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Bomb radiocarbon and lead–radium disequilibria in otoliths of bocaccio rockfish (*Sebastes paucispinis*): a determination of age and longevity for a difficult-to-age fish

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Abstract. Longevity estimates for the bocaccio rockfish (*Sebastes paucispinis*) using traditional techniques range from less than 20 years to approximately 50 years. Otoliths of bocaccio are difficult to age, and previous attempts to validate ages have been unsuccessful. Because otolith age suggests the bocaccio are reasonably long-lived, lead–radium dating was used in an attempt to independently age bocaccio otoliths. The measured ^{210}Pb and ^{226}Ra activities were among the lowest reported and resulted in poor radiometric age resolution; however, the break-and-burn technique clearly underestimated age in some cases with the longevity of the bocaccio being at least 31 years. To provide better age resolution, the bomb radiocarbon approach was applied to individual otoliths. Based on measured radiocarbon levels relative to a reference time-series, several specimens were aged at approximately 30–40 years. To evaluate these determinations, the remaining otolith of the pair was sectioned and aged blind. The result was an excellent fit to the reference time-series and a validation of the age estimates. The maximum age from growth zone counts was 37 ± 2 years, which is consistent with a reported maximum age of approximately 50 years.

Extra keywords: growth, lead–radium dating, longevity, Scorpaenidae.

Introduction

The bocaccio rockfish (*Sebastes paucispinis*) has been an important component of the long history of California rockfish fisheries (Ralston *et al*. 1996), but has more recently been deemed one of the most severely depleted deep-water rockfish fisheries (Starr *et al*. 2002). Annual landings of bocaccio along the western coast of the United States during the late 1960s to early 1980s frequently exceeded 5000 *t* and have decreased to less than 100 *t* since that period, partly as a result of the implementation of catch limits (MacCall 2003*a*). A stock assessment of the California bocaccio fishery in the Conception/Monterey/Eureka areas under the International North Pacific Fishery Commission, estimated that the spawning output for 1999 was 2.1–4.1% of the unfished levels (MacCall *et al*. 1999), although the estimated unfished levels were arguably too high, based on the low abundance from 1951 to 1965 (15–27% of the estimated unfished abundance; MacCall 2003*a*). Additional concerns were trends over the past several decades that indicated: (*1*) the average size of landed female bocaccio in the California recreational fishery had decreased to below the size at 50% maturity (Mason 1998); and (*2*) the catch per unit effort for California trawl-based fishing had decreased considerably (Ralston 1999). In the 1999 ‘Report to Congress: Status of Fisheries of the United States’ by the National Marine Fisheries Service (NMFS), the bocaccio was listed as being overfished, and it was mandated that a rebuilding programme be designed and implemented for the bocaccio rockfish fishery. Most recently, the unfished abundance was adjusted for lower abundances determined for 1951–1965, and the spawning biomass was estimated as 7.4% of the virgin stock level. It was further estimated that rebuilding the fishery would take a few decades, depending on the level of exploitation and success of the inherently variable bocaccio recruitment (MacCall 2003*b*; Berkeley *et al*. 2004*a*).

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Life history information, such as age and growth characteristics, must be known to properly evaluate the status of the bocaccio population. For example, in a report on the status of the bocaccio rockfish off British Columbia, Canada proclaimed there was not enough information to carry out a stock assessment, partly because of the highly variable and largely unknown recruitment success (Stanley *et al.* 2004). Some life history information has been described for the bocaccio (for a synopsis see Love *et al.* 2002), but longevity estimates remain unresolved. Recent and historic longevity estimates based on a variety of traditional techniques (scale rings and otolith surface ageing, break-and-burn, and transverse otolith sectioning) range from less than 20 years to approximately 50 years (Phillips 1964; Westrheim and Harling 1975; Wilkins 1980; Love *et al.* 2002). When determining a recovery time for the bocaccio rockfish fishery, a maximum age of 45 years was assumed, based on supporting evidence that was not presented in the report (MacCall 2003*a*).

The history of rockfish age estimation began with counting rings or growth zones in various structures, like scales, whole otoliths, and bony parts. These early age estimates provided evidence that rockfishes were a relatively fast-growing group (Phillips 1964). The validity of these early estimates was often evaluated and sometimes assumed by using precision and/or a form of verification (comparison of ages between structures within the same fish). The methods are in contrast to true age validation methods, which require a temporal context to establish the annual periodicity of growth zones. For some of the smaller near-shore rockfish species, relatively rapid growth may be accurate, but larger and deeper-dwelling species were deemed older, with the discovery that transversely sectioned otoliths provided much higher age estimates (Beamish 1979). This finding led to an even greater need for age validation because many people in the fishing and fisheries management communities did not believe estimated ages that were decades to more than 100 years. Perhaps the reason for greatest concern was that high longevity had serious implications for fisheries management, indicating probable low productivity rates and an overdue need for more conservative and restrictive fishing measures. It is reasonably certain that underestimation of age and longevity has had serious consequences for rockfish fisheries (Campana 2001), and that counting growth zones in the transverse plane of the sagittal otolith provides the best estimate of age for rockfish (Committee of Age Reading Experts (CARE) 2000). There are now numerous rockfishes that are estimated to attain ages that approach or exceed 100 years (Cailliet *et al.* 2001; Munk 2001).

Validating the annual periodicity of growth zones in sagittal otoliths of rockfishes has had an interesting evolution that has become increasingly technical (Kastelle *et al.* 2000; Cailliet *et al.* 2001). The problem with traditional age validation techniques is limited applicability to deep-water or long-lived fishes (Burton *et al.* 1999). Deep-water rockfishes are highly susceptible to barotrauma because of changes in pressure when brought to the surface, which precludes the use of tag–mark–recapture techniques for all except the most shallow-dwelling rockfish species. Rockfishes with high estimates of age cannot be validated using otolith marginal growth or modal length studies because of the fine growth structure and lack of a detectable change in fish length, respectively, with increasing age. Two techniques that can be used to validate high age estimates for rockfishes are: (*1*) lead–radium dating; and (*2*) the time-specific, bomb-produced radiocarbon (^{14}C) marker in otoliths as a natural chronometer (Campana 2001; Kalish 2001).

Because interpretations of growth zones in otoliths suggest bocaccio are long-lived and no consistent ageing methodology has been resolved (Ralston and Ianelli 1998; MacCall 2003*a*), application of an independent ageing technique to the otoliths of bocaccio can test hypotheses about age and longevity. In the present study, otolith break-and-burn age estimates were tested for validity by comparing the age estimates for: (*1*) otolith groups with age determined from lead–radium dating using ^{210}Pb (lead-210) and ^{226}Ra (radium-226) disequilibria; and (*2*) individual otoliths with age determined from the time-specific, bomb-produced ^{14}C chronometer. Based on observations made during the study, maximum age was estimated from these techniques.

