Radiometric validation of age, growth, and longevity for the blackgill rockfish (*Sebastes melanostomus*)

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Abstract—As nearshore fish populations decline, many commercial fishermen have shifted fishing effort to deeper continental slope habitats to target fishes for which biological information is limited. One such fishery that developed in the northeastern Pacific Ocean in the early 1980s was for the blackgill rockfish (*Sebastes melanostomus*), a deep-dwelling (300–800 m) species that congregates over rocky pinnacles, mainly from southern California to southern Oregon. Growth zone-derived age estimates from otolith thin sections were compared to ages obtained from the radioactive disequilibria of ^{210}Pb, in relation to its parent, ^{226}Ra, in otolith cores of blackgill rockfish. Age estimates were validated up to 41 years, and a strong pattern of agreement supported a longevity exceeding 90 years. Age and length data fitted to the von Bertalanffy growth function indicated that blackgill rockfish are slow-growing (k=0.040 females, 0.068 males) and that females grow slower than males, but reach a greater length. Age at 50% maturity, derived from previously published length-at-maturity estimates, was 17 years for males and 21 years for females. The results of this study agree with general life history traits already recognized for many *Sebastes* species, such as long life, slow growth, and late age at maturation. These traits may undermine the sustainability of blackgill rockfish populations when heavy fishing pressure, such as that which occurred in the 1980s, is applied.

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The blackgill rockfish (*Sebastes melanostomus*) is a deep-water rockfish that is found mainly along the continental slope between 300 and 800 m depth off central and southern California (Moser and Ahlstrom, 1978; Cross, 1987; Williams and Ralston, 2002). Although not as heavily targeted in relation to other commercially important rockfish species, a directed commercial fishery for blackgill rockfish has existed since the mid-1970s, beginning off southern California (Point Conception area) and spreading northward (Monterey area) as stocks of other heavily fished rockfishes declined (Butler et al., 1999). Using acoustic sonar and set nets, the commercial fleet was able to catch large aggregations of previously unexploited blackgill rockfish. Landings peaked in 1983 with 1346 metric tons (t) caught coast-wide, but declined over the next decade, presumably because of the disappearance of the large concentrations that could be located with acoustical gear (Butler et al., 1999). In 2001, 141 t were reportedly landed along the entire west coast (PacFIN[1])—less than half of the allowable catch (343 t; NOAA, 2001) for blackgill rockfish that year.

The first stock assessment of blackgill rockfish was made by Butler et al. (1999). One objective of this assessment was to determine age and growth characteristics, which were then applied to estimate age-at-maturity, natural mortality, and stock biomass. Using conventional aging methods (i.e., otolith increments), we estimated that blackgill rockfish live at least 87 years and reach full (100%) maturity from 13 to 26 years for females, and from 13 to 24 years for males. Although such estimates are useful and should be considered whenever available, validation of the age-estimation procedure is needed to be certain of accurate age estimates (Beamish and McFarlane, 1983; Campana, 2001). Inaccurate age determinations in some cases have led to overharvesting of stocks such as Pacific ocean perch (*Sebastes alutus*)

[1] PacFIN (Pacific Fisheries Information Network). 2002. Commercial fisheries landing data. http://www.PacFIN.org. [Accessed 9 August 2002].

and orange roughy (*Hoplostethus atlanticus*; Beamish, 1979; Archibald et al., 1983; Mace et al., 1990). These historical examples of fishery collapses necessitate that age validation be achieved before age and growth information is applied to management.

In the last decade, radiometric age validation has been applied successfully to over 20 species of rockfishes and other marine teleosts (Burton et al., 1999; Kastelle et al., 2000; Andrews et al., 2002). The most common technique uses the disequilibria between two radioisotopes, radium-226 (^{226}Ra) and lead-210 (^{210}Pb), present in the otolith (Bennett et al., 1982; Smith et al., 1991). Radium-226 is a naturally occurring radioisotope and calcium analogue that is incorporated from the surrounding seawater into the aragonitic crystalline matrix of fish otoliths. Radium-226 decays through a series of short-lived radioisotopes to ^{210}Pb. Because the half-lives of these isotopes are known, the ratio of activity between them (^{210}Pb:^{226}Ra) gives a measure of elapsed time since the initial incorporation of ^{226}Ra into the otolith (Campana et al., 1990). Radium-226 decays very slowly (a 1600 year half-life) in relation to ^{210}Pb (a 22 year half-life), allowing the activity ratio of these radioisotopes to build into secular equilibrium (1:1 ratio; Smith et al., 1991). Based on this relationship (also referred to as ingrowth), the ^{210}Pb: ^{226}Ra activity ratio is suitable for age determination in fishes up to 5 half-lives of ^{210}Pb, or approximately 120 years of age (Andrews et al., 1999b; Campana, 2001). This approach is therefore ideally suited to the blackgill rockfish, whose longevity has been estimated at almost 90 years (Butler et al., 1999).

The objectives of this study were 1) to estimate age from otolith growth zone counts, 2) to describe growth, and 3) to validate the annual periodicity of growth zones used to estimate longevity for the blackgill rockfish with the radiometric aging technique. An ancillary objective was to create a reliable predictive relationship between average otolith weight and estimated age for use as a timesaving tool in the management of this species. Growth zones quantified in sectioned otoliths were used to estimate age, and growth was described by using the von Bertalanffy growth function. Final age estimates were directly compared to radiometric ages to evaluate agreement between the two methods and ultimately were used to validate age estimation procedures, age-at-maturity, and longevity for this species.

Materials and methods

Approximately 1210 blackgill rockfish sagittal otoliths were available for this study. Otoliths were collected by National Marine Fisheries Service (NMFS) personnel from commercial vessels in 1985 at ports along the California coastline (Long Beach to Fort Bragg), and during NMFS research surveys from 1998 to 2000 from central California to the Oregon-Washington border. Thirty-two juvenile blackgill rockfish, collected from spot prawn traps along the central California coast, were provided by Robert Lea of the California Department of Fish and Game (CDFG). Fish total length (TL; cm or mm), catch area (port or geographic location), and otolith weights (right and left, 1985 samples only) were provided. Otoliths were first considered for age estimation (sectioning), and the remainder were reserved for radiometric analysis. Otolith weights (left and right, male and female) were measured to the nearest milligram and compared with *t*-tests to determine if significant differences in mass existed between sides or sexes.

Estimation of age and growth

Based on previous aging studies and the need to conserve samples for radiometric analysis, approximately 310 otoliths (25% of the collection) were assumed to be sufficient for age estimation. The left otolith from 5 to 30 fish, depending upon the number available in each 50-mm size class (ranging from 100 mm to 600 mm), was randomly chosen by using a basic resampling tool. Otoliths were thin-sectioned and mounted onto glass slides. Approximately 50 otoliths were damaged in the sectioning process, leaving 260 otoliths available for age estimation.

