Lead–radium dating of orange roughy (*Hoplostethus atlanticus*): validation of a centenarian life span

Allen H. Andrews, Dianne M. Tracey, and Matthew R. Dunn

Abstract: Life-span estimates for orange roughy (*Hoplostethus atlanticus*) range from ~20 years to well over 100 years. In this study, an improved lead–radium dating technique provided independent age estimates from sagittal otoliths. This technique used the known properties of radioactivity for lead-210 and radium-226 to determine the validity of fish age estimates. An improvement to lead–radium dating using mass spectrometry allowed the use of smaller samples than previously possible; therefore, an application was made to otolith cores, the first few years of otolith growth. This approach circumvented the use of whole otoliths and alleviated many of the assumptions that were necessary in previous lead–radium dating applications. Hence, it was possible to critically evaluate lead–radium dating as a tool in fish age validation. The measurement of lead–radium ratios for a series of age groups that consisted of otolith cores, grouped based on growth-zone counts from thin sections, showed a high degree of correlation to the expected lead–radium ingrowth curve. This finding provided support for age estimation procedures using thin otolith sectioning. As independent estimates of age, the results indicated that fish in the oldest age group were at least 93 years old, providing robust support for a centenarian life span.

Résumé : Les estimations de la longévité de l'hoplostèthe orange (*Hoplostethus atlanticus*) varient de ~20 ans à nettement plus d'un siècle. Dans notre étude, une méthode améliorée de détermination de l'âge basée sur le plomb et le radium fournit des estimations de l'âge indépendantes à partir des otolithes sagittaux. La technique utilise les propriétés connues de radioactivité du plomb-210 et du radium-226 pour déterminer la validité des estimations de l'âge chez les poissons. Une amélioration de la détermination de l'âge basée sur le plomb et le radium par l'utilisation de la spectrométrie de masse permet l'analyse d'échantillons plus petits qu'il n'était possible antérieurement; c'est pourquoi nous l'avons appliquée aux noyaux des otolithes qui représentent les premières années de croissance des otolithes. Cette méthodologie évite l'utilisation d'otolithes entiers et atténue plusieurs des présuppositions antérieurement nécessaires pour la détermination de l'âge à l'aide du plomb–radium. Il est ainsi possible d'évaluer de manière critique la détermination de l'âge par le plomb–radium comme outil de validation de l'âge chez les poissons. Les mesures des rapports plomb–radium pour une série de classes d'âge représentées par des noyaux d'otolithes regroupés d'après le nombre de zones de croissance sur des coupes minces, présentent une forte corrélation avec la courbe attendue de recrutement plomb–radium. Cette observation vient valider les procédures d'estimation de l'âge basées sur les coupes minces d'otolithes. En tant qu'estimations indépendantes de l'âge, nos résultats indiquent que les poissons appartenant au groupe le plus âgé ont au moins 93 ans, ce qui appuie solidement l'hypothèse d'une longévité d'un siècle.

[Traduit par la Rédaction]

Introduction

Orange roughy (*Hoplostethus atlanticus*, family Trachichthyidae) is widely distributed at depths of 600–1400 m in most temperate oceans and is a common target species for deepwater trawl fisheries around the world. The development of deepwater fisheries has been relatively recent, with the first major orange roughy fisheries developing off New Zealand in the late 1970s, followed by fisheries off Australia in the mid-1980s, smaller fisheries in the northeastern Atlantic Ocean in the early 1990s, and fisheries off Namibia, Chile, and the southern Indian Ocean through the mid- to late 1990s (Bax et al. 2005; Japp and James 2005; Large and Bergstad 2005). Orange roughy fisheries have proven difficult to manage sustainably; many of these areas have supported boom-and-bust fisheries, with much of the catch

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occurring in the first few years, followed by a period of substantial catch rate declines, and culminating in fishery closures or abandonment (Branch 2001; Clark et al. 2007; Sissenwine and Mace 2007).

The most well developed and productive orange roughy fisheries in the world have been from the waters off New Zealand (Branch 2001). Of these, the largest fishery has been situated on the Chatham Rise, where annual catch levels of around 40 000 tonnes (t) were reached in the late 1980s. However, by 2007–2008, these were reduced to about 10 500 t following a series of total allowable commercial catch (TACC) reductions, and sustainability at this level has been a growing concern (Ministry of Fisheries 2008). A similar scenario was realized for orange roughy fisheries off Australia, where catch quotas were reduced over time (Bax et al. 2005); in 2006, orange roughy were declared threatened by the Australian Department of Environment and Heritage. An approach perceived as conservative was applied to recent seamount fisheries off Namibia with the aim of establishing sustainability. The fisheries appeared to have suffered quickly from overexploitation (Boyer et al. 2001; Butterworth and Brandão 2005); however, an intermittent spawning aggregation is being considered as a hypothesis for the observed changes in the fishery (McAllister and Kirchner 2001; Oelofsen and Staby 2005).

Although major efforts have gone into managing orange roughy fisheries, after three decades of exploitation, almost all stocks have been fished down substantially, and concerns are raised regularly about whether sustainability is attainable (Clark et al. 2007; Sissenwine and Mace 2007). High vulnerability to fishing pressure combined with rapid development of the fishery led to a substantial catch before management was introduced (Clark 2001; Lack et al. 2003; Morato and Clark 2007). When the accumulated biomass of a stock has been fished down, the sustainability of the fishery will be dependent on stock productivity. The productivity of orange roughy stocks is believed to be especially low but remains poorly understood (Francis and Clark 2005; Sissenwine and Mace 2007).

