



Age determination and validation studies of marine fishes: do deep-dwellers live longer?

G.M. Cailliet^{a,*}, A.H. Andrews^a, E.J. Burton^a, D.L. Watters^b,
D.E. Kline^c, L.A. Ferry-Graham^d

^aMoss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA

^bCalifornia Department of Fish and Game, 411 Burgess Drive, Menlo Park, CA 94025, USA

^cPSC 811, Box 354, FPO AE 09699-1001, USA

^dSection of Evolution and Ecology, University of California, Davis, CA 95616, USA

Abstract

Age determination and validation studies on deep-water marine fishes indicate they are difficult to age and often long-lived. Techniques for the determination of age in individual fish includes growth-zone analysis of vertebral centra, fin rays and spines, other skeletal structures, and otoliths (there are three sets of otoliths in most bony fish semicircular canals, each of which is made of calcium carbonate). Most have regular increments deposited as the fish (and its semicircular canals) grows. The most commonly used otolith for age determination is the largest one called the sagitta. Age validation techniques include: (1) tag–recapture, often combined with oxytetracycline injection and analysis in growth-zones of bone upon recapture; (2) analysis of growth-zones over time; and (3) radiometric approaches utilizing a known radioactive decay series as an independent chronometer in otoliths from bony fishes. We briefly summarize previous studies using these three validation approaches and present results from several of our radiometric studies on deep-water, bony fishes recently subjected to expanding fisheries. Radiometric age validation results are presented for four species of scorpaenid fishes (the bank, *Sebastes rufus*, and bocaccio, *S. paucispinis*, rockfishes, and two thornyhead species, *Sebastolobus altivelis* and *S. alascanus*). In addition, our analysis of scorpaenids indicates that longevity increases exponentially with maximum depth of occurrence. The reason that the deep-water forms of scorpaenid fishes are long-lived is uncertain. Their longevity, however, may be related to altered physiological processes relative to environmental parameters like low temperature, high pressures, low light levels, low oxygen, and poor food resources. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Age; Deep sea; Growth; Longevity; Marine fishes; Radiochemistry; Rockfishes; Scorpaenidae; Validation

* Corresponding author. Tel.: +1-831-632-4432; fax: +1-831-632-4403.

E-mail address: cailliet@mlml.calstate.edu (G.M. Cailliet).

1. Introduction

Age estimation provides information on fish life histories that is essential for effective fishery management. Common techniques used for determining the age of (“ageing” Bagenal, 1974) fishes include growth-zone analysis of vertebral centra (Cailliet, 1990), fin rays and spines (Brennan and Cailliet, 1989), other skeletal structures, and most commonly, otoliths (Bagenal, 1974; McFarlane and Beamish, 1995). Indeed, there have been two recent international symposia focused entirely on the importance of otoliths in fish life history studies (Secor et al., 1995; Fossum et al., 2000). Often, these structures are sectioned, polished, and stained to enhance the readability of their growth-zones (Cailliet et al., 1986). The growth-zones are then counted and the fish’s age determined.

In many fish studies, the annual periodicity of growth-zones in these structures has been assumed but seldom validated (Beamish and McFarlane, 1983). Growth-zones can be correlated with environmental fluctuations affecting the growth of the fish (Williams and Bedford, 1974). Thus, environmental cycles on a variety of time scales may cause growth rings to be laid down in calcified structures leading to error in age estimates. Further, in many deep-water fishes, discernible growth-zones exist in otoliths despite the relative constancy of the environment in which they live, but they are often very difficult to count accurately. This is mainly because they grow slowly and produce fine growth-zone structure, especially in the larger specimens (Mace et al., 1990; Bergstad, 1995; McFarlane and Beamish, 1995).

Such problems make validation essential for accurate age and growth studies, and three main age validation techniques have been developed. The first is tag–recapture, often combined with oxytetracycline injection, and analysis of growth-zones upon recapture. This involves collecting a wide range of sizes of a given species, keeping them alive so they can be tagged, injected, and released, and collecting sufficient numbers of individuals over time to demonstrate the rate at which growth-zones are deposited. However, keeping deep-water fishes alive after capture and transport to the surface is difficult because they suffer barotrauma (Mace et al., 1990; Bergstad, 1995; McFarlane and Beamish, 1995).

The second age validation technique is to analyze growth-zone characteristics (opacity, translucency) and increment dimensions over time (also known as marginal increment analysis). This again requires collecting large numbers of samples, but in this case covering all seasons, and even depths because in some species (e.g. sablefish, *Anoplopoma fimbria*, and thornyheads, *Sebastolobus* spp.), different stages or ages live at different depths. There is a certain amount of subjectivity involved in characterizing the margins, but this can be a powerful tool. However, in the deep sea, which is so remote and expensive to sample, obtaining sufficient samples to validate growth using this technique is difficult. Plus, growth-zones in deep-sea animals are often narrow and difficult to discern, let alone measure.

Recently, a third, very promising technique has been developed which utilizes a known radioactive decay series in the cores of previously aged fish otoliths to provide an independent age estimate of bony fishes (Bennett et al., 1982; Campana et al., 1990). This technique has proven most valuable to long-lived fishes, especially those from deep water which are difficult to sample and keep alive. The most common approach exploits the disequilibria of lead-210 (^{210}Pb) and radium-226

(^{226}Ra) in otoliths as a natural chronometer (Smith et al., 1991; Bergstad, 1990, 1995).