Sections were viewed by three readers under magnification (25 and 40×) with transmitted or reflected light. Each reader obtained age estimates by inspecting all available growth axes, choosing the most discernible axis, and reading it three times consecutively. A growth zone (here termed an “annulus”) was defined as one pair of translucent (winter-forming) and opaque (summer-forming) bands. A final age, based on each reader’s most confident estimate, was chosen. Precision between and within readers was compared by using average percent error (APE; Beamish and Fournier, 1981), index of precision (D) and coefficient of variation (CV; Chang, 1982). Percent agreement among readers was also calculated. Reader 1 (author) determined the final age estimate for each section as described in Mahoney (2002). Ages that could not be confidently resolved (through re-examination or discussion) were removed from analysis.

Length and age estimates for males, females, and sexes combined were fitted to the von Bertalanffy growth function (VBGF). A small portion of juvenile samples (n=16) were included in each function. Because there was strong agreement between facility aging techniques (MLML and NMFS, La Jolla, Butler et al. 1999), additional aged samples were added to strengthen the VBGF and age prediction models (n=119). Estimates of age at first, 50%, and 100% maturity were calculated by inserting existing size at maturity data (Echeverria, 1987) into the VBGF and solving for age (t).

Age prediction, age group determination, and core extraction

Campana et al. (1990) was the first to circumvent the assumption of constant ^{226}Ra uptake throughout the life of the fish by eliminating younger growth layers from adult otoliths, leaving just the oldest layers of otolith growth (i.e., the core, representing the first few years of life). Radium-226 is present at such low activity levels, however, that many otolith cores from fish of a similar age and same sex must be pooled to acquire the mass of material needed for detection (~0.5 to 1 gram; Andrews et al., 1999a, 1999b). Because we possessed a limited number of blackgill rockfish otoliths (~1200), an age prediction model was created to conserve otolith material for radiometric analysis. It was appropriate to assume from the results of Francis (2003) that within-sample heterogeneity with respect to otolith age and mass growth rate was negligible in the core material.

To determine age groups for radiometric analyses, final ages for fish whose otoliths were sectioned, along with their corresponding average otolith weight (left and right, n=2), were used to predict age for the remaining fish in the collection. Several parameters were regressed to determine a predictive relationship between average otolith weight (henceforth termed "otolith weight") and estimated age (i.e., section age). The following regressions were compared to estimated age by using Kruskal-Wallis (nonnormal) ANOVA: 1) otolith weight (to the nearest 0.001 g), 2) otolith weight and fish length (to the nearest 1 mm), and 3) otolith weight plus otolith length (to the nearest 0.001 mm) multiplied by otolith weight (as an interaction term). A power function was also investigated but did not result in a better fit than that provided by a simple linear regression (either log-transformed or normal). A paired sample t-test and student's t-test for slopes were used to determine if a significant difference existed between male and female otolith weight, and between male and female otolith weight-to-age regressions, respectfully. The final regression equations were applied to the average otolith weight for all individual remaining fish to obtain a predicted age. Age groups were created if there was sufficient otolith material from fish of the same sex and of a similar predicted age.

The predicted age range for each group was kept as narrow as possible while permitting enough material for analysis; approximately 25 to 50 otoliths were needed at a target core weight of 0.02 g. Fish that had both otoliths intact (not sectioned or broken) were preferred to reduce the number of fish for each radiometric sample. To better insure sample conformity, 90% confidence intervals with respect to fish length and otolith weight were used to eliminate from each group dissimilar fish that may have varied significantly from predicted age. In addition to this discriminating technique, groups were further confined by capture year and location. Only samples caught in the same year and similar geographic location (based on the majority of port locations within 300 miles) were included in the same group.

Core size was determined by viewing several whole juvenile blackgill rockfish otoliths with estimated ages between 1 and 7 years. The first annulus was determined to be approximately 2 mm wide, and a 3-year-old otolith was measured at 3 mm wide, 4 mm long, and 1 mm thick, and having a weight of 0.02 g. These dimensions were chosen as the target core size because a core of this size could be easily extracted, yet was young enough to minimize the possible error associated with variable ^{226}Ra uptake in the first few years of growth. Otoliths from adult fish were ground down to the target core size with a lapping wheel and 80- to 120-grit silicon-carbide paper. Otoliths from selected juveniles, if older than age 3 (core size), were also ground to the target core size.

Radiometric analysis

The radiometric analysis was conducted as described in Andrews et al. (1999a, 1999b). Because previous studies have revealed extremely low levels of ^{210}Pb and ^{226}Ra in otolith samples, trace metal precautions were employed throughout sample cleaning and processing (Bennett et al., 1982; Campana et al., 1990; Andrews et al.,1999a). Acids were double distilled (GFS Chemicals®, Powell, OH) and all dilutions were made using Millipore® filtered Milli-Q water (18 MΩ/cm). Samples were thoroughly cleaned, dried, and weighed to the nearest 0.0001 g prior to dissolution. Whole juvenile otoliths groups were analyzed first to determine if exogenous ^{210}Pb was a significant factor, and to determine baseline levels of ^{226}Ra activity.

Because of the low-level detection problems associated with (beta) β-decay of ^{210}Pb, the activity ^{210}Pb was quantified through the autodeposition and (alpha) α-spectrometric determination of its daughter proxy, polonium-210 (^{210}Po, half-life=138 days; Flynn, 1968). In preparation for ^{210}Po analysis, samples were dissolved in acid and spiked with a calibrated yield tracer, ^{208}Po, estimated to be 5 times the activity of ^{210}Po in the otolith sample. Polonium isotopes from the sample were autodeposited onto a purified silver planchet (A.F. Murphy Die and Machine Co., North Quincy, MA) held in a rotating Teflon™ holder over a 4-hour period (Flynn, 1968). The activity of ^{208}Po and ^{210}Po on the planchets was measured with ion-implant detectors in a Tennelec (Oak Ridge, TN) TC256 α-spectrometer interfaced with a multichannel analyzer and an eight channel digital multiplexer. Counts were recorded with Nucleus® software (Nucleus Personal Computer Analyzer II, The Nucleus Inc., Oak Ridge, TN) on an IBM computer. Counts measured over periods that ranged from 28 to 50 days accumulated from 160 to 919 total counts. Lead-210 activity, along with uncertainty, was calculated in a series of equations that corrected for background and reagent counts, as well as error associated with count statistics and procedure (pipetting error, yield-tracer uncertainty, etc; Andrews et al., 1999a). The remaining sample was dried and conserved for ^{226}Ra analysis.

Determination of ^{226}Ra employed an elemental separation procedure followed by isotope-dilution thermal ionization mass spectrometry (TIMS) as described in Andrews et al. (1999a, 1999b). The sample was spiked with a known amount of ^{228}Ra yield tracer estimated to produce a ^{226}Ra:^{228}Ra atom ratio close to one. The samples were dissolved in strong acid and dried repeatedly (~90–100°C) until the sample color was bright white, indicating that most organic material had been removed. A three-step elemental separation procedure was used to remove calcium and barium, elements that interfere with the detection of radium in the TIMS process. This involved passing the samples through three cation exchange columns, two containing a slurry of BioRad AG® 50W-X8 resin (first and second column), and one containing EiChroM Sr® resin (third column). The samples were introduced to a highly acidic medium within the columns, which separated the elements according to elution characteristics (Andrews et al., 1999b).

