Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique

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Abstract: Current and historic longevity estimates for the Pacific grenadier (*Coryphaenoides acrolepis*) range from 6 to greater than 60 years. Age estimates in this study using growth increment counts in thin otolith sections indicate the Pacific grenadier is a long-lived fish. To validate this growth information, age was determined using the radioactive disequilibria of ^{210}Pb and ^{226}Ra in otolith cores from adult Pacific grenadier. Radiometric ages closely agreed with age estimates from counting growth increments, which confirms their annual periodicity. Radiometric results indicate the Pacific grenadier can live at least 55.8 years (–7.4, +10.1 years). Growth increment counts from large fish indicate longevity may approach 73 years. Because the Pacific grenadier is long-lived and matures late in life, it may be vulnerable to heavy fishing pressure. Therefore, conservation measures need to be taken to sustain this rapidly developing fishery.

Résumé : Selon les estimations actuelles et passées, la longévité du grenadier à écailles rudes (*Coryphaenoides acrolepis*) serait de 6 ans à plus de 60 ans. Les estimations de l'âge de la présente étude, dans laquelle on a dénombré les incréments de croissance sur des coupes fines d'otolithes, indiquent que ce poisson vit longtemps. Pour valider cette information issue des incréments de croissance, on a déterminé l'âge au moyen du déséquilibre radioactif du ^{210}Pb et du ^{226}Ra dans des coupes d'otolithes de grenadier à écailles rudes adultes. Les âges obtenus par mesures radiométriques coïncidaient étroitement avec les estimations de l'âge par dénombrement des incréments de croissance, ce qui confirme la périodicité annuelle de ces derniers. Les résultats des mesures radiométriques indiquent que ce poisson peut vivre au moins 55,8 ans (–7,4, +10,1 ans). Les dénombrements des incréments de croissance chez de gros poissons indiquent que la longévité de l'espèce peut approcher 73 ans. Comme le grenadier à écailles rudes vit longtemps et atteint la maturité à un âge avancé, il peut être vulnérable aux fortes pressions de pêche. C'est pourquoi on doit prendre des mesures de conservation pour assurer la durabilité de cette pêche en pleine croissance.

[Traduit par la Rédaction]

Introduction

The Pacific grenadier, *Coryphaenoides acrolepis* (family Macrouridae), is a benthopelagic, deepwater fish species that inhabits the continental slopes of the northern Pacific Ocean. Its range is circum-north Pacific from Baja California, Mexico, to northern Japan and into the Bering Sea (Iwamoto and Stein 1974; Cohen et al. 1990). Its typical depth range is from 600 to 2500 m (Iwamoto and Stein 1974) with a population density maximum near 1500 m (Stein and Pearcy 1982; Matsui et al. 1990).

Until recently, fishermen regarded the Pacific grenadier as a trash fish because the fillets were small (~25% of the total fish weight) and had low market value (US$0.08 to US$0.16 per pound ex-vessel). In recent years, the Pacific grenadier has been discovered to have desirable culinary attributes (Matsui et al. 1990) and has become a large commercial fishery in California and Oregon (Fig. 1). Landings for California until 1992 were primarily from Eureka, California. After 1992, landings from Monterey Bay, California, increased substantially to nearly 900 t (~2 million pounds) in 1996 (Leos 1996 and 1997). Before 1995, greater than 95% of the landings were from trawlers. For 1995 and 1996, greater than 90% of the landings were from set lines targeting the Pacific grenadier (Leos 1997). Because of these landings, the Pacific grenadier is no longer in the "other" category and has become the fifth largest fishery in Monterey Bay, California, and thirteenth in the state of California at 1130 t (~2.5 million pounds) for 1996 (Leos 1996 and 1997).

To properly manage this rapidly developing fishery, the age structure and growth characteristics of the Pacific grenadier must be known along with other life history characteristics. Some life history aspects are known (Stein and Pearcy 1982; Matsui et al. 1990), but longevity estimates have been variable. Recent and historic age and longevity estimates range from 6 to greater than 60 years (Kulikova 1957; Brothers et al. 1976; Mulcahey et al. 1979; Wilson 1982; Matsui et al. 1990).

Fisheries management strategies rely heavily on accurate

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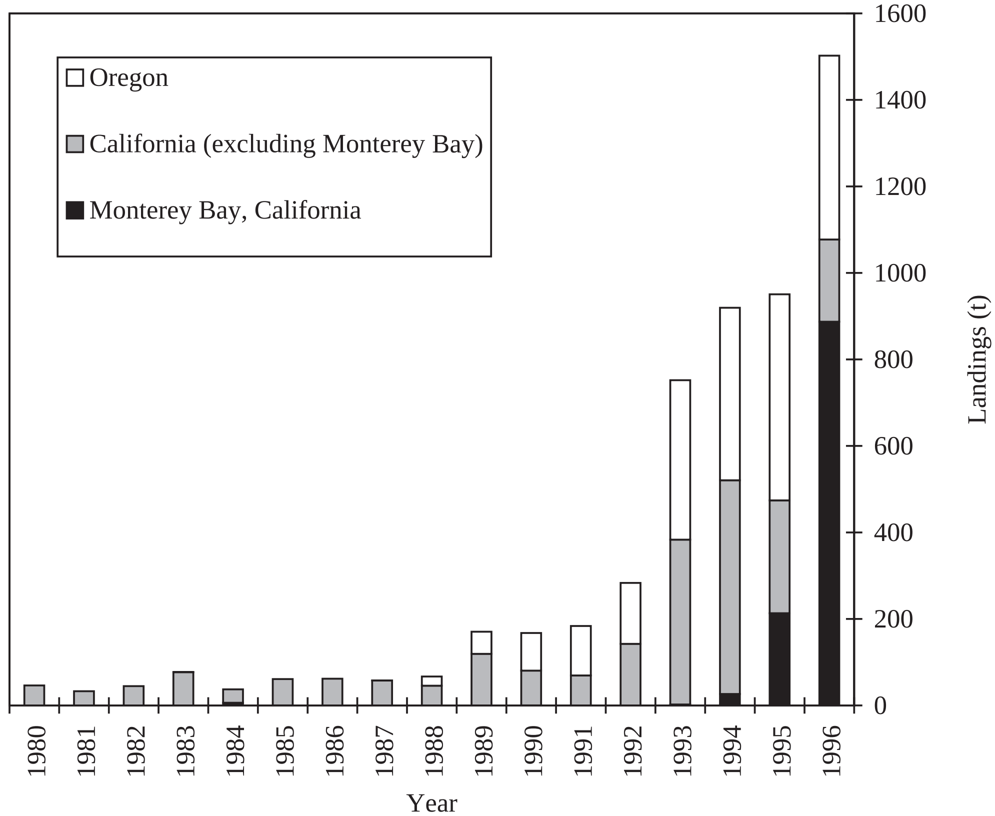
Fig. 1. Landings of Pacific grenadier for California and Oregon from 1980 to 1996 given in metric tons (t). Landings for Washington, Canada, and Alaska have been 0 or negligible.



age determinations. Age of fishes is typically determined by using one of several techniques, with growth increment counts in calcified structures being most common (Beamish and McFarlane 1987). The annual periodicity of growth increments in these structures is often assumed. Until recently this assumption was rarely validated (Beamish and McFarlane 1983). As a consequence, underestimation of longevity and overfishing may have led to the decline of the Pacific Ocean perch (*Sebastes alutus*) of the northeastern Pacific Ocean and the orange roughy (*Hoplostethus atlanticus*) off New Zealand (Beamish 1979; Smith et al. 1995).

