008.2	20.6 ± 3	42.2 ± 1	721
Niihau Kauai-4	121.9 ± 4.9	2008.2	21.8 ± 3	41.9 ± 1	700
Niihau Kauai-5	125.8 ± 6.0	2008.2	23.2 ± 3	41.7 ± 1	712
Niihau Kauai-6	128.1 ± 4.7	2008.1	24.0 ± 3	41.4 ± 1	730
Penguin-1	127.9 ± 3.9	2008.3	24.1 ± 3	41.7 ± 1	708

Table 6.--Bomb radiocarbon dating results for recently collected opakapaka otoliths collected from Twin Banks to Pioneer Bank within the Northwestern Hawaiian Islands in 2007-2008. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 14). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
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
N 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

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

Table 7.--Bomb radiocarbon dating results for archive opakapaka otoliths from Necker to French Frigate Shoals within the Northwestern Hawaiian Islands in 1978-1988. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 15). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample Number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
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

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

Table 8.--Bomb radiocarbon dating results for archive opakapaka otoliths from Gardner Pinnacles to Raita Bank within the Northwestern Hawaiian Islands in 1978-1988. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 16). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample Number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
Gardner-4 ^a	148.3 ± 4.3	1981.6	NA	21.6 ± 1	577
Gardner-5	170.6 ± 4.4	1981.6	1.9 + 3	27.7 ± 1	507
Gardner-6	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

a. Sequence continued from Table X2.

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

Table 9.--Bomb radiocarbon dating results for archive opakapaka otoliths from Maro Reef within the Northwestern Hawaiian Islands in 1978-1988. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 17). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample Number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
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	$-0.9 + 3^a$	9.3 ± 2	577

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

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

Table 10.--Bomb radiocarbon dating results for archive opakapaka otoliths from Laysan Island within the Northwestern Hawaiian Islands in 1978-1988. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with either the rise or decline in $\Delta^{14}\text{C}$ from regional records is provided where applicable (Decline-age and Rise-age). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 18). Sample numbering was segregated by island region to make data interpretation easier in tables and plots.

Sample Number	$\Delta^{14}\text{C}$ (‰)	Collection year	Decline-age (yr)	Rise-age (yr)	Fish length (mm FL)
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	$-0.4 + 3^a$	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

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

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.

Table 11.--Bomb radiocarbon dating results for archive opakapaka otoliths from the Mariana Islands in 1982. Age determination from the correlation of measured $\Delta^{14}\text{C}$ levels in otolith cores with the rise in $\Delta^{14}\text{C}$ for the regional records (NWHI or Okinawa) is provided (Age-FFS and Age-Okinawa). Projection from collection year at the measured $\Delta^{14}\text{C}$ level to the regional calibration $\Delta^{14}\text{C}$ records led to the respective age determinations (Fig. 19).

Sample Number	$\Delta^{14}\text{C}$ (‰)	Collection year	Age-FFS (yr)	Age-Okinawa (yr)	Fish length (mm FL)
Mariana-1	-24.8 ± 4.0	1982.4	15.9 ± 1^a	13.9 ± 1^a	521
Mariana-2	11.9 ± 5.2	1982.4	16.3 ± 1^a	14.3 ± 1^a	512
Mariana-3	138.1 ± 4.3	1982.3	20.4 ± 1	20.4 ± 1	491
Mariana-4	144.0 ± 4.4	1982.4	24.4 ± 1	26.9 ± 1^b	453

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

b. Small peak in Okinawa $\Delta^{14}\text{C}$ record with duration of <8 months was unlikely, but possible.

Table 12.--Diagnostic opakapaka age determinations for fish from NWHI and sorted by fish length. These data were used in the determination of VBGF parameters, in concert with other sources of validated length-at-age data (Fig. 20). Rise-age over Decline-age for some samples was based on validated length-at-age from previous early growth studies.

Sample Number	Fish length (mm FL)	Decline-age (yr)	Rise-age (yr)	$\Delta^{14}\text{C}$ (‰)
FFS-7	576	0.3 + 3 ^a	11.1 ± 2	158.2 ± 4.3
Gardner-4	577	NA	21.6 ± 1	148.3 ± 4.3
Maro-9	577	-0.9 + 3 ^{ab}	9.3 ± 2	171.0 ± 5.0
Necker-1	600	NA	22.6 ± 1	-17.9 ± 3.6
FFS-6	603	NA	21.7 ± 1	143.8 ± 5.5
Necker-2	604	NA	15.1 ± 1	135.3 ± 4.4
Raita-4	614	0.5 + 3 ^a	11.1 ± 2	170.5 ± 4.5
Maro-8	626	NA	13.9 ± 1	150.2 ± 7.6
FFS-5	627	NA	22.2 ± 1	136.6 ± 4.8
FFS-4	631	NA	13.1 ± 1	117.7 ± 4.9
FFS-2	642	NA	27.7 ± 1	-1.6 ± 3.6
Raita-2	649	NA	22.2 ± 1	160.7 ± 5.2
Maro-7	655	NA	13.9 ± 1	150.0 ± 4.1
Raita-1	656	NA	13.1 ± 1	102.7 ± 8.8
Laysan-5	660	-0.4 + 3 ^{ab}	21.1 ± 1	152.8 ± 4.4
FFS-3	662	NA	15.1 ± 1	61.6 ± 4.0
Raita-3	665	1.2 + 3 ^a	21.7 ± 1	169.1 ± 5.5
Laysan-6	665	1.0 + 3 ^a	21.0 ± 1	155.6 ± 4.9
FFS-1	672	NA	21.6 ± 1	-31.6 ± 4.1
Maro-3	673	NA	27.1 ± 2	-45.5 ± 4.8
Maro-4	682	NA	27.6 ± 2	-45.5 ± 3.8
Laysan-3	702	NA	22.8 ± 1	111.4 ± 4.8
Maro-6	716	NA	24.8 ± 2	-38.2 ± 3.9
Twin-1	718	7.5 + 3 ^a	41.9 ± 1	129.1 ± 10.1
Gardner-2	718	3.3 + 3 ^a	41.9 ± 1	121.3 ± 5.2
N Hampton-1	719	NA	35.4 ± 2	186.2 ± 4.8
Laysan-7	721	2.3 + 3 ^a	20.8 ± 1	158.3 ± 4.3
Laysan-2	723	NA	32.2 ± 2	-38.6 ± 3.9
Laysan-8	729	3.0 + 3 ^a	20.7 ± 1	159.6 ± 4.8
Gardner-1	730	NA	43.1 ± 1	96.2 ± 5.6
Laysan-4	738	NA	21.6 ± 1	145.4 ± 5.6
Maro-5	742	NA	26.6 ± 2	-42.3 ± 4.2
Laysan-1	768	NA	34.4 ± 2	-45.1 ± 4.0

a. Length-at-age from the estimated decline in $\Delta^{14}\text{C}$ unlikely based on validated daily age and growth information (Ralston and Miyamoto 1983, DeMartini et al. 1994).

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

NA = Not applicable because collection year precluded application to $\Delta^{14}\text{C}$ reference record.



Figure 1.--Opakapaka or pink snapper (*Pristipomoides filamentosus*) captured in the Hawaiian Islands.

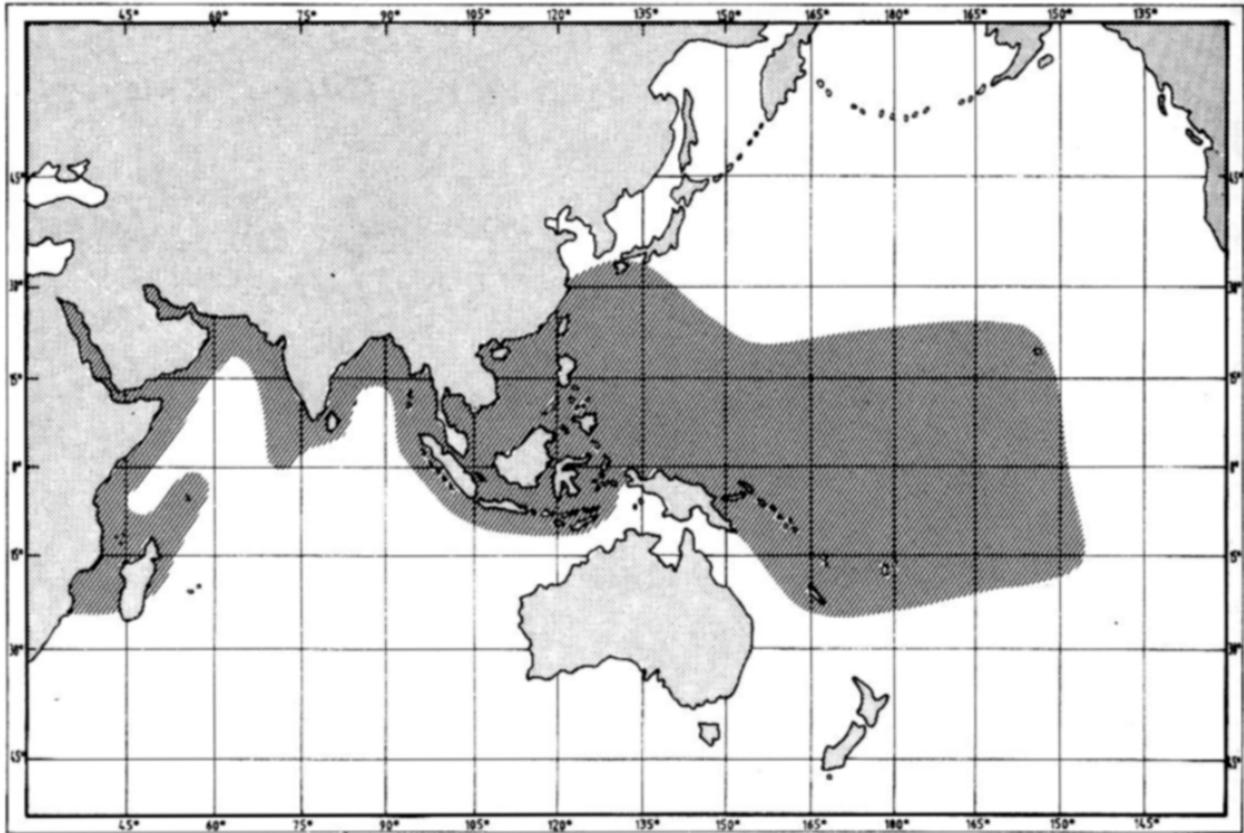


Figure 2.--Known distribution of *P. filamentosus* (Snappers of the World, FAO; Allen, 1985).