Radiometric age for each group was determined by inserting the measured ^{210}Pb and ^{226}Ra activities into the secular equilibrium model (Smith et al., 1991) and correcting for the elapsed time between capture and autodeposition. Because these activities were measured from the same sample, the calculation was independent of sample mass (Andrews et al., 1999a, 1999b). Propagated uncertainty associated with the final ^{210}Pb activity was based on count statistics, and procedural error and uncertainty for the final ^{226}Ra activity was based on procedural error and an instrumental TIMS analysis routine (Wang et al., 1975; Andrews et al., 1999b). The combined errors were used to calculate high and low radiometric ages.

Accuracy of age estimates

Measured ^{210}Pb:^{226}Ra activity ratios for each age group, along with their total sample age (predicted age + time since capture), were plotted with the expected ^{210}Pb:^{226}Ra growth curve. Each age group range was widened by multiplying the minimum and maximum age in the range by the age estimate CV, which was determined from the variability in age estimates among three readers. Agreement between the measured ratio with respect to estimated age and the expected ratio (ingrowth curve) provided an indication of the age estimate accuracy. Radiometric age was compared to the average predicted age for each group by using two tests: 1) a paired sample t-test to determine if a significant difference existed between the two age estimates for the groups and 2) predicted age was plotted against radiometric age and the correlation was compared to a hypothetical agreement line (slope of 1) by using t-tests for slope and elevation.

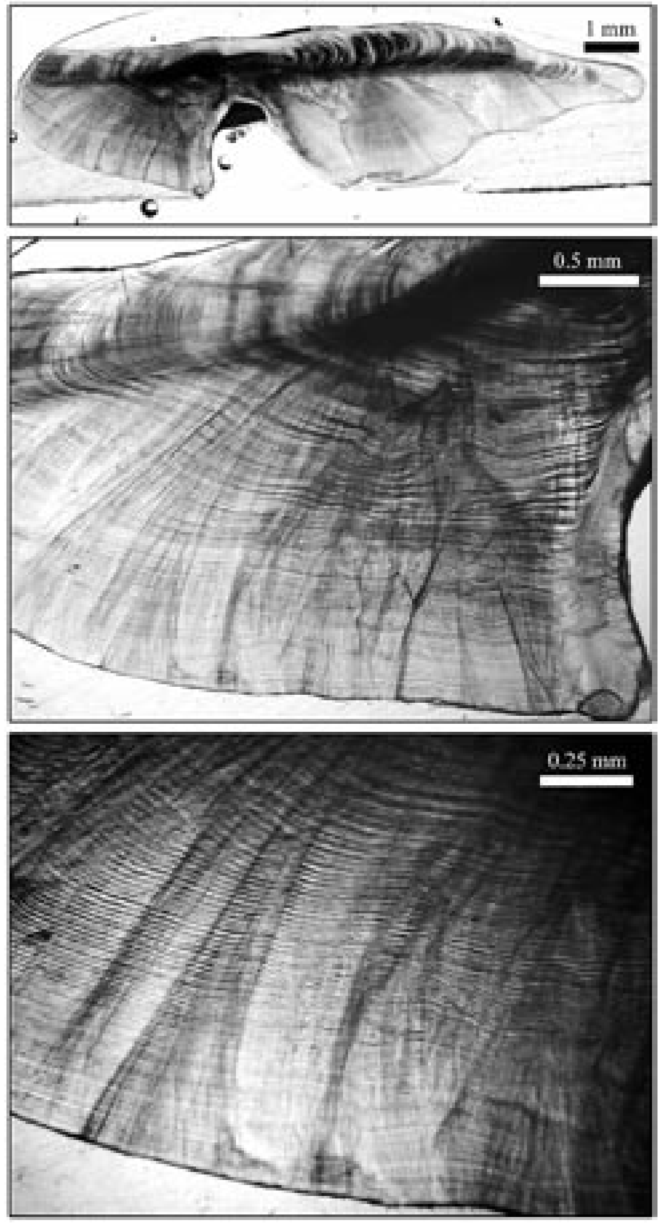

Figure 1

Three images of a blackgill rockfish (*Sebastes melanostomus*) otolith section viewed with transmitted light at 25× magnification (top), 40× (center), and 80× magnification (bottom). This section was aged most consistently as 90 years under a microscope, but because of finer digital resolution and contrast, the section pictured can be aged as high as 102 years.

Results

Estimation of age and growth

Growth zones observed within otolith sections of most blackgill rockfish were difficult to interpret. Distinction of the first annulus was often ambiguous, and the banding pattern during the first several years (1 to ~10) of growth was, in some sections, wide and inconsistent. After approximately 8 to 12 growth zones, the zone width transitioned to a narrower zone, which became extremely compressed after 20–40 growth zones. In some sections, these older zones were beyond optical resolution, whereas in others they were remarkably clear (Fig. 1).

Table 1

Comparison of von Bertalanffy growth function parameters for this study and Butler et al. (1999; in parentheses), for combined sexes, females, and males. All lengths are total lengths (mm). Note that the sample size for females and males does not sum to 332 because the same juvenile samples (n=16) were used for each sex, and only once for combined sexes. N.R.= not reported.

	Combined sexes	Females	Males
L_∞ (mm)	509 (524[1])	548 (554[1])	448 (467[1])
95% CI	491–528 (N.R.)	520–576 (N.R.)	434–462 (N.R.)
k	0.045 (0.040)	0.040 (0.040)	0.068 (0.060)
95% CI	0.038–0.052	0.033–0.047	0.058–0.078
t_0	−4.86 (−5.02)	−4.49 (−4.66)	−2.37 (−2.98)
95% CI	−6.60 to −3.12	−6.30 to −2.67	−3.55 to −1.19
n	332 (335)	181 (98)	167 (78)
r^2	0.81 (0.79)	0.87 (0.90)	0.87 (0.92)

[1] Total lengths from some samples in Butler et al., 1999 were estimated from fork length (FL in mm) by using an equation from Echeverria and Lenarz (1984).

The most consistent axis in the otolith section for which confident interpretations could be made was along either the sulcus ridge, or along the dorsoventral margin. Final age estimates were resolved for 197 fish, or approximately 76% of the 260 successfully sectioned otoliths. Agreement among readers was relatively low: approximately 24% of age estimates were within ±1 year, 61% were within ±5 years, and 87% were within ±10 years. The mean difference in age estimates between readers was 2.9 ±4.0 years. Among the three readers, APE was 10.7%, D was 8.4%, and CV was 14.6%. Average percent error, D, and CV estimates were comparable within readers; reader 1 APE was 5.2%, D was 4.1%, and CV was 7.0%. The two oldest fish to be aged were a 90-year-old male (450 mm TL) collected in 1999 and an 87-year-old female (546 mm TL) collected in 1985. Both individuals were caught south of Point Conception, California.