The problem with typical growth increment age validation techniques is that they have limited applicability to deep-water or long-lived fishes (Mace et al. 1990; McFarlane and Beamish 1995). One technique that can be used to validate age estimates for these fishes is the radiometric ageing technique, which uses the disequilibria of ^{210}Pb and ^{226}Ra in otoliths as a natural chronometer (Smith et al. 1991; Bergstad 1995). This technique has been successfully applied to 12 fish species (Bennett et al. 1982; Campana et al. 1990; Fenton et al. 1991; Kastelle et al. 1994; Fenton and Short 1995; Milton et al. 1995; Smith et al. 1995; Stewart et al. 1995; Watters 1995; Kline 1996).

In this study, the age and growth of the Pacific grenadier was estimated using a traditional ageing technique, validated using an improved radiometric ageing technique, and compared with other age and growth studies of the Pacific grenadier. Improvements made to the radiometric ageing technique in a concurrent study have been used here (Andrews et al. 1999). Ageing results were discussed in the context of known life history information and management recommendations were made.

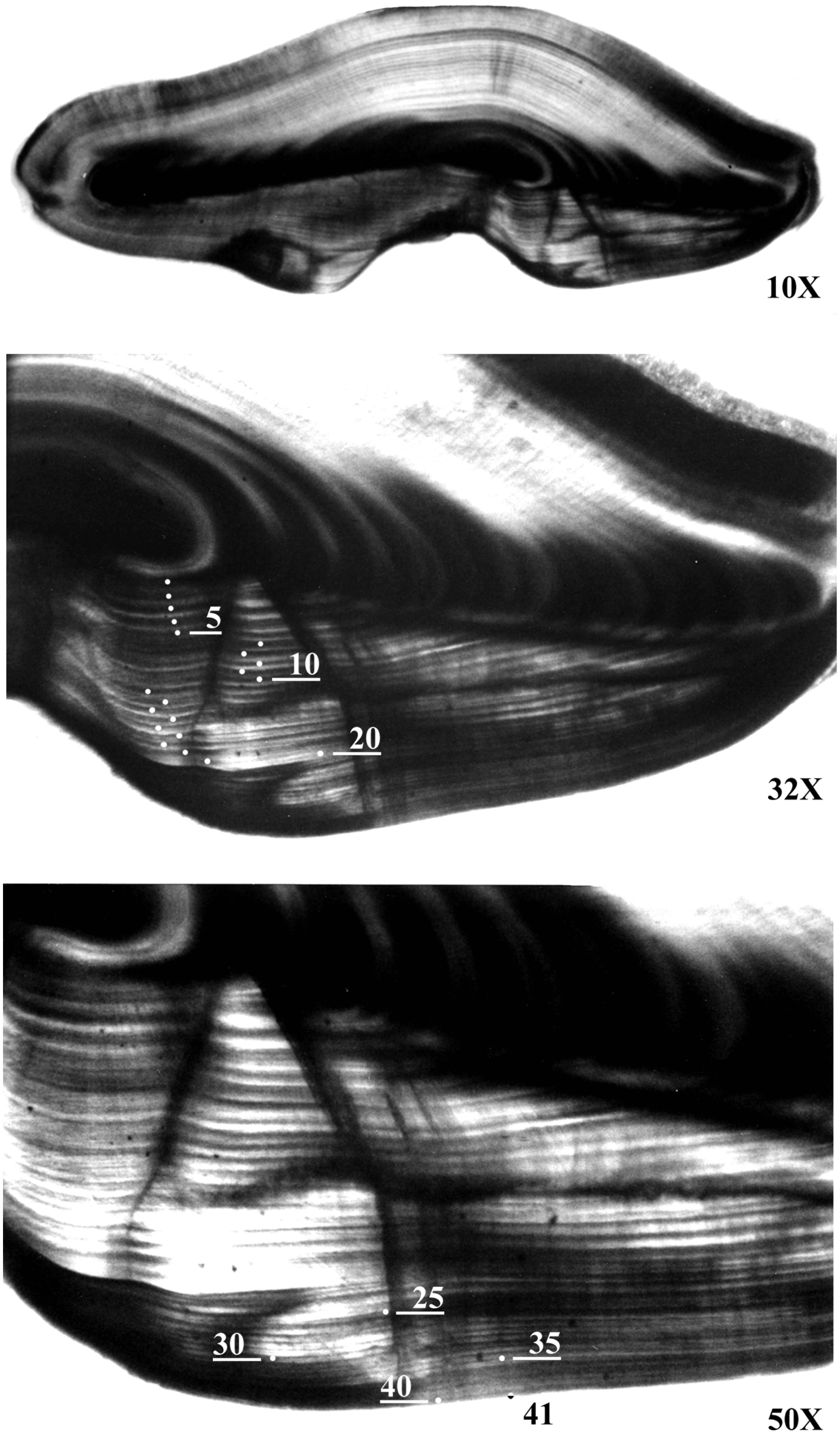
Materials and methods

Pacific grenadier were collected east of Santa Cruz, California, in November 1992 and off of Oregon and Washington in October 1992 and December 1993. As sagittal otoliths were extracted, fish total length (TL), pre-anal fin length (PAF), snout to dorsal fin (SD), and head length (HL) were recorded to the nearest millimetre. PAF was defined as snout to the base of the first anal fin ray. SD was defined as snout to the base of the first dorsal fin ray. HL was defined as snout to the posterior-most tip of the operculum. A partial length analysis was conducted on fish with intact tails. Otolith weight was measured to the nearest milligram, and length, width, and height were measured to the nearest 0.1 mm. Extracted otoliths were temporarily stored in de-ionized water and ethanol (50%) buffered with marble chips. Cleaned otoliths were stored dry in glass vials.