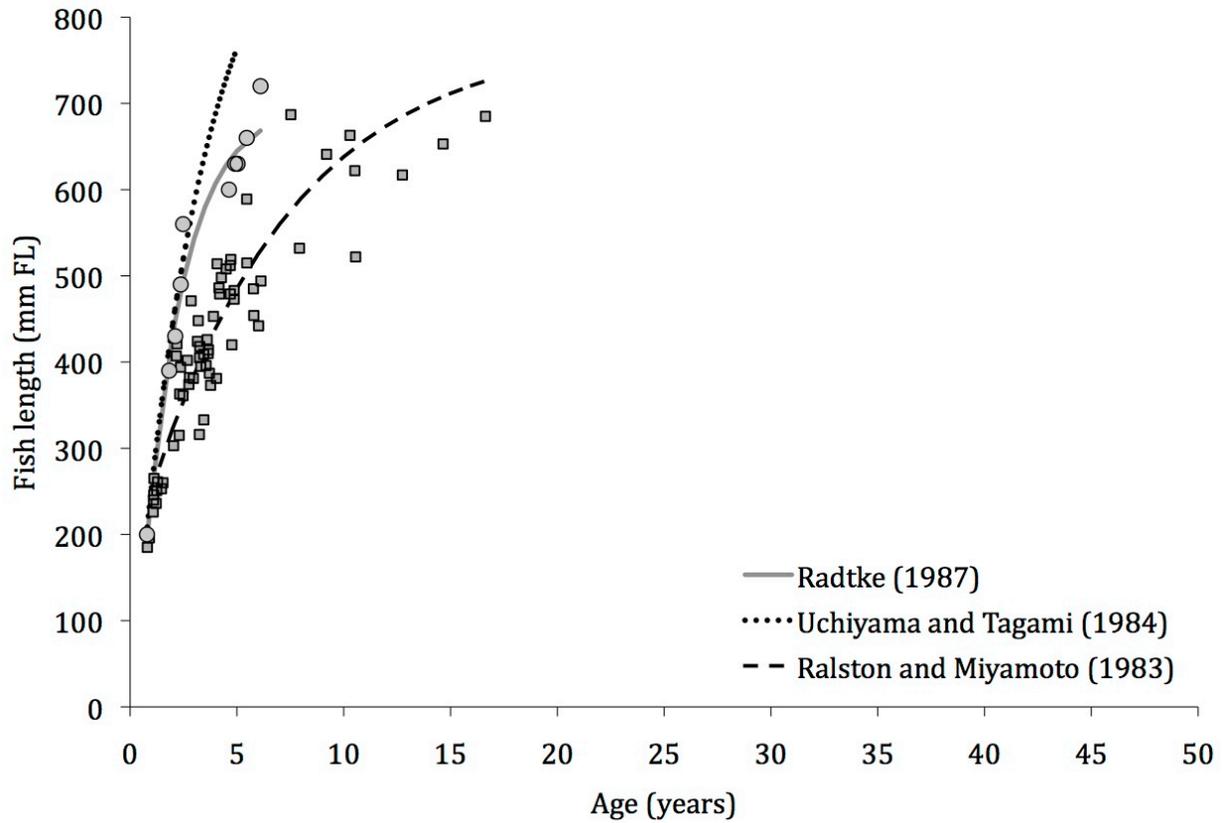


Figure 3.--An assimilation of the earliest von Bertalanffy growth functions for *P. filamentosus* with age data from Ralston and Miyamoto (1983) and Radtke (1987). Uchiyama and Tagami (1984) was an extrapolation of early growth estimates to the largest fish. Length-at-age data used to fit a VBGF (Cope, 2000) to Radtke (1987) because function was unconventional.

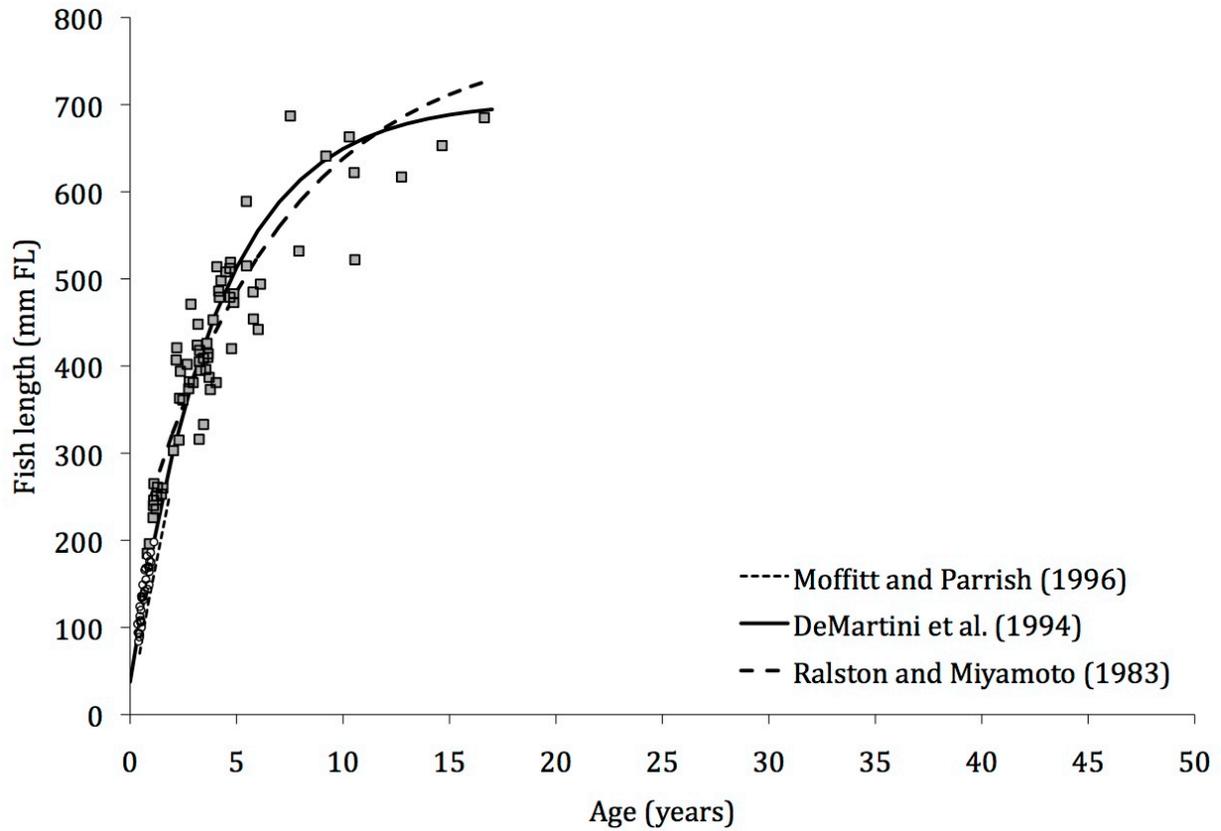


Figure 4.--Reliable age data for *P. filamentosus* from Ralston and Miyamoto (1983) and DeMartini et al. (1994) with von Bertalanffy growth functions. Moffitt and Parrish (1996) show a length frequency analysis for early growth. See Table 1 for growth function parameters.



Figure 5.--Assimilation of *P. filamentosus* age and growth estimation in the Seychelles using various methods. Age data estimated from presumed annual growth zone counting is presented from Pilling et al. (2000) with fitted VBGF. See Table 1 for growth function parameters.

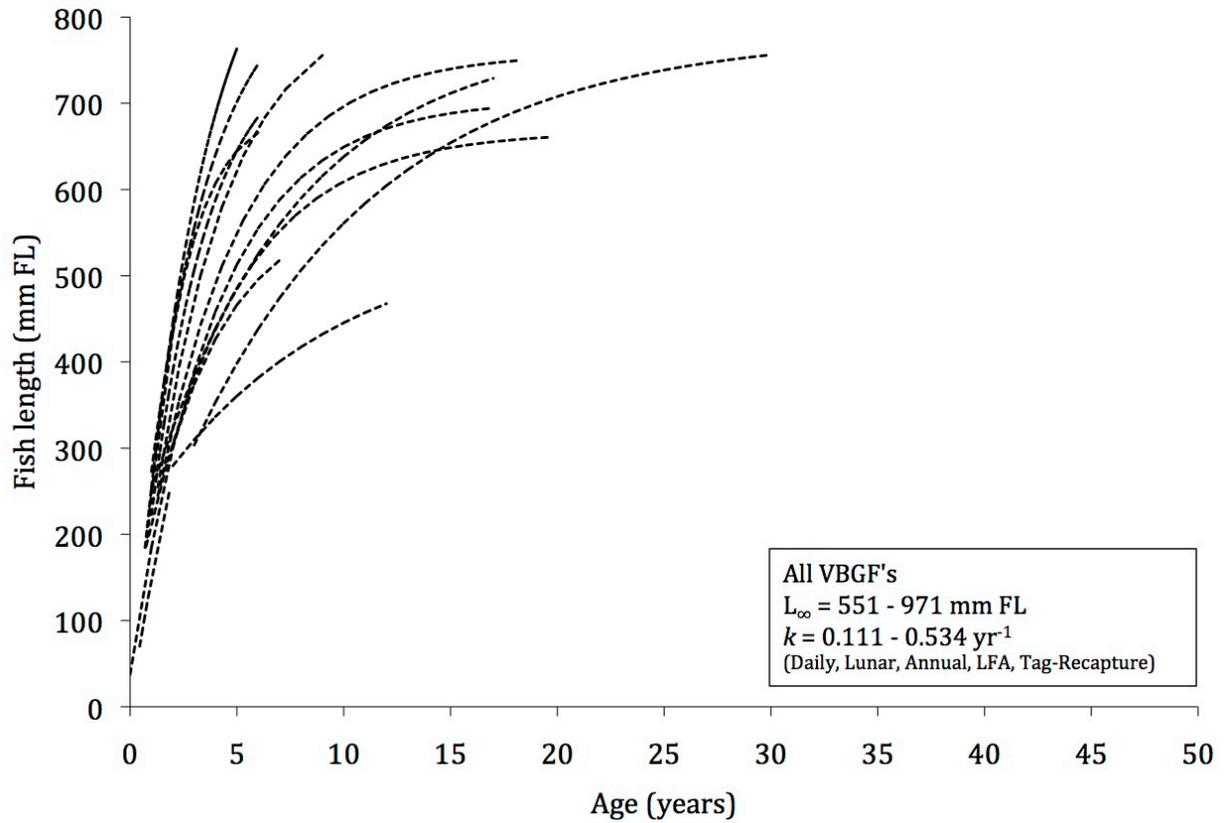


Figure 6.--Assimilation of all known von Bertalanffy growth functions for *P. filamentosus* throughout its geographical range. Age estimation procedures and results vary considerably and to date there was no age validation for the largest fish. See Table 1 for growth function parameters for all studies considered here.