The VBGF fitted to age and length data resulted in distinct growth curves for male and female blackgill rockfish (Fig. 2). This difference is also represented by non-overlapping confidence intervals with respect to the primary VBGF parameters (L_∞, k; Table 1). The growth coefficient, k, ranged from 0.040 (±0.007, female) to 0.068 (±0.010, male), and asymptotic length was 448 ±14 mm for males to 548 ±28 mm for females. The asymptotic length for females was 32 mm less than the largest female fish sampled (580 mm TL), and for males, was 74 mm less than the largest male sampled (522 mm TL). The fit for all three functions was satisfactory (r^2=0.81, 0.87; Table 1, Fig. 2). Estimated ages at first, 50%, and 100% maturity, derived from inserting published estimates of length-at-maturity (Echeverria, 1987) into the growth model for each sex, were 15, 21, and 22 years for females and 13, 17, and 28 years for males (Table 2).

Table 2

Age at maturity estimates, in years, for male and female blackgill rockfish (95% confidence intervals are in parentheses). Maturity estimates were derived by inserting published estimates of length at maturity into the von Bertalanffy growth function.

	First maturity	50% maturity	100% maturity
Females	15 (12–22)	21 (16–31)	22 (17–33)
Length at maturity[1] (mm)	300	350	360
Males	13 (11–15)	17 (14–20)	27 (22–35)
Length at maturity[1] (mm)	290	330	390

[1] Echeverria (1987).

Age prediction, age group determination, and core extraction

A paired sample t-test indicated that there was a significant difference between male and female average otolith weight (t=4.54, P<0.001), and a student's t-test for slopes indicated a significant difference between male and female average otolith weight-to-age regressions (t_{crit}=1.967, t=2.87, P<0.05). Therefore, male and female age estimates and regressions were treated separately. There was no statistical difference between regressions involving fish length and average otolith weight (Kruskal-Wallis one-way ANOVA on ranks, H=4.834, P=0.089). A simple linear regression, with average otolith weight as the independent variable and estimated age as the dependent variable, was sufficient to predict age. Log normalizing the regressions to stabilize the variance in older age estimates was unsuccessful (Cochran's test: α=0.05, 36 df, C=0.4748, P=0.486). The final regressions are given in Figure 3.

Fourteen age groups based on the predicted ages of unsectioned otoliths were chosen. These groups consisted of four juvenile groups, and five male and five female adult groups (Table 3). Fish lengths ranged from 82 mm to 580 mm TL, and predicted age ranged from 1 to 69 years. The number of otolith cores per age group ranged from 11 to 59, representing 7 to 32 fish per group. Total sample weight for each age group ranged from 0.4649 g to 1.6424 g. Whole otolith weight ranged from 0.041 to 0.842 g, and average individual core weight for the adult age groups ranged from 0.025 g to 0.028 g. The process of extracting the core inadvertently destroyed some otoliths in the grinding process, leading to smaller samples for some groups.

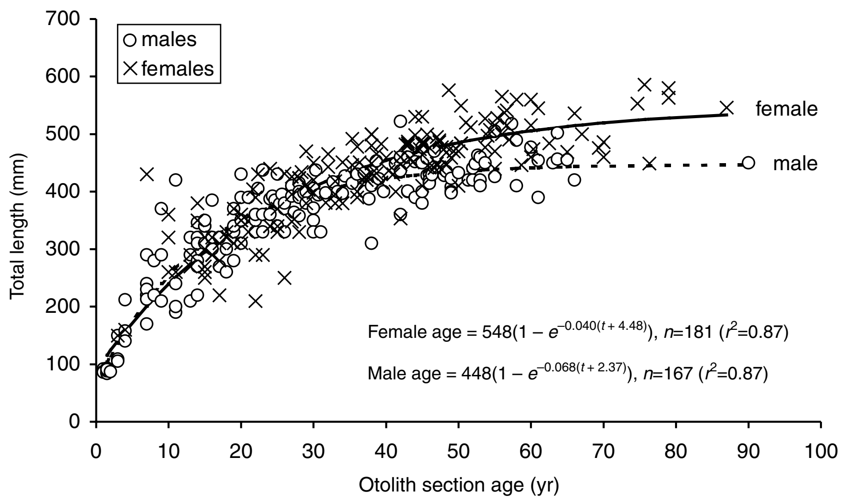

Figure 2

Blackgill rockfish (*Sebastes melanostomus*) von Bertalanffy growth functions plotted for males and females. Observed and expected values, as well as the parameters of the equations, are given. Note that the same juvenile samples (n=16) were included in both male and female equations.

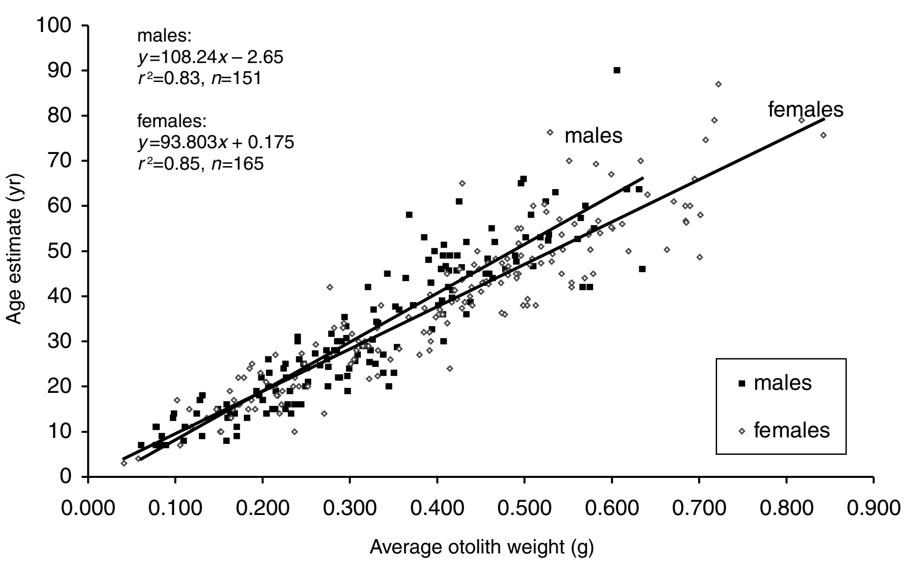

Figure 3

Predictive relationship between average otolith weight and estimated age for blackgill rockfish (*Sebastes melanostomus*). These regression equations were used to predict the age of fish whose otoliths were reserved for radiometric analysis.