Three assumptions must be met to use the radiometric approach (Bennett et al., 1982; Campana et al., 1990). First, the calcified structure acts as a closed system for radium and its daughter products. Second, the initial activity ratio of ^{210}Pb : ^{226}Ra in the calcified structure should be much smaller than one, ideally close to zero, and is known or measured. Third, the uptake rate of ^{226}Ra is proportional to mass growth of the structure during the lifetime of the fish. The second and third assumptions can be minimized or eliminated if otolith cores (otolith material at the center or nucleus) are used.

An essential requirement for utilizing ^{210}Pb : ^{226}Ra disequilibria for age determination is the capability of measuring the activity of these radioisotopes with high precision and accuracy at very low levels (Andrews et al., 1999b). In age determination of fishes, the measurement of ^{210}Pb has been accomplished using α -spectrometry on its daughter product, polonium-210 (^{210}Po ; Flynn, 1968). For ^{226}Ra , however, three techniques have been used: (1) scintillation counting of its daughter radon-222 (^{222}Rn) via radon emanation; (2) direct α -spectrometry of ^{226}Ra in a filtered precipitate; and (3) direct determination of ^{226}Ra via isotope-dilution Thermal Ionization Mass Spectrometry (TIMS; Cohen and O’Nions, 1991). Most recently, a technique that measures both isotopes has been used and has shown promise (Baker et al., 2001a,b). Each of these techniques has been successful in validating age estimations, but each has varying degrees of error and advantage.

Early radiometric studies on four species of sharks were unsuccessful due to violation of two of the three assumptions (closed system and constant incorporation of radionuclides into the porous cartilage) used to age these fishes (Welden et al., 1987). Similar problems have been encountered when attempting to use radiometric techniques with sturgeon pectoral fin rays (Burton et al., 1999). This is unfortunate because several studies have found that sturgeon are long-lived and slow growing (Probst and Cooper, 1954; Brennan and Cailliet, 1989, 1991; Rien and Beamesderfer, 1994), but validation has only been possible using tag–recapture and oxytetracycline marking of bone growth-zones.

The radon emanation technique has been applied in radiometric determination of age of ten fish species, in which nine were members of the family Scorpaenidae (Burton et al., 1999; Kastle et al., 2000). This technique uses the α -decay of ^{222}Rn as a proxy for ^{226}Ra and has typically had a large error associated with each determination (Andrews et al., 1999b). Refinement of the technique in studies over time, however, have eliminated violation of the mass growth assumption and reduced the margin of error by using otolith core material, the first few years of growth (Burton et al., 1999), and by increasing the sensitivity of the radon emanation system (Craig Kastle, NOAA, NMFS, Alaska Fisheries Science Center, Seattle, WA, personal communication).

Direct α -spectrometry of ^{226}Ra has been used in radiometric age determination studies of six fish species (see Table 1 in Burton et al., 1999). This technique has been used primarily by researchers in Australia and New Zealand, where ^{226}Ra is isolated by coprecipitation with barium, using barium-133 (^{133}Ba) as a yield tracer (Fenton et al., 1990). Because this technique is more sensitive, relatively low sample weights have been used (~ 1 g), but the error associated with this technique has been relatively high (~ 12 – 21%) (Andrews et al., 1999b).

Determining ^{226}Ra in otoliths using radon emanation and direct α -spectrometry has

been an effective tool in radiometric age determination, but aspects of each technique made improvement desirable (Andrews et al., 1999b). Because some fish species have a longevity that may exceed 100 yr, the utility of the radiometric technique becomes increasingly dependent on the error of the technique. As the activity of ^{210}Pb asymptotically approaches the activity of ^{226}Ra ; the error becomes a larger proportion of the age estimate. A reduction of this error would reduce the age estimate uncertainty and would increase the applicability of the technique to fish approaching 150 yr (Andrews et al., 1999b).

In recent studies, the use of TIMS has been refined and applied to the radiometric age validation of four species of deep-sea fishes, the Pacific and giant grenadiers (Family Macrouridae, *Coryphaenoides acrolepis*; Andrews et al., 1999a and *Albatrossia pectoralis*; Burton, 1999), the Atlantic tarpon (Family Megalopidae, *Megalops atlanticus*; Andrews et al., 2001), and the bocaccio rockfish (Family Scorpaenidae, *Sebastes paucispinis*; Andrews et al., 2000a). The use of TIMS has reduced the error associated with the measurement of ^{226}Ra and made it possible to apply the radiometric technique successfully to samples with lower weight and lower ^{226}Ra than previously attempted (Andrews et al., 1999b). We are also using TIMS in our radiometric age validation studies of additional scorpaenid fishes as well as deep-sea corals (Andrews et al., 2000b; Wilson et al., 2000).

These radiometric age validation techniques have been used on marine fishes, summarized by Burton et al. (1999), with Kastle et al. (2000) adding results for *Sebastolobus alascanus* (shortspine thornyhead) and four species of *Sebastes* (*S. aleutianus*, rougheye rockfish; *S. alutus*, Pacific ocean perch; *S. borealis*, shortraker rockfish; and *S. polyspinis*, northern rockfish). In addition, recent studies on fishes such as the snappers (family Lutjanidae) and drums (family Sciaenidae) have also used this approach (Baker et al., 2001a,b).