In most stock assessments, productivity is determined using ageing analyses to estimate growth, age at maturity, longevity, rate of natural mortality, and recruitment variability. Although there is growing confidence in current age interpretations of deepwater fish species and in proposed mechanisms for how some may attain high longevity (Cailliet et al. 2001), many age estimates are based solely on sagittal otolith growth zone counts. In some cases, the lack of a convincing age validation associated with these counts has lead to disbelief in the age interpretations; the orange roughy, believed to live to ages over 100 years, has been one of the most debated species (Gauldie and Cremer 1998; Branch 2001).

Numerous age estimation studies have been performed on orange roughy, the majority on populations from New Zealand and Australia. These studies have provided estimated age at maturity of between 23 and 40 years, a maximum age exceeding 100 years, and some estimates of ages exceeding 150 years (Smith et al. 1995; Tracey and Horn 1999; Green et al. 2002). Age estimation studies of populations in the North Atlantic and off Chile and Namibia have been guided by the New Zealand and Australian protocol and similarly concluded that orange roughy have centenarian life spans (Clark et al. 1999; Allain and Lorance 2000; Payá et al. 2006). However, there are alternative hypotheses based on an alternative interpretation of growth zones and modeling studies of otolith growth arguing that orange roughy are a relatively rapid-growing, short-lived species (e.g., Romanek and Gauldie 1996; Gauldie and Sharp 2001).

The most recent estimations of orange roughy age have utilized growth-zone counts from longitudinal thin sections of sagittal otoliths and made the assumption that the zone counts represent age (Tracey and Horn 1999). The resolution of growth zones in older otoliths has proven difficult, and the zone counts can have high uncertainty. In addition, a between-institute bias in zone count interpretation was documented (Francis 2006). Although the general consensus in the international community has been that orange roughy are a slow-growing, long-lived species, the argument that they are actually short-lived and fast-growing, combined with limited age validation studies to date and the imprecision and potential bias in otolith zone counts, has highlighted the need for further and conclusive age validation.

The age validation techniques that have been applied to deepwater fishes range widely in efficacy and precision (Campana 2001). Some techniques rely on establishing a temporal context to early growth by measuring changes in otolith zones or fish length; for instance, marginal increment analysis and length frequency analysis have been applied to orange roughy (Mace et al. 1990). The disadvantage of these techniques is that it is necessary to extrapolate the findings to provide support for older ages because of a loss of growth-zone or length-mode resolution. Other age validation methods rely on marking and recapturing older fish (e.g., oxytetracycline injection and tagging), but recovery of deepwater fishes is time-consuming and the survival rates are likely to be low (Campana 2001). Advances in the use of radioactive proxies for age have provided opportunities for independent age determination of deepwater fishes, and the primary techniques currently in use are bomb radiocarbon ($\Delta^{14}C$) and lead–radium dating, both of which can work well either independently or together (e.g., Andrews et al. 2007). However, for orange roughy, bomb radiocarbon dating is unsuitable because the species lacks an epipelagic phase in its life cycle, a requirement if the timing of the influx of bomb radiocarbon is to provide an accurate temporal marker (Kalish 2002).

Lead–radium dating relies on the incorporation of radium-226 (^{226}Ra), a naturally occurring calcium analog, from the environment into the otolith and its subsequent decay to lead-210 (^{210}Pb). By measuring the disequilibria of these two radioisotopes in otolith material, an independent estimate of age can be determined based on the known ingrowth rate of ^{210}Pb from ^{226}Ra (Smith et al. 1991). Fenton et al. (1991) applied lead–radium dating to orange roughy otoliths and provided radiometric age estimates that were the first to support a centenarian life span. In this study, it was necessary to pool a large number of whole otoliths to acquire enough material for measurement of ^{226}Ra, because the technology used at the time was not sensitive enough to detect ^{226}Ra at the low levels typically present in otolith material. It was also necessary to assume that ^{226}Ra was incorporated in constant proportion to otolith mass growth. In addition, when considering the decay of ^{226}Ra to ^{210}Pb with respect to otolith growth, a gradient of ^{210}Pb activity is formed where core material has the highest ^{210}Pb:^{226}Ra activity ratio (the oldest part) decreasing to the outer layer (the youngest part). Because of the gradient, it was necessary to make an additional assumption: mass growth must be modeled by assuming that growth rates are known to some degree, which introduces circularity with respect to radiometric age determination. Francis (1995) described two approaches to avoid this assumption, reanalyzed the Fenton et al. (1991) lead–radium data, and reached a similar conclusion: a centenarian longevity was likely for orange roughy.

Increased sensitivity in the techniques used to determine ^{226}Ra activity has made it possible to reduce the sample size necessary to detect ^{226}Ra in otolith material with increased precision and accuracy. As a result, the first few years of growth can now be extracted from the core of orange roughy otoliths and analyzed for both ^{210}Pb and ^{226}Ra; hence, there is no need for sample weight dependence in calculating age or the assumption that ^{226}Ra uptake was constant (Andrews et al. 1999*a*; Campana 2001). In addition, advances in mass spectrometry have significantly reduced the error and processing time associated with the measurement of ^{226}Ra, which makes the measurement of ^{210}Pb the limiting factor in lead–radium dating (Andrews et al. 1999*b*). By using the same small sample of core material (the first few years of growth) for the measurement of both ^{210}Pb and ^{226}Ra activities, the problems associated with mass growth assumptions or variable uptake of ^{226}Ra are largely circumvented (Campana et al. 1990; Kimura and Kastelle 1995).

The goals of this study were (*i*) to provide independent age validation of orange roughy using the improved lead–radium dating procedure on orange roughy otolith cores and (*ii*) to address long-standing concerns over the validity of lead–radium dating as a tool for age determination in fishes. In addition, these findings provided an opportunity to discuss orange roughy age estimation and the importance of valid age determinations in light of recent research advances and perspectives.