Radiometric analysis

Radiometric analysis of all age groups (n=14) resulted in the successful determination of ^{210}Pb activity for all samples, and limited success for ^{226}Ra (Table 4). Activities of ^{210}Pb increased, as expected, fivefold from juvenile to adult age groups, and ranged from near 0.01 dpm/g for the juvenile samples to over 0.05 dpm/g for the oldest age groups. Error associated with these measurements ranged from 3.7 to 9.2 % (1s). The detection of ^{226}Ra activity was met with some technical difficulties. Because of poor radium recovery, radium measurements were unreliable in three samples and radium was lost in four samples. Therefore, an average of the reliable ^{226}Ra measurements was used because of the relative consistency of levels measured in these samples (0.0643 ±0.0035 dpm/g, n=7). The use of a single estimate for ^{226}Ra activity was acceptable prior to refinement of the technique (Andrews et al., 1999b). Calculated ^{210}Pb:^{226}Ra ratios increased as expected from 0.172 to 0.845 and 0.912 for the oldest groups (Table 4).

Age estimate accuracy

Radiometric ages were in agreement with predicted ages, as evidenced by concordance of ^{210}Pb:^{226}Ra activity

Table 3

Summary data for 14 pooled otolith age groups of blackgill rockfish. The age range and sample weight of each age group was based on the age prediction model and otolith availability. Groups were confined by year of capture, and for the 1985 samples, by port location. Mean total length (±1 standard deviation) of individuals per group is provided, along with the number of fish and otoliths, total sample weight, and average core weight.

Sample number	Age group (yr)	Sex	Capture year	Mean length $\pm\sigma$ (TL mm)	Number of fish,[1] number of otoliths	Sample weight (g)	Avg. core weight (g)
BG1	1–3	Juvenile	1998	154 ±26	7, 11[2]	0.4649	0.042
BG2	4	Juvenile	1998	200 ±8	10, 8[2]	1.1687	0.065
BG3	4–5	Juvenile	1999	217 ±9	15,19[2]	1.6630	0.088
BG4	1–7	Juvenile	2000	119 ±37	25, 36[2]	0.7854	0.022
BG5	29–31	Female	1985	400 ±20	25, 46	1.2510	0.027
BG6	26–28	Male	1985	379 ±19	22, 35	0.8866	0.025
BG7	11–17	Female	1998	276 ±20	22, 33	0.9018	0.027
BG8	39–41	Female	1985	458 ±22	31, 53	1.3332	0.025
BG9	48–54	Male	1985	459 ±21	25, 48	1.2491	0.026
BG10	60–69	Female	1985	525 ±30	19, 30	0.8254	0.028
BG11	19–23	Male	1998	329 ±16	21, 39	1.0313	0.026
BG12	56–59	Female	1985	502 ±28	13, 25	0.6989	0.028
BG13	39–41	Male	1985	428 ±24	31, 59	1.6424	0.028
BG14	42–47	Male	1998	423 ±26	32, 54	1.4267	0.026

[1] Both otoliths were not available for every fish chosen.

[2] Whole juvenile otoliths.

Table 4

Summary of radiometric results for pooled otolith age groups. Samples are listed in order of increasing age-group range. Activities are expressed as disintegrations per minute, per gram (dpm/g). Radium-226 activity was averaged among samples with low analytical error (<10%; n=7) and was determined to be 0.0643 (±0.0035) dpm/g. This value was then applied to all samples to gain an estimate of ^{226}Ra activity and radiometric age. Agreement between radiometric age and predicted age was qualified by the degree of overlap between the two age ranges. Radiometric age incorporates the time between capture and analysis.

Sample number	^{210}Pb activity (dpm/g) ±%s[1]	^{210}Pb:^{226}Ra activity ratio	Radiometric age (yr)	Radiometric age range (yr)	Predicted age group range[2]	Average age[3] (yr)	Age range agreement[4]
BG1	0.0154 ±8.6	0.234	7.1	5.4–8.7	0–3	2	Exceeds
BG2	0.0124 ±6.7	0.193	5.5	4.3–6.5	4–5	4	Overlaps
BG3	0.0118 ±5.5	0.184	5.5	4.5–6.4	4–6	4.5	Overlaps
BG4	0.0111 ±9.2	0.172	6.0	5.3–6.7	0–8	3.5	Encompasses
BG7	0.0300 ±5.6	0.467	18.0	15.2–21.4	9–19	14	Overlaps
BG11	0.0276 ±5.8	0.430	15.7	13.2–18.7	16–26	21	Overlaps
BG6	0.0440 ±4.7	0.684	22.3	16.2–30.3	22–32	27	Overlaps
BG5	0.0439 ±4.4	0.683	22.1	16.2–30.3	25–35	30	Overlaps
BG13	0.0481 ±3.8	0.749	29.3	21.8–40.4	33–47	40	Overlaps
BG8	0.0494 ±4.0	0.769	32.1	23.7–45.1	33–47	40	Overlaps
BG14	0.0499 ±3.8	0.777	45.8	37.3–59.1	36–54	45	Overlaps
BG9	0.0560 ±3.7	0.871	50.7	35.8–85.1	41–62	51	Encompasses
BG12	0.0586 ±4.7	0.912	62.9	40.7–undef.	48–67	57	Encompasses
BG10	0.0543 ±4.4	0.845	44.8	31.6 – 71.6	51–79	65	Overlaps

[1] Error calculation based on the standard deviation of ^{210}Pb activity (Wang et al., 1975).

[2] Predicted age range was extended by 14.6% of coefficient of variation (CV) associated with growth-zone–derived age estimates.

[3] The average predicted age of each radiometric age group.

[4] Definition of terms: Exceeds = radiometric age range is greater than predicted age range; Overlaps = radiometric age range partially agrees with predicted age range; Encompasses = radiometric age range was in agreement with predicted age range.

in otolith cores with expected ingrowth curves through time (Fig. 4). Of the 14 pooled otolith groups, three had radiometric age ranges that fully encompassed the predicted age range, ten resulted in overlapping age ranges, and one exceeded predicted age (Table 4). In addition, radiometric ages were in close agreement with predicted ages in a direct comparison (r^2=0.88; Fig. 5). Further t-tests indicated no significant difference in slope (t=1.92, P=0.092) or elevation (t=0.163, P=2.201) between the regression and a hypothetical agreement line (slope of 1), confirming the close agreement of radiometric age and predicted age.

Discussion

Estimation of age and growth

The growth pattern present in otoliths of blackgill rockfish was often difficult to interpret. Complications inherent to the growth pattern were the following: obscure growth zones up to age 10–15 (the ages when the otolith begins to thicken laterally), rapid transition to slower growth, conflicting or ambiguous growth patterns, and poor resolution of extremely compressed zones in old-age fish. Irregular patterns may have led to enumeration of false growth zones (checks), and the compression of the outer layers may have concealed growth zones present in older fish. This finding has been consistent among previous studies of rockfishes (Chilton and Beamish, 1982).