Because the inshore areas along most coastlines are heavily fished, fishing activities are concentrating more and more on deep-water fishes (Moore, 1999; Moore and Mace, 1999). In addition, it appears that many of these deeper-dwelling fishes are long-lived. Thus, it would be interesting to find out, what features of their life histories and physiology might account for this longevity.

The objectives of this paper are to compare growth-zone and radiometric age estimates for four species of scorpaenids (bank rockfish, *Sebastes rufus*; bocaccio rockfish, *S. paucispinis*; and two thornyheads, longspine thornyhead, *Sebastolobus altivelis*, and shortspine thornyhead; Fig. 1). Then we present a preliminary analysis of the relationship between scorpaenid longevities and their maximum depth of occurrence, with a discussion of the possible physiological mechanisms that might help account for increased longevity with depth.

2. Materials and methods

2.1. Traditional methods to determine age

Otoliths from thornyheads, and bank and bocaccio rockfishes were collected from various locations in the nearshore and offshore marine environment along the coast of California in three separate studies conducted during the 1990s (Watters, 1993; Cailliet et

al., 1996; Kline, 1996; Andrews et al., 2000a). Age of individual fish in each study was estimated using one of the two techniques. Transverse sections were taken from otoliths for all species, mounted to glass slides, and read under a dissecting microscope. Some bocaccio age estimates used the break-and-burn technique (Don Pearson, NMFS, personal communication). Growth-zones visible in these cross sections were used as an estimate of age for each fish, where either reflected or transmitted light was used to enhance the detail in the sections. In each study, the hypotheses tested were that traditional age estimates were the same as those produced using radiometry (Watters, 1993; Kline, 1996; Burton et al., 1999; Andrews et al., 2000a).

2.2. Radiometric determination of age

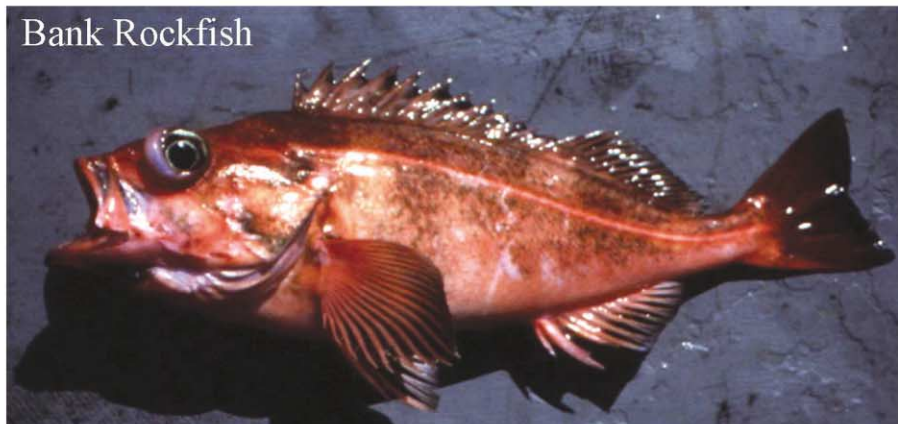
The naturally occurring uranium-238 (^{238}U) decay series contains the radioisotope pair ^{226}Ra and its daughter product ^{210}Pb ; the pair used for age determination of long-lived fishes. Radium-226 has a half-life of approximately 1600 yr, and decays through a series of short-lived daughter isotopes, with half-lives of only days, minutes, or seconds, to the more stable isotope ^{210}Pb , which has a half-life of 22.26 yr.

Radiometric age determination of fishes relies on the incorporation of ^{226}Ra , a water soluble calcium analog, from the environment into the calcium carbonate matrix of otoliths and its subsequent decay into ^{210}Pb (Smith et al., 1991; Fenton and Short, 1992). Because the parent and daughter isotopes of radium are not calcium analogs and are relatively insoluble or short-lived in seawater, therefore less abundant, they are not readily incorporated into calcified tissues. Lead-210 is generated in situ within the otolith by radioactive decay of ^{226}Ra , a process called ingrowth (Fenton and Short, 1992). Because the half-life of ^{226}Ra is so much greater than the half-life of ^{210}Pb , ^{226}Ra activity can be considered constant. As ^{210}Pb decays, its activity approaches the activity of ^{226}Ra (Fig. 2; Ivanovich, 1992; Cowart and Burnett, 1994). It can be said that ^{210}Pb builds into secular equilibrium with ^{226}Ra over time. By measuring both ^{210}Pb and ^{226}Ra , the disequilibrium of these isotopes can be used as a natural chronometer which is useful in determining ages of fishes up to 120–150 yr.