Materials and methods

^{210}Pb and ^{226}Ra disequilibria

Bocaccio otoliths collected off the central coast of California in 1983 and 1984 by NMFS were used to determine radiometric age. These years were selected because there was a sufficient number of otoliths available for the radiometric analyses. Although otoliths collected more recently were available, they were fewer in number and the maximum estimated age for the collection years was lower. We chose to use the older collections because the traditional ageing technique (break-and-burn) for the bocaccio had not changed during this time. One otolith of the pair was aged at the National Oceanic and Atmospheric Association (NOAA), NMFS, Santa Cruz Laboratory, CA, USA. Surface ageing (whole otolith ageing) was used for juvenile otoliths and the break-and-burn technique for adult otoliths. Towards the end of the study, age was not estimated by using any technique other than radiometric ageing for reasons that are discussed later. For fish that were aged, the unused otolith was used for radiometric age determination at Moss Landing Marine Laboratories (MLML). Otolith core size was determined from seven whole juvenile otoliths, with an estimated age of 3 years. Core dimensions were approximately 12.5 mm long by 5.5 mm wide by 1.2 mm thick with a weight of approximately 0.11 g. Adult otolith samples were pooled into age groups based on break-and-burn age or whole otolith weight and cored to the size and weight of a 3-year otolith. Coring of adult otoliths was performed by hand-grinding to core dimensions on a Buehler Ecomet III lapping wheel with 320 grit silicon-carbide paper. The contribution of each adult fish to a group varied based on sample availability; (*1*) where pooled sample weight was sufficient, only the unbroken otolith was used; and (*2*) where pooled sample weight was insufficient, either the unbroken otolith and the unburned half of the aged otolith were used or both whole otoliths (juvenile and high otolith weight groups) were used. Radiometric analysis of the age groups involved the use of well-established protocols; the activity of ^{210}Pb and ^{226}Ra was determined via alpha-spectrometry and thermal ionization mass spectrometry (TIMS) respectively (Andrews *et al*. 1999*b*).

Break-and-burn age estimates and their respective whole otolith weights were compared before conducting radiometric analyses. A large range and variation in otolith weight was observed for otoliths with middle and older age estimates. Age determination using the break-and-burn technique, therefore, may not be an effective discriminating tool for pooling otoliths into age groups (i.e. estimates could be incorrect) for radiometric age determination. To better elucidate true age and minimise potential errors owing to pooling otoliths into age groups, break-and-burn age estimates and/or whole otolith weight were the criteria considered for pooling adult otoliths.

Otoliths were pooled into 12 samples, which were organised into three thematic sets (four groups each) based on several criteria: (*1*) juvenile surface age estimates (groups A–D); (*2*) low and high otolith weight groups for adult samples with similar break-and-burn estimated age (groups E–H); and (*3*) high whole otolith weight for presumably the oldest adults (groups I–L). Typically, lead–radium studies require approximately 1 g of otolith material based on the usual levels of ^{226}Ra encountered in previous studies (Andrews *et al.* 1999*b*); hence, pooled samples are necessary to acquire measurable ^{210}Pb and ^{226}Ra activities. Age-group sets were analysed consecutively, in a step-wise manner, to better determine the composition of the next set of samples. First, whole juvenile otoliths were analysed to determine the baseline activity levels of ^{210}Pb and ^{226}Ra (groups A–D). Second, a set of otoliths was selected based on similar break-and-burn age estimates with a broad variation in otolith weight. Within that set, four groups were formed (two male and two female); two of which were 'low' otolith weight and two were 'high' otolith weight (groups E–H). This approach was used to elucidate potential differences in age that may not have been detected in the traditional ageing procedures.

Finally, based on the results from the first and second age group sets, whole otolith weight (rather than age) was used to pool otoliths for the third set of samples. High otolith weight groups (two male and two female) were formed to assess maximum age; assuming whole otolith weight could be related to age (groups I–L). In these groups, both otoliths from each fish (when available) were used for radiometric age determination to increase sample weight and total sample activity. Otoliths that had the highest weight were selected to form these groups. Once enough otoliths were selected to form approximately 1 g of cored material for males and females, a second set was selected from the next largest otoliths. To increase the sample weight, the collection period (initially only 1983) for these groups was expanded to include 1984. This approach was used as a last effort to determine a maximum age based on the observation that estimated age from growth zone counts appeared to be underestimating actual age in the second thematic set of otolith groups. To proceed, we needed to assume the heaviest otoliths would come from the oldest fish and that existing ageing methodologies could not determine valid estimates of age.

Radiometric age was determined by using the measured $^{210}\mathrm{Pb}:{}^{226}\mathrm{Ra}$ activity ratios as an independent indicator of age. The error and analytical uncertainty was propagated through to the final radiometric age, resulting in a radiometric age range. This age range was compared with the growth-zone derived age range (groups A–H) to determine the accuracy of growth-zone derived age estimates. For the high otolith weight groups, the radiometric age was simply determined and considered relative to estimates of longevity from other studies.

Bomb radiocarbon

Otoliths from female bocaccio rockfish were selected from the archive at the National Marine Fishery Service, Santa Cruz Laboratory. In addition, a coast-wide search was made for large otoliths from bocaccio collected elsewhere to increase the chances that we had the largest and presumably oldest fish available. The result of this search was otoliths from two additional fish collected by the Department of Fisheries and Oceans, Nanaimo, British Columbia, Canada (collection year, 2002). The criterion for search and selection was the highest otolith weight attainable from a series of collection years dating from close to present day to as far back as possible. Because age determined from otolith growth zone counts seemed unreliable, the approach was to assume the heaviest otoliths represented the oldest fish. By analysing otoliths of this nature for ^{14}C in the core material dating back as far as possible, we posited that eventually we would see a reduction in measured ^{14}C from post-bomb to pre-bomb levels; hence, relating these Δ^{14}C measurements to a reference time-series would give an indication of age and perhaps longevity.

Ten otoliths from fish collected along the central California coast and two otoliths collected from fish off British Columbia were used in the ^{14}C analyses. These otoliths were the heaviest available from the largest female bocaccio (females are known to attain a larger size than males; MacCall 2003*a*). Birth years were not estimated initially; only otolith weight was used as a proxy for the assumption that the oldest fish were represented by the heaviest otoliths. This is not the typical approach; usually, age is estimated in some manner (e.g. growth zone counts) and a birth year is assigned. Conformity of these dates with the reference time-series created by the atmospheric detonation of thermonuclear weapons is typically used to determine the validity of the age estimates. In this case, because age estimation from growth zone counts seemed unreliable, we measured ^{14}C levels first, and then looked for conformity to the Δ^{14}C reference time-series. For the present study, we used the previously determined yelloweye rockfish (*Sebastes ruberrimus*) ^{14}C record (Kerr *et al.* 2004*a*). Use of this time-series as a reference tool was further supported by the determinations made for a fish from a similar region, the Pacific halibut (*Hippoglossus stenolepis*; Piner and Wischniowski 2004). Use of these time-series makes the assumption that ^{14}C levels in the Gulf of Alaska were similar to the coastal waters of central California, a factor discussed later.

The core of each otolith, which constituted less than the first year of growth, was analysed for ^{14}C because it is known that at least the first year's growth was formed while the fish inhabited the ocean mixed layer. This technique is most reliable for fishes that inhabit the surface mixed layer of the ocean, at least during a portion of their life history. Uncertainty regarding mixing rate at depth and limited data on the Δ^{14}C signal in deeper waters make it difficult to use this technique for organisms that live below the mixed layer throughout their lives (Kalish 2001).

The average length and width, and maximum thickness of this first year's growth was determined by using an Olympus dissecting microscope (Tokyo) from whole and sectioned otoliths from juvenile and adult bocaccio. Extracted cores were well within these measurements using a milling machine with a 3.2 mm (1/8′) diameter end mill. Visual alignment of the milling machine bit with the centre of the distal side of the otolith allowed for correction owing to the individual variability; the first year's growth was easily recognisable because more recent accretion on the distal surface was negligible. Coring produced small powdered samples that were weighed to the nearest 0.1 mg. For ^{14}C analysis, otolith calcium carbonate ($CaCO_3$) was converted to pure carbon in the form of graphite and measured for ^{14}C content using accelerator mass spectrometry (AMS) at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, California, USA. The ^{14}C values were reported as Δ^{14}C (Stuvier and Polach 1977).