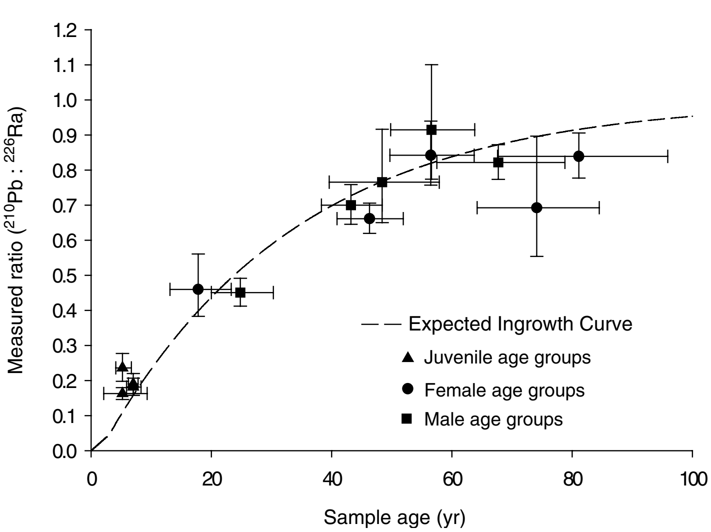

Figure 4

Measured ^{210}Pb:^{226}Ra ratio plotted against total sample age (mean predicted age plus time since capture) of blackgill rockfish (*Sebastes melanostomus*), with respect to the expected ^{210}Pb:^{226}Ra activity ratio. Horizontal error bars represent the predicted age range (based on age prediction model extended by 14.6% CV). Vertical error bars represent high and low activity ratios based on the analytical uncertainty associated with ^{210}Pb and ^{226}Ra measurements.

Because of the difficulty involved in interpreting growth patterns, aging of blackgill rockfish otoliths involved a high degree of individual subjectivity, as evidenced by the relatively low precision (D=8.4%) and high variation (CV=15%) between readers. However, there were some remarkably clear otoliths and for these we were highly confident of age estimates (Fig. 1). Overall, 87% of between-reader age estimates were within 10 years, emphasizing that although the method of interpretation of growth can be imprecise, it provides a reasonable indication of the growth characteristics and longevity of this species.

The von Bertalanffy growth parameters for male and female blackgill rockfish appear to indicate that blackgill rockfish possess distinct patterns of growth (Table 1). Female blackgill rockfish exhibited a slower growth rate than males up to approximately 25–30 years of age (Fig. 2). At this point, the male growth rate slows and approaches an asymptotic length of 448 mm, but females continue to grow in length, reaching an asymptotic length of 548 mm. This trend of slower growing, but ultimately larger females has been observed in other slope-dwelling *Sebastes* species, such as the darkblotched (*S. crameri*; Rogers et al., 2000), and splitnose (*S. diploproa*; Wilson and Boehlert, 1990) rockfishes. For both sexes, the growth coefficient is low (k=0.040–0.068) when compared to shallower-dwelling (50–200 m) rockfishes, such as the greenstriped (*S. elongates*, 0.10–0.12; Love et al., 1990) and widow (*S. entomelas*, 0.20–0.25; Williams et al., 2000) rockfishes, but very similar to other deep-dwelling, long-lived species, such as the shortspine thornyhead (*Sebastolobus alascanus*, k=0.020; Cailliet et al., 2001), yelloweye (*S. ruberrimus*, k=0.046; Andrews et al., 2002), and bank (*S. rufus*, k=0.041; Cailliet et al., 2001) rockfishes.

Previous maturity estimates for blackgill rockfish (7–9 yr males, 6–10 yr females; Echeverria 1987), based on whole otolith counts, were much lower than estimates obtained from section ages in the present study (Table 2). Maturity estimates from our study support those derived by Butler et al. (1999), largely because the aging protocol was the same between facilities. Although our growth model included some age estimates (37%) from Butler et al. (1999), our results further confirm age at maturity (Table 2). Compared to other species of the genus, blackgill rockfish have a late maturity that resides at the upper end of the range for rockfishes (Cailliet et al., 2001; Love et al., 2002).

Extraordinarily old ages in average-size fish exhibited by the blackgill rockfish should not be dismissed as an anomaly. In this study the oldest blackgill rockfish was a 90-year-old male (aged as high as 102 years) that was 450 mm TL. This fish was 160 mm less than the maximum reported length (Love et al., 2002). According to an experienced rockfish age and growth researcher, "some of the oldest specimens [rockfish] are rarely the largest (lengthwise), and most, if not all, are males." (Munk[2]) The reasons for this age-length pattern are beyond the scope of this study, but the implications for stock dynamics and management are that it is worthy of further consideration.

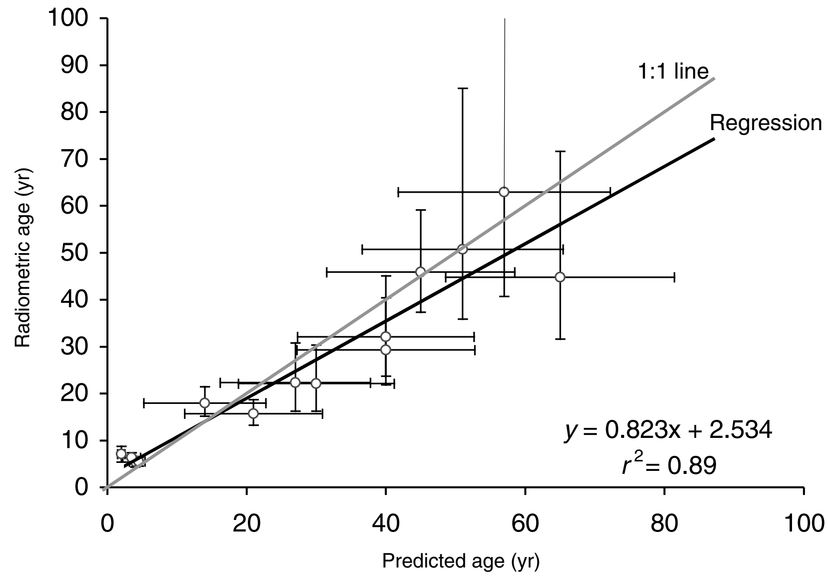

Figure 5

Direct comparison of mean predicted age and radiometric age for 14 pooled otolith age groups for blackgill rockfish (*Sebastes melanostomus*). A regression of the data points and 1:1 line of agreement are included for comparison. Horizontal error bars represent the error associated with age estimation (average predicted age multiplied by 14.6% CV), plus the standard error of the regression (1*s*) used to predict age for radiometric samples. Vertical error bars represent high and low radiometric age estimates based on the analytical uncertainty associated with ^{210}Pb and ^{226}Ra measurements.