Materials and methods

Samples of orange roughy otoliths used in this study were from archival collections previously aged using the growth-zone count method. The first otolith from each fish had been longitudinally thin-sectioned to allow growth-zone counting and the second “sister” otolith was used for the radiometric analyses. Otoliths were selected to form estimated age groups, which were chosen to create as narrow an age range for each age group, while covering as much of the life span as possible. In a feasibility study (Andrews and Tracey 2003), only samples aged by National Institute for Water and Atmospheric Research (NIWA) were used, but to obtain sufficient samples for older age groups, otoliths collected by the New Zealand Seafood Industry Council (SeaFic) and aged by Central Ageing Facility (CAF) in Australia were also used in the complete study. The number of otoliths required for orange roughy age groups was based on lead–radium information determined from the feasibility study. The specifics of sample composition (i.e., collection details of each fish used) were tabulated elsewhere (Andrews 2009).

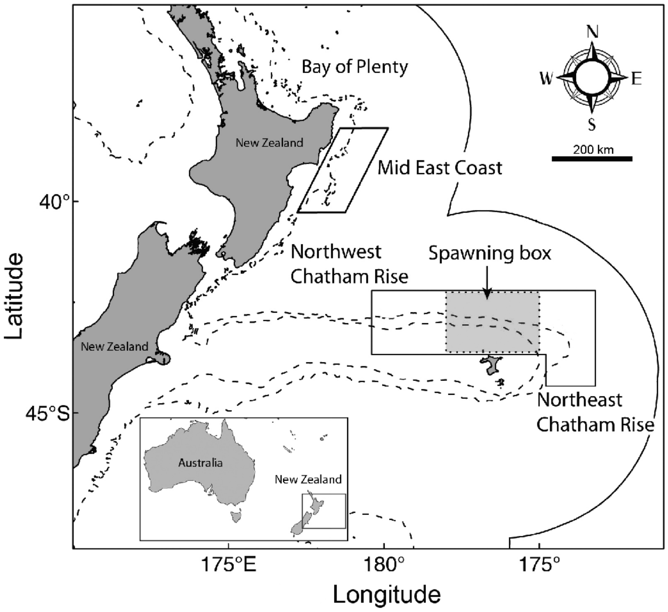
The orange roughy otoliths were selected from various regions off the north island of New Zealand (Fig. 1). For organizational purposes, the feasibility study remains separated from the follow-up age groups because of minor differences in protocol and development of the procedure used for the other groups. The youngest group analyzed was part of the feasibility study and consisted of whole juvenile otoliths collected from the Northwest Chatham Rise region in 1989 (group 0–2 years). The otoliths used in the adult samples were collected from the Chatham Rise and Bay of Plenty regions in 1984 (group 34–38 years), 1990 (group 61–71 years), and 1996 (group 70–81 years). In the following study, the samples analyzed primarily filled in the older age groups. These otoliths came from four regions (Spawning Box, Northeast and Northwest Chatham Rise, and Mid East Coast) and were all collected in 2002 and 2003. The age groups were as follows: ORH 1, 25–30 years; ORH 2, 40–45 years; ORH 3, 60–69 years; ORH 4, 70–80 years; ORH 5, 81–88 years; ORH 6, 90–108 years. Samples from the Spawning Box contributed exclusively to ORH 1 and ORH 2 and composed part of ORH 3 with Mid East Coast samples. The oldest age groups (ORH 4, ORH 5, and ORH 6) consisted of otolith samples from all regions. Note that each sample was a collection of aged otoliths that was processed once; no replication was possible in this study because of low sample availability and the limitations of sample size in the application of lead–radium dating (for a detailed discussion on lead–radium dating, see Andrews 2009).

Sample preparation and processing

Based on the dimensions and weight of 4-year-old whole otoliths from several samples made available for the feasibility study and from information on juvenile otolith weight data available from Mace et al. (1990), a target core sample size of 5.5 mm long × 2.5 mm wide × 0.8 mm thick, weighing approximately 0.012 g, was chosen. The proximal surfaces of each otolith were ground down by hand on a Buehler Ecomet III lapping wheel with 120- to 320-grit wet–dry silicon–carbide paper until the otolith was the target dimensions and weight. The resulting core looked very similar to a juvenile otolith in shape (pyramidal) and size. An exception was the group 0–2 years, which was processed whole. Hand-grinding was chosen for this study over the use of a micromilling machine primarily to follow the method used in the feasibility study and also because of the ease of this method.

It was ascertained from the feasibility study that dimensions alone were not enough to be certain that the core was not heavier than targeted size, as the average weight of cored otoliths was often found to be greater than expected (~0.024 g). To correct for this in this study, each core was first ground down using otolith dimensions as a guide, then weighed, and reground if the weight was greater than targeted. This was repeated until the target dimensions were achieved; in these cases, a weight of just under 0.02 g was targeted to avoid the loss of too much material and to allow for mass loss during the cleaning process (typically 3%–5%). Samples were cleaned of any adhering contamination following Andrews et al. (1999*b*). The weight of all of the cores and pooled otolith age groups were measured to the nearest 0.1 mg.

Fig. 1. Areas within the New Zealand exclusive economic zone (EEZ) referred to in the text from which orange roughy (*Hoplostethus atlanticus*) otolith samples were collected and used in the lead–radium analyses.



Radiochemical protocol

A detailed protocol describing sample preparation, chromatographic separation of ^{226}Ra from barium and calcium, and analysis of ^{226}Ra using mass spectrometry was described by Andrews et al. (1999*b*). These procedures have not changed for this study, except for two aspects of the analysis: (*i*) radium recovery was improved by shifting the collection interval on the final chromatography column to begin after the first 200 μL (as opposed to after 250 μL), and (*ii*) purified radium samples were analyzed using an improved inductively coupled plasma mass spectrometry (ICPMS) technique, which is less prone to ionization suppression (Craig Lundstrom, University of Illinois–Urbana Champaign, Department of Geology, Urbana, Illinois, USA, unpublished data).