The Δ^{14}C values measured in bocaccio rockfish otolith cores were plotted with respect to corresponding collection year and projected to the yelloweye rockfish time-series to estimate a birth year range, effectively establishing a minimum longevity. Blind retrospective ageing (i.e. without knowing details about fish size, date of capture, etc.) of these otoliths was performed by reading a thin transverse section from the remaining otolith of the pair. Agreement of the estimated age range determined from the reference time-series with the section ages was used to demonstrate age confirmation and the potential utility of age determination using transverse otolith sections for bocaccio rockfish.

Results

^{210}Pb and ^{226}Ra disequilibria

Total sample weights for the age groups ranged from 0.8315 to 1.8165 g and were composed of otolith material from six to 12 fish (Table 1). To increase the sample weight of five groups, the unburned portion of the aged otolith was cored and used in addition to the unaged otolith (e.g. group E consisted of 10 otoliths, that included four unburned portions, from six fish). The total lengths of fish used ranged from 296 mm, in a juvenile group, to 824 mm in a large adult group; however, fish length was not available for all otoliths used.

The first thematic set (juveniles, groups A–D) had low ^{210}Pb activities that ranged from $0.0044 \pm 17\%$ to $0.0049 \pm 17\%$ dpm g^{-1}, except one sample that had very high activity (Table 2). This sample was suspected of having ^{210}Pb or ^{210}Po contamination because of the unusually high activity (group C, $0.424 \pm 4.0\%$ dpm g^{-1}). This was attributed to a few dirty otoliths that were permeated with an organic material from adhering tissue on the uncored otolith, staining it orange. As a result, otoliths with this kind of staining were avoided in the samples that followed.

The measured ratios of ^{210}Pb : ^{226}Ra were relatively high for juvenile samples; however, this was expected because of the large amount of time that had elapsed since capture (15–16 years). Once age was calculated and corrected for this elapsed time, the radiometric age of the juvenile samples was reasonable. For the three samples that had ratios between 0 and 1, two radiometric ages were close to what was expected (groups A and D) and one was slightly lower (group B). Negative age calculated for some groups can be considered age zero. The wide margin of error is a result of the very low activities, approaching background levels. Typically, an initial uptake ratio (R_0) can be determined from

Table 1. Data for pooled otolith groups for bocaccio rockfish

Age range of age groups was based on the break-and-burn method for age estimation. Capture date ranges are listed with the time span. Total length ranges are listed for fish with data available (number of fish noted in parentheses). The number of otoliths and otolith portions used in each sample are listed with the number of fish and, in some cases, the number of unburned half otoliths in parentheses (fish, half otoliths). The sample weight is the total weight of the pooled otolith sample after cleaning

Group label	Age group (years)	Average age (years)	Sex	Capture date range (span years)	Total length (mm)	No. otoliths	Sample weight (g)
A	2–3	2.5	♂	1/13–7/13/83 (0.50)	296–401	16 (8)	1.1437
B	2–3	2.9	♀	1/13–5/26/83 (0.36)	384–426 (6)	14 (7)	1.2461
C	5	5.0	♂	1/4–7/14/83 (0.52)	442–505 (6)	15 (10)	1.0923
D	6	6.0	♀	4/18–10/3/83 (0.46)	482–567 (4)	20 (12)	1.8165
E	12–15	13.3	♀	8/16–11/4/83 (0.22)	NA	10 (6, 4)	0.8315
F	12–15	14.0	♀	5/9–10/27/83 (0.47)	680–765 (5)	12 (7, 5)	1.0930
G	12–16	13.4	♂	7/21–10/12/83 (0.23)	570–640 (3)	17 (9, 8)	1.4618
H	13–16	14.4	♂	7/20–10/14/83 (0.24)	591–681 (5)	12 (8, 4)	1.0903
I	NA[A]	NA	♀	5/15–12/5/84 (0.56)	715–791	11 (6)	1.2856
J	NA[A]	NA	♀	5/6/83–8/4/84 (1.25)	744–824 (6)	12 (7)	1.3372
K	NA[A]	NA	♂	5/10–10/12/84 (0.42)	591–698	12 (6)	1.2536
L	NA[A]	NA	♂	8/24/83–10/12/84 (1.13)	642–687 (3)	10 (6, 3)	0.8803

[A] Estimated age not used as a consideration for grouping based on observations discussed in the text. NA, Not available.

Table 2. Radiometric results for the first thematic set

Juvenile age groups were analysed first to determine baseline levels of ^{210}Pb and ^{226}Ra. Activities are expressed as disintegrations per minute per gram (dpm g^{-1}). The measured activity ratio of ^{210}Pb : ^{226}Ra was used to determine the overall age of the sample, which was corrected for elapsed time between collection and sample processing (15–16 years)

Group label	Age (years)	Average age (years)	Sex	^{210}Pb (dpm g^{-1}) ± % error[A]	^{226}Ra (dpm g^{-1}) ± % error[B]	^{210}Pb : ^{226}Ra activity ratio	Radiometric age (years)	Radiometric age range (years)
A	2–3	2.5	♂	0.0049 ± 17	0.0111 ± 1.5	0.44	4	0 to 9
B	2–3	2.9	♀	0.0044 ± 17	0.0137 ± 1.4	0.32	−2[C]	−4 to 1
C	5	5.0	♂	0.424 ± 4.0	0.0128 ± 2.0	33.1	NA[D]	
D	6	6.0	♀	0.0049 ± 14	0.0123 ± 2.0	0.40	3	0 to 7

[A] Calculation based on standard deviation of ^{210}Pb activity and incorporation of background count uncertainty using the delta method; [B] Calculation based on TIMS analysis routine (± 1 s.e.) and the delta method; [C] Sample activity may have been too low to effectively separate from background; [D] Possible sample contamination resulted in a ratio greatly exceeding 1.0. NA, Not applicable.

the baseline determinations of the juvenile age groups. In this case, we found that the results were quite variable and, therefore, assumed the initial uptake ratio was zero.

The second thematic set (low and high otolith weight groups of similar growth-zone derived age, groups E–H) had ^{210}Pb activities that were slightly higher than the juvenile samples, as was expected relative to the fairly consistent radium levels measured thus far (Table 3). Low otolith weight groups (groups E and G) had radiometric ages that were younger than the high otolith weight groups (groups F and H). The two low weight age groups had a radiometric age range that broadly (as a result of low activity) encompassed the growth zone derived ages. The high weight groups had radiometric ages that were older than the growth zone derived age; hence age was underestimated for these samples by using the break-and-burn method. The apparent trend of increasing age with increasing otolith weight led to the otolith weight-based thematic set of samples.

The third thematic set (high whole otolith weight set representing presumably the oldest fish, groups I–L) had ^{210}Pb activities that varied considerably relative to the fairly consistent radium levels (Table 4), resulting in quite variable radiometric ages. Unexpectedly, none of the groups in this set produced the highest radiometric ages of the study. More unexpected was that the group with the heaviest otolith weights (group J) ended up having the lowest radiometric age of 11 years (range of 5–19 years) among the adult samples in the present study. All samples again had a broad range of radiometric age because of low activity.