Traditional otolith ageing

Transverse otolith sections mounted to slides and viewed under a dissecting microscope with transmitted light were used to estimate age. The ageing criteria was based on several very well-defined sections (Fig. 2). The sulcal region was usually used, but the distal margin was also used for some samples. Otolith sections that did not have quantifiable increments were removed from the analysis. Readable otoliths were aged independently by two readers three times each. Average percent error (APE) and index of precision (D) were used to test the reproducibility of ageing between readers (Beamish and Fournier 1981; Chang 1982). Consul-

Fig. 2. Three views of a transverse otolith section with increasing magnification centered on the sulcal region. The full section view is at a magnification of 10× and shows some of the growth increments visible toward the distal margin (top of section). The two are successive views are at magnifications of 32× and 50×. Markers indicate quantified growth increments, which rapidly become compressed toward the margin. This growth pattern was used as a search image in ageing other otolith sections. This section was aged at 41 years.



tation between readers on ageing criteria was used to resolve differences and final age estimates were assigned by the first reader. A von Bertalanffy growth function was fitted, using FISHPARM software (Saila et al. 1988), to the final age estimates to describe growth parameters.

Age-group determination and core extraction

Before otoliths were selected for ageing using growth increment counts, sample weight requirements were considered for age-groups consisting of pooled otolith cores. Dimensions and weight of otoliths from juvenile fish (estimated age 5 years) were used to determine core size and weight. The number of otoliths needed to perform the analysis was determined and a subsample of otoliths were held aside for radiometric analysis.

Because otoliths were difficult to age and the amount of otolith material must be maximized for radiometric analysis, age was determined using a simple linear regression of otolith weight to section age. Sexes were separated and age groups were formed using both otoliths from each fish. To discriminate dissimilar fish from potential age-group members, a multiple linear regression, incorporating fish length (PAF), otolith weight, and an interaction term (otolith length multiplied by PAF), was used to determine age. Agreement of ages determined for each fish by each regression was used to determine group membership. Fish with regression ages that differed by greater than an arbitrary 10% were not included in the age-group. The age of the age-group members was determined from the simple linear regression. The age range for each age-group was kept as narrow as was permitted by the amount of otolith mass needed. The average age of the age-group was an age-weighted average based on the estimated age of each core in the sample. An age-group weight of 1 g was targeted, but lower amounts were used where sufficient sample was unavailable.

The otoliths selected for each age-group were cored to the size of a 5-year-old otolith. Average dimensions determined from three juvenile otoliths were 5.0 mm long, 3.0 mm wide, and 1.0 mm thick. Each core was extracted by cutting a 6 mm transverse section and hand grinding to the core dimensions. A weight of approximately 0.02 g per otolith core was targeted based on an average of the three juvenile otoliths.

Radiometric analysis

To address some of the assumptions of this technique, whole juvenile and adult otoliths were analyzed. To determine if exogenous ^{210}Pb was incorporated during otolith formation, a sample of whole otoliths from juvenile fish was included as an age-group. For comparative purposes, an adult whole-otolith pair was analyzed for ^{226}Ra to assess if an ontogenetic difference occurs in ^{226}Ra uptake.

Each pooled otolith core sample was analyzed for ^{210}Pb and ^{226}Ra. To determine ^{210}Pb, α-spectrometry of ^{210}Po, its daughter product, was performed. Determination of ^{226}Ra was performed using a new technique that uses isotope-dilution thermal ionization mass spectrometry (TIMS; Andrews et al. 1999). The details of ^{210}Pb determination are described here, but only the details of ^{226}Ra determination that vary from Andrews et al. (1999) are stated here.

Because of the extremely low levels of ^{210}Pb and ^{226}Ra, trace-metal precautions were exercised during sample cleaning and processing (Watters 1995). All acids used were double distilled (GFS Chemicals®) and dilutions were made using Millipore® filtered Milli-Q water (18 MΩ·cm^{-1}). Thorough cleaning and repeated dissolution of the core samples was performed prior to radiometric analysis (Andrews et al. 1999).

To determine ^{210}Pb activity in samples where it is very low, ^{210}Pb activity was determined by proxy using the autodeposition and α-spectrometric determination of its daughter, ^{210}Po (Flynn 1968). To ensure that all of the ^{210}Po was due to ingrowth from ^{210}Pb and that ^{210}Po:^{210}Pb was in secular equilibrium, all samples were at least 2 years old (from date of capture). Samples prepared for ^{210}Po analysis were spiked with a yield tracer, ^{208}Po, calibrated against NBS and geological standards. The amount added was estimated to be 5 times the activity of ^{210}Po in the otolith sample to reduce counting error in the determination of ^{210}Pb activity.

To isolate the polonium isotopes for the purpose of α-spectrometry, the isotopes were autodeposited onto a silver planchet. Spiked samples were redissolved in approximately 50 mL of 0.5 N HCl on a hot plate covered with a watch-glass. Samples were completely dissolved and the temperature was elevated to ~90°C before plating. The ^{210}Po and ^{208}Po-tracer were autodeposited at this temperature onto a purified silver planchet (99.999%, A.F. Murphy Die and Machine Co., North Quincy, Mass.) held in a rotating teflon holder over a 4-h period (Flynn 1968). Planchets were counted using both silicon surface barrier detectors and ion implant detectors in 8 Tennelec TC256 α-spectrometers interfaced with a multichannel analyzer and an 8-channel digital multiplexer. Counts were collected with Nucleus® software on an IBM-PC. Radium blanks were included in these steps to account for any potential radium contamination. The sample remaining after polonium autodeposition was recovered for ^{226}Ra analysis.

The activity of ^{210}Po was calculated using the α-spectrometry counts for ^{210}Po and ^{208}Po. These counts were corrected for background counts (reagent counts not above background) by subtracting the amount of counts calculated to occur for the counting period. Adjusted sample counts for ^{208}Po and ^{210}Po were corrected for decay during the counting period and the activity of ^{210}Po was calculated based on the known ^{208}Po activity (Andrews 1997). Because the activity of ^{210}Po was in secular equilibrium with ^{210}Pb, the activity of ^{210}Po was equal to the ^{210}Pb activity. This activity was corrected for ^{210}Pb ingrowth from ^{226}Ra to the time of capture (Andrews 1997).

Determination of ^{226}Ra was performed using an elemental separation procedure and isotope-dilution TIMS, described elsewhere (Andrews et al. 1999). The only exception to the procedure used for these samples was the collection intervals used for each column separation. In the first two column passes, where calcium removal occurs, the collection interval was from 35 to 120 mL, instead of 40 to 120 mL. For the third column pass, where radium is isolated, the collection interval was from 300 to 700 µL, instead of 250 to 700 µL. These intervals were changed as a result of this study to improve radium separation and recovery and to further reduce calcium.