^{226}Ra analyses were performed by isotope dilution techniques following the procedure of Andrews et al. (1999*b*), except that analyses in this study were performed using a Multicollector ICPMS in place of TIMS. The new mass spectrometer analysis took place on a Nu Plasma$^{\text{TM}}$ HR instrument located in the Department of Geology at University of Illinois–Urbana, Champagne. The analysis introduced the chemically purified radium into a desolvating nebulizer as a 2% HNO_3 solution. The sample was converted into dry aerosols, which were swept into the argon plasma and the mass spectrometer. Sensitivity during radium analysis corresponds to approximately 25 counts per second (cps)·ppq^{-1} radium at an uptake rate of 70 μL·min^{-1}. Once in the spectrometer, isotope ratios were measured by switching the magnet back and forth between atomic mass units (amu) 226 and 228 after a 1-min background taken at amu 225.5 or 227.5. An individual sample analysis consisted of 10 measured ratios representing 10 s integrations on each amu peak. After each analysis, the system was washed successively with 5% HNO_3 and 2% HNO_3 for 10 min until no residual radium signal could be observed. Count rates on samples in this study were usually >100 cycles·s^{-1} for each radium isotope, compared with the nominal background on clean acid, which was <1 cycle·s^{-1}.

Radiometric age was determined from the measured ^{210}Pb and ^{226}Ra activities. Because the activities were measured using the same sample, the calculation was independent of sample mass. Radiometric age was calculated using an equation derived from Smith et al. (1991) to compensate for the ingrowth gradient of ^{210}Pb–^{226}Ra in the otolith core:

$$t_{\text{age}} = \left[\ln \left(\frac{1 - \left(\frac{A^{210}\text{Pb}}{A^{226}\text{Ra}} \right)}{(1 - R_0)\left(\frac{1 - e^{-\lambda t}}{\lambda t} \right)} \right) / (-\lambda) \right] + T$$

where t_{age} was the radiometric age at the time of analysis, A^{210}Pb was the measured ^{210}Pb activity at time of analysis (reported as disintegrations per minute per gram (dpm·g^{-1})), A^{226}Ra was the ^{226}Ra activity measured using ICPMS (reported as dpm·g^{-1}), R_0 was the activity ratio of ^{210}Pb and ^{226}Ra initially incorporated, λ was the decay constant for ^{210}Pb (ln(2)·22.26 year^{-1}), and T was the estimated core age based on the first few growth zones. An initial uptake ratio of $R_0 = 0.0$ was used based on the close agreement of the measured juvenile age group lead–radium ratio with the expected ingrowth curve; however, other studies have accounted for what appeared to be exogenous ^{210}Pb with minor adjustments necessary (e.g., Kastelle et al. 2000; Stransky et al. 2005). A radiometric age range, based on the analytical uncertainty, was calculated for each sample by using error propagation through to the final age determinations (2 standard errors, SE). Calculated error included the standard sources of error (i.e., pipetting, spike, and calibration uncertainties, etc.), alpha-counting statistics for ^{210}Pb, and the ICPMS analysis routine.

The 95% confidence interval (2 SE) from lead–radium dating was used to interpret the validity of growth-zone counts and to determine the strength and limits of age confirmations. To describe the trend between age estimation from growth-zone counts and lead–radium dating, a simple linear regression was applied. Age agreement or disagreement between the methods, in terms of potential ageing bias, were given considering the potential error (2 SE).

Results

The six age groups ORH 1 to ORH 6 covered a range of prerecruitment juveniles to old adults and consisted of groups of 13 to 32 individual otolith cores, with an age group sample weight of 0.227–0.464 g (Table 1). The mean core weight was consistent and close to the target weight of a 4-year-old otolith (~0.012 g). The results from three of the four feasibility study age groups were added to provide more lead–radium dating results, but a sample that experienced accidental loss of ^{228}Ra tracer during the spike addition process (group 61–71 years) was not included (Andrews and Tracey 2003). Sample weight for the feasibility study ranged from a very low weight for the juvenile sample (0.040 g) to the highest group weight approaching 1 g (0.842 g). Mean core weights for the feasibility study were slightly higher because they were extracted in the exploratory phase of the overall study.

Table 1. Summary of the orange roughy (*Hoplostethus atlanticus*) samples processed in this study and in the previous feasibility study.

	Zone count group (years)	Mean zone count (years)	Time since capture (years)	No. of otoliths	Sample weight (g)	Mean core weight (g)
ORH sample series						
ORH 1	25–30	28	2.7	31	0.426	0.0137
ORH 2	40–45	42	2.7	32	0.464	0.0145
ORH 3	60–69	65	3.0	24	0.402	0.0168
ORH 4	70–80	74	3.1	26	0.339	0.0130
ORH 5	81–88	85	2.9	14	0.242	0.0173
ORH 6	90–108	98	2.7	13	0.227	0.0175
Feasibility study	0–2	2	13.3	9	0.040	0.0044
	34–38	36	18.7	37	0.842	0.0228
	61–71[a]	66	12.7	20	0.474	0.0237
	70–81	76	7.0	28	0.701	0.0250

Note: Mean estimated growth-zone count and average time since capture for each group, with resultant pooled sample number and weight, are given. An average core weight for each sample is given as an indicator of the consistency of coring.

[a] This sample was not considered further in this study because of the accidental loss of the radium-228 tracer during the spike addition process (Andrews and Tracey 2003).

Table 2. Radiometric results for orange roughy (*Hoplostethus atlanticus*).