Overall, the activity of ^{226}Ra was fairly constant and, as expected, ^{210}Pb activity was variable. The activity of ^{226}Ra ranged from 0.00871 ± 1.5 to 0.0148 ± 1.5% dpm g^{-1} with an average of 0.0115 ± 17% dpm g^{-1} (s.d. of the sample set). The error associated with the ^{226}Ra analyses was low and ranged from 1.1 to 3.3% (s.e. of the measurement precision), where 31 to 223 ratios were measured in the TIMS analysis routine and 20–69% of the measured radium-226 was from the sample material. Activity of ^{210}Pb was very low and near the detection limits of the alpha-spectrometer. The 11 samples ranged from 0.0044 ± 17 to 0.012 ± 14% dpm g^{-1}. The error associated with the ^{210}Pb analysis was relatively high because of the very low activity and ranged from 14 to 23%

Table 3. Radiometric results for the second thematic set

Low and high otolith weight groups for adult samples, with similar break-and-burn age, composed the groups within this thematic set. Breaks in the otolith weight range were arbitrarily chosen to separate the age groups (approximately 12 to 16 years for each sex) into relatively low weight (E and G) and relatively high weight (F and H) groups. Activities are expressed as disintegrations per minute per gram (dpm g^{-1}). The measured activity ratio of ^{210}Pb : ^{226}Ra was used to determine the overall age of the sample, which was corrected for elapsed time between collection and sample processing (15–16 years)

Group label	Age group (years)	Average age (years)	Sex	Otolith weight range (g)	Average otolith weight (g)	^{210}Pb (dpm g^{-1}) ± % error[A]	^{226}Ra (dpm g^{-1}) ± % error[B]	^{210}Pb : ^{226}Ra	Radiometric age (years)	Radiometric age range (years)
E	12–15	13.3	♀	0.259–0.313	0.282	0.0068 ± 23	0.0120 ± 1.7	0.57	13	4 to 25
F	12–15	14.0	♀	0.321–0.354	0.340	0.0096 ± 16	0.0105 ± 1.8	0.91	65	31 to undef.[C]
G	12–16	13.4	♂	0.241–0.278	0.264	0.0068 ± 15	0.0102 ± 3.3	0.67	21	11 to 36
H	13–16	14.4	♂	0.282–0.311	0.294	0.012 ± 14	0.0148 ± 1.5	0.81	36	21 to 65

[A]Calculation based on standard deviation of ^{210}Pb activity and incorporation of background count uncertainty using the delta method; [B]Calculation based on TIMS analysis routine (± 1 s.e.) and the delta method; [C]Analytical uncertainty caused the upper limit to exceed 1.0, therefore, the upper radiometric age range is undefined.

Table 4. Radiometric results for the third thematic set

High whole otolith weight presumably represented the oldest adults in this sample set. Activities are expressed as disintegrations per minute per gram (dpm g^{-1}). The measured activity ratio for ^{210}Pb : ^{226}Ra was used to determine the overall age of the sample, which was corrected for elapsed time between collection and sample processing (15–16 years)

Group label	Sex	Otolith weight range (g)	Average otolith weight (g)	^{210}Pb (dpm g^{-1}) ± % error[A]	^{226}Ra (dpm g^{-1}) ± % error[B]	^{210}Pb : ^{226}Ra activity ratio	Radiometric age (years)	Radiometric age range (years)
I	♀	0.361–0.388	0.374	0.0067 ± 18	0.00953 ± 1.4	0.70	25	13 to 45
J	♀	0.379–0.421	0.403	0.0055 ± 16	0.0101 ± 1.7	0.54	11	5 to 19
K	♂	0.284–0.315	0.301	0.0054 ± 17	0.00871 ± 1.5	0.62	18	9 to 30
L	♂	0.319–0.390	0.348	0.010 ± 14	0.0129 ± 1.1	0.78	34	20 to 58

[A]Calculation based on s.d. of ^{210}Pb activity and incorporation of background count uncertainty using the delta method; [B]Calculation based on TIMS analysis routine (± 1 s.e.) and the delta method.

Table 5. Otolith and fish data for fish collected from 1983 to 2002
Average otolith weight is derived from the weight of both sagittal otoliths for each fish. Mass is the amount of core material extracted from the otolith. The corresponding radiocarbon and stable carbon levels from accelerator mass spectrometry are listed

Collection year	Fish length (FL mm)	Average otolith weight (g)	Mass (mg)	Δ^{14}C (‰)	s.d.	δ^{13}C (‰)[A]
1983	821	0.387	6.00	−69.3	3.2	−3.2
1985	816	0.392	7.63	5.5	3.5	−3.4
1987	840	0.450	6.00	−72.1	3.2	−3.2
1989	818	0.378	5.26	65.8	3.7	−3.3
1992	775	0.381	4.97	45.8	3.6	−4.2
1996	754	0.400	4.86	28.4	3.6	−4.0
1997	760	0.402	7.86	5.4	3.6	−3.2
1998	763	0.385	8.35	41.7	5.2	−3.9
2000	732	0.333	6.87	52.5	3.7	−3.3
2001	763	0.452	4.89	45.3	3.0	−4.3
2002*a*	810	0.404	5.35	58.7	3.7	−4.3
2002*b*	860	0.517	6.10	52.5	3.7	−4.4

[A] Measured sample values with respect to Pee Dee Belemnite (Stuvier and Polach 1977).

(s.d. including background count uncertainty), excluding one outlier (group C). Count times to minimise this error were high and ranged from 27 to 63 days. The oldest radiometric age for each sex for the present study was 65 years (range of 31 years to an undefined age) for a female group and 36 years (range of 21 to 65 years) for a male group.

Bomb radiocarbon

Radiocarbon was determined for the largest female fishes with the heaviest otoliths, collected from 1983 to 2002 (Table 5). Fish lengths ranged from 732 to 860 mm SL (standard length) with otolith weights remaining relatively high for all fish and ranging from 0.333 in 2000 to 0.517 in 2002. Core extractions were consistent and small, ranging from 4.86 to 8.35 mg. As expected, the ^{14}C levels for otoliths from earlier collection years tended to be lower than those of otoliths from more recent years.

Based on the projection of the ^{14}C values from the collection year to the yelloweye rockfish time-series for samples at the extremes of the distribution (Fig. 1), a reference time-series birth year range was estimated (Table 6). This was done for the extremes of the distribution in terms of ^{14}C levels and collection date. The birth year ranges that were possible from the rise and decline of the yelloweye rockfish time-series ranged from as early as 1956 to as late as the collection year itself. Ages estimated from these possible birth years ranged from 0 to approximately 37 years.

The retrospective blind age estimations from transverse sections ranged from 16 ± 4 to 37 ± 2 years (Table 6). Growth zones in some transverse sections were quite clear and easy to read (Fig. 2), contrary to that reported for the break-and-burn technique. Growth zone age estimates were in agreement for four fish, in agreement within the age uncertainty for two fish, and low by approximately 5–7 years for two fish. For the 1985 and 1997 samples, where two age ranges were possible, the high age range for both samples was in agreement. These findings were exemplified by the concordance of the data with the yelloweye rockfish time-series, and further supported by data recently collected for the Pacific halibut (Fig. 3; Piner and Wischniowski 2004). The agreement was good and the distribution of post-peak age estimates that did not agree with the yelloweye rockfish time-series were better represented by the Pacific halibut distribution. If these age data were taken into consideration with otolith weight, there was a trend of increasing age with increasing otolith weight (age = 145 (otolith weight) −36; $R^2 = 0.76$), and a scattered relationship for fish length relative to age (Table 7).

Discussion

^{210}Pb and ^{226}Ra disequilibria

The values and ranges of measured ^{226}Ra activity in the otoliths of bocaccio were among the lowest observed in the literature (Kastelle and Forsberg 2002). Lower activities were reported for whole otoliths (as low as 0.004 dpm g^{-1}), but these values were from an unsuccessful application of the method to the blue grenadier (*Macruronus novaezelandiae*, Family Merlucciidae; Fenton *et al.* 1990). The lowest ^{226}Ra activity reported in a successful application was 0.0179 dpm g^{-1} in a follow-up study of the blue grenadier, in which otolith cores were used instead of whole otoliths (Fenton and Short 1995). The results of the present study range from slightly lower (0.0148 dpm g^{-1}) to approximately two times lower (0.00871 dpm g^{-1}) than that of the blue grenadier. However, this factor had little effect on the capability of TIMS to detect radium, as indicated by the low error associated with these measurements (1.1 to 3.3%).