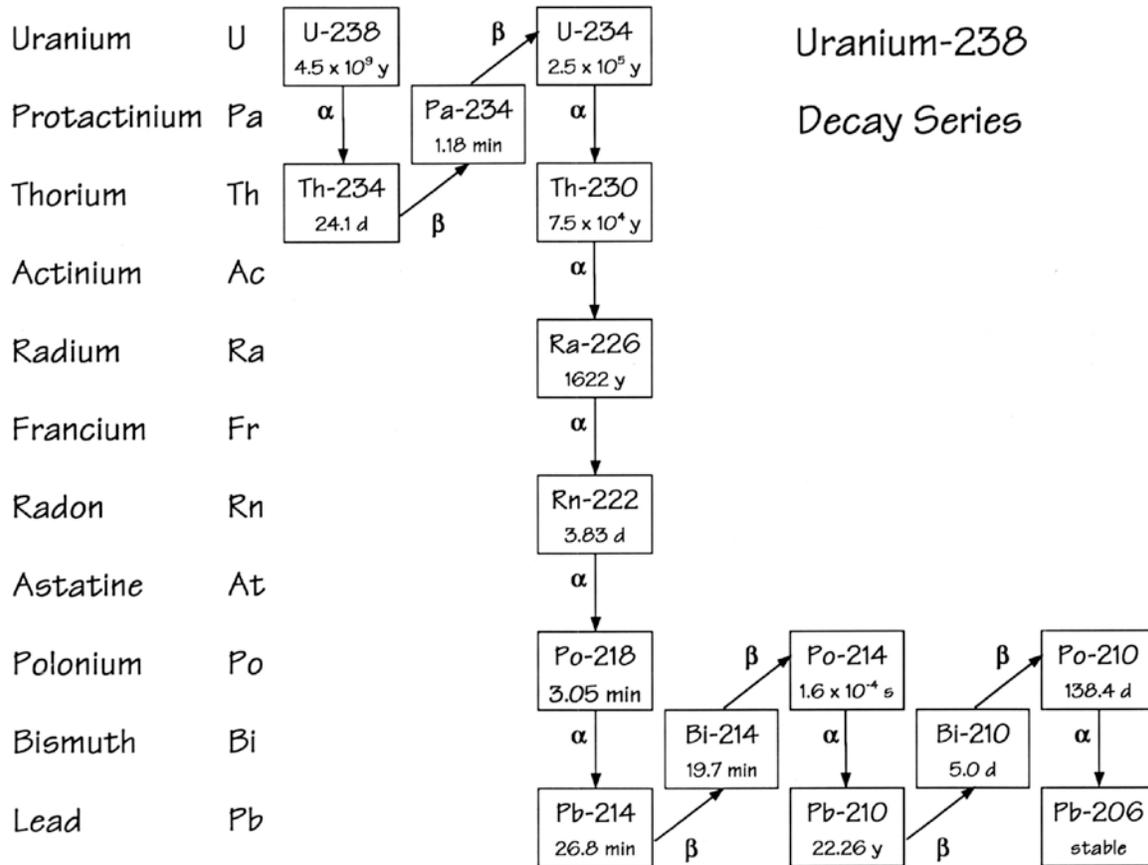


Figure 7.--Diagram of the uranium-238 decay series with the half-life for individual isotopes given in each cell. Of interest to lead-radium dating is the isolation of radium-226 from the environment and its subsequent decay to lead-210. Note that the half-lives of the intermediate isotopes are far less than the half-life of lead-210, hence the decay of radium-226 over the period of interest for fishes (decades) can be simplified to a direct decay to lead-210 and a disequilibrium relative to time (see Fig. 8).

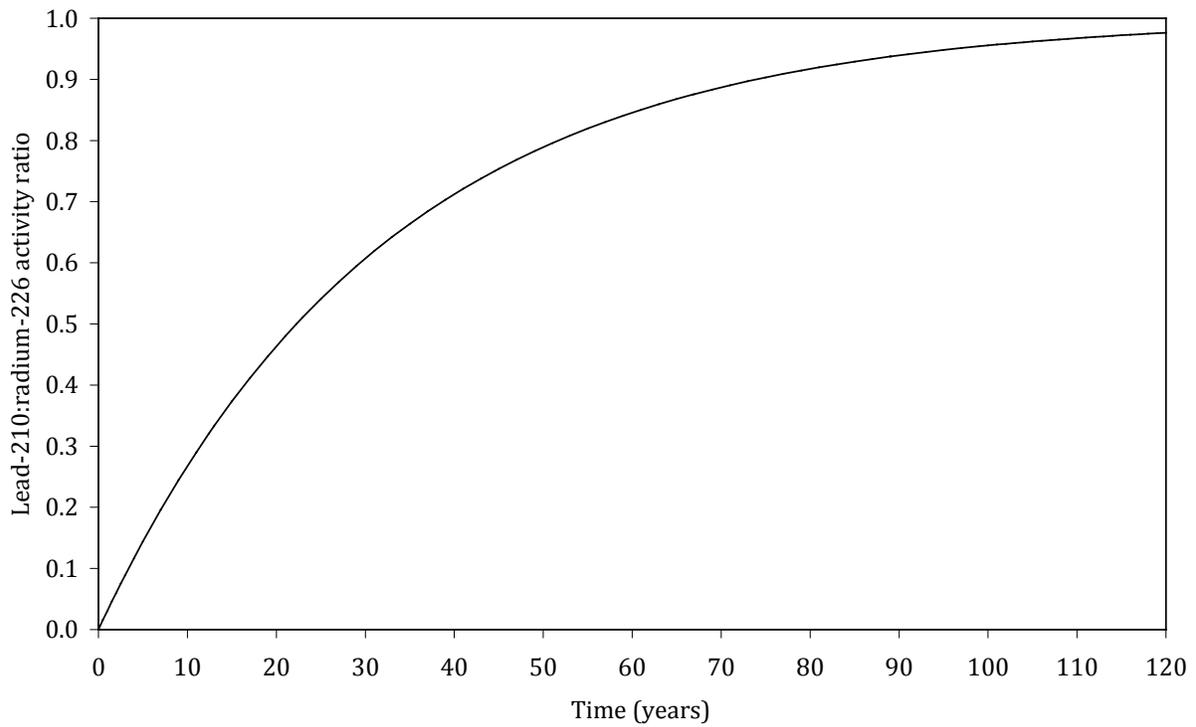


Figure 8.--The relationship used for lead-radium dating begins with the ingrowth of lead-210 activity from radium-226 at time zero. Over time, the activity ratio of lead-210 to radium-226 approaches secular equilibrium (decay activity is equal for the two isotopes), measured as a ratio of one. It is the measured disequilibria of lead-210 and radium-226 activities that provide a measure of time, or age in the case of fish otoliths.

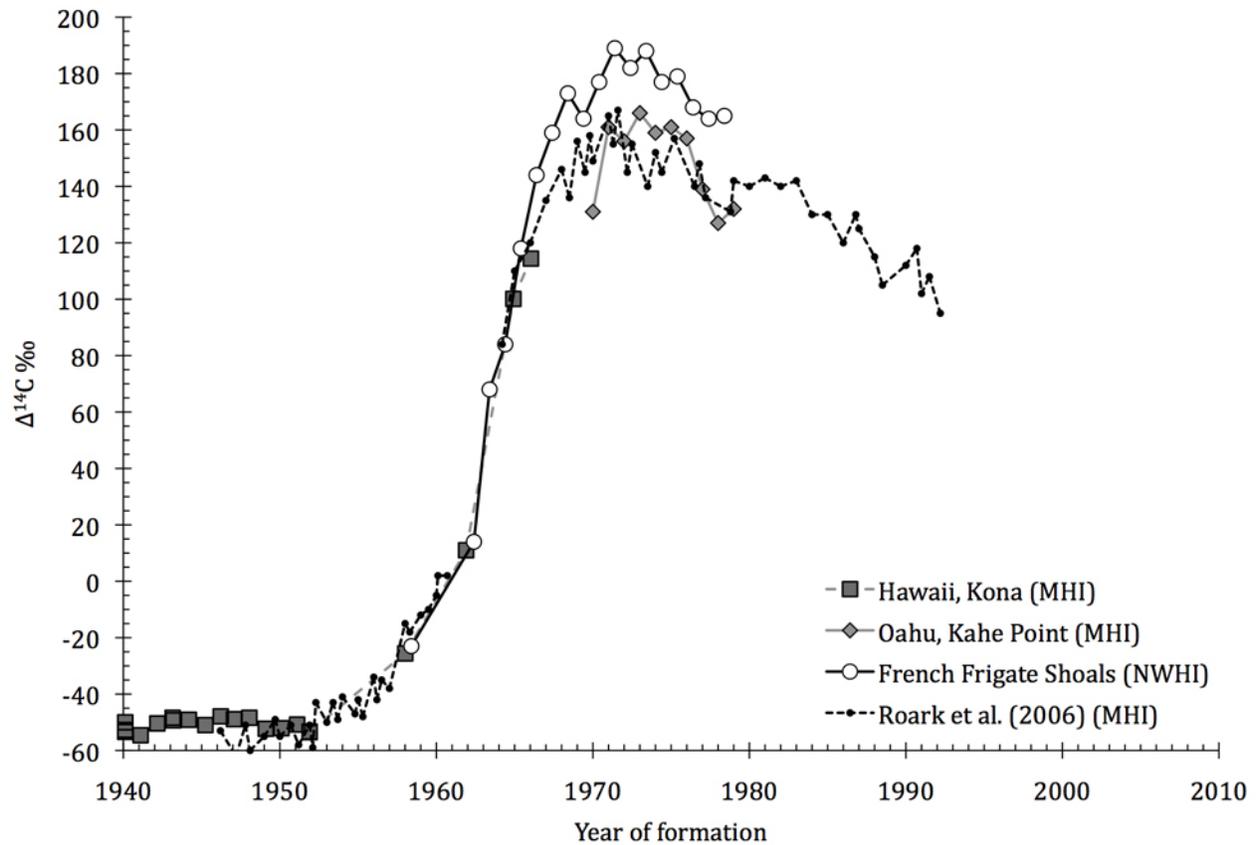


Figure 9.--Available reference records from hermatypic corals showing the change in $\Delta^{14}\text{C}$ over time in the Hawaiian Islands. The rise in $\Delta^{14}\text{C}$ was the result of atmospheric testing to thermonuclear devices in the 1950s and 1960s. Hence, these coral records provide a reference for the bomb radiocarbon signal in the marine environment and can be used in the validation of fish age using otoliths. The Kona, Hawaii, Kahe Point, Oahu and French Frigate Shoals were from published records (Druffel, 1987; Druffel et al., 2001). The fourth record is from Kona, Hawaii and was roughly digitized from Figure 8 of Roark et al. (2006).

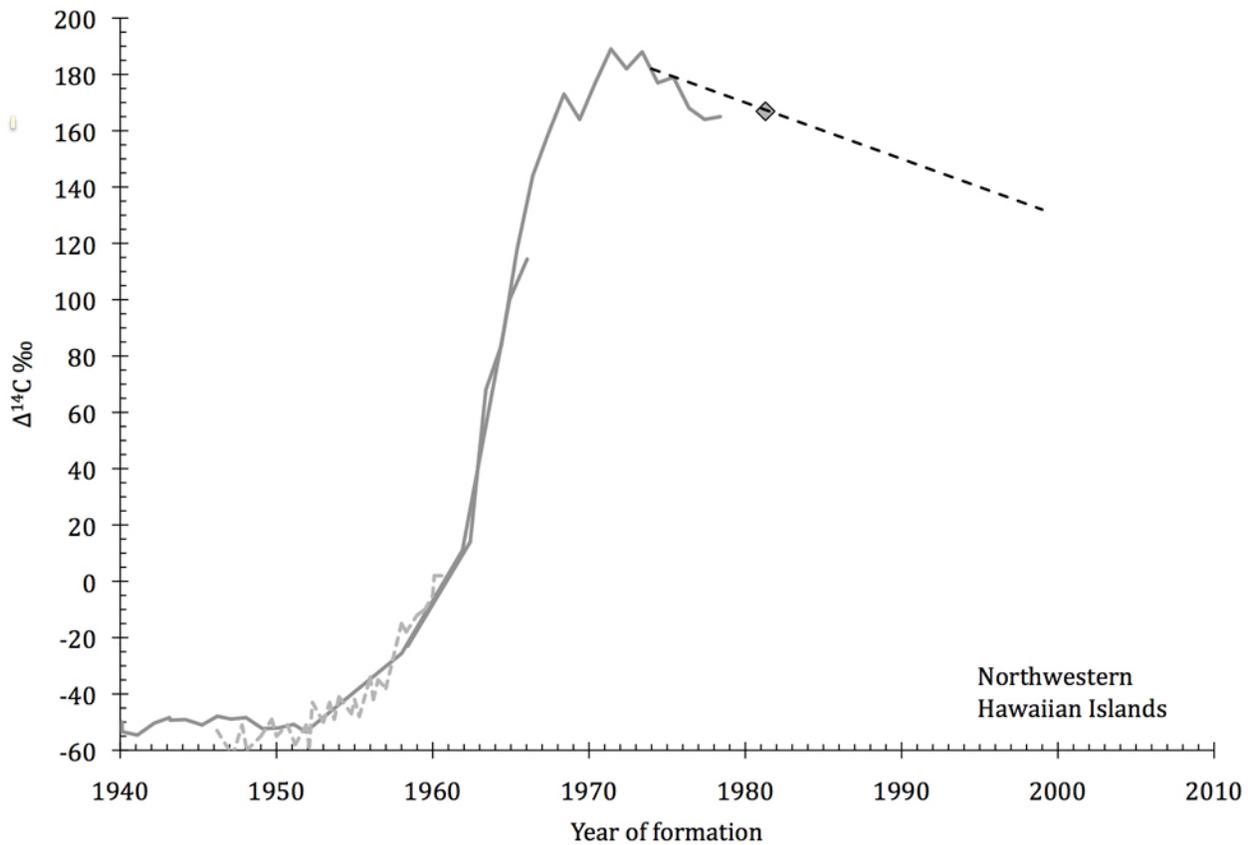


Figure 10.--Bomb radiocarbon references used in correlating measured $\Delta^{14}\text{C}$ values from otolith cores of fish collected in the NWHI. The most informative period (rise in $\Delta^{14}\text{C}$) was primarily the FFS record, which was supplemented with pre-bomb and rise data from the MHI because no other records exist. In addition, the decline rate for the post-bomb period was estimated based on a single juvenile otolith (diamond symbol) collected in 1981 and regional oceanographic data (Druffel et al., 2008). The trend was a decrease in $\Delta^{14}\text{C}$ of seawater at a rate of 2‰ per year.