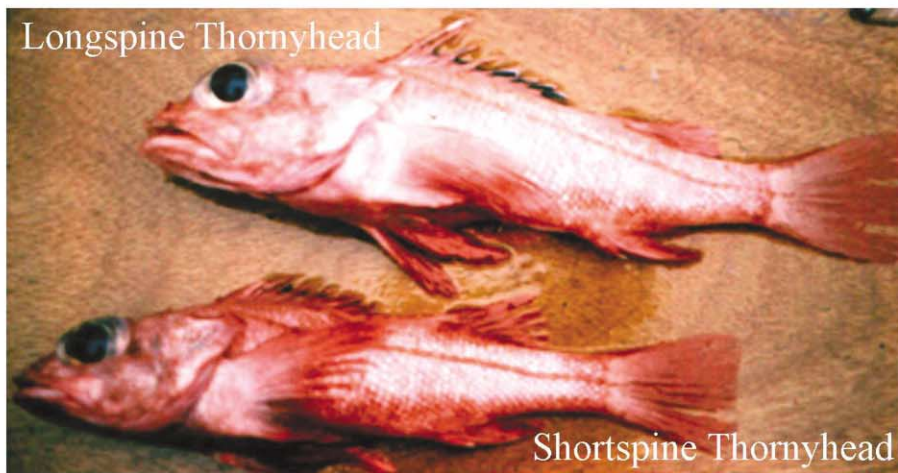
Radiometric ages for the species presented here were calculated by measuring the activity of these isotopes in whole- and core-otolith (first few years of growth) material using α -spectrometry to determine ^{210}Pb and one of two techniques to determine ^{226}Ra . Because of the extremely low levels of ^{210}Pb and ^{226}Ra , trace-metal precautions were exercised during sample cleaning and processing (Watters, 1993). All acids used were double distilled (GFS Chemicals[®]) and dilutions were made using Millipore[®] filtered Milli-Q water ($18\ \Omega\ \text{cm}^{-1}$). Thorough cleaning and repeated dissolution of the core samples were performed prior to radiometric analysis (Andrews et al., 1999b).

The procedures using α -spectrometry to determine ^{210}Pb are well established and have changed little over many years of application (Flynn, 1968). Determining ^{226}Ra , however, has evolved considerably, where ^{226}Ra was determined using the radon emanation technique for the bank rockfish and thornyheads, and our refined technique including TIMS was used for the bocaccio rockfish. Determination of ^{210}Pb in the rockfish samples, where activity was very low, required the use of its daughter ^{210}Po and a yield tracer, Polonium-208 (^{208}Po ; Flynn, 1968). To ensure that all of the ^{210}Po was ingrowth from ^{210}Pb and that ^{210}Po : ^{210}Pb was in

Bank Rockfish



Longspine Thornyhead



Shortspine Thornyhead

Bocaccio Rockfish



secular equilibrium, all samples were at least 2 yr old (from date of capture). The polonium isotopes were plated on to a silver planchet (99.999%, A.F. Murphy Die and Machine Co.) and α -spectrometric determination of the plated sample was used to determine the activity of ^{210}Pb by proxy (Andrews et al., 1999a).

Because this technique is very sensitive, otolith core material was used to avoid problems with developing otolith mass-growth models (Campana et al., 1990; Kimura and Kastle, 1995). In the analysis of the bocaccio rockfish, the sample remaining after polonium plating was recovered for TIMS analysis of ^{226}Ra . The analyses of the bank and thornyheads, however, were performed before the TIMS technique was developed, and the radon emanation technique was, therefore, used for ^{226}Ra determination in these species (Watters, 1993; Kline, 1996).

The radon emanation technique was applied to whole otoliths of the bank rockfish (Watters, 1993) and shortspine and longspine thornyheads (Kline, 1996). This technique used the α -decay of ^{222}Rn to determine ^{226}Ra by proxy. Because the instrumentation used for the radon emanation technique had relatively low sensitivity, the use of whole otoliths in large numbers (>10 g) was required to increase the activity and reduce the error of the ^{226}Ra determination. This approach required the assumption that the ontogenetic uptake of ^{226}Ra by the otolith was in a constant proportion to the mass growth of the otolith. This approach was used because the amount of ^{226}Ra in otolith core material (~1 g), used to determine ^{210}Pb , was not large enough to determine ^{226}Ra via radon emanation. The constant uptake of ^{226}Ra was indirectly tested for the shortspine and longspine thornyhead rockfishes by measuring ^{226}Ra activity in a series of otolith-weight stratified samples, but was assumed to be true for the bank rockfish.

To reduce error and avoid the ^{226}Ra uptake assumption in the determination of bocaccio rockfish age, ^{226}Ra was measured using a more sensitive technique that employs TIMS on the same otolith core sample used for ^{210}Pb determination (Andrews et al., 1999b). After coring, cleaning, dissolution, and plating in a similar manner to the thornyhead and bank rockfish studies, the residue was processed for ^{226}Ra determination by spiking the samples with a radium-228 (^{228}Ra) tracer and then passing the samples through a series of chromatography columns. These columns separated the radium in the samples from interfering quantities of calcium and barium, where the final sample was processed on a thermal ionization mass spectrometer. By determining ^{210}Pb and ^{226}Ra in the same sample, this technique made the calculation of radiometric age independent of sample mass and alleviated any concerns over the ontogenetic uptake of ^{226}Ra by the otolith. In all three studies, radiometric age was determined by applying the ratio of the measured isotopes (^{210}Pb : ^{226}Ra disequilibria) to the secular equilibrium model. To compare age determinations and accuracy of growth-zone age estimates, radiometric ages were compared directly

Fig. 1. Photographs of specimens of the four scorpaenid species for which age and longevity results were presented. The bank rockfish (*Sebastes rufus*) was collected and photographed by Milton Love (University of California, Santa Barbara). The longspine (*Sebastolobus altivelis*) and shortspine (*Sebastolobus alascanus*) thornyheads were collected in the Monterey Submarine Canyon, California and photographed by Donna Kline. The bocaccio rockfish (*Sebastes paucispinis*) was also collected in the Monterey Submarine Canyon at 120 m and photographed by Gregor Cailliet.