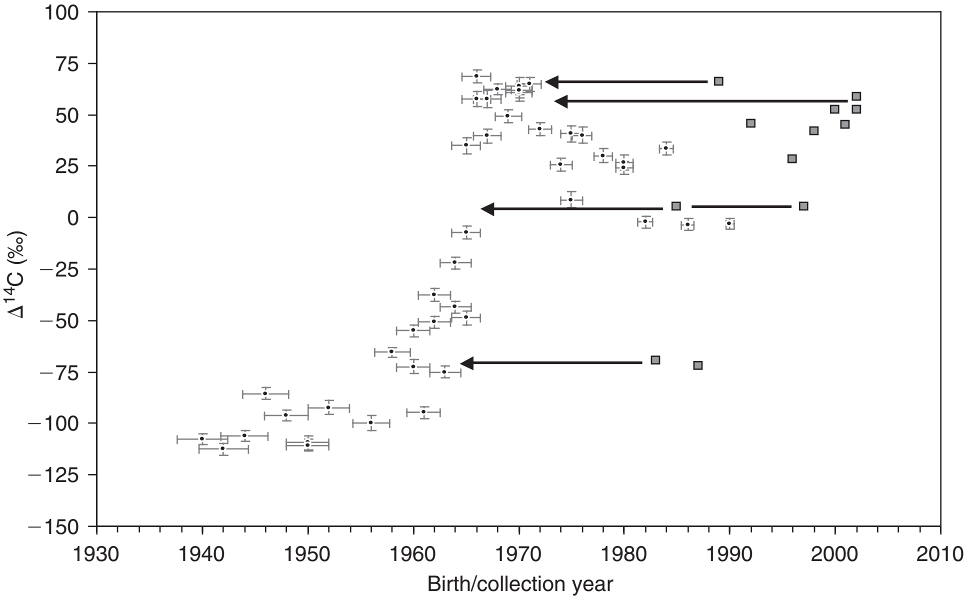

Fig. 1. Plot of measured Δ^{14}C levels in otolith cores of bocaccio rockfish with respect to the collection date (grey squares). To estimate a birth year for selected bocaccio collection dates, the yelloweye rockfish reference time-series (black dots) was used as a chronological reference for the measured Δ^{14}C levels. Error bars represent the analytical uncertainty of the Δ^{14}C measurements and the potential range for the birth date of the yelloweye rockfish used in the chronology. The arrows pointing left indicate the region of the yelloweye time-series where an estimate of the birth year range was determined. The difference between the collection year and the birth year range was used as an estimate of age range for each sample.

Table 6. Age estimates for bocaccio from the yelloweye reference time-series

Ages were determined from the yelloweye rockfish reference time-series by projecting the measured radiocarbon levels back to the reference time-series and estimating a range of birth years (Fig. 1); the difference between collection date and birth years resulted in an estimated age range. The otolith remaining from each fish was used, in retrospect, for 'blind' age estimation using transverse sections and to check for agreement

Collection year	Reference time-series birth year range	Age range from reference time-series (years)	Section age and range (± 1 s.d.)
1983	1956–1963	20–27	21 ± 1 years
1985	1975–1985 or 1964–1966[A]	0–10 or 19–21[A]	19 ± 2 years
1987	1956–1963	24–31	26 ± 1 years
1989	1965–1972	17–24	16 ± 4 years
1997	1967–1975 or 1964–1966[A]	10–22 or 31–33[A]	29 ± 3 years
2000	1965–1975	35–25	18 ± 2 years
2002*a*	1965–1972	30–37	22 ± 2 years
2002*b*	1965–1972	30–37	37 ± 2 years

[A] Two ranges because the possibilities include the timing of the rise and post-bomb decline in radiocarbon values.

The greatest effect of low ^{226}Ra activity values was on the determination of ^{210}Pb activity from ingrowth. Because bocaccio can attain ages that were estimated to be only slightly greater than one ^{210}Pb half-life (22.26 years), the activity of ^{210}Pb was expected to be approximately half the level of ^{226}Ra activity. This posed real challenges for alpha-spectrometric determination of ^{210}Po, detected as a proxy for ^{210}Pb, because the resultant activity of ^{210}Po was close to detection limits. The most active samples (estimated to be the oldest) had alpha-spectrometer counts that were only 3.6 to 4.4 counts per day, where an estimated 26–36% of these counts were from background counts. Based on the McCroan/MARLAP/ISO Decision Rule, the counts were significantly above background (Strom and MacLellan 2001)

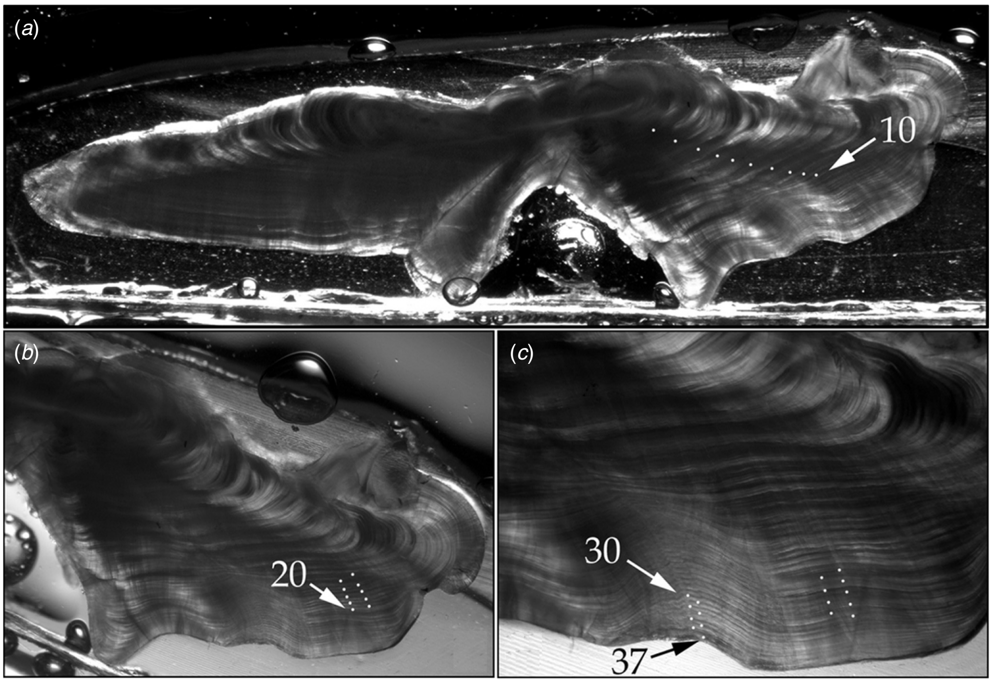

Fig. 2. From our retrospective 'blind' age estimation performed on the remaining otolith of the pair using transverse sectioning and growth zone counts, this otolith section, shown at three successively greater magnifications (A–C, 10×–32×) was collected in 2002 and was the oldest fish aged (37 ± 2 years).