Figure 11.--Otolith core extraction using the micromilling machine. The small pile of carbonate powder at the surface was analyzed for $\Delta^{14}\text{C}$ and was typically 3 mg of core material.

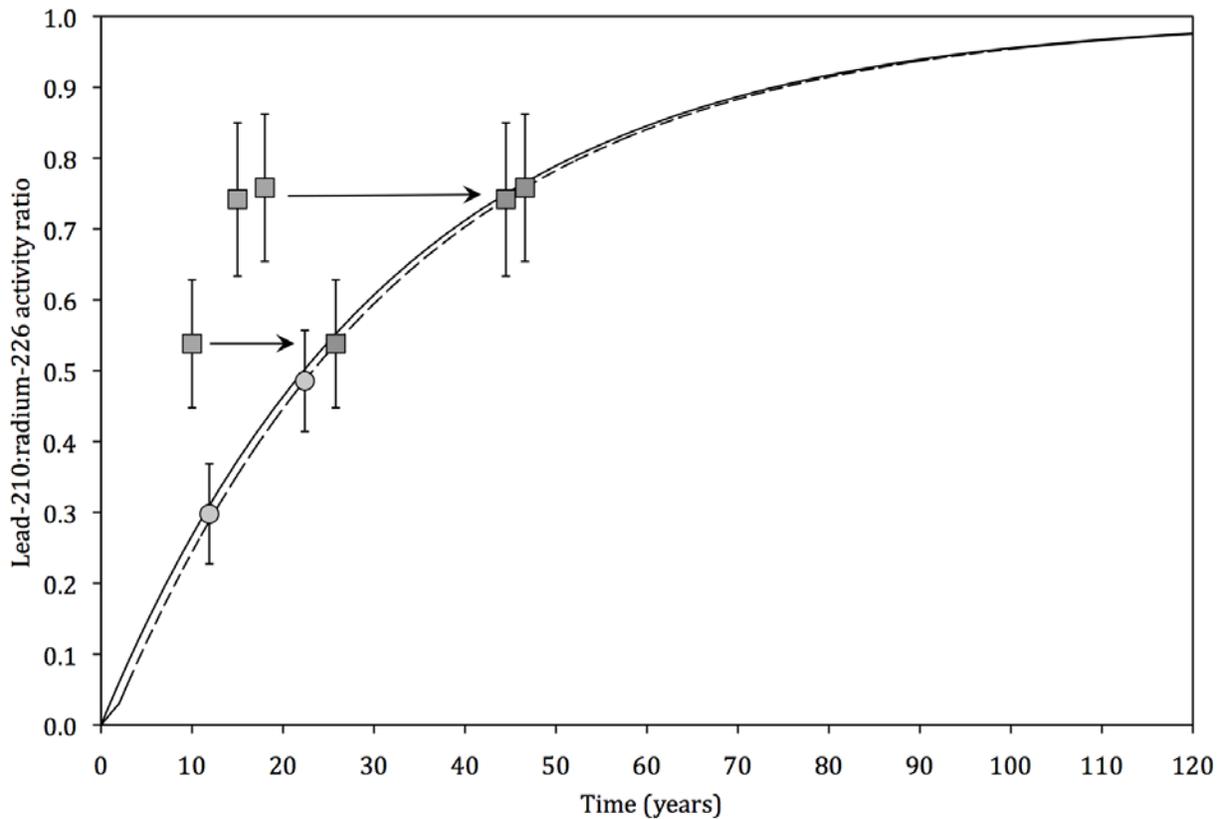


Figure 12.--Total sample age for each juvenile group (time since collection plus half of the average fish age) was plotted (grey circles) relative to measured lead-radium activity for each sample. Comparison with the ingrowth model for lead-radium ingrowth provided a baseline assessment of the radium-226 daughter product conservation within the otolith over time spent in storage. Placement of the measured ratios for the adult age groups (grey 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 SE for the measured ratio from the measurement of lead-210 and radium-226 activities.

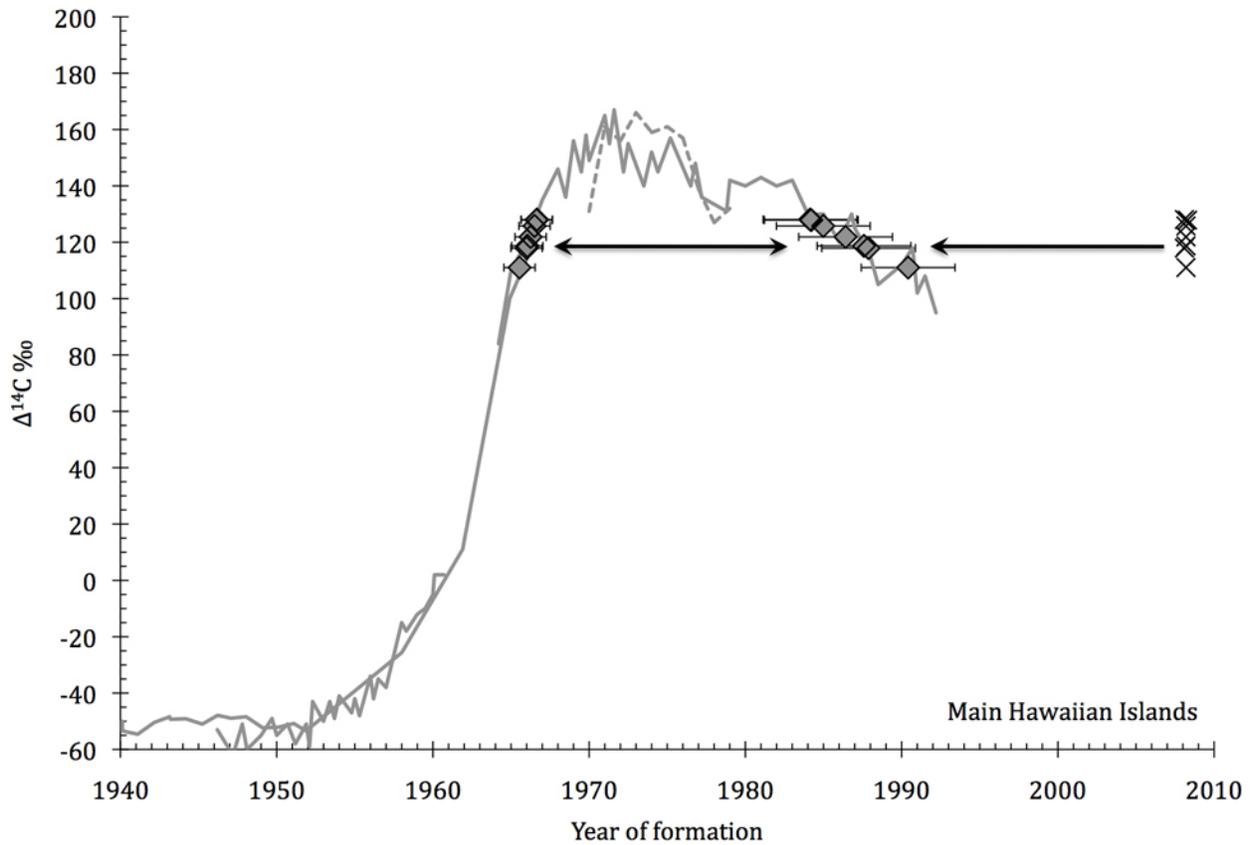


Figure 13.--Measured $\Delta^{14}\text{C}$ levels from recently collected *P. filamentosus* in the MHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise and decline in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and Kahe Point, Oahu (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006).

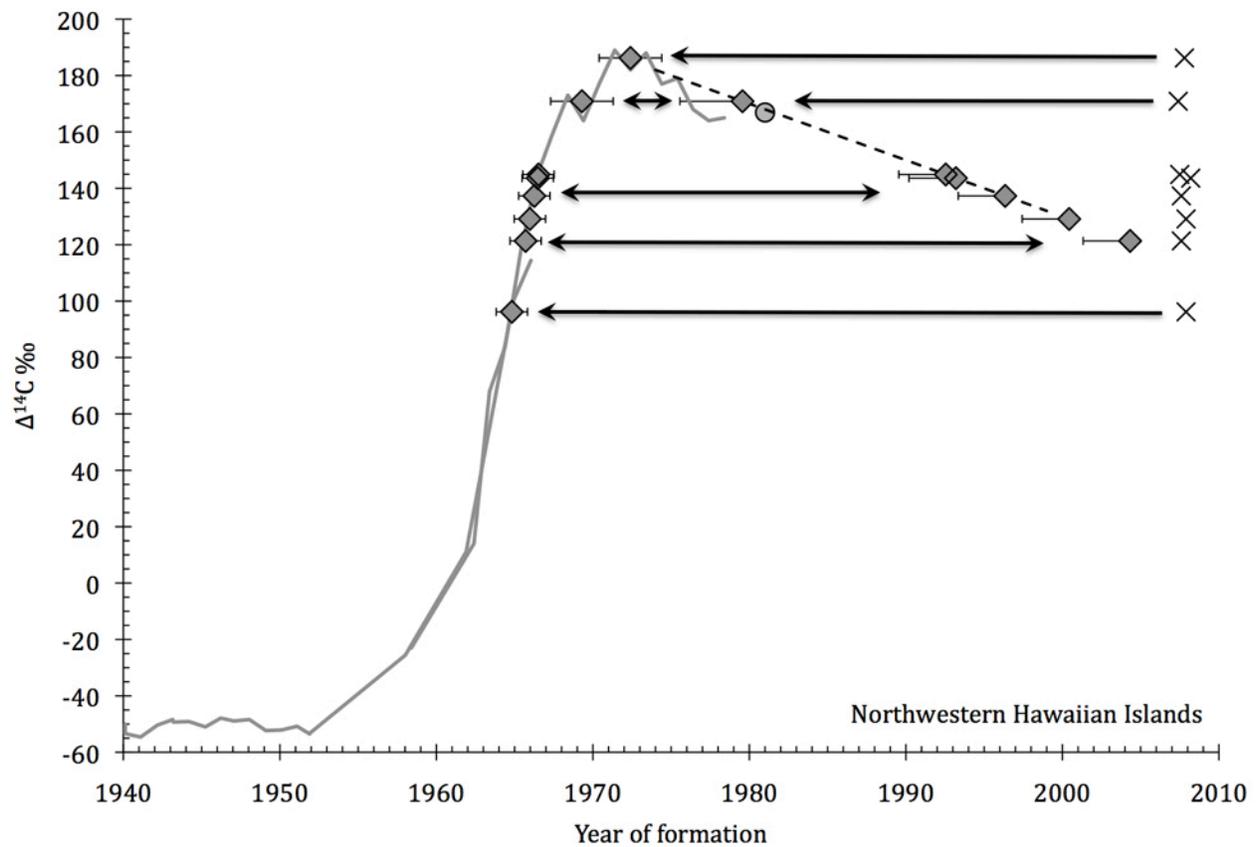


Figure 14.--Measured $\Delta^{14}\text{C}$ levels from recently collected *P. filamentosus* in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise and decline in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period and a rough estimate of 3 years prior for the calculated post-bomb decline. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001). The circle is a reference juvenile otolith from 1981.