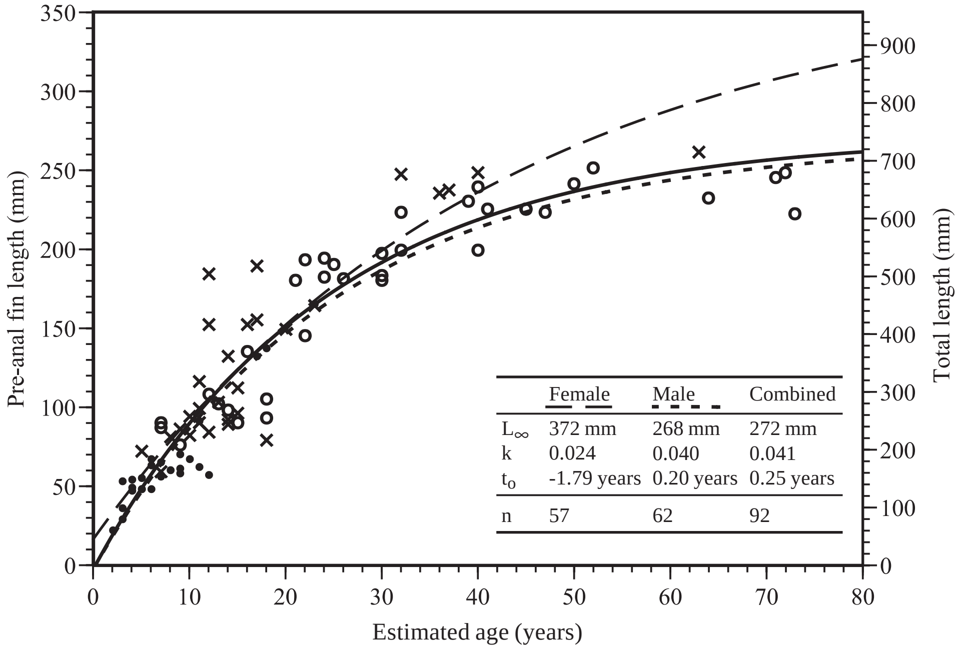
Radiometric age determination

Age determination was performed using the measured ^{210}Pb and ^{226}Ra activities in the following equations. Because the activities were measured using the same sample, the calculation was independent of sample mass. For adult samples, where estimated age was greater than the 5-year core, radiometric age was calculated as follows using an equation derived from Smith et al. (1991) to compensate for the ingrowth gradient of ^{210}Pb:^{226}Ra in the otolith core,

$$t_{\mathrm{age}} = \frac{\ln\left(\dfrac{\dfrac{1 - A^{210}\mathrm{Pb}_{\mathrm{tc}}}{A^{226}\mathrm{Ra}_{\mathrm{TIMS}}}}{(1 - R_0)\left(\dfrac{1 - \mathrm{e}^{-\lambda T}}{-\lambda T}\right)}\right)}{-\lambda} + T,$$

where t_{age} is the radiometric age at the time of capture, $A^{210}\mathrm{Pb}_{\mathrm{tc}}$ is the ^{210}Pb activity corrected to time of capture, $A^{226}\mathrm{Ra}_{\mathrm{TIMS}}$ is the ^{226}Ra activity measured using TIMS, R_0 is the ratio of ^{210}Pb:^{226}Ra initially incorporated, λ is the decay constant for ^{210}Pb (ln(2)/22.26 years), and T is the core age (5 years). The radiometric age calcula-

Fig. 3. Von Bertalanffy growth functions were fitted to estimated ages from growth zone counts and pre-anal fin lengths (PAF) for females (χ), males (○), and immature (●). Immature fish were used in each growth function. Total length (TL), shown on the right vertical axis, was calculated based on PAF.



tion for the juvenile age-group was determined by iteration of an equation derived from Smith et al. (1991):

$$\frac{A^{210}\mathrm{Pb}_{\mathrm{tc}}}{A^{226}\mathrm{Ra}_{\mathrm{TIMS}}} = 1 - (1 - R_0)\left(\frac{1 - \mathrm{e}^{-\lambda t_{\mathrm{age}}}}{\lambda t_{\mathrm{age}}}\right),$$

where all equation components were as defined above.

Age estimate accuracy

A comparison of estimated age versus radiometric age was performed in two plots and one statistical analysis. First, the estimated age of the age-groups and measured ^{210}Pb:^{226}Ra activity ratios were plotted with expected ^{210}Pb:^{226}Ra ingrowth curves. Concordance of these data with the expected ingrowth curves were used as an indicator of age estimate accuracy. A direct comparison of estimated age was also performed by plotting the radiometric age opposite estimated age. A linear regression was applied to these data and plotted with a line of agreement. A paired two-sample *t*-test was used to determine if a significant difference existed between the age estimates.

Results

A total of 747 Pacific grenadier was collected from waters off California, Oregon, and Washington. Of these fish, 128 with intact tails were used in the partial length analysis. All three partial lengths (PAF, SD, and HL) had linear relationships which predicted total length well with coefficients of determination close to 1. Head length had an r^2 = 0.988 (TL = 4.69(HL) + 20.2), snout to dorsal length had an r^2 = 0.987 (TL = 4.31(SD) + 21.2), and preanal fin length had an r^2 = 0.985 (TL = 2.53(PAF) + 73.0). Fish used in this analysis ranged in size from 124 mm to 688 mm TL. Because PAF had the largest proportion of the total length, it was chosen as the length used in growth analyses and was used to determine total length.

Traditional ageing

Fish chosen for traditional age determination numbered 178 and ranged in size from 22 mm to 272 mm PAF. Transverse sections were very difficult to age. APE was comparable between readers at about 6%, but *D* indicated precision was better for the first reader (6 and 10%, respectively). Forty-three percent of the readings between readers were within 1 year, 55% within 2 years, 80% within 5 years, and 95% within 10 years. Most of the differences between readers resulted from lower age estimates made by the second reader on old otolith sections (69%). Precision estimates were 6.3% (APE) between readers. Consultation between readers usually resolved differences greater than 10%. Age estimates were ultimately finalized by the first reader. For 32 of the specimens, the second otolith of the pair was sectioned for another attempt at ageing. Twenty could not be aged after examining both sections. Ninety-two of the otoliths selected could be aged (52%).

Three von Bertalanffy growth functions were fitted to the PAF lengths and estimated ages from growth zone counts to describe growth characteristics for females, males, and combined sexes; juveniles were factored into each determination (Fig. 3). The growth curves for males and combined sexes have similar growth curves, but females appear to have slower growth and a greater maximum length.