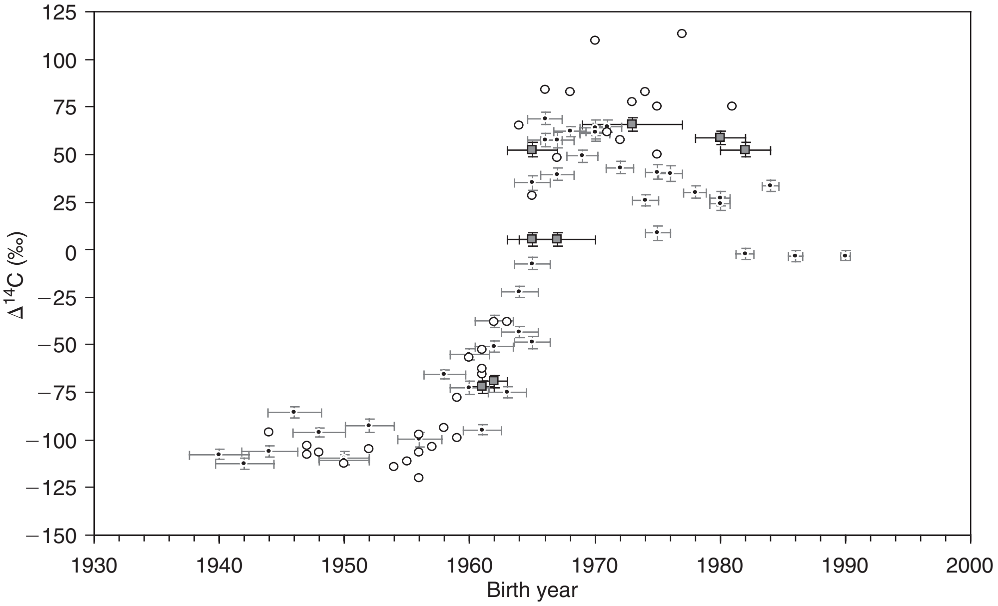

Fig. 3. Plot of measured Δ^{14}C values for the bocaccio otoliths with respect to the estimated age from growth zone counts (grey squares). The horizontal error bars represent the standard deviation (s.d.) of the age estimates with highest confidence. Note there is strong agreement with the estimated birth year determinations made earlier relative to the yelloweye rockfish reference time-series (black dots), with the exception of the post-bomb decline. The addition of Pacific halibut data (*Hippoglossus stenolepis*; Piner and Wischniowski 2004) strengthens the utility of the bomb radiocarbon chronology in this region (open circles). Note that the pre-bomb levels, time of first increase, and the slope of the rise are concordant between the yelloweye rockfish and the Pacific halibut. Only the post-bomb Δ^{14}C values differ in magnitude, and it is interesting to note that the bocaccio post-bomb levels appear to be in better agreement with the Pacific halibut record.

Table 7. Otolith and fish data for fish collected between 1983 and 2002

Average otolith weight was derived from the weight of both sagittal otoliths for each fish. Age estimates from growth zone counts, and the associated range of counts with the highest confidence, are given for otoliths that were sectioned after $\Delta^{14}C$ analyses. Aged samples were selected to cover the earliest to latest collection dates and the lowest to highest $\Delta^{14}C$ values

Collection year	Fish length (FL mm)	Average otolith weight (g)	Section age and range (± 1 s.d.)	Estimated age range (years)
1983	821	0.387	21 ± 1.3	20–22
1985	816	0.392	19 ± 1.7	18–22
1987	840	0.450	26 ± 0.8	25–27
1989	818	0.378	16 ± 4.0	12–20
1992	775	0.381	Not aged[A]	–
1996	754	0.400	Not aged[A]	–
1997	760	0.402	29 ± 2.7	27–33
1998	763	0.385	Not aged[A]	–
2000	732	0.333	18 ± 1.9	16–20
2001	763	0.452	Not aged[A]	–
2002*a*	810	0.404	22 ± 1.5	20–24
2002*b*	860	0.517	37 ± 2.0	33–39

[A] These otoliths were not section aged because we concentrated on the extremes of the collection and $\Delta^{14}C$ distribution.

but the low count rates increased the dependence of error on the background variability resulting in wide ranging age determinations.

One remedy for the low activity problem would be to increase sample size, but this increases the potential variation in the age of the pooled sample, which was already high. In addition, sample availability for any given collection year was low for the largest, and presumably oldest, bocaccio. In contrast, the Atlantic tarpon (*Megalops atlanticus*) was successfully aged and its longevity determined using single otoliths (Andrews *et al.* 2001). This was possible because ^{226}Ra activity was up to 27 times higher in Atlantic tarpon otoliths (0.401 dpm g^{-1}). As a consequence, ^{210}Pb activity was much higher and the error associated with background variability was negligible.

The results for the juvenile and young samples (groups A–D) indicated there was little concern for exogenous ^{210}Pb incorporation in the otoliths of bocaccio. Other studies have indicated that exogenous ^{210}Pb was a problem in poorly calcified structures like elasmobranch vertebrae and sturgeon fin rays (Welden *et al.* 1987; Burton *et al.* 1999), but it does not appear to be a major factor in otoliths (Smith *et al.* 1995; Andrews *et al.* 1999*a*).

Analysis of the second thematic set of four age groups (groups E–H), in which growth zone-derived ages were similar (12–16 years) and otolith weights varied considerably, indicated that otolith weight was related to age. This is similar to recent results for the blackgill rockfish (*Sebastes melanostomus*; Stevens *et al.* 2004). Both of the low weight groups (groups E and G) had estimated ages within the margin of uncertainty of the radiometric ages, indicating the age estimates may be correct; however, the high weight groups (groups F and H) had radiometric ages that clearly indicated age was underestimated for those fish when the break-and-burn technique was used. The groups were older by at least 7 years (group H) and at least 17 years (group F) based on the low end of the radiometric age range. Based on this observation, the next set of four samples was grouped based on otolith weight, with an attempt to age the largest, and presumably oldest, bocaccio (groups I–L).

Radiometric ages for the final thematic set of four groups (groups I–L) did not follow the expected weight-to-age trend for the female groups, but were in fairly close agreement for the male groups. The sample with the highest otolith weight range was a female group with an unexpectedly low radiometric age of 11 years (range of 5–19 years). However, if we subjectively remove this sample from consideration because it deviates from what is expected (assuming there was a problem with the sample), there is a general increase in radiometric age with otolith weight.

Because of the low precision of the radiometric results, we can only make rough conclusions about age and the ageing methodology. Despite the large uncertainty in the radiometric determinations, it is certain that age was underestimated in some cases that used the break-and-burn method. In a study of routine ageing of bocaccio otoliths using the break-and-burn method, disparities as high as 19 years were revealed between readers (Don Pearson, NOAA, NMFS, Santa Cruz, California, USA, personal communication). As an ancillary part of the project, we took a small set of otoliths that ranged from young to old, based on break-and-burn ages, and transversely sectioned the remaining otoliths. The transverse sections were typically aged older. Based on other rockfish ageing studies, in which age agreement between break-and-burn and sectioning techniques was good (Andrews *et al.* 2002; Stevens *et al.* 2004), it is clear there is a problem with age estimation when the break-and-burn method is used for bocaccio. Furthermore, the otoliths from three known-age bocaccio raised in the Monterey Bay Aquarium, Monterey, California, USA, were aged by transverse sectioning. The estimated age based on growth zone counts was highly uncertain for these 8-year-old fish because of the difficulty of determining the first few years of growth and in deciding whether to split or lump some of the finer zones. Despite the problems with ageing the otoliths using traditional growth-zone-based techniques, we can use the low end of the age range determined from the radiometric uncertainty to conclude that bocaccio can reach an age of at least 31 years. The low precision of these findings led to the follow-up study using the time-specific bomb ^{14}C chronometer to elucidate the age of bocaccio.