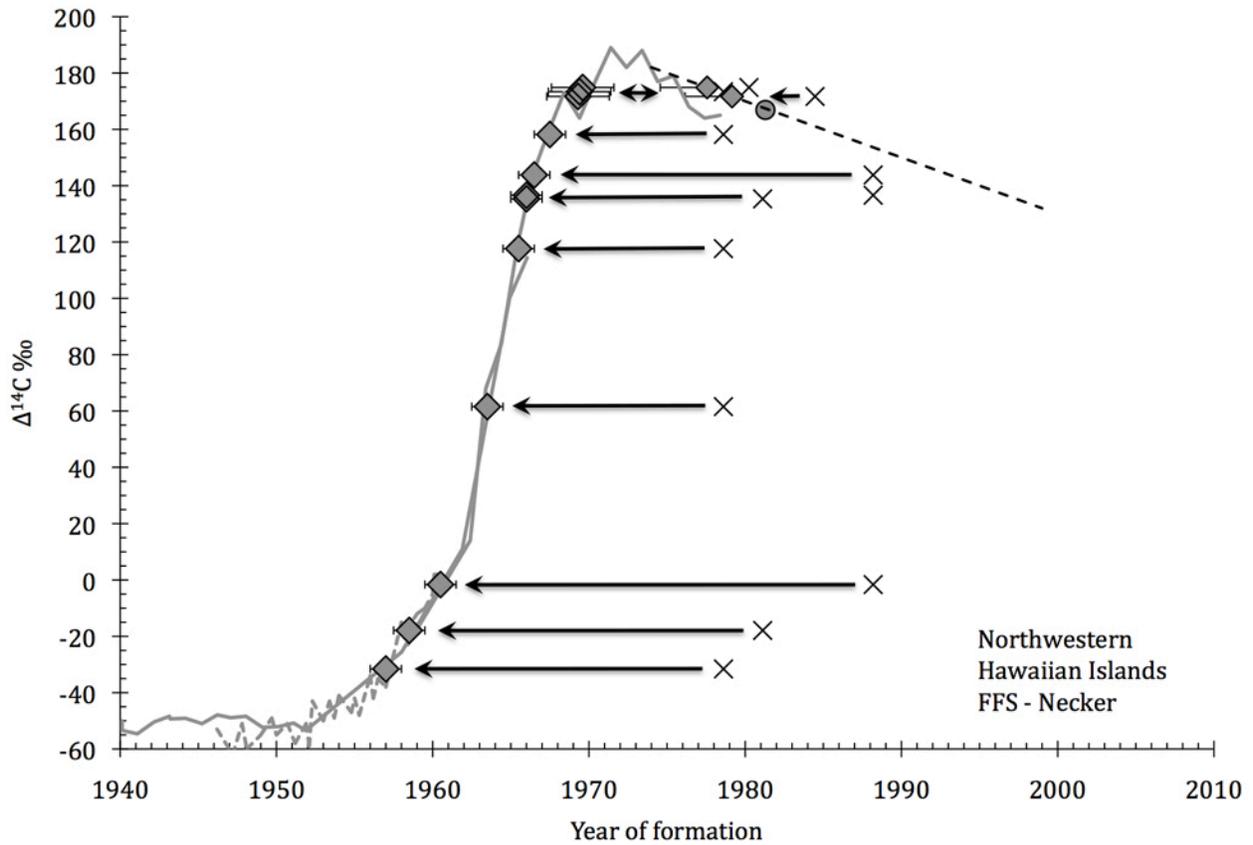


Figure 15.--Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from French Frigate Shoals and Necker Island in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise and decline in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period and a rough estimate of 3 years prior for the calculated post-bomb decline. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006). The circle is a reference juvenile otolith from 1981.

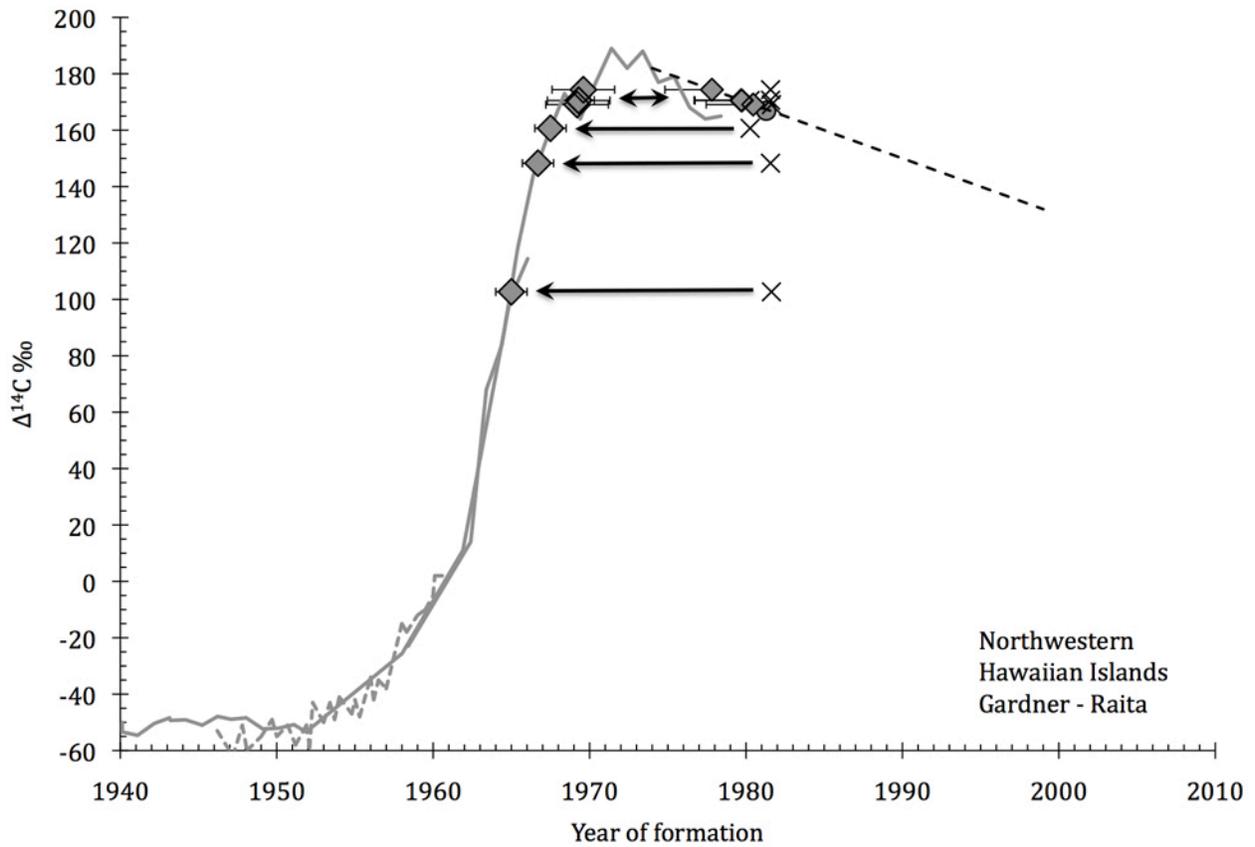


Figure 16.--Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from Gardner Pinnacles and Raita Bank in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise and decline in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period and a rough estimate of 3 years prior for the calculated post-bomb decline. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006). The circle is a reference juvenile otolith from 1981.

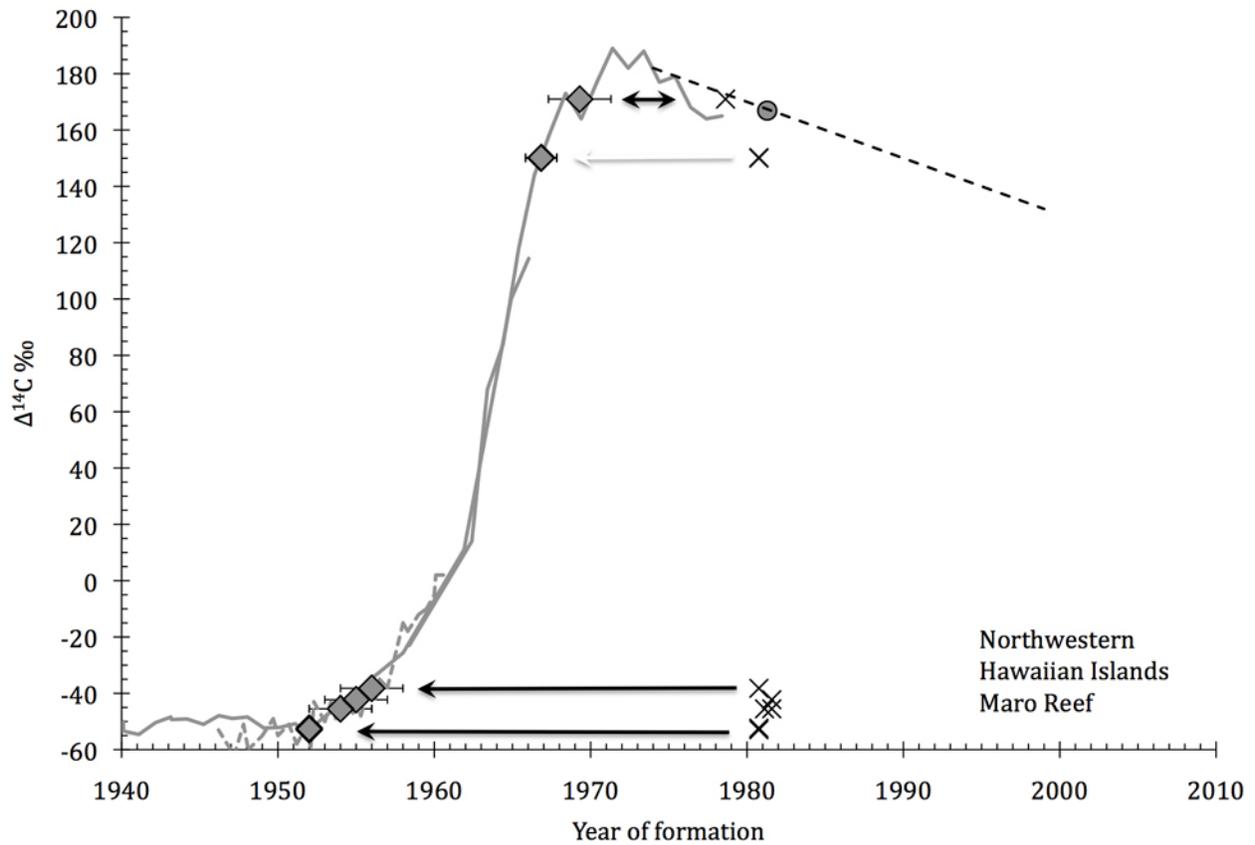


Figure 17.--Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from Maro Reef in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006). The circle is a reference juvenile otolith from 1981.