Age-group determination and core extraction

Otolith weight predicted section age for each sex well with coefficients of determination close to 1. Female regression age had an r^2 = 0.863 (regression age = 88.6(otolith weight) + 4.8) and male regression age had an r^2 = 0.927 (regression age = 91.3(otolith weight) + 4.6).

Six adult age-groups (3 female, 3 male), as determined by the age regressions, and one juvenile age-group were selected for radiometric analysis (Table 1). Age-groups ranged

Table 1. Composition of age-groups used for radiometric age determination. Mean length (PAF, mm) is given for comparison.

Age-group (years)	Sex	Number of fish	Number of otoliths	Sample size (g)	Mean length ± SD (PAF, mm)
1–3	Juvenile	46	92	0.9147	44 ± 2
14–20	Female	19	35	1.2279	143 ± 14
30–41	Female	15	29	0.9823	224 ± 19
43–54	Female	10	19	0.6242	245 ± 13
34–38	Male	21	39	0.5315	196 ± 12
40–45	Male	21	41	0.7458	207 ± 16
46–56	Male	12	23	0.4717	216 ± 19

from as low as 1 year for the juvenile sample to a maximum of 56 years for the oldest age-group. Dissimilar fish eliminated from the age-groups by comparing age regressions resulted in the removal of 9–33% of the potential group members. The number of fish in the adult age-groups ranged from 10 to 21, but the juvenile age-group numbered higher at 46 because the otoliths were smaller than the cores. Both otoliths were used from each fish, except where otoliths were lost in the coring process. Target sample size was 1 g. Some samples were closer to 0.5 g because sufficient sample was unavailable. Average core weight for the female samples, processed first, were slightly higher (0.03 g) than the targeted core weight (0.02 g). Male samples were cored a little smaller and more closely approached the target core weight. Total sample weight for each age-group ranged from 0.4717 g to 1.2279 g. Mean length was also calculated for each age-group (± SD).

Radiometric analysis

The results of the radiometric determinations are given in the form of activity (dpm·g^{-1}, disintegrations per minute per gram) and a ratio of activities (Table 2). The activity of ^{210}Pb increased, as expected, 25 times from 0.0022 dpm·g^{-1} in the juvenile samples to 0.0568 dpm·g^{-1} in the oldest adult sample. Standard error for this determination ranged from 4.4 to 7.8%. The activity of ^{226}Ra ranged from 0.0419 to 0.1245 dpm·g^{-1}, where the highest activity was from the juvenile sample. This was 2.2 times higher than the mean adult sample activity (0.0568 ± 0.01 dpm·g^{-1}) and nearly 3 times the lowest activity measured. The activity of the adult whole-otolith pair was similar to the lowest adult sample. Error for ^{226}Ra was very low and ranged from 1.07 to 4.35% (1 SE). The activity ratio of ^{210}Pb:^{226}Ra increased, as predicted by estimated age, from a low of 0.018 for the juvenile age-group to 0.798 for the oldest adult age-group.

Radiometric age determination

Radiometric age determined using the activity ratio was in close agreement with the average estimated age of the age-groups (Table 3). Each age-group range overlapped the radiometric age range. The low radiometric age for the 1–3 age-group indicated that uptake of exogenous ^{210}Pb (R_0, Campana et al. 1990) by juveniles was insignificant. Therefore, radiometric age was determined based on the measured activity ratios and no adjustment was necessary.

Age estimate accuracy

A graphical comparison of the age-groups versus the measured ^{210}Pb:^{226}Ra activity ratio plotted with the expected ingrowth curves indicated that age estimate accuracy was good (Fig. 4). The 1–3 age-group was closely associated with the ingrowth curve for an R_0 of 0.0. This indicated uptake of exogenous ^{210}Pb was insignificant and that it was the most accurate model for what to expect in adult otolith cores. The horizontal bar for each data point was the range of otolith weight derived age estimates. The 95% confidence interval from the otolith weight regression broadened the age group ranges by 3 to 7 years. This is a liberal estimate of this variation because outlying otoliths were eliminated with the multiple linear regression comparison (age estimates that differed between the two regressions by more than an arbitrary 10% were removed). The strong concordance of the data points with the expected ingrowth curve indicated the otolith weight regression was a good predictor of age and that growth zone age estimates were accurate.

A direct comparison of estimated age with radiometric age indicated ages were statistically in agreement (Fig. 5). Data points were all in close proximity to the line of agreement. A regression of these data showed a high correlation and a slope very close to 1 with an intercept near the origin. A paired two-sample *t*-test comparison indicated that there was no significant difference between estimated age and radiometric age (t = 0.427, P = 0.684).

Discussion

Partial length defined

Partial lengths have been used to indicate total length of grenadier from the north Atlantic (Atkinson 1991). The Pacific grenadier often has a tail that is apparently intact, but a few centimetres can be missing with little evidence. Most broken tails occurred during capture by trawling. In some cases, tails were lost during life and regenerated, where regenerated means growth of fin rays from the severed edge. For a few fish, approximately 10 to 20% of the total length was lost during life. In this study, approximately 80% of the fish collected had damaged, broken, or regenerated tails. For fish greater than 500 mm TL, calculated tail loss from trawling was as high as 18% of the total length.

Use of a standardized partial length is needed for consistency in grenadier fishery data collection. Many different partial lengths have been used and some are poorly defined and ambiguous (Atkinson 1991; Wilson 1982; Bergstad 1990; Matsui et al. 1990; Kelly et al. 1997). Because the anus is often distorted by barotrauma, the distance from the first anal fin ray to the snout is the most easily measured. This distance is best defined as pre-anal fin length and should be given the unambiguous acronym PAF. For these reasons, PAF was chosen as the partial length for the Pacific grenadier in this study. It is further proposed that the partial length measurement for grenadier be standardized in these terms and that use of HL or SD be used where the anal fin is missing or badly damaged.

Traditional age estimation

A graphical comparison of growth curves from this study and other studies revealed differences and similarities

Table 2. Results of radiometric analysis for ^{210}Pb and ^{226}Ra activity determinations for each age-group. A single whole otolith pair from one fish is also listed for comparison with core results.