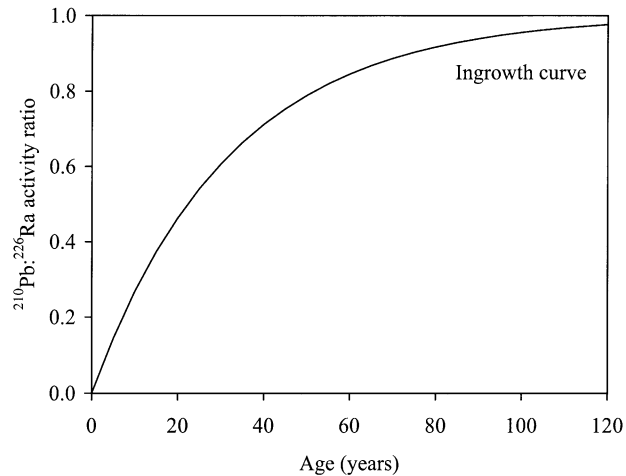


Fig. 2. Typical ingrowth curve ($^{210}\text{Pb}:^{226}\text{Ra}$) showing how the radio-isotopes decay, causing the ratio to asymptotically approach one at a rate predicted by the known half-lives of the isotope in question.

with otolith growth-zone ages using simple linear regression and a paired two-sample *t*-test.

2.3. Analysis of longevity versus depth of occurrence in the family Scorpaenidae

To explore the relationship of maximum estimated age to depth of occurrence, a literature search was performed and personal communications were sought to collect the latest longevity information for as many rockfish (genus *Sebastes*) species as possible. Maximum depth was used because the oldest individuals of these fishes are commonly the deepest. This estimate was recorded from the deeper of either Miller and Lea (1972) or Kramer and O'Connell (1995) for each species plus newly compiled depth information (Milton S. Love, Personal Communications, University of California, Santa Barbara, CA 93106). This information was used to plot maximum depth versus maximum age, where an exponential function was used heuristically to describe the relationship, if any, between longevity and depth of occurrence. Information on distribution was also used in the plot to differentiate species that had distributions either north or south of the northern California border, or distributions that covered the full range of northeastern Pacific rockfishes, from Baja California, Mexico to Alaska.

3. Results

3.1. Traditional and radiometric determination of age

Growth-zone and radiometric ages were similar for all of the four scorpaenid species examined (Fig. 3). However, there was a tighter fit between the two estimates for the bank rockfish and the two thornyheads than for the more variable bocaccio rockfish (Fig. 3d).

For the bank rockfish, five pooled otolith age-groups were examined, ranging in mean growth-zone age from 13.2 to 39.7 yr (Fig. 3a; Watters, 1993). There was no significant difference between growth-zone and radiometric age estimates (paired two-tail *t*-test, *df* = 4, *t* = -0.6424, *P* = 0.5556). The oldest growth-zone age-group was composed of otoliths ranging in age from 35 to 53 yr (mean age 39.7 yr); maximum radiometric age was determined to be 40.7 yr (range of 33.6–49.7 yr).

For the shortspine thornyhead, fourteen pooled otolith age-groups were examined, ranging in mean growth-zone age from 10.6 to 71.7 yr (Fig. 3b; Kline, 1996). There was no significant difference between growth-zone and radiometric ages (paired two-tail *t*-test, *df* = 13, *t* = -0.7907, *P* = 0.4433). The oldest growth-zone age-group was 71.7 ± 12.0 yr SD; radiometric age was determined to be 84.8 yr (range of 62.2 yr to an undefined upper limit).

For the longspine thornyhead, thirteen pooled otolith age-groups were examined, ranging in mean growth-zone age from 3.3 to 35.6 yr (Fig. 3c; Kline, 1996). There was no significant difference between growth-zone and radiometric ages (paired two-tail *t*-test, *df* = 12, *t* = -0.5739, *P* = 0.5766). The oldest growth-zone age-group was 35.6 ± 4.9 yr SD; radiometric age was determined to be 36.5 yr (range of 29.6–45.8 yr).

For the bocaccio rockfish, 10 pooled otolith age-groups were examined, ranging in mean age from 2.5 to 19.4 yr (Fig. 3d; Andrews et al., 2000a). There was no significant difference between growth-zone and radiometric ages (paired two-tail *t*-test, *df* = 9, *t* = -0.1933, *P* = 0.8510). The oldest growth-zone age-group was composed of otoliths ranging in age from 13 to 29 yr (mean age 19.4 yr); radiometric age was determined to be 28.7 yr (range of 23.8–34.6 yr). The greatest variation was in the growth-zone age estimates, whereas the radiometric ages were usually less variable.