	Zone count group (years)	^{210}Pb activity	^{226}Ra activity	^{210}Pb:^{226}Ra activity ratio	2 SE
ORH sample series					
ORH 1	25–30	0.0426±6.1	0.0784±2.20	0.5437	0.0350
ORH 2	40–45	0.0591±4.9	0.0755±2.17	0.7824	0.0418
ORH 3	60–69	0.0696±5.3	0.0795±2.18	0.8761	0.0498
ORH 4	70–80	0.0759±5.2	0.0826±2.24	0.9189	0.0524
ORH 5	81–88	0.0624±9.3	0.0672±3.19	0.9285	0.0915
ORH 6	90–108	0.0693±5.5	0.0688±2.56	1.0067	0.0606
Feasibility study[a]	0–2	0.0647±18	0.2090±5.43	0.3096	0.0583
	34–38	0.0522±4.4	0.0692±2.99	0.7549	0.0399
	70–81	0.0561±4.6	0.0599±5.14	0.9365	0.0644

Note: Listed are the estimated growth-zone count ranges and measured ^{210}Pb and ^{226}Ra activities for all samples ± 2 standard errors (SE) for the measured activities. Sample activities for ^{210}Pb and ^{226}Ra were reported in disintegrations per minute per gram (dpm·g^{-1} ± percent error).

[a] One sample was eliminated from the original four age groups because of the accidental loss of the radium-228 tracer during the spike addition process (Andrews and Tracey 2003).

The activities of ^{210}Pb and ^{226}Ra were measured for all samples (Table 2). The activity of ^{210}Pb was relatively inconsistent with increasing age, as would be expected for samples with consistent ^{226}Ra levels; however, the variable activity of ^{226}Ra compensated for what would have been a random age distribution, the result being a steady increase in the ^{210}Pb:^{226}Ra activity ratio with increasing estimated age. It is interesting to note that the measurable activities from the extraordinarily small juvenile sample were possible because the activity of ^{226}Ra was relatively high and the overall age (time since collection plus average age) was 14 years. The range of sample contribution of ^{226}Ra to the measured radium ratios using ICPMS was 9%–72%, which accounts for some of the variability in measurement error.

The estimated age of the samples from the growth-zone counts were similar to the radiometric ages determined from the measured ^{210}Pb:^{226}Ra activity ratios (Table 3). There was considerable agreement for the sample series, with one age group not in agreement (feasibility study age group 34–38 years) based on the margin of error from lead–radium dating (2 SE). This sample was aged lower using lead–radium dating than the estimate from growth-zone counts.

Correspondence of the measured ^{210}Pb:^{226}Ra ratios with the expected ingrowth curve indicated that growth zone derived age estimates were precise (Table 3), within a level of uncertainty that increases with age, and provides support for orange roughy age estimation procedures (Fig. 2). This plot is only possible for total sample age (age from growth-zone counts plus the time since capture). For all but two of the samples, the measured ratio fell within 2 SE of the expected ingrowth curve. The youngest sample (total sample age of about 14 years) was in close agreement with the expected ratio, indicating that the effect of exogenous ^{210}Pb was low or negligible. This was the basis for choosing an initial uptake ratio (R_0) equal to zero.

Table 3. Summary of growth-zone counts and radiometric ages for orange roughy (*Hoplostethus atlanticus*).

	Zone count group (years)	Mean zone count (years)	Radiometric age (years)	Radiometric age range (years)
ORH sample series				
ORH 1	25–30	28 (±10)	24	22–27
ORH 2	40–45	42 (±15)	48	42–55
ORH 3	60–69	65 (±23)	66	55–82
ORH 4	70–80	74 (±26)	79	63–113
ORH 5	81–88	85 (±30)	83	57–undefined
ORH 6	90–108	98 (±35)	Undefined	93–undefined
Feasibility study	0–2	2 (±2)	1	0–3
	34–38	36 (±13)	29	24–34
	70–81	76 (±27)	83	61–undefined

Note: Mean growth-zone age and radiometric age were calculated from the measured ^{210}Pb:^{226}Ra activity ratios and corrected for time since capture. Radiometric age range is 2 standard errors (SE) from the analytical uncertainty and error propagation. A potential uncertainty for otolith zone counts using 2 SE from the age-misclassification matrix, used in New Zealand stock assessments, is provided to illustrate potential age determinations.

Fig. 2. Plot of the measured ^{210}Pb:^{226}Ra ratios with respect to total sample age (mean growth-zone count plus the time since capture) for orange roughy (*Hoplostethus atlanticus*) samples processed in this study (shaded circles) and in the feasibility study (open squares), plotted with the expected ^{210}Pb:^{226}Ra ingrowth curve. Horizontal error bars (some within the symbol size) represent 2 standard errors (SE) around the mean of the sample growth-zone age determined by National Institute of Water and Atmospheric Research (NIWA) and Central Ageing Facility (CAF). The vertical error bars represent the analytical uncertainty associated with measuring the ^{210}Pb:^{226}Ra ratio (2 SE).