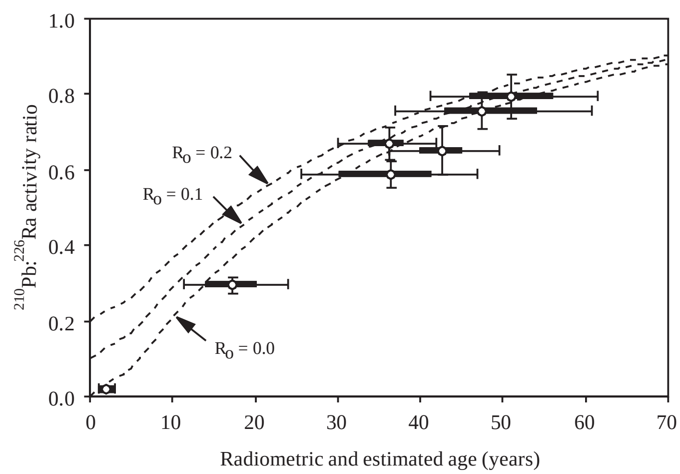
Age-group (years)	Sample size (g)	^{210}Pb activity ($dpm \cdot g^{-1}$)[a]	^{210}Pb % error (SE)	^{226}Ra activity ($dpm \cdot g^{-1}$)	^{226}Ra % error (SE)	^{210}Pb:^{226}Ra activity ratio
1–3	0.9147	0.0022	7.8	0.1245	1.94	0.018
14–20	1.2279	0.0124	5.9	0.0419	1.38	0.295
30–41	0.9823	0.0320	4.4	0.0546	1.26	0.587
43–54	0.6242	0.0385	5.1	0.0510	1.37	0.755
34–38	0.5315	0.0391	5.4	0.0583	1.07	0.670
40–45	0.7458	0.0415	5.5	0.0639	4.35	0.649
46–56	0.4717	0.0568	4.8	0.0711	2.45	0.798
Otolith pair[b]	1.2826	NM	NA	0.0419	2.88	NA

Note: NM, not measured; NA, not applicable.
[a]Corrected to time of capture.
[b]Whole otolith pair from an individual adult fish.

Table 3. Comparison of estimated and radiometric ages for each age-group.

Age-group (years)	Average estimated age (years)	Radiometric age (years)	Radiometric age range (years)
1–3	2	1.2	1.1–1.3
14–20	17	14.0	13.1–14.9
30–41	36	31.9	29.6–34.4
34–38	36	39.2	35.5–43.3
40–45	43	37.5	32.6–43.7
43–54	48	49.2	43.7–55.9
46–56	51	55.8	48.4–65.9

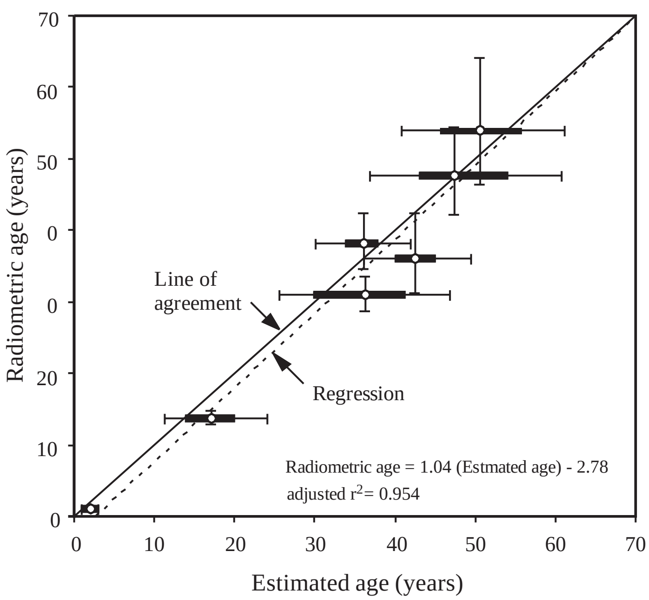
Fig. 4. Observed ^{210}Pb:^{226}Ra activity ratios for age-groups plotted with expected activity ratio ingrowth curves. Horizontal bars represent age range of the otolith cores in the age-group (with 95% confidence interval). Vertical bars indicate analytical uncertainty in the determination of ^{210}Pb and ^{226}Ra activities. Expected activity ratio ingrowth curves also incorporate possible initial uptake ratios (R_0) of ^{210}Pb:^{226}Ra.



(Fig. 6). Kulikova (1957) did not calculate growth parameters, but for comparative purposes, growth parameters were calculated using the average length given for each estimated age. In that case, the growth constant was very high (k = 0.435) and longevity was very low (~6 years) relative to validated estimates in this study (Fig. 3). This growth constant was unrealistically greater than many fast-growing fishes (i.e., tuna and billfishes; Prince and Pulos 1983). The growth curve fitted to age estimates determined by Matsui et al. (1990) was very similar to the male and combined sexes growth curves in this study. It must be noted that Matsui et al. (1990) used snout to anus length (less than PAF by approximately 1%). The upper end of the female growth curve in this study is largely unsupported by data, but it is important to mention that some otoliths from females greater than 300 mm PAF were aged greater than 90 years. These otoliths were not included in this study because growth increments were very fine and confusing toward the margin and were also aged as low as 65 years. The difficulty of ageing otolith sections for this species was similar to recent findings for the roundnose grenadier (Kelly et al. 1997). The asymptotic length of the female growth curve more closely approximates the maximum size reported (~900 mm TL, Cohen et al. 1990). Therefore, it is possible that females get larger than males with increasing age, as may also be indicated by Matsui et al. (1990).

A comparison of historic and recent age estimates indicates the age and growth of the Pacific grenadier was variable and age was usually underestimated (Table 4). The first Pacific grenadier age estimates were for specimens collected in the Bering and Okhotsk seas and the Kuril-Kamchatka trench, where scales were used to estimate a longevity of 6 years (Kulikova 1957). Scales can be unreliable, however, as a conserved record of age (Simkiss 1974; Yoklavich and Boehlert 1987). This result is an underestimate by a factor of 10 or more. Brothers et al. (1976) used extrapolation of daily increments to estimate the age of one fish. A Pacific grenadier with similar length would actually be about 3 times older. The first attempt at quantification of annual growth increments in transverse otolith sections used 15 fish collected off San Diego, California (Mulcahey et al. 1979). They found otoliths difficult to age and cautiously estimated age at 15 to 25 years for the size range of fish used. In this study, similarly sized fish would be 2 to 3 times older. A detailed examination of scales, vertebrae, and otoliths from 130 fish collected off southern California resulted in an estimated longevity of approximately 20 years (Wilson 1982). Otolith sections were determined, however, to be too ambiguous for age estimation. This was true for about half of the otoliths used in this study, but Wilson's (1982) longevity es-

Fig. 5. Comparison of estimated age versus radiometric age. The solid line represents agreement between age estimates (slope of 1). The broken line was a regression of the compared ages. Bars for estimated ages represent the age range of each age-group (with 95% confidence interval). Bars for the radiometric ages represent the range between high and low age based on analytical uncertainties.



timate was low by a factor of 3 to 4. Most recently, otolith break-and-burn was used on 60 fish collected off northern Baja California, Mexico, to central California (Matsui et al. 1990). Longevity was estimated to be greater than 60 years, which is very similar to the result of this study.