Of the ~56 known rockfish species (genus *Sebastes*) from the northeastern Pacific Ocean, maximum age or longevity estimates are available for 47 species (Table 1). For all of these species, the maximum depth recorded ranged from 37 m for the black-and-yellow rockfish (*S. chrysomelas*) to at least 874 m for the shortraker (*S. borealis*) and rougheye (*S. aleutianus*) rockfishes. The lowest estimates of maximum age were 12 and 14 yr for calico (*S. dalli*) and rosy (*S. rosaceus*) rockfishes, respectively, where maximum depths were ~250 m. The highest estimates of maximum age were 157 and 205 yr for the shortraker and rougheye rockfishes, respectively, both of which live to the north and had a maximum-recorded depth of 874 m, the deepest recorded for the rockfishes listed.

A plot of maximum-recorded depth versus these maximum estimated ages (longevity) revealed a pattern that appeared exponential for the known species of *Sebastes* (Fig. 4). The relationship was described heuristically as longevity (years) = $38 + 4.1 \times 10^{-7}$ (depth, m)^{2.9}, where the distribution showed a fair amount of scatter with a relatively low, but significant, $r^2 = 0.51$ (*P* < 0.001). The thornyheads are plotted even though they were excluded from the statistical analysis, because they are in a different genus, with morphological and physiological differences, and occupy very deep water.

Distributional information revealed that rockfish residing primarily south of the Oregon–California border tended to have lower maximum ages and live at shallower depths (Fig. 4). Rockfishes that were found only north of California tended toward greater depth and higher longevities. The northern rockfish (*S. polyspinis*) has the deepest distribution (626 m) for those species found only north of California. The oldest rockfishes, in

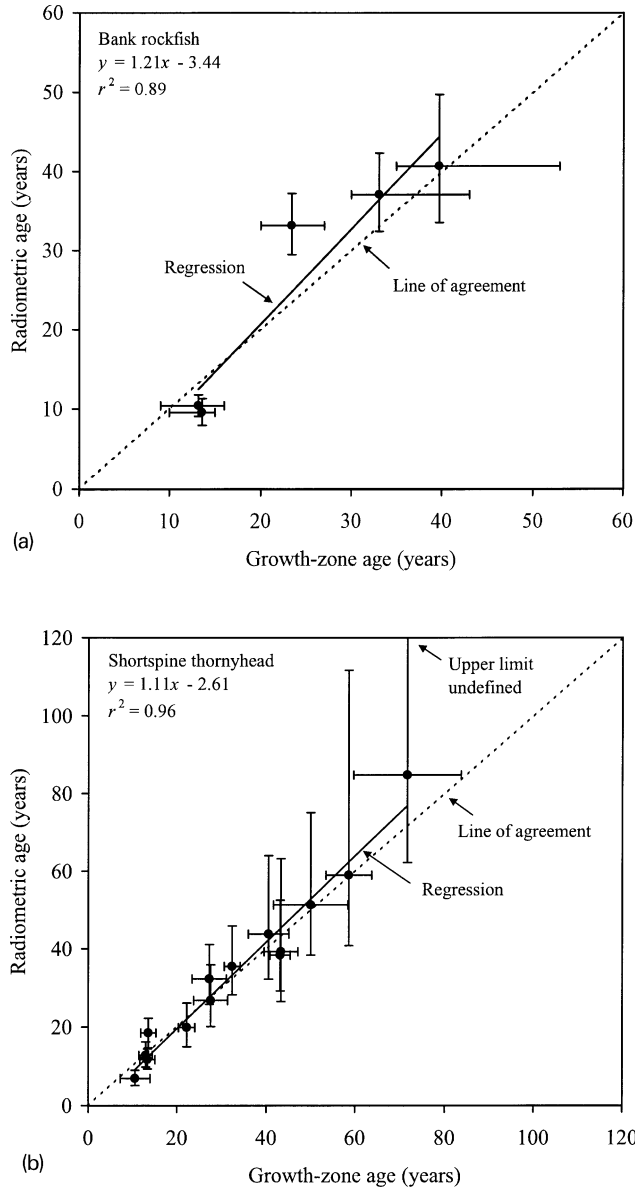


Fig. 3. Comparison of mean otolith growth-zone ages and radiometric ages for four species: (a) Bank rockfish (*Sebastes rufus*; paired two-tail t -test, $df = 4$, $t = -0.6424$, $P = 0.5556$); (b) shortspine thornyhead (*Sebastolobus alascanus*; paired two-tail t -test, $df = 13$, $t = -0.7907$, $P = 0.4433$); (c) longspine thornyhead (*Sebastolobus altivelis*; paired two-tail t -test, $df = 12$, $t = -0.5739$, $P = 0.5766$); and (d) bocaccio rockfish (*Sebastes paucispinis*; paired two-tail t -test, $df = 9$, $t = -0.1933$, $P = 0.8510$). A linear regression and a line of agreement are drawn for comparison and the regression coefficient (r^2) noted. Vertical bars represent low and high radiometric age estimates, based on analytical uncertainty of ^{210}Pb and ^{226}Ra measurements. Horizontal bars represent the range of otolith-derived ages for each pooled otolith age group. There was no significant difference between growth-zone and radiometric age estimates.