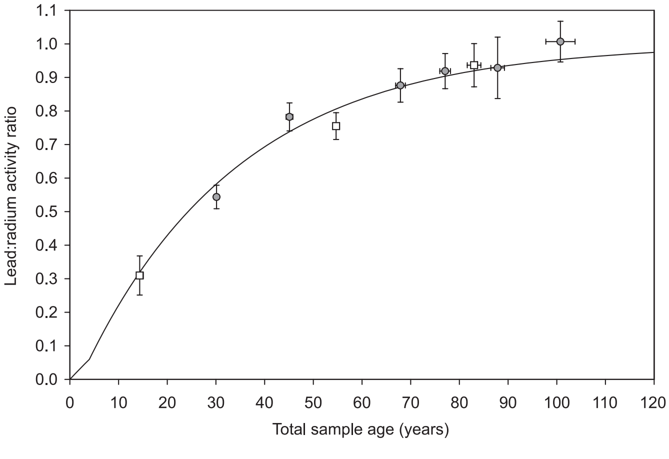
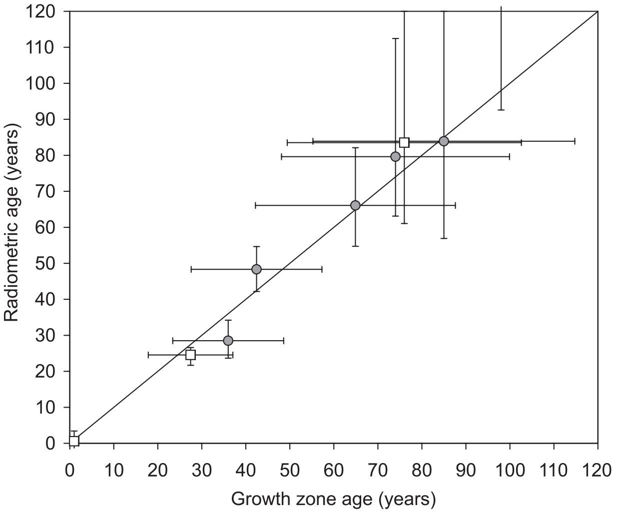


Fig. 3. Orange roughy (*Hoplostethus atlanticus*) age agreement plot of growth-zone age estimates versus radiometric age estimates (corrected to time of capture) for samples processed in this study (shaded circles) and in the feasibility study (open squares), plotted with a line of agreement for comparison. Out of interest, the horizontal error bars indicate the potential uncertainty in otolith zone counts (2 standard errors, SE), derived from an age-misclassification matrix used in New Zealand stock assessments (Dunn 2006; A. Hicks, University of Washington, School of Aquatic and Fishery Sciences, Seattle, WA 98105, USA, unpublished data). Vertical error bars represent the analytical uncertainty associated with measuring ^{210}Pb and ^{226}Ra (2 SE). The upper end of some error bars and the age of one sample exceed the figure limits because age (or its upper bound) was undefined (the ^{210}Pb:^{226}Ra ratio exceeded 1.0).



An age-agreement plot allowed for direct comparison between the mean growth-zone count and the radiometric age (Fig. 3). One data point (ORH 6) could not be plotted as it had a measured ratio that narrowly exceeded 1.0 (Table 2), resulting in an undefined radiometric age (Table 3). Correlation between the two ageing methods was good (R^2 = 0.979). The slope of the regression was close to 1.0 (regression slope = 1.08), indicating that there was general agreement between the methods; however, this result does not take into consideration the change in radiometric age uncertainty as the measured ^{210}Pb:^{226}Ra activity ratio increases. An estimate of zone-count error from other studies was included in Fig. 3 out of interest and provided an indication of a potentially wide margin of uncertainty (Dunn 2006; A. Hicks, School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98105, USA, unpublished data). By treating the radiometric age determinations as independent estimates of age, using core material, and making no assumptions with regard to otolith growth, the results indicated that otoliths in the oldest age group were at least 93 years old.

Discussion

The application of lead–radium dating to orange roughy otolith cores was successful, with good agreement between the mean age from growth-zone counts and the lead–radium technique. Use of otolith core material avoided potential problems associated with the application of otolith mass growth models and provided the most accurate age determinations to date for orange roughy. The minor assumption typically associated with the use of a known-age core was well supported by the age validation study performed by Mace et al. (1990) on otolith margin type, where the first few years of growth were well documented. The radiometric findings provided refined support for age estimates that exceed 100 years, even though the uncertainty in radiometric age increased as lead–radium ratios approached one. Independent of other age estimation procedures, lead–radium dating in this study provided support for a centenarian life span.

Making precise and accurate growth-zone counts appears to be difficult for orange roughy. Francis (2006) described calibration data sets used in New Zealand and Australia in which the same otoliths were read twice, some involving replicate readings by the same reader and some involving different readers from the same or different institutions. The variability in growth-zone counts was found to be least when a single reader re-read the otoliths, then greater for two readers from the same institute, and greater again for two readers from different institutions. There was also substantial variability in what each reader considered to be a readable otolith. An age-misclassification (error) matrix was constructed from these data for use in stock assessment models and was estimated from the between-institute comparisons, as it was believed that this would introduce a larger and more appropriate variation for the assigned age range around the true range (Dunn 2006; A. Hicks, School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98105, USA, unpublished data). The imprecision in ageing estimated from this analysis was substantial; for example, the 95% confidence interval for an orange roughy aged at 40 years was estimated to be 26–54 years.

Perhaps of more concern has been a suspected bias in age estimation. This suspected bias resulted in age-frequency data being excluded from use in stock assessments in New Zealand, the rationale being that there was insufficient confidence that differences observed between samples were real and not simply artifacts arising from ageing problems. One possible source of bias appears to be associated with the detection of the transition zone (TZ), a region on the otolith where the width of the growth zone changes from wide to narrow, assumed to be the result of a switch from primarily somatic growth to gamete production at the onset of maturity (Francis and Horn 1997). Francis (2006) found that there was a tendency to count more growth zones, therefore to age older, when a TZ was recorded, with a relative bias of about 6 years. This would result in an ageing problem around the ages when the TZ was formed, roughly between 20 and 45 years, and could explain the offset in the age group 34–38 years.

Francis (2006) also found that estimated age at length varied substantially between years and areas in a way that could not be attributed easily to real changes in population structure. For example, estimated mean age at length in one specific area changed by 30% over a 2-year period. If orange roughy were growing slowly, then it should not be possible for age at length to change so much over a short period: this observation is therefore likely to be either a sampling or an ageing bias. Francis (2006) then demonstrated likely ageing biases occurring in the calibration data sets; the estimated biases were greatest between institutes, at about 10%, but varied in direction depending on the otolith sample considered. For the present study, imprecision in growth-zone counts adds uncertainty to the age composition of the age groups but does not change the conclusions about overall longevity.