Age prediction, age-group determination, and core extraction

The use of otolith weight as a proxy for age has benefits over conventional otolith aging methods by reducing cost, increasing sample size, and allowing greater objectivity (Boehlert, 1985; Pawson, 1990; Fletcher, 1991; Pilling et al., 2003). In this study, predicting ages from otolith weight increased the number of unsectioned otoliths that could be used in the radiometric analysis, but the prediction model also amplified the uncertainty associated with estimates of age, especially in older fish. The variance around the regression line increased with otolith weight, and log normalizing the data did not eliminate this problem. Older predicted ages, therefore, were more uncertain than younger ages (Fig. 3). Although limited to a specific otolith weight range, the prediction model presented here may provide managers with a more efficient and less costly way to investigate the age structure of blackgill rockfish stocks.

In an ideal study, otoliths from the entire estimated age range for blackgill rockfish would be available in the sample set. Otoliths from fish with predicted ages greater than 70 years, however, were not present in our study in sufficient numbers to allow age determination by radiometric methods. This was so, even though more than half of the 1200 otolith pairs obtained for ourstudy were sampled directly from commercial fishing vessels in 1985 along the coast of central and southern California, where the bulk of the fishery occurred. Because fishermen often target adult aggregations, the absence of these older individuals may be an indication that the population had already experienced depletion of older age classes at the time of sample collection, particularly if natural mortality is thought to be low for most rockfishes (Bloeser[3]). However, it is possible that the largest, oldest fish are naturally rare, even at the start of an intensive commercial fishery. Knowledge of blackgill rockfish pre-exploitation stock structure and population dynamics would help to elucidate which (depletion of older age classes or a natural situation of low numbers of older fish) is the more likely scenario.

Radiometric analysis

In previous studies the analytical uncertainty of ^{226}Ra was the limiting factor in radiometric age determination (Andrews et al., 1999a). Typically, TIMS determination of ^{226}Ra reduces error to less than 1–3% of the determined value, but technical difficulties (improperly mixed nitric acid) led to poor recovery and loss of radium in seven samples. The remaining seven samples were deemed reliable because of relatively high radium recovery, longer run times, and low analytical uncertainty as determined by the TIMS analysis routine. The ^{226}Ra activity determined for these samples was consistent

[2] Munk, K. 2002. Personal commun. Alaska Department of Fish and Game, P.O. 25526, Juneau, AK 99802.

[3] Bloeser, J. A. 1999. Diminishing returns: the status of West Coast rockfish, 94 p. Pacific Marine Conservation Council, P.O. Box 59, Astoria, OR 97103.

enough that we could assume that ^{226}Ra activities were similar among all samples and that use of an average was valid (0.0643 [±0.0035] dpm/g). This approach is acceptable because ^{226}Ra activities measured in previous radiometric studies on Pacific rockfishes were relatively constant. For example, the activity of cored yelloweye rockfish (*S. ruberrimus*) otoliths had a mean ^{226}Ra activity of 0.0312 (±0.0026) dpm/g (n=18; Andrews et al., 2002), and the rougheye rockfish (*S. aleutianus*), another deepwater species (to 730 m; Love et al., 2002), had a similar otolith core ^{226}Ra activity averaging 0.065 (±0.003) dpm/g (Kastelle et al., 2000).

Accuracy and uncertainty of ages estimates

Radiometric activities measured in blackgill rockfish otoliths generally agreed with expected activity ratios for ^{210}Pb and ^{226}Ra (Fig. 4), confirming the validity of growth-zone–derived age estimates. In addition, a direct comparison between radiometric age and predicted age resulted in a strong agreement (r^2=0.89; Fig. 5), which was further supported by slope and elevation tests that revealed no significant difference from a 1:1 agreement line.

The most critical sources of error involved in age estimation, prediction, and radiometric age determination were the following: 1) age estimate uncertainty, 2) regression error associated with predicted ages, and 3) analytical uncertainty associated with the radiometric aging technique (TIMS and α-spectrometry). Conventional aging techniques are inherently subjective (Boehlert, 1985; Campana, 2001) and thus create uncertainty associated with an estimated age. This uncertainty is transferred to the prediction model, where the natural variability associated with individual otolith weight must also be considered. For most samples, however, the error bars either overlapped or were in contact with the agreement line (Figs. 4 and 5), further confirming the concordance of radiometric age with predicted age.

Implications for management

When considering the longevity of rockfishes for which a maximum age has been reported (Munk, 2001; Cailliet et al., 2001), a longevity exceeding 90 years places the blackgill rockfish within the top 20% of long-lived rockfishes. There is a trend for rockfishes that may indicate that longevity increases as maximum depth of occurrence increases, and physiological adaptations to the environmental conditions of deep-sea living could provide an explanation (Cailliet et al., 2001). The confirmed longevity and the maximum depth of occurrence (~800 m) for the blackgill rockfish provide further support for this concept.

Longevity in the rockfishes has been central to its evolutionary success in relation to other marine teleosts. The suite of life history characters implicit with a long lifespan (slow adult growth, late age-at-maturity, low adult natural mortality) represent a "slow and steady" adaptive strategy, whereby the energy allocated towards individual growth is prolonged, eventually contributing to greater fecundity (due to larger size at maturity) over the lifespan of the individual. This reproductive strategy serves to propagate genetic material across several generations, as well as to diffuse the effect of mortality associated with each reproductive event (Leaman, 1991). In this sense, longevity may act to buffer the species against short-term (El Niño) and long-term environmental change (Pacific Decadal Oscillations), and the stochasticity inherent in the Pacific Ocean system (Moser et al., 2000).

In the absence of fishing pressure, the genetic contribution of a slow-growing, longer-lived species may be more conserved in the collective species' gene pool (Munk[2]). In the presence of fishing pressure, however, this "slow and steady" adaptation may be detrimental (Musick, 1999). Although modeling fish populations for the purpose of management typically involves some or all of these parameters, the focus is often on determining sustainable biomass and this approach largely ignores the unknown effects of changes in age structure due to removal of the oldest individuals from the population (Craig, 1985), as well as a loss of genetic diversity that could prevent full recovery of severely depleted populations (Hauser et al, 2002). Given the current depressed condition of many heavily fished rockfish stocks, species-specific life history characteristics, such as longevity, growth rate, and age-at-maturity estimates, should be given thorough consideration in the development of an effective management strategy. Management regulations that account for these characteristics, such as a limited fishing season, or designation of harvest refugia (Yoklavich, 1998), would provide a stronger basis for conservation and sustainability of the resource.

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Literature cited

Andrews, A. H., G. M. Cailliet, and K. H. Coale.
1999a. Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. Can. J. Fish. Aquat. Sci. 56:1339–1350.

Andrews, A. H., K. H. Coale, J. Nowicki, C. Lundstrom, A. Palacz, and G. M. Cailliet.
1999b. 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. Can. J. Fish. Aquat. Sci. 56:1329–38.

Andrews, A. H., G. M. Cailliet, K. H. Coale, K. M. Munk, M. M. Mahoney and V. M. O'Connell.
2002. Radiometric age validation of the yelloweye rockfish (*Sebastes ruberrimus*) from south-eastern Alaska. Mar. Freshw. Res. 53:1–8.