Radiometric analysis

Use of otolith cores for radiometric age determination was typically limited to a minimum of approximately 1 g of material because of instrument detection limits (Kastelle et al. 1994; Fenton and Short 1995). Because of cleaner procedures and the application of isotope-dilution TIMS, sample size can be lower than 0.5 g (Table 2). Reduced error associated with ^{226}Ra determination make the analytical uncertainty of ^{210}Pb determination the limiting factor in radiometric ageing. In this study, uncertainty in ^{210}Pb activity contributes 7.8% of the error where activity was very low (juvenile sample) and decreases to approximately 5% as age and activity increase (Table 2). Typically, the error for ^{226}Ra determination was lower than 2%. In this study, reported error greater than 2% was attributed to high calcium in the sample. An alteration of the technique remedied this problem (Andrews et al. 1999).

In some radiometric ageing studies, ^{226}Ra activity was inferred from other samples, rather than measured directly, because of the detection limits of ^{222}Rn emanation (Bennett et al. 1982; Campana et al. 1990; Watters 1995; Kline 1996). Results from this study indicate ^{226}Ra activity can vary among samples and presumably among individuals (Table 2). The ^{226}Ra activity for the juvenile sample was the highest activity measured in this study. Some juvenile specimens were collected from upper slope areas near the Columbia River mouth. Because freshwater is a source of ^{226}Ra, elevated environmental levels of ^{226}Ra may explain the higher activity (Osterberg et al. 1963; Moore 1996). Use of an average ^{226}Ra activity in this study causes significant changes to radiometric age. This emphasizes the necessity of measuring ^{210}Pb and ^{226}Ra for each sample in future studies.

Assumption clarification

The radiometric ageing technique requires several assumptions depending on the analytical circumstances. The typical assumptions are as follows. (*i*) The otolith is a closed system with no loss or migration of post-formational radionuclides in the ^{226}Ra decay series through to ^{210}Po; this is necessary because loss of nuclides would result in lower ^{210}Pb activity and subsequently underestimated age. (*ii*) Uptake of exogenous nuclides in the ^{226}Ra decay series is negligible relative to ingrowth from ^{226}Ra; this is necessary to attribute ^{210}Pb activity in the otolith to ingrowth from ^{226}Ra. (*iii*) Uptake of ^{226}Ra is in constant proportion to the otolith mass growth rate; this assumption is necessary when whole otoliths are used and is largely circumvented when otolith cores are used (Kimura and Kastelle 1995).

The assumption that an otolith is a closed system is well supported by studies of coraline carbonate properties and of otolith structure and formation. A proposed violation of this assumption is the loss of ^{222}Rn, the daughter of ^{226}Ra, from the otolith via diffusion as a noble gas (West and Gauldie 1994). Although loss of ^{222}Rn seems possible because it is a non-reactive gas that can enter the interstitial lamellar spaces via α-recoil (Fleischer et al. 1975) and diffuse out of the otolith, there is strong evidence that indicates this does not occur in the in vivo otolith. Any ^{222}Rn that enters the lamellar spaces is entering a matrix of water and otolin, a secreted neuroprotein (Pannella 1980). A recent study of the sorption characteristics of ^{222}Rn in the presence of organic matter indicated that the ^{222}Rn would tend to remain in the sorbent otolin (Morawska and Phillips 1993).

The lack of Ostwald ripening and cementation in otoliths support the assumption that there is no post-formational migration of nuclides. Ostwald ripening, a process in which small crystals (more soluble than larger ones) dissolve and reprecipitate onto larger crystals, has been demonstrated not to occur in otoliths. Studies using ^{45}Ca indicate that once calcium is incorporated it remains immobilized in otoliths (Simkiss 1974; Campana 1983; Yoklavich and Boehlert 1987). This suggests that the crystalline structure of the otolith is conserved and well regulated during and after growth. This is supported by the existence of polyanions in the organic matrix, called nucleation barriers, which confine crystalline growth to one direction (Wheeler and Sikes 1984).

The only exogenous nuclide in the ^{226}Ra decay series that is an uptake concern for samples that are greater than 2 years old (from date of collection) is ^{210}Pb. Any exogenous ^{210}Po would have decayed away and all nuclides from ^{226}Ra through to ^{210}Pb are very short lived (seconds to minutes). Because ^{210}Pb exists in the natural environment, it must be assessed as a potential contaminant. Measuring ^{210}Pb in juvenile otoliths is currently the most applicable technique for assessing the possibility of direct incorporation of ^{210}Pb.

The assumption that ^{226}Ra uptake is in constant proportion to mass growth-rate is only necessary when whole otoliths

Fig. 6. Comparison of von Bertalanffy growth functions from two other studies with the results of this study. The growth function for Kulikova (1957) was calculated using the published average length-at-age where total lengths were converted to PAF.

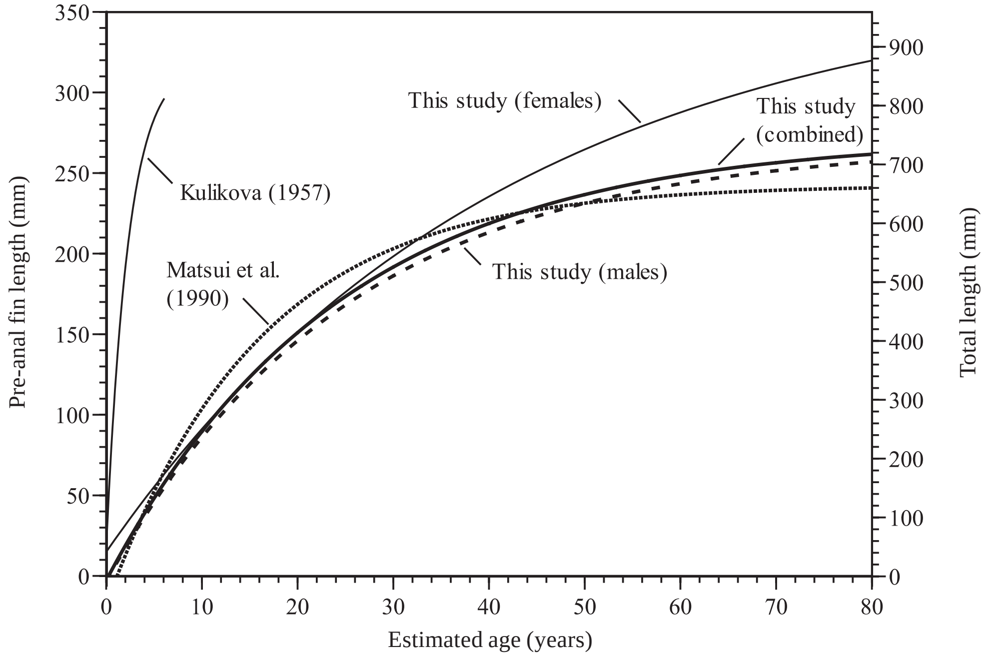


Table 4. Comparison of age and longevity estimates for the Pacific grenadier. Age estimates for fish of the given length(s) are listed with the ageing technique and number of fish.