For orange roughy, examination of otolith margin growth and length frequencies provided the first temporal evidence for a life span greater than 50 years, but this estimate was based on trends observed with small fish extrapolated to the largest fish (Mace et al. 1990). Further support for relatively high longevity came from one of the earliest applications of lead–radium dating to fishes (Fenton et al. 1991; Francis 1995) and shortly thereafter with an application of radiocarbon dating (Kalish 2002). Although radiocarbon dating (not to be confused with bomb radiocarbon dating) provided support for a centenarian life span, with rough age estimates that were complicated by other factors, lead–radium dating was the first to begin to provide more concrete evidence.

The seminal radiometric study on orange roughy by Fenton et al. (1991) used pooled whole otolith samples and an approach that made it necessary to make some educated assumptions. The study did not perform any growth zone derived age estimations, but instead sought to independently determine age for groups of fish with similar length and otolith weight. For the method to work, there needed to be little or no (*i*) between-individual variability in otolith mass growth rate and (*ii*) variability in ^{226}Ra uptake throughout the growth of the otolith. In addition to these factors, there were important assumptions about the very nature of the lead–radium dating technique; the otolith needed to be a closed system to (*i*) the ingrowth of ^{210}Pb from ^{226}Ra with no loss of ^{226}Ra daughter products and (*ii*) the incorporation of exogenous sources of the decay series radionuclides (not from the decay of incorporated ^{226}Ra). Within these assumptions, the most conceivable problems were (*i*) the potential loss of ^{222}Rn (daughter product of ^{226}Ra and a noble gas) and (*ii*) the incorporation of exogenous ^{210}Pb or polonium-210 (used as a proxy for ^{210}Pb in alpha-spectrometry). These concerns could not be thoroughly addressed when Fenton et al. (1991) performed the analyses on orange roughy otoliths, but subsequent studies have provided support for the assumptions that were necessary (Francis 1995; Smith et al. 1995). In some cases, the assumptions have been tested directly.

The veracity of the lead–radium technique was questioned by a number of papers addressing the assumptions. In a perspective paper, West and Gauldie (1994) argued that there were uncontrollable errors that invalidated the technique for fish age estimation but provided a series of observations and conclusions that failed to consider equally viable explanations that do not discredit the radiometric technique. In an attempt to measure loss of ^{222}Rn from orange roughy otoliths, Gauldie and Cremer (1998) openly recognized anomalous results, a faulted technique, and negative values that imply the contrary; nevertheless, they concluded from weak trends in rather dubious data that loss of ^{222}Rn was a problem and that this invalidated old ages. The inconclusive quality of those data was reiterated in a follow-up application that reported a loss of 26%–28% (Gauldie and Cremer 2000), but these findings are inconsistent with determinations made in this study because large losses as such would create an upper limit to the measured lead–radium ratios. Furthermore, evidence supporting the author's conclusions was cited (e.g., incomplete concepts from a report by Whitehead and Ditchburn (1996)), but a prior publication that (*i*) specifically addressed ^{222}Rn diffusion from orange roughy otoliths and (*ii*) provided evidence to support a long life span (Whitehead and Ditchburn 1995) was ignored (i.e., Gauldie and Cremer 1998, 2000; Gauldie and Romanek 1998).

Perhaps the most scientifically robust study to date on potential loss of ^{222}Rn from otoliths was performed on red snapper (*Lutjanus campechanus*) and red drum (*Sciaenops ocellatus*) from the Gulf of Mexico (Baker et al. 2001). In this study, two species with relatively large otoliths and some of the highest ^{226}Ra activities recorded from otolith material were analyzed; the study resulted in low ($\leq$4.1%) to no loss of ^{222}Rn. The measured loss was further considered more of a surface emanation because larger otoliths liberated relatively less ^{222}Rn. They concluded that such losses were probably insignificant relative to other sources of error associated with lead–radium dating. This would be especially true in the case of otolith cores because the loss would be temporary and much less significant with time. In another study, Pacific halibut (*Hippoglossus stenolepis*) otoliths revealed no evidence of ^{222}Rn loss, but experimental error from low lead–radium levels led to somewhat inconclusive results (Kastelle and Forsberg 2002).

In the present study, a small group of juvenile otoliths provided indirect evidence, similar to the approach used by Kastelle and Forsberg (2002), that ^{222}Rn loss was not a significant factor for orange roughy. These whole otoliths were aged at 0 to 2 years but were collected 13.3 years prior to analysis for lead–radium content. The measured ratio was consistent with the total sample age of approximately 14 years with a margin of error of about 2 years. If the loss of ^{222}Rn for this sample was on the order of 25%, as was proposed by Gauldie and Cremer (2000), then radiometric age would have been approximately 6 years less than the known age of 14 years of the sample itself. The scenario was similar for other studies in which juvenile otoliths have been used to determine early ingrowth ratios (e.g., Andrews et al. 2005, 2007).

Another scenario to consider with regard to loss of ^{222}Rn is the potential affect on the measured lead–radium ratio as age approaches 100 years. In a study performed on yelloweye rockfish (*Sebastes ruberrimus*), otolith cores provided measured lead–radium ratios that were very close to secular equilibrium (Andrews et al. 2002). If there was a consistent problem with the loss of ^{222}Rn throughout the period of otolith growth, then secular equilibrium would not and could not be attained. It was at approximately 99 years that secular equilibrium was approached to within 95% for the ingrowth model used in the present study (core age of 4 years). Provided that there was a ^{222}Rn loss on the order of 25% for the oldest orange roughy age group (90–108 years with an average age of 98 years), the measured ratio (1.007, 2 SE low of 0.9461) would have been far less, approximately 0.675 and a radiometric age of 30–40 years. In addition, none of the samples analyzed in this study, as well as other studies (e.g., Andrews et al. 2002), would have exceeded this ratio. The findings presented here for orange roughy support the hypothesis that loss of ^{222}Rn was not a significant factor in the determination of age from lead–radium dating.