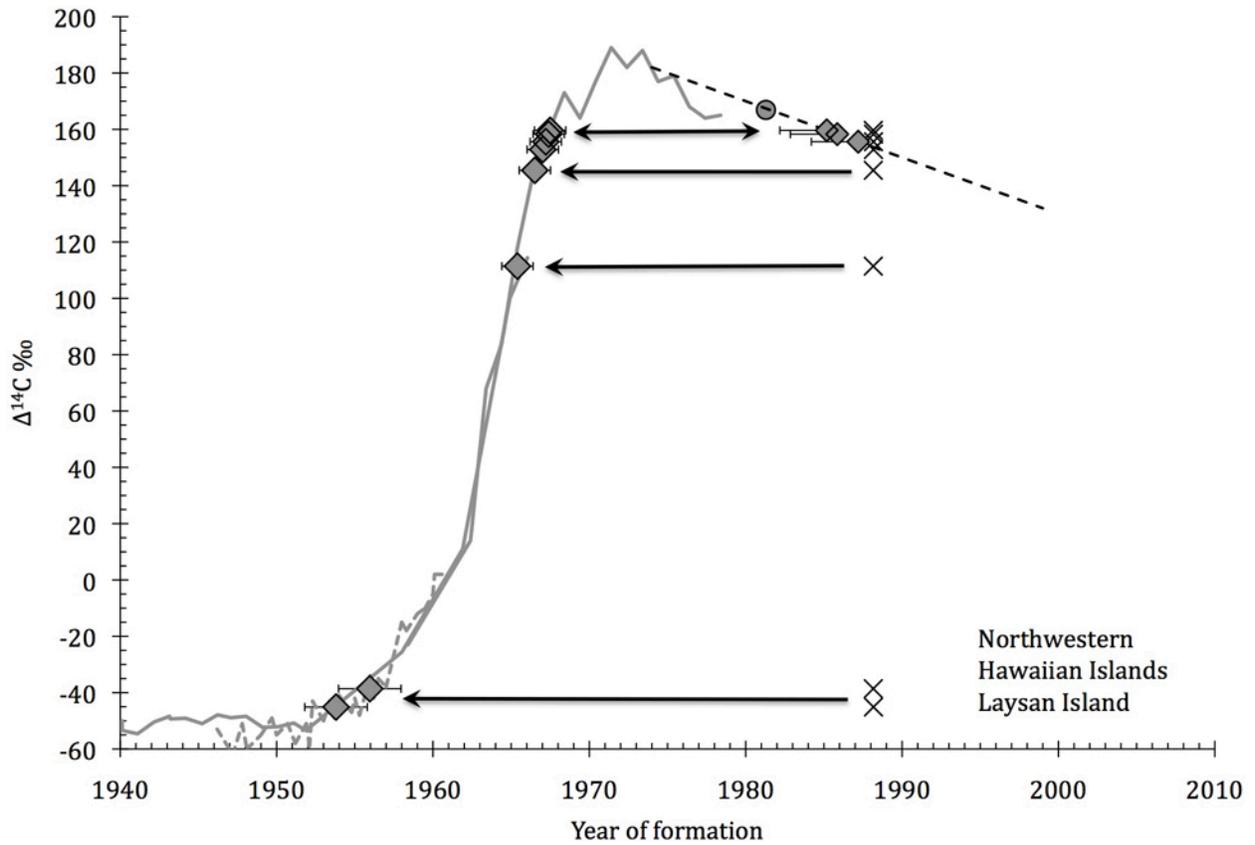


Figure 18.--Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from Laysan Island in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise and decline in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record for the associated reference time period and a rough estimate of 3 years prior for the calculated post-bomb decline. Reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006). The circle is a reference juvenile otolith from 1981.

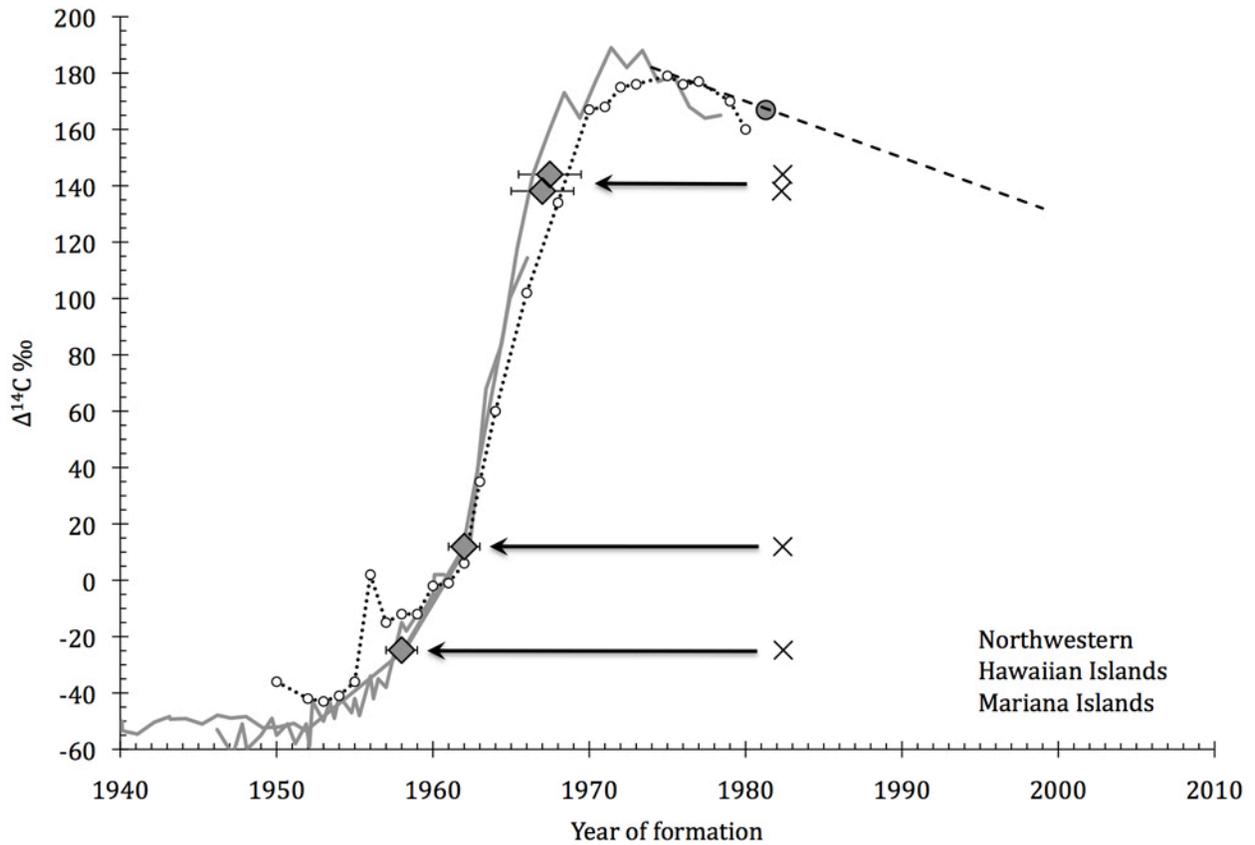


Figure 19.--Measured $\Delta^{14}\text{C}$ levels from *P. filamentosus* collected from Mariana Islands in the NWHI plotted both at the collection year (x symbol) and projected to the MHI $\Delta^{14}\text{C}$ reference records (diamond symbol). Age was determined from correlated birth years at the rise in $\Delta^{14}\text{C}$. Uncertainty was based nominally on the variability of the record 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). Other reference $\Delta^{14}\text{C}$ records were from Kona, Hawaii and French Frigate Shoals (Druffel, 1987; Druffel et al., 2001; Roark et al., 2006). The circle is a reference juvenile otolith from 1981.

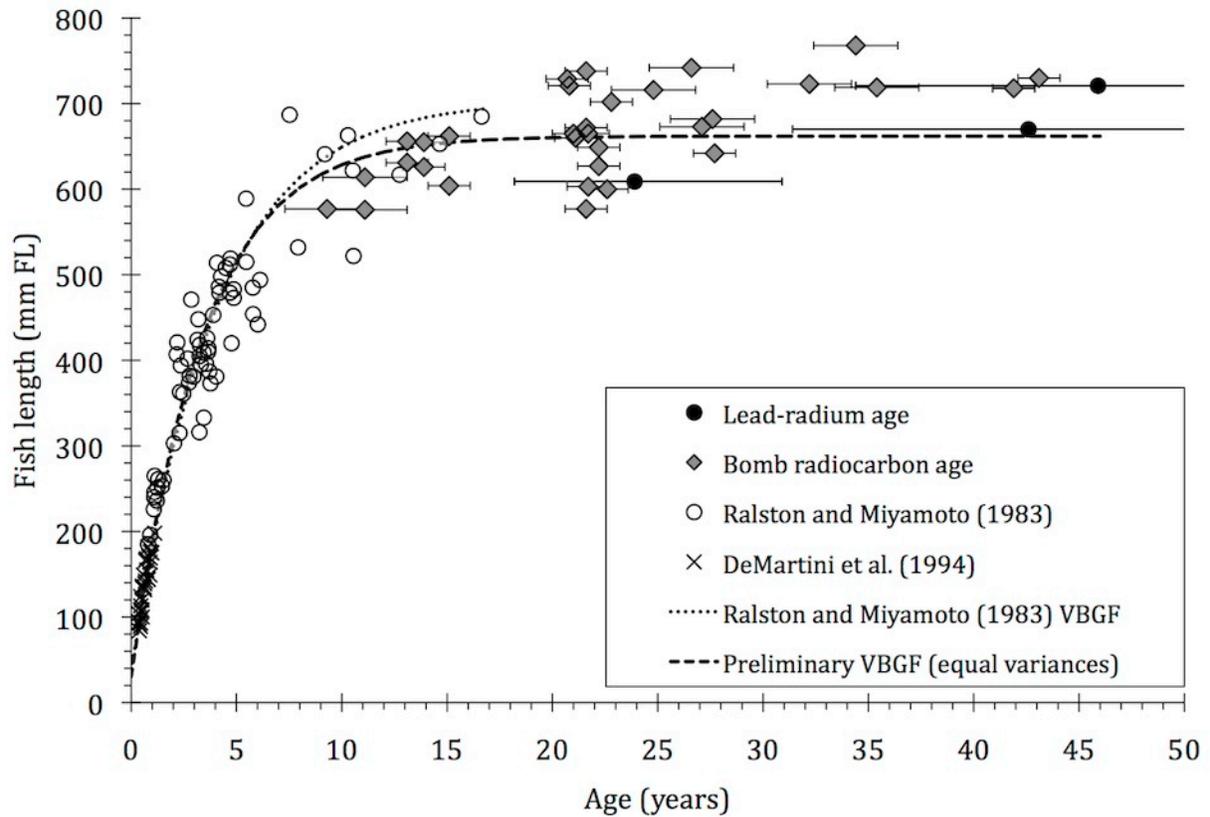


Figure 20.--Revised von Bertalanffy growth curve plotted with all age data considered reliable for *P. filamentosus*. The revised curve is considered preliminary because the assumption for the curve fit was that variances were equal among the various age estimation techniques. VBGF parameter estimates for the preliminary curve were $L_{\infty} = 662$, $k = 0.294$, $t_0 = -0.16$.