Bomb radiocarbon

The optimal sampling strategy for this approach would have been to acquire the heaviest otoliths from the largest female fish with collection dates ranging back to the mid-1970s to better ascertain the pre-bomb (~pre-1958) levels of Δ^{14}C for bocaccio otoliths. Because it is reasonably certain that these large female fish with heavy otoliths were at least 20 years old, establishing a firm series of otoliths with levels that can be qualified as pre-bomb would have made for better certainty on the minimum age without having to consider otolith growth zone counts. As the present study stands, we could only assume that the data were approaching pre-bomb levels in two of the samples (collection dates 1983 and 1987). This assumption was probably valid based on the graphical comparison of the pre-bomb levels measured for yelloweye rockfish and Pacific halibut; both species have similar pre-bomb levels, averaging just below $-100‰$ Δ^{14}C. These relatively low pre-bomb Δ^{14}C values for the coastal north-eastern Pacific waters are generally ascribed to the influence of ^{14}C depleted deeper waters upwelling in the coastal regions (Druffel and Williams 1991; Kerr *et al.* 2004*a*, 2004*b*).

By projecting the measured Δ^{14}C data points to a reference time-series, we can obtain information about sample age and potential longevity. In our study, comparing the bocaccio Δ^{14}C data to the yelloweye rockfish and Pacific halibut reference time-series made the assumption that ^{14}C levels available to the bocaccio collected off central California were similar to the waters of the Gulf of Alaska. Currently, there are no chronological time-series for Δ^{14}C off California, but there is evidence from seawater and organismal studies that indicate it is likely that that pre-bomb Δ^{14}C levels were lower in the Gulf of Alaska than for the central coast of California and sites further south in the California Current (Druffel and Williams 1991). The average Δ^{14}C value for museum bivalve specimens collected at locations along the central California coast, ranging from Stinson Beach to Carmel Bay, was $-84.2 \pm 3.7‰$ with a high of $-75.9 \pm 6.3‰$ at Carmel Bay (Ingram and Southon 1996). Hence, it is possible that the bocaccio otoliths with the lowest Δ^{14}C values (-72.1 ± 3.2 and $-69.3 \pm 3.2‰$) do represent pre-bomb levels and could be found to be much older than estimated using the yelloweye reference time-series. It is the retrospective age estimation from growth zone counts, however, that make a strong argument that these samples reside at the very beginning of the rise in ^{14}C and that age can be accurately determined from growth zones in transverse sections.

The timing of peak ^{14}C values can be offset by a few years, and the maximum peak value is often different from species to species because of regional differences in oceanography. This is demonstrated by Pacific halibut and quillback rockfish; Δ^{14}C values that range higher than, and do not drop as quickly as, the yelloweye rockfish record (Kerr *et al.* 2004*b*). The Δ^{14}C values that were measured for birth dates that were younger than expected (samples 2000 and 2002*a*), relative to the yelloweye rockfish time-series, can be explained by regional or species-related variation in the post-bomb decline. The age and corresponding birth dates are almost certainly accurate for these samples, even though they are in disagreement with what was expected from the yelloweye rockfish time-series. Despite these uncertainties, the distribution of the retrospective ages relative to the measured Δ^{14}C values for bocaccio provides strong support for age estimation using transverse sections and a longevity of at least 37 ± 2 years (Fig. 3).

Conclusions

The lead–radium dating in the present study demonstrates the dependence of the technique on sample mass, coupled with radium-226 activity. This application pushed the limits to a point where results were of marginal use. When considering an application of the lead–radium technique to any given species, probably the most important factor is the uptake of radium-226 and its activity relative to sample weight. In this case, the activity of radium-226 was very low, which was exacerbated by low sample availability in old ages. This was further complicated by the lack of well-defined age reading criteria; confidence in the age estimates was low for the otoliths used in the age groups of the present study. However, within the constraints of analytical uncertainty, we could conclude from lead–radium dating that the minimum age that bocaccio can attain is approximately 31 years.

The bomb ^{14}C technique provided the age resolution that we had hoped for with the lead–radium dating. A few otoliths, well placed in time, were all that was required to answer the question of bocaccio longevity. From the results of the present study, there is strong support for developing an age reading criteria based on thin transverse otolith sections, and it is certain that bocaccio longevity is at least 37 ± 2 years.

The age findings in the present study emphasise the requirement for standardised ageing criteria and provide a valid age basis for stock assessment modelling. An interagency decision needs to be made regarding either: (*1*) calibration of the break-and-burn technique relative to section age determination; or (*2*) resort to ageing strictly with transverse sections. Clearly, the longevity of bocaccio exceeds the early estimates on the order of 20 years, not surprisingly invalidating some of the older techniques used to estimate age for the largest fish. Retrospective examination of archival otoliths used to determine age through the history of the bocaccio fishery may be required to better understand how age structure has changed over time.

The longevity of the bocaccio is moderate relative to other rockfishes, but recent findings emphasise the importance of determining longevity and maintaining the age structure of a population. It is common to find that modelling and management of fisheries focuses on sustainability of biomass, with little or no regard to the possible long-term effects of fishing down age and genetic structure (Hauser *et al.* 2002; Berkeley *et al.* 2004*a*). It is a common trait among rockfishes that fecundity drastically increases with increasing size and age, and this is exemplified by the extreme fecundity of large bocaccio (Love *et al.* 2002). In addition, recent findings indicate that older fish can produce better offspring, which has been documented for the rockfishes by the black rockfish (*Sebastes melanops*) where growth rates and survivorship were drastically higher for adult fish with greater age (Berkeley *et al.* 2004*b*; Palumbi 2004). Clearly, the importance of accurate age determination over the time of fishery exploitation must not be underestimated and that harvest refugia may be the only recourse in providing for the recovery of the bocaccio rockfish fishery.

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References

Andrews, A. H., Cailliet, G. M., and Coale, K. H. (1999*a*). Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1339–1350. doi:10.1139/CJFAS-56-8-1339

Andrews, A. H., Coale, K. H., Nowicki, J. L., Lundstrom, C., Palacz, Z., Burton, E. J., and Cailliet, G. M. (1999*b*). Application of an ion-exchange separation technique and thermal ionization mass spectrometry to ^{226}Ra determination in otoliths for radiometric age determination of long-lived fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1329–1338. doi:10.1139/CJFAS-56-8-1329

Andrews, A. H., Burton, E. J., Coale, K. H., Cailliet, G. M., and Crabtree, R. E. (2001). Radiometric age validation of Atlantic tarpon, *Megalops atlanticus. Fishery Bulletin* **99**, 389–398.

Andrews, A. H., Cailliet, G. M., Coale, K. H., Munk, K. M., Mahoney, M. M., and O'Connell, V. M. (2002). Radiometric age validation of the yelloweye rockfish (*Sebastes ruberrimus*) from southeastern Alaska. *Marine and Freshwater Research* **53**, 139–146. doi:10.1071/MF01126

Beamish, R. J. (1979). New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *Journal of Fisheries Research Board of Canada* **36**, 1395–1400.

Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. (2004*a*). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**(8), 23–32.

Berkeley, S. A., Chapman, C., and Sogard, S. M. (2004*b*). Maternal age as a determinant of larval growth and survival in marine fish, *Sebastes melanops. Ecology* **85**, 1258–1264.

Burton, E. J., Andrews, A. H., Coale, K. H., and Cailliet, G. M. (1999). Application of radiometric age determination to three long-lived fishes using ^{210}Pb:^{226}Ra disequilibria in calcified structures: A review. In 'Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals'. (Ed. J. A. Musick.) pp. 77–87. (American Fisheries Society Symposium 23: Bethesda, MD.)

Cailliet, G. M., Andrews, A. H., Burton, E. J., Watters, D. L., Kline, D. E., and Ferry-Graham, L. A. (2001). Age determination and validation studies of marine fishes: do deep-dwellers live longer? *Experimental Gerontology* **36**, 739–764. doi:10.1016/S0531-5565(00)00239-4

Campana, S. E., Zwanenburg, K. C., and Smith, J. N. (1990). ^{210}Pb/^{226}Ra determination of longevity in redfish. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 163–165.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197–242. doi:10.1111/J.1095-8649.2001.TB00127.X

CARE (2000). Manual on the generalized age determination procedures for groundfish. Prepared by: Committee of age reading experts: Pacific coast groundfish ageing technician. Pacific States Marine Fisheries Commission, Portland, OR.