Author	Technique	Number of fish	Length (TL, mm)	Age at length (years)
Kulikova (1957)	Scales	92	820 (max.)	6+
Brothers et al. (1976)	Daily increment extrapolation	1	580	10–11
Mulcahey et al. (1979)	Sagittal otolith sections	15	640–840	15–25
Wilson, R.R., Jr. (1982)	Scales and vertebrae	130	820 (max.)	18–20
Matsui et al. (1990)	Sagittal otolith break and burn	60	600–700	>60

and an otolith mass growth model are used (Bennett et al. 1982). A violation of this assumption was documented for the blue grenadier (Gadidae: *Macruronus novaezelandiae*; Fenton et al. 1990). The radiometric ageing technique could not be used on whole otoliths because the activity of ^{226}Ra decreased in otoliths from juveniles to adults. This was attributed to an ontogenetic movement from estuarine and inshore waters, where environmental ^{226}Ra can be significantly higher (Moore 1996), to deeper, offshore waters. A radiometric analysis of otolith cores from this species, however, was successful (Fenton and Short 1995).

The two most important assumptions in this study were: (*i*) the otolith was a closed system and (*ii*) the incorporation of exogenous ^{210}Pb was negligible. These assumptions can be more closely scrutinized with the increased accuracy of the radiometric ageing technique using cleaner techniques and isotope-dilution TIMS (Andrews et al. 1999). If ^{222}Rn loss was a problem, the radiometric disequilibria of ^{210}Pb:^{226}Ra would consistently underestimate fish age. In this study, it is very unlikely that the traditional age estimates of each age-group were underestimated by the precise amount necessary to compensate for ^{222}Rn loss. Because the use of TIMS has increased the accuracy of the radiometric ageing technique, tolerance for such an error was very low. Exogenous ^{210}Pb was eliminated as a possible factor by ageing the juvenile age-group (1–3 years). It was highly unlikely that uptake of ^{210}Pb in adults would be different from juveniles.

Age estimate accuracy

The strong concordance of measured ^{210}Pb:^{226}Ra with the expected ingrowth curves validated age estimation using growth increments in the Pacific grenadier (Fig. 4). Because the 1–3 age-group showed extremely low ^{210}Pb activity, the most applicable ingrowth model was for an R_0 of 0.0. Variation of the data points around the ingrowth curve could be explained by the analytical uncertainty associated with the technique and the age-group age range. Although variation of otolith weight derived age could have been as high as ±10 years for the oldest fish, use of the multiple linear regression as a tool to discriminate dissimilarities reduced this variability to 10% of the regression age estimate. Because this variation could not be accurately assessed, the 95% confidence interval for the otolith weight regressions was used to estimate the contribution of this error to the age range.

Statistical agreement between estimated age and radiometric age further supports validation of the age estimates (Fig. 5). Radiometric age determinations confirm a longevity of at least 55.8 years (–7.4, +10.1 years) and validate the annual periodicity of the growth increments used to estimate age. Based on similar growth increment interpretations, the longevity of the Pacific grenadier may be at least 73 years.

Life histories

Longevity estimates for two similar grenadier species of the North Atlantic differ considerably. The roundnose grenadier has longevity estimates that range from 50 to 72 years, which were similar to the Pacific grenadier (Bergstad 1990; Kelly et al. 1997). Age validation of these estimates was limited to young fish using marginal increment analysis (Gordon and Swan 1996). This species can attain a greater length (1.5 to 2 m TL) and appears to have a higher growth rate than the Pacific grenadier. In contrast, the roughhead grenadier has a relatively low estimated longevity of 13 years for males and 22 years for females (Savvatimsky 1994). Age estimates, however, were based largely on scales and validation has not been performed. Grenadier from other parts of the world are also thought to have a relatively low longevity (Rannou 1976; Middleton and Musick 1986; Morales-Nin 1990; Specchi et al. 1995). It is possible that the grenadier family consists of a series of species complexes that differ in growth characteristics, as is thought to be the case for the eastern Pacific Ocean rockfishes (*Sebastes* spp.; Mary Yoklavich, National Marine Fisheries, Pacific Fisheries Environmental Laboratory, Pacific Grove, CA 93950, personal communication), but age validation is necessary for most members of both families.

Maturity at length from several studies can be used to estimate age at maturity for the Pacific grenadier. Length at maturity is estimated to occur at approximately 500 mm TL (ca. 170 mm PAF) for males and from 460 to 650 mm TL (ca. 153 to 230 mm PAF) for females (Stein and Pearcy 1982; Matsui et al. 1990). Based on the growth functions calculated for each sex, maturity may occur between 20 and 40 years for females and at 20 years for males. This is much later in life than the typically larger and faster-growing roundnose grenadier, where 50% maturity occurs at 8 to 11 years (Kelly et al. 1997).

It is important to consider the potential age of Pacific grenadier being landed in Oregon and Monterey Bay, California, because landings have increased substantially (Fig 1). Landings for Oregon have been about 91% male, where most range in size from about 450 to 650 mm TL (Mike Hosie, Oregon Department of Fish and Wildlife, PO Box 5430, Charleston, OR 97420, personal communication). The small percentage of females landed were typically larger (550 to 650 mm TL). Based on the calculated growth functions, fish being landed may range in age from 20 to 50 years for males and 30 to 40 years for females. Landings for Monterey Bay, California, consist of fish ranging in size from 550 to 650 mm TL (~95%) with some small individuals at approximately 300 mm TL (~5%). Sex composition was not known. Based on both growth functions, age of the large fish may be from 30 to 50 years and the small fish may be approximately 10 years old. Because maturity occurs late in life, some of the smaller fish being landed may be sexually immature.

Much remains unknown about the Pacific grenadier that would be necessary to develop a sustainable fishery. Population size and distribution and the movement of individuals in the population are probably the most important aspects of this fishery that need research. Catch per unit effort information needs to be compiled and analyzed for abundance estimates in areas already being fished. Other studies including break-away tag and recapture coupled with deep trawling and submersible transects could be used to estimate population characteristics at depths greater than current commercial fishing depths. Until this information is gathered, the Pacific grenadier fishery should be managed cautiously by setting strict and small quotas.

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