Archibald, C. P., D. Fournier, and B. M. Leaman.
1983. Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manag. 3:283–294.

Beamish, R. J.
1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36:1395–1400.

Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112(6):735–743.

Bennett, J. T., G. W. Boehlert, and K. K. Turekian.
1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from ^{210}Pb/^{226}Ra measurements in otoliths. Mar. Biol. 71:209–215.

Boehlert, G. W.
1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull. 83:103–117.

Burton, E. J., A. H. Andrews, K. H. Coale, and G. M. Cailliet.
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 (J. A. Musick, ed.,), p. 77–87. Am. Fish. Soc. Symp. 23.

Butler, J. L., L. D. Jacobson, and J. T. Barnes.
1999. Stock assessment for blackgill rockfish. *In* Appendix to the status of the Pacific coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999: stock assessment and fishery evaluation, 93 p. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, Oregon, 97201.

Cailliet, G. M., A. H. Andrews, E. J. Burton, D. L. Watters, D. E. Kline, and L. A. Ferry-Graham.
2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Exp. Gerontology 36:739–764.

Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biology 59:197–242.

Campana, S. E., K. C. Zwanenburg, and J. N. Smith.
1990. ^{210}Pb/^{226}Ra determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47:163–165.

Chang, W. Y. B.
1982. A statistical method of evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 48:734–750.

Chilton, D. E., and R. J. Beamish.
1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station, 102 p. Can. Spec.Pub. Fish. Aquat. Sci. 60.

Craig, J. F.
1985. Aging in fish. Can. J. Zoology 63:1–8.

Cross, J. N.
1987. Demersal fishes of the upper continental slope off southern California. CalCOFI Report 28:155–167.

Echeverria, T. W.
1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85:229–249.

Echeverria, T. W., and W. H. Lenarz.
1984. Conversions between total, fork, and standard length in 35 species of *Sebastes* from California. Fish. Bull. 82:249–251.

Fletcher, W. J.
1991. A test of the relationship between otolith weight and age for the pilchard *Sardinops neopilchardus*. Can. J. Fish. Aquat. Sci. 48:35–38.

Flynn, W. W.
1968. The determination of low levels of polonium-210 in environmental materials. Anal. Chimica Acta. 43: 221–227.

Francis, R. I. C. C.
2003. The precision of otolith radiometric ageing of fish and the effect of within-sample heterogeneity. Can. J. Fish. Aquat. Sci. 60:441–447.

Hauser, L., G. J. Adcock, P. J. Smith, J. H. Bernal Ramirez, and G. R. Carvalho.
2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). Proc. Nat Acad. Sci. 99(18):11742–11747.

Kastelle, C. R., D. K. Kimura, and S. R. Jay.
2000. Using Pb^{210}/Ra^{226} disequilibrium to validate conventional ages in Scorpaenids (*sic*) (genera *Sebastes* and *Sebastolobus*). Fish. Res. 46:299–312.

Leaman, B. L.
1991. Reproductive style and life history variables relative to exploitation and management of *Sebastes* stocks. Environ. Biol. Fishes 30: 253–271.

Love, M. S., P. Morris, M. McCrae, and R. Collins.
1990. Life history aspects of 19 rockfish species (Scorpaenidae: Sebastes) from the southern California Bight, 38 p. NOAA Technical Report. NMFS 87.

Love, M. S., M. M. Yoklavich, L. Thorsteinson, and J. Butler.
2002. The rockfishes of the Northeast Pacific, 405 p. Univ. California Press, Berkeley, CA.

Mace, P. M., J. M. Fenaughty, R. P. Coburn, and I. J. Doonan.
1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. New Zealand J. Mar. Fresh. Res. 24:105–109.

Mahoney, M. M.
2002. Age, growth and radiometric age validation of the blackgill rockfish, *Sebastes melanostomus*. M.Sc. thesis, 70 p. California State Univ., San Francisco, CA. [Available from: Moss Landing Marine Labora-

tories, 8272 Moss Landing Road, Moss Landing, CA 95039.]

Moser, H. G., and E. H. Ahlstrom.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981–996.

Moser, H. G. R. L. Charter, W. Watson, D. A. Ambrose, J. L. Butler, S. R. Charter, and E. M. Sandknop.
2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the southern California Bight in relation to environmental conditions and fishery exploitation. CalCOFI Report 41:132–147.

Musick, J. A.
1999. Ecology and conservation of long-lived marine animals. *In* Life in the slow lane: ecology and conservation of long-lived marine animals (J. A. Musick, ed.), p. 1–10. Am. Fish. Soc. Symp. 23.

Munk, K. M.
2001. Maximum ages of groundfishes in waters off Alaska and British Columbia and considerations of age determination. Alaska Fish. Res. Bull. 8(1):12–21.

NOAA (National Oceanic and Atmospheric Administration).
2001. Magnuson-Stevens Act Provisions; Fisheries off West Coast states and in the western Pacific; Pacific coast groundfish fishery; annual specifications and management measures. Federal Register 66:8, 2338–2355.

Pawson, M. G.
1990. Using otolith weight to age fish. Fish. Biol. 36:521–531.

Pilling, G. M., E. M. Grandcourt, and G. P. Kirkwood.
2003. The utility of otolith weight as a predictor of age in the emperor *Lethrinus mahsena* and other tropical fish species. Fish. Res. 60:493–506.

Rogers, J. B., R. D. Methot, T. L. Builder, K. Piner, and M. Wilkins.
2000. Status of the darkblotched rockfish (*Sebastes crameri*) resource in 2000. *In* Appendix to the status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001: stock assessment and fishery evaluation, 79 p. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Smith, J. N., R. Nelson, and S. E. Campana.
1991. The use of Pb-210/Ra-226 and Th-228/Ra-228 disequilibria in the ageing of otoliths of marine fish. *In* Radionuclides in the study of marine processes (P. J. Kershaw and D. S. Woodhead, eds.), p. 350–359. Elsevier Applied Science, New York, NY.

Wang, C. H., D. L. Willis, and W. D. Loveland.
1975. Radiotracer methodology in the biological, environmental, and physical sciences, 480 p. Prentice Hall, Englewood Cliffs, NJ.

Williams, E. H., A. D. MacCall, S. V. Ralston, and D. E. Pearson.
2000. Status of the widow rockfish resource in 2000. *In* Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000, 75 p. Pacific Fishery Management Council, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

Williams, E. K., and S. R. Ralston.
2002. Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fish. Bull. 100:836–855.

Wilson, C. D., and G. W. Boehlert.
1990. The effects of different otolith ageing techniques on estimates of growth and mortality for the splitnose rockfish, *Sebastes diploproa*, and canary rockfish, *S. pinniger*. Calif. Fish Game 76:146–160.

Yoklavich, M. (ed).
1998. Marine harvest refugia for West Coast rockfish: a workshop, 162 p. NOAA-Tech. Memo. NMFS-SWFSC-255.