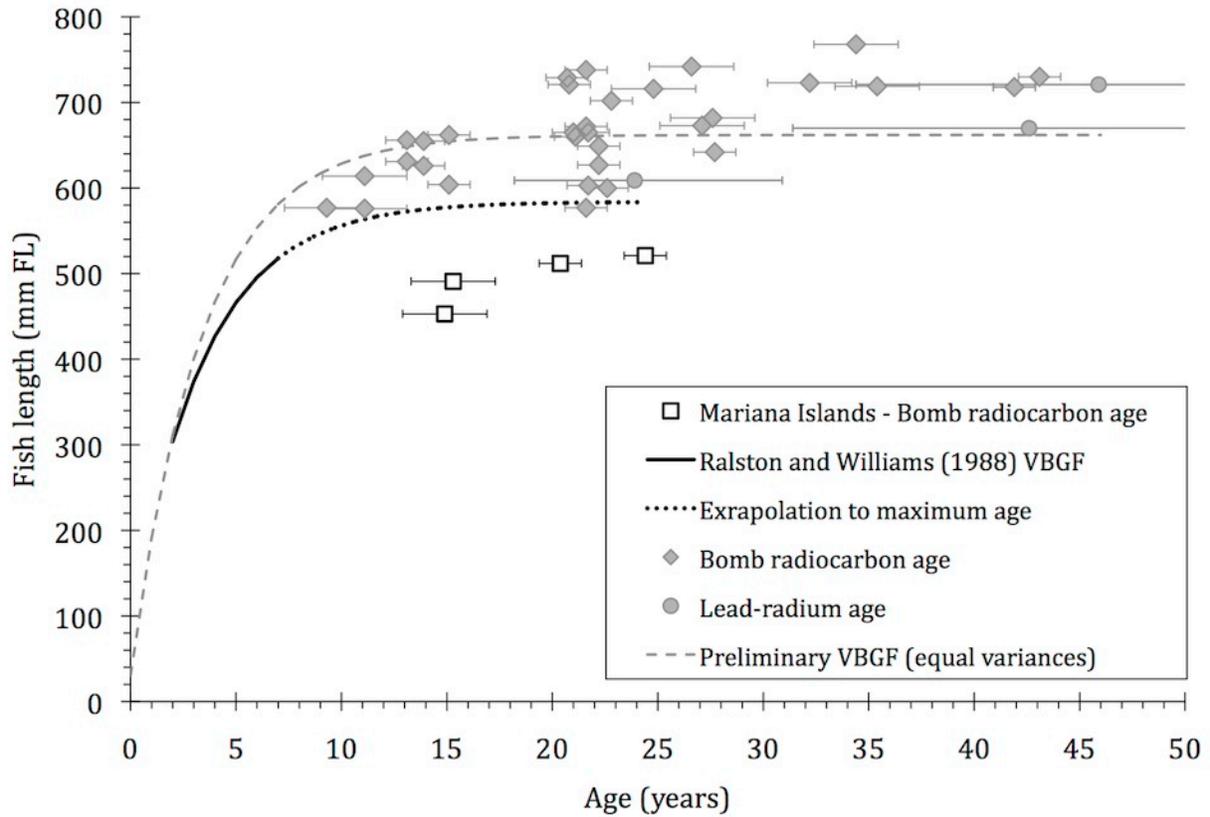


Figure 21.--Bomb radiocarbon age data for the Mariana Islands, plotted relative to the results from the Hawaiian Islands, indicated growth characteristics were different for *P. filamentosus* in the region. For comparison, the VBGF determined from early growth interpretations by Ralston and Williams (1988) is plotted and extrapolated to the greatest bomb radiocarbon age (24 years).

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Appendix A: Data associated with juvenile otolith groups collected in 1987 and 1997-98.

Sample group	ID	FL (mm)	Capture date	Location	Otolith wt. (g)
OP 1987	176	342	11/4/1987	Oahu	0.0802
	193	344	11/4/1987	Oahu	0.0931
	194	322	11/4/1987	Oahu	0.0892
	195	324	11/4/1987	Oahu	0.0822
	196	335	11/4/1987	Oahu	0.0858
	197	337	11/4/1987	Oahu	0.0838
	198	326	11/4/1987	Oahu	0.1005
	199	323	11/4/1987	Oahu	0.0823
	200	329	11/4/1987	Oahu	0.0889
	201	324	11/4/1987	Oahu	0.0928
	202	344	11/4/1987	Oahu	0.0965
	203	337	11/4/1987	Oahu	0.0866
	204	347	11/4/1987	Oahu	0.0906
	219	346	11/5/1987	Oahu	0.0832
		Mean	334	11/4/1987	Total

Sample group	ID	FL (mm)	Capture date	Location	Otolith wt. (g)
OP 1997	2 OP	205	12/26/1997	Oahu	0.0490
	5 OP	138	12/27/1997	Oahu	0.0208
	6 OP	156	12/27/1997	Oahu	0.0260
	7 OP	185	12/27/1997	Oahu	0.0389
	12 OP	192	12/21/1997	Oahu	0.0368
	13 OP	204	12/18/1997	Oahu	0.0410
	14 OP	214	12/18/1997	Oahu	0.0413
	15 OP	136	12/23/1997	Oahu	0.0220
	18 OP	206	12/23/1997	Oahu	0.0491
	20 OP	204	12/22/1997	Oahu	0.0445
	21 OP	208	12/22/1997	Oahu	0.0456
	22 OP	190	12/22/1997	Oahu	0.0455
	32 OP	190	12/22/1997	Oahu	0.0422
	49 OP	106	1/27/1998	Oahu	0.0137
	54 OP	132	2/10/1998	Oahu	0.0194
	55 OP	143	2/10/1998	Oahu	0.0231
	62 OP	140	2/19/1998	Oahu	0.0201
	63 OP	125	2/19/1998	Oahu	0.0163
	64 OP	106	2/19/1998	Oahu	0.0141
		Mean	167	1/8/1998	Total

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Appendix B: Data associated with cored adult otolith samples for the 600 to 610 mm group.

Sample group	ID	FL (mm)	Capture date	Location	Otolith wt. (g) ¹
OP 600-610	LA2-4-8-236	602	4/28/2007	Maro	0.257
	M2-2-5-188	602	12/21/2007	Kauai	na
	LA5-4-6-419	603	9/21/2007	N. Hampton	na
	LA2-4-2-225	604	4/25/2007	N. Hampton	na
	LA6-5-2-445	606	11/09/2007	Raita	0.201
	M6-2-1-154	607	2/13/2008	Niihau	0.246
	LA2-4-6-232	608	4/26/2007	N. Hampton	0.289
	CK6-3-3-23	609	1/07/2008	Penguin Bank	na
	M9-2-8-322	609	2/23/2008	Niihau	na
	CK11-1-9-9	610	3/05/2008	Penguin Bank	na
	M9-2-9-323	611	2/23/2008	Niihau	0.266
	M9-3-5-332	611	2/23/2008	Niihau	0.242
	LA5-5-2-407	612	9/17/2007	Lisianski	0.282
	LA2-4-4-217	613	4/21/2007	Lisianski	0.245
	M8-4-2-392	614	2/20/2008	Niihau	0.198
	LA6-5-5-459	616	11/11/2007	N. Hampton	0.318
		Mean	609	11/22/2007	

1. Whole otolith weight prior to extraction of core material. Some otoliths were not weighed (na = not available) because of prior damage and mass loss.

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Appendix C: Data associated with cored adult otolith samples for the 660 to 680 mm group.

Sample group	ID	FL (mm)	Capture date	Location	Otolith wt. (g) ¹	
OP 660-680	LA5-5-3-426	661	9/22/2007	Maro	0.281	
	M13-3-2-488	662	3/09/2008	Kailua	0.290	
	LA5-5-4-425	663	9/22/2007	Maro	0.270	
	IM1-3-2-224	665	8/29/2007	Nihoa	na	
	M1-1-5-212	665	12/09/2007	Niihau	na	
	M3-2-9-118	665	12/31/2007	Kauai	0.296	
	M13-3-1-437	665	3/08/2008	Niihau	na	
	LA6-5-4-475	666	11/17/2007	Gardner	0.195	
	M7-4-4-246	667	2/17/2008	Niihau	0.275	
	M7-4-2-231	668	2/17/2008	Niihau	na	
	M10-4-4-399	668	2/28/2008	Niihau	0.282	
	IM3-4-9-264	671	1/02/2008	Nihoa	na	
	LA4-3-1-317	675	7/13/2007	Raita	0.211	
	M3-3-1-139	675	12/31/2007	Kauai	0.318	
	LA4-3-6-336	676	7/15/2007	Gardner	na	
	M5-1-6-208	676	1/20/2008	Kauai	0.318	
		Mean	670	11/25/2007		

1. Whole otolith weight prior to extraction of core material. Some otoliths were not weighed (na = not available) because of prior damage and mass loss.

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Appendix D: Data associated with cored adult otolith samples for the 700+ mm group.

Sample group	ID	FL (mm)	Capture date	Location	Otolith wt. (g) ¹
OP 700+	M11-471	700	3/2/2008	Kauai	0.366
	KP6-391	706	2/16/2008	Twin Banks	0.437
	IM3-274	707	¼/2008	Nihoa	na
	CK10-12	708	3/9/2008	Penguin Bank	0.401
	M10-269	712	2/28/2008	Niihau	0.375
	M3-131	716	12/31/2007	Kauai	0.321
	LA3-278	718	6/8/2007	Gardner	0.416 ^a
	LA4-338	718	7/15/2007	Gardner	0.320
	KP5-366	718	11/2/2007	Twin Banks	0.336
	LA5-420	719	9/21/2007	N. Hampton	0.480
	M11-481	721	3/1/2008	Niihau	0.331 ^a
	M10-379	725	2/28/2008	Niihau	0.296
	LA6-441	730	11/8/2007	Gardner	0.580
	M5-219	730	1/20/2008	Kauai	0.479
	LA4-337	745	7/15/2007	Gardner	0.367
	LA2-222	746	4/23/2007	Pioneer	0.561
		Mean	720	11/21/2007	

1. Whole otolith weight prior to extraction of core material. Some otoliths were not weighed (na = not available) because of prior damage and mass loss.

a. Whole otolith broken with all pieces present or loss was deemed negligible

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Appendix E. Sample and measurement data from recent opakapaka otolith collections in 2007-2008 (Tables 5 and 6).