Druffel, E. R. M., and Williams, P. M. (1991). Radiocarbon in seawater and organisms from the Pacific coast of Baja California. *Radiocarbon* **33**, 291–296.

Fenton, G. E., Ritz, D. A., and Short, S. A. (1990). ^{210}Pb/^{226}Ra disequilibria in otoliths of blue grenadier, *Macruronus novaezelandiae*; problems associated with radiometric ageing. *Australian Journal of Marine and Freshwater Research* **41**, 467–473.

Fenton, G. E., and Short, S. A. (1995). Radiometric analysis of blue grenadier, *Macruronus novaezelandiae*, otolith cores. *Fishery Bulletin* **93**, 391–396.

Hauser, L., Adcock, G. J., Smith, P. J., Bernal Ramirez, J. H., and Carvalho, G. R. (2002). Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences of the United States of America* **99**, 11 742–11 747. doi:10.1073/PNAS.172242899

Ingram, B. L., and Southon, J. R. (1996). Reservoir ages in eastern Pacific coastal and estuarine waters. *Radiocarbon* **38**, 573–582.

Kalish, J. M. (2001). Use of the bomb radiocarbon chronometer to validate fish age. Final Report FRDC Project 93/109. Fisheries Research and Development Corporation, Canberra, Australia.

Kastelle, C. R., Kimura, D. K., and Jay, S. R. (2000). Using ^{210}Pb/^{226}Ra disequilibrium to validate conventional ages in scorpaenids (genera *Sebastes* and *Sebastolobus*). *Fisheries Research* **46**, 299–312. doi:10.1016/S0165-7836(00)00155-7

Kastelle, C. R., and Forsberg, J. E. (2002). Testing for loss of ^{222}Rn from Pacific halibut (*Hippoglossus stenolepis*) otoliths. *Fisheries Research* **57**, 93–98. doi:10.1016/S0165-7836(01)00339-3

Kerr, L. A., Andrews, A. H., Frantz, B. R., Coale, K. H., Brown, T. A., and Cailliet, G. M. (2004*a*). Radiocarbon in otoliths of yelloweye rockfish (*Sebastes ruberrimus*): a reference time series for the coastal waters of southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 443–451. doi:10.1139/F04-009

Kerr, L. A., Andrews, A. H., Frantz, B. R., Coale, K. H., Brown, T. A., Munk, K., and Cailliet, G. M. (2004*b*). Age validation of quillback rockfish (*Sebastes maliger*) using bomb radiocarbon. *Fishery Bulletin* **103**, 97–107.

Love, M. S., Yoklavich, M., and Thorsteinson, L. (2002). 'The Rockfishes of the Northeast Pacific'. (University of California Press: Berkeley, CA.)

MacCall, A. D., Ralston, S., Pearson, D., and Williams, E. (1999). Status of bocaccio off California in 1999 and outlook for the next millennium. In 'Status of Pacific Coast Groundfish Fishery through 1999 and Recommended Acceptable Biological Catches for 2000: Stock Assessment and Fishery Evaluation.' (Pacific Fisheries Management Council: Portland.)

MacCall, A. D. (2003*a*). 'Status of Bocaccio Off California in 2003.' (Santa Cruz Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service: Santa Cruz.)

MacCall, A. D. (2003*b*). Bocaccio rebuilding analysis for 2003. In 'Status of the Pacific Coast Groundfish Fishery Through 2003 Stock Assessment and Fishery Evaluation: Volume 1'. (Pacific Fishery Management Council: Portland.)

Mason, J. E. (1998). Declining rockfish lengths in Monterey Bay, California, recreational fishery, 1959–94. *Marine Fisheries Review* **60**, 15–28.

Munk, K. M. (2001). Maximum ages of groundfishes in waters off Alaska and British Columbia and considerations of age determination. *Alaska Fisheries Research Bulletin* **8**, 12–21.

National Marine Fisheries Service (1999). 'Report to Congress: Status of Fisheries of the United States.' (Washington, DC.)

Palumbi, S. R. (2004). Why mothers matter. *Nature* **430**, 621–622. doi:10.1038/430621A

Phillips, J. B. (1964). Life history studies on ten species of rockfish (genus *Sebastodes*). California Department of Fish and Game, Fish Bulletin No. 126.

Piner, K. R., and Wischniowski, S. G. (2004). Pacific halibut chronology of bomb radiocarbon in otoliths from 1941 to 1981 and a validation of ageing methods. *Journal of Fish Biology* **64**, 1060–1071. doi:10.1111/J.1095-8649.2004.0371.X

Ralston, S. (1999). Trend in standardized catch rate of some rockfishes (*Sebastes* spp.) from the California trawl logbook database. NMFS Santa Cruz/Tiburon Laboratory Administration Report, SC-99-01.

Ralston, S., and Ianelli, J. N. (1998). When lengths are better than ages: the complex case of bocaccio. In 'Fishery Stock Assessment Models'. (Eds F. Funk, T. J. Quinn II, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C.-I. Zhang.) pp. 451–468. (Alaska Sea Grant College Program No. AK-SG-98–01, University of Alaska: Fairbanks.)

Ralston, S., Ianelli, J. N., Miller, R. A., Pearson, D. E., Thomas, D., and Wilkins, M. E. (1996). Status of bocaccio in the Conception/Monterey/Eureka INPAC areas in 1996 and recommendations for management in 1997. Appendix B: Status of the Pacific Coast groundfish fishery through 1996 and recommended biological catches from 1997, stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland.

Smith, D. C., Fenton, G. E., Robertson, S. G., and Short, S. A. (1995). Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 391–401.

Stanley, R. D., Starr, P., and Olsen, N. (2004). Bocaccio update. Research document 2004/027. Canadian Science Advisory Secretariat. Fisheries and Oceans Canada, Nanaimo, British Columbia.

Starr, R. M., Cope, J. M., and Kerr, L. A. (2002). Trends in fisheries and fishery resources associated with the Monterey Bay National Marine Sanctuary from 1981–2000. Publication number T-046. California Sea Grant College Program. University of California, La Jolla.

Stevens, M. M., Andrews, A. H., Cailliet, G. M., Coale, K. H., and Lundstrom, C. C. (2004). Radiometric validation of age, growth, and longevity for the blackgill rockfish, *Sebastes melanostomus*. *Fishery Bulletin* **102**, 711–722.

Strom, D. J., and MacLellan, J. A. (2001). Evaluation of eight decision rules for low-level radioactivity counting. *Health Physics* **81**, 27–34. doi:10.1097/00004032-200107000-00005

Stuvier, M., and Polach, H. A. (1977). Discussion: reporting of ^{14}C data. *Radiocarbon* **19**, 355–363.

Welden, B. A., Cailliet, G. M., and Flegal, A. R. (1987). Comparison of radiometric vertebral band age estimates in four California elasmobranchs. In 'The Age and Growth of Fish'. (Eds R. C. Summerfelt and G. E. Hall.) pp. 301–315. (Iowa State University Press: Ames.)

Westrheim, S. J., and Harling, W. R. (1975). Age-length relationships for 26 scorpaenids in the Northeastern Pacific Ocean. Technical report number 565. Department of the Environment, Fisheries and Marine Service, Nanaimo, Canada.

Wilkins, M. E. (1980). Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. *Marine Fisheries Review* **42**, 64–73.

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