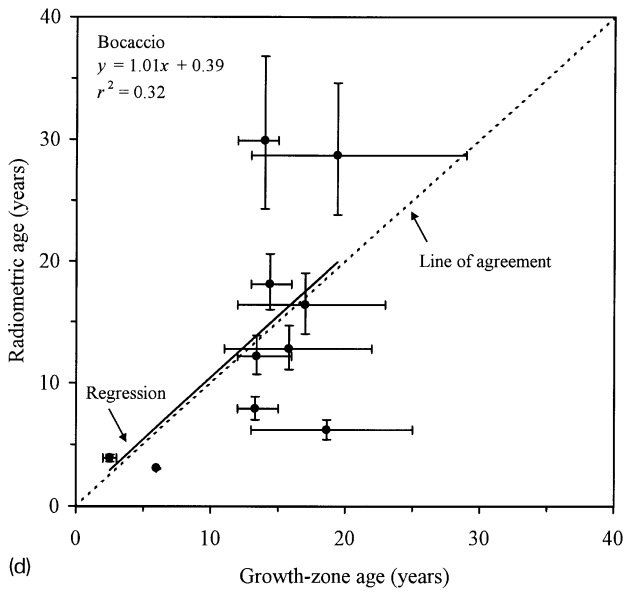
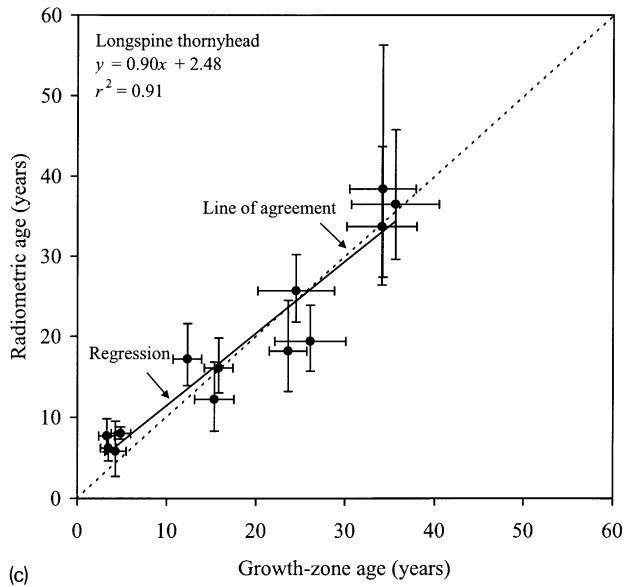


Fig. 3. (continued)

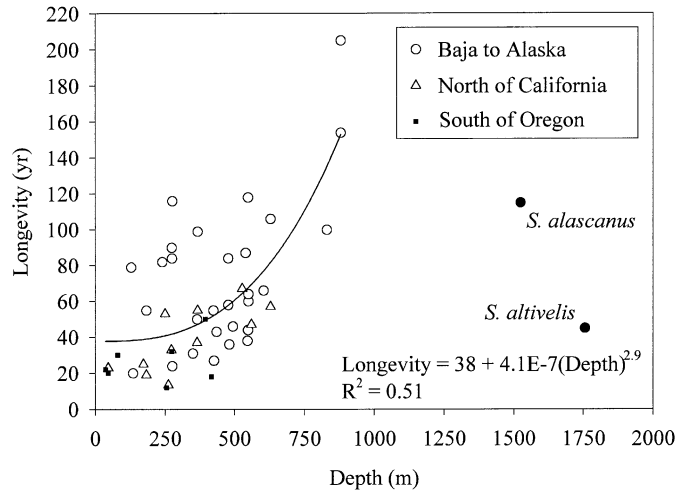


Fig. 4. Plot of maximum depth of occurrence (m) versus longevities (years) of 49 species of fishes in the family Scorpaenidae, based upon this paper and a review of the literature on age and growth of this group. The curvilinear regression is only for fishes in the genus *Sebastes*, with the two species of *Sebastolobus* plotted to the right, but not included statistically.

general, had a broad distribution (Baja California, Mexico to Alaska) and ranged from relatively shallow to the greatest depths.

4. Discussion

4.1. Radiometric age validation and longevity estimates

The best traditional age validation methods require examination of known-age fish obtained through tag–recapture studies or laboratory rearing (Beamish and McFarlane, 1983). However, tag–recapture techniques are impractical for deep-water fishes, because barotrauma precludes vital marking, and recapture probability is low. Laboratory rearing is also difficult, because generally little is known of the early life histories of deep-sea fishes. Thus, many of the species studied from deep-water areas rely on marginal increment analysis, which is good only if one has sufficient samples covering all seasons.

Radiometric age determination of fishes is most useful for difficult-to-age or difficult-to-sample species, especially for relatively long-lived species. The technique is not routinely used for all age determination studies, because it is costly and few laboratories have the specialized equipment necessary to process and age calcified structures. The radiometric technique is only useful for fishes in which the three assumptions are satisfied for a given calcified structure. Because these assumptions are violated in chondrichthyan (shark) and chondrosteian (sturgeon and paddle fishes) structures used for age determination (vertebrae

Table 1
List of maximum estimated age for 47 rockfishes (*Sebastes* spp.)