Regional sample #	Original sample #	Collection Date	Fish length (mm FL)	Fish wt. (kg)	Otolith wt. (g)	Sample wt. (mg)	$\delta^{13}\text{C}$ (‰)	Fraction mod. (Fm)	Correction year	$\Delta^{14}\text{C}$ (‰)	NOSAMS number
Niihau Kauai-1	M10-379	2/28/2008	725	na	0.296	3.2	-5.98	1.1148	1978	111.0 ± 5.3	OS-76557
Niihau Kauai-2	M3-131	12/31/2007	716	5.96	0.321	3.0	-4.9 ^a	1.1217	1978	117.9 ± 5.7	OS-76585
Niihau Kauai-3	M11-481	3/1/2008	721	5.78	0.331 ^b	2.8	-4.9 ^a	1.1225	1978	118.7 ± 6.4	OS-76590
Niihau Kauai-4	M11-471	3/2/2008	700	5.52	0.366	3.0	-4.9 ^a	1.1257	1978	121.9 ± 4.9	OS-76587
Niihau Kauai-5	M10-269	2/28/2008	712	na	0.375	2.8	-4.9 ^a	1.1296	1978	125.8 ± 6.0	OS-76595
Niihau Kauai-6	M5-219	1/20/2008	730	6.14	0.479	3.2	-4.9 ^a	1.1319	1978	128.1 ± 4.7	OS-76586
Penguin-1	CK10-12	3/9/2008	708	5.78	0.401	3.0	-5.49	1.1317	1978	127.9 ± 3.9	OS-76584
Twin-1	KP5-366	11/2/2007	718	6.94	0.336	3.1	-4.9 ^a	1.1309	1963	129.1 ± 10.1	OS-76592
Twin-2	KP6-391	2/16/2008	706	6.70	0.437	2.7	-4.9 ^a	1.1454	1963	143.6 ± 5.0	OS-76594
Gardner-1	LA6-441	11/8/2007	730	6.52	0.580	2.6	-4.9 ^a	1.0979	1963	96.2 ± 5.6	OS-76593
Gardner-2	LA4-338	7/15/2007	718	6.32	0.320	2.7	-4.9 ^a	1.1231	1963	121.3 ± 5.2	OS-76934
Gardner-3	LA4-337	7/15/2007	745	7.14	0.367	2.7	-4.84	1.1391	1963	137.3 ± 5.0	OS-76588
Gardner-4	LA3-278	6/8/2007	718	6.40	0.416 ^b	2.6	-4.9 ^a	1.1467	1963	144.9 ± 10.6	OS-76942
N Hampton-1	LA5-420	9/21/2007	719	5.74	0.480	3.1	-4.67	1.1894	1972	186.2 ± 4.8	OS-76591
Pioneer-1	LA2-222	4/23/2007	746	6.54	0.561	2.9	-5.18	1.1740	1972	170.9 ± 4.9	OS-76589

a. Mean measured $\delta^{13}\text{C}$ value from all opakapaka samples where the determination was made by NOSAMS ($n = 11$)

b. Whole otolith broken with all pieces present or loss was deemed negligible

na = not available

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Appendix F. Sample and measurement data from archive opakapaka otolith collections in 1978-1988 (Table 7 and 8).

Regional sample #	Original sample # (lab #)	Collection date	Fish lgth. (mm FL)	Fish wt. (Kg)	Otolith wt. (g)	Sample wt. (mg)	$\delta^{13}\text{C}$ (‰)	Fraction mod. (Fm)	Correction year	$\Delta^{14}\text{C}$ (‰)	NOSAMS number
Necker-1	TC81-01 (Paka 41)	2/12/1981	600	3.94	0.315	3.6	-4.9 ^a	0.9835	1963	-17.9 ± 3.6	OS-76557
Necker-2	TC81-01 (Paka 37)	2/11/1981	604	3.76	0.242	3.2	-4.9 ^a	1.1370	1963	135.3 ± 4.4	OS-76585
Necker-3	TC84-06 (Paka 35)	6/20/1984	622	na	0.243 ^b	3.3	-4.9 ^a	1.1749	1972	171.7 ± 4.5	OS-76590
Necker-4	TC80-02 (Paka 39)	3/28/1980	603	3.97	0.192 ^b	3.3	-4.9 ^a	1.1779	1972	174.9 ± 4.2	OS-76587
FFS-1	TC78-03 (Paka 40)	8/11/1978	672	4.80	0.372	3.3	-4.9 ^a	0.9698	1963	-31.6 ± 4.1	OS-76595
FFS-2	TC88-02 (Paka 34)	3/9/1988	642	5.03	0.357 ^b	3.4	-4.9 ^a	0.9998	1963	-1.6 ± 3.6	OS-76586
FFS-3	TC78-03 (Paka 43)	8/9/1978	662	4.66	0.283	3.3	-4.9 ^a	1.0631	1963	61.6 ± 4.0	OS-76584
FFS-4	TC78-03 (Paka 44)	8/9/1978	631	na	0.293 ^b	3.3	-4.9 ^a	1.1193	1963	117.7 ± 4.9	OS-84031
FFS-5	TC88-02-128 (Paka 36)	8/9/1988	627	4.18	0.212 ^b	3.3	-4.9 ^a	1.1383	1963	136.6 ± 4.8	OS-84041
FFS-6	TC88-02 (Paka 38)	8/9/1988	603	3.49	0.194	3.1	-4.9 ^a	1.1455	1963	143.8 ± 5.5	OS-84026
FFS-7	TC78-03 (Paka 49)	8/9/1978	576	3.11	0.293	3.3	-4.9 ^a	1.1599	1963	158.2 ± 4.3	OS-84026
Gardner-4	TC81-04-25 (Paka 9)	7/25/1981	577	3.20	0.243 ^b	3.2	-4.68	1.1501	1963	148.3 ± 4.3	OS-76592
Gardner-5	TC81-04 (Paka 21)	7/26/1981	507	2.14	0.225	3.4	-4.9 ^a	1.1736	1972	170.6 ± 4.4	OS-76594
Gardner-6	TC81-04 (Paka 8)	7/27/1981	564	2.93	0.229	3.2	-4.9 ^a	1.1773	1972	174.4 ± 4.6	OS-76593
Raita-1	TC81-04 (Paka 31)	8/15/1981	656	4.66	0.255	3.5	-4.9 ^a	1.1043	1963	102.7 ± 8.8	OS-76934
Raita-2	TC80-02 (Paka 30)	4/5/1980	649	4.50	bkn-m	3.9	-4.9 ^a	1.1624	1963	160.7 ± 5.2	OS-76588
Raita-3	TC81-04 (Paka 33)	8/16/1981	665	5.27	bkn-m	3.5	-4.9 ^a	1.1721	1972	169.1 ± 5.5	OS-76942
Raita-4	TC80-02-18 (Paka 32)	4/4/1980	614	3.86	0.213	3.5	-4.9 ^a	1.1735	1972	170.5 ± 4.5	OS-76591

a. Mean measured $\delta^{13}\text{C}$ value from all opakapaka samples where the determination was made by NOSAMS ($n = 11$)

b. Whole otolith broken with all pieces present or loss was deemed negligible

na = not available

bkn-m = whole otolith broken with pieces missing

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Appendix G. Sample and measurement data from archive opakapaka otolith collections in 1978-1988 (Tables 9 and 10).

Regional sample #	Original sample # (lab #)	Collection date	Fish lgth. (mm FL)	Fish wt. (Kg)	Otolith wt. (g)	Sample wt. (mg)	$\delta^{13}\text{C}$ (‰)	Fraction mod. (Fm)	Correction year	$\Delta^{14}\text{C}$ (‰)	NOSAMS number
Maro-1	TC80-04 (Paka 14)	10/3/1980	645	4.01	0.403	3.2	-4.9 ^a	0.9470	1950	-52.9	OS-81419
Maro-2	TC80-04 (Paka 19)	10/3/1980	728	6.05	0.436	3.6	-4.9 ^a	0.9475	1950	-52.3	OS-81405
Maro-3	TC81-01 (Paka 16)	2/12/1981	673	5.69	0.412 ^b	3.2	-4.68	0.9560	1963	-45.5	OS-81378
Maro-4	TC 81-04 (Paka 17)	7/31/1981	682	5.34	0.482 ^b	3.6	-4.9 ^a	0.9559	1963	-45.5	--
Maro-5	TC81-04 (Paka 20)	7/31/1981	742	5.99	0.491 ^b	3.7	-4.89	0.9592	1963	-42.3	--
Maro-6	TC80-04 (Paka 18)	10/3/1980	716	5.76	0.482	na	-4.9 ^a	0.9632	1963	-38.2	--
Maro-7	TC 80-04 (Paka 15)	10/3/1980	655	4.50	0.260	3.4	-4.9 ^a	1.1517	1963	150.0	OS-81415
Maro-8	TC80-04 (Paka 1)	10/3/1980	626	3.81	0.237	3.2	-4.9 ^a	1.1519	1963	150.2	OS-81421
Maro-9	TC78-03 (Paka 2)	8/16/1978	577	5.99	0.194	3.1	-5.02	1.1741	1972	171.0	OS-81420
Laysan-1	TC88-02-85 (Paka 3)	3/2/1988	768	3.23	0.472 ^b	3.4	-4.47	0.9564	1963	-45.1	OS-81422
Laysan-2	TC88-02-44 (Paka 6)	2/27/1988	723	6.22	0.460 ^b	3.3	-4.9 ^a	0.9628	1963	-38.6	OS-81418
Laysan-3	TC88-02-70 (Paka 13)	2/27/1988	702	5.80	0.385 ^b	3.1	-4.9 ^a	1.1130	1963	111.4	--
Laysan-4	TC88-02-35 (Paka 4)	2/27/1988	738	6.21	bkn-m	3.3	-4.9 ^a	1.1471	1963	145.4	OS-81423
Laysan-5	TC88-02-76 (Paka 10)	3/2/1988	660	4.55	0.264 ^b	3.3	-4.9 ^a	1.1545	1963	152.8	OS-81424
Laysan-6	TC88-02-114 (Paka 11)	3/3/1988	665	4.60	0.247	3.3	-4.9 ^a	1.1573	1963	155.6	OS-81377
Laysan-7	TC88-02-101 (Paka 7)	3/2/1988	721	5.72	0.289 ^b	3.4	-4.9 ^a	1.1600	1963	158.3	--
Laysan-8	TC88-02-46 (Paka 5)	2/27/1988	729	6.65	0.355	3.3	-4.9 ^a	1.1613	1963	159.6	OS-81417

a. Mean measured $\delta^{13}\text{C}$ value from all opakapaka samples where the determination was made by NOSAMS ($n = 11$)

b. Whole otolith broken with all pieces present or loss was deemed negligible

bkn-m = whole otolith broken and piece was missing

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Appendix H. Sample and measurement data from archive opakapaka otolith collections from Mariana Islands (Table 11).

Regional sample #	Original sample # (lab #)	Collection date	Fish lgth. (mm FL)	Fish wt. (Kg)	Otolith wt. (g)	Sample wt. (mg)	$\delta^{13}\text{C}$ (‰)	Fraction mod. (Fm)	Correction year	$\Delta^{14}\text{C}$ (‰)	NOSAMS number
Mariana-1	Paka 42, TC82-02-1279	5/29/1982	521	2.42	0.336	3.2	-4.9 ^a	0.9766	1963	-24.8	OS-84030
Mariana-2	Paka 45, TC82-02-602	5/17/1982	512	2.27	0.313 ^b	3.3	-4.9 ^a	1.0134	1963	11.9	OS-84040
Mariana-3	Paka 47, TC82-02-23	4/20/1982	491	2.20	0.189	3.4	-4.9 ^a	1.1398	1963	138.1	OS-84023
Mariana-4	Paka 48, TC82-02-599	5/17/1982	453	1.59	0.209 ^b	3.1	-4.82	1.1457	1963	144.0	OS-84034

a. Mean measured $\delta^{13}\text{C}$ value from all opakapaka samples where the determination was made by NOSAMS ($n = 11$)

b. Whole otolith broken with all pieces present or loss was deemed negligible

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