The potential problem of ^{226}Ra uptake variability was largely circumvented with the use of otolith cores (Campana et al. 1990), but detection limits for ^{226}Ra combined with the small otolith core size for orange roughy precluded an analysis of otolith core material by Fenton et al. (1991). Although it is possible that otoliths with consistent ^{226}Ra levels were measured in the whole otolith study, more support was necessary to alleviate concerns about this assumption. Based on a comprehensive synopsis, ^{226}Ra uptake can vary considerably for orange roughy, with a range of approximately 0.05–0.2 $\text{dpm}\cdot\text{g}^{-1}$ (Andrews 2009); however, the present study provided additional support that ^{226}Ra activity levels can also be relatively consistent among the core samples (average activity of $^{226}\text{Ra} = 0.0740 \pm 0.0053\ \text{dpm}\cdot\text{g}^{-1}$, $n = 9$). The notable exception was the whole juvenile age group ($0.209 \pm 0.011\ \text{dpm}\cdot\text{g}^{-1}$). This group consisted of otoliths that were very small, with an average weight that was about three to five times lower than the average core weight. This finding implies that within the first 2 years of growth, ^{226}Ra uptake may be greater relative to later in life. The reason for this finding is unknown but may be attributed to differences in habitat, diet, metabolism, or all of the above. Relatively high variability of ^{226}Ra activities measured in other studies reinforce the hypothesis that uptake can be highly variable and that mass growth rate models using an average ^{226}Ra activity provide radiometric ages that should have greater uncertainty than was assumed at the time. Although the radiometric ages in this study support those of Fenton et al. (1991), this study also places emphasis on the necessity for sample-specific lead–radium measurements to avoid ^{226}Ra uptake assumptions (Francis 2003).

In an age and growth study of Northeast Atlantic orange roughy, lead–radium dating was applied to whole otoliths following a technique similar to that of Fenton et al. (1991), but the results were considered somewhat inconclusive (Allain and Lorance 2000). In the study, age estimates were made by counting growth zones in whole and thin-sectioned otoliths and indicated a high degree of age-estimate departure between whole otolith and thin-section ageing beginning at approximately 40 years. The finding was similar to the classical plot discovered for Pacific ocean perch (*Sebastes alutus*; Beamish 1979), indicating that there were differences in age on the order of decades between whole otolith and thin-section ageing. Allain and Lorance (2000) did not consider the lead–radium results as conclusive because of ageing imprecision and what appeared to be inconclusive lead–radium results (P. Lorance, IFREMER, 150 quai Gambetta, BP 699, 62321 Boulogne-sur-mer, France, personal communication). Use of successive dissolutions on one otolith by Allain and Lorance (2000) provided similar results to the findings of Whitehead and Ditchburn (1996). Both dissolution studies were performed making the assumption that the core material (youngest) was at the center of the otolith and that successive acid dissolutions would provide greater and greater ^{210}Pb activities; however, both studies revealed anomalous distributions of ^{210}Pb and concluded that the growth of the otolith was not concentric (Whitehead and Ditchburn 1996; P. Lorance, personal communication). The findings in Whitehead and Ditchburn (1996) have been cited as support for the argument that lead–radium dating cannot be applied to otolith material (Gauldie and Cremer 1998, 2000), yet the observable reason for the anomalous results was invalid assumptions about otolith growth geometry.

Allain and Lorance (2000) cite that the mean ages for the four otolith groups analyzed ranged from 29 to 80 years. An analysis of the lead–radium data (provided by P. Lorance, personal communication) and the margin of error associated with the measurements of ^{210}Pb and ^{226}Ra revealed that the minimum age for fish in the samples was 45 years (2 SE). This determination was conservative because the measured ratios were from whole otolith samples and age would have been diluted by younger material. These findings provided support for older age estimates obtained from thin sections in that study and provided additional support for hypotheses that challenge low longevity estimates for orange roughy.

Although there have been challenges to the centenarian longevity assertion for orange roughy, this assumption has been accepted for some time in stock assessment and fishery management. The alternative hypothesis of low longevity and rapid growth would be associated with greater productivity, but the repeated failure of orange roughy stocks to rebuild rapidly following catch reductions gives further evidence that this hypothesis is not correct. Moreover, recent stock assessments and analyses have suggested productivity since the inception of the fisheries may be even lower than is currently being assumed (Sissenwine and Mace 2007; M.R. Dunn, unpublished data). Fishing down the age structure may have additional impacts on sustainability that have yet to be fully considered (Berkeley et al. 2004; Beamish et al. 2006; Cailliet and Andrews 2008). For a long-lived species like orange roughy, relatively low fecundity and highly episodic recruitment also contribute to their low productivity (Pankhurst and Conroy 1987; Longhurst 2002).

Based on reasonable assumptions that were supported by orange roughy growth data (Smith et al. 1995), the radiometric data presented by Fenton et al. (1991) supported a maximum age for orange roughy that exceeded 84 years (Francis 1995). The findings of the present study provide even more robust support for the centenarian age estimates obtained from otolith thin sections. As independent estimates of age, the radiometric results indicated that fish in the oldest age group were at least 93 years old, and by circumventing assumptions that were previously necessary, lead–radium dating of otolith core material has validated a centenarian life span for orange roughy.

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