Common name	Species	Longevity (years)	References for age
Calico	<i>S. dalli</i>	12	Reilly et al. (1994)
Rosy	<i>S. rosaceus</i>	14	Reilly et al. (1994)
Flag	<i>S. rubrivinctus</i>	18	Reilly et al. (1994)
Squarespot	<i>S. hopkinsi</i>	19	Casillas et al. (1998)
Kelp	<i>S. atrovirens</i>	20	Reilly et al. (1994)
Brown	<i>S. auriculatus</i>	20	Love and Johnson (1998)
Black-and-yellow	<i>S. chrysomelas</i>	22	Zaitlin (1986)
Grass	<i>S. rastrelliger</i>	23	Love and Johnson (1998)
Pygmy	<i>S. wilsoni</i>	24	S. MacLellan, pers. commun. ^a
Olive	<i>S. serranoides</i>	25	Casillas et al. (1998)
Chilipepper	<i>S. goodei</i>	27	Love et al. (1998)
Gopher	<i>S. carnatus</i>	30	Bloeser (1999)
Shortbelly	<i>S. jordani</i>	31	D. Pearson, per. commun. ^b
Starry	<i>S. constellatus</i>	32	Reilly et al. (1994)
Greenspotted	<i>S. chlorostictus</i>	33	Reilly et al. (1994)
Bocaccio	<i>S. paucispinis</i>	36	Chilton and Beamish (1982)
Speckled	<i>S. ovalis</i>	37	Reilly et al. (1994)
Stripetail	<i>S. saxicola</i>	38	Reilly et al. (1994)
Greenstriped	<i>S. elongatus</i>	42	Shaw (1999)
Vermilion	<i>S. miniatus</i>	43	Paul Reilly, per. commun. ^c
Blue	<i>S. mystinus</i>	44	T. Laidig, pers. commun. ^d
Harlequin	<i>S. varigatus</i>	47	S. MacLellan, pers. commun. ^a
Black	<i>S. melanops</i>	50	K. Munk, pers. commun. ^c
Greenblotched	<i>S. rosenblatti</i>	50	Casillas et al. (1998)
Bank	<i>S. rufus</i>	53	Watters (1993)
Redstripe	<i>S. proriger</i>	55	S. MacLellan, pers. commun. ^a
Copper	<i>S. caurinus</i>	55	Love et al. (1998)
Cowcod	<i>S. levis</i>	55	Butler et al. (1999)
Northern	<i>S. polyspinis</i>	57	K. Munk, pers. commun. ^c
Sharpchin	<i>S. zacentrus</i>	58	K. Munk, pers. commun. ^c
Widow	<i>S. entomelas</i>	60	K. Munk, pers. commun. ^c
Yellowtail	<i>S. flavidus</i>	64	K. Munk, pers. commun. ^c
Darkblotched	<i>S. crameri</i>	66	Love et al. (1998)
Dusky	<i>S. ciliatus</i>	67	K. Munk, pers. commun. ^c
China	<i>S. nebulosus</i>	79	S. MacLellan, pers. commun. ^a
Silvergray	<i>S. brevispinis</i>	82	S. MacLellan, pers. commun. ^a
Canary	<i>S. pinniger</i>	84	S. MacLellan, pers. commun. ^a
Splitnose	<i>S. diploproa</i>	84	Wilson and Boehlert (1990)
Rosethorn	<i>S. helvomaculatus</i>	87	K. Munk, pers. commun. ^c
Quillback	<i>S. maliger</i>	90	K. Munk, pers. commun. ^c
Yellowmouth	<i>S. reedi</i>	99	S. MacLellan, pers. commun. ^a
Pacific ocean perch	<i>S. alutus</i>	100	S. MacLellan, pers. commun. ^a
Redbanded	<i>S. babcocki</i>	106	K. Munk, pers. commun. ^c
Tiger	<i>S. nigrocinctus</i>	116	K. Munk, pers. commun. ^c
Yelloweye	<i>S. ruberrimus</i>	118	K. Munk, pers. commun. ^c
Shortraker	<i>S. borealis</i>	157	K. Munk, pers. commun. ^c
Rougheye	<i>S. aleutianus</i>	205	K. Munk, pers. commun. ^c

^a Shayne MacLellan, Department of Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC, Canada V9R 5K6.

^b Donald Pearson, National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, Tiburon, CA 94920, USA.

^c Paul Reilly, California Department of Fish and Game, 20 Lower Ragsdale, Monterey, CA 93940, USA.

^d Tom Laidig, National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060, USA.

^e Kristen Munk, Alaska Department of Fish and Game, Mark Tag and Age Lab, PO Box 25526, Juneau, AK 99802, USA.

and fin ray sections, respectively), age validation for these fishes will require a combination of techniques, including tag–recapture and marking (Burton et al., 1999).

The pioneering study by Bennett et al. (1982) has led to the use and further refinement of the radiometric age validation technique to many different groups of fishes, some of which live in deep water (Burton et al., 1999; Kastle et al., 2000; Baker et al., 2001b). To date, there have been at least 18 scientific papers written on radiometric age determination of fishes. The majority of these have successfully confirmed age or longevity estimates.

The results presented here for four species of scorpaenid fishes add useful information for understanding both the growth rates and longevities of deep-water fishes. The comparison of age estimates from otoliths compared favorably with those from radiometric analysis. The agreement was quite close for the bank rockfish and the two deeper-dwelling thornyhead species. However, there still was variability in both otolith and radiometric age estimates. This is probably due to the difficulty in estimating the ages from sectioned otoliths and to the requirement to combine the cores of many otoliths to provide sufficient material for the radiometric measurements. The agreement was not as tight for the shallow-dwelling bocaccio rockfish. The main source of variation was in the otolith estimates, indicating that these fish are difficult to age (Andrews et al. 2000a).

Even though variability exists in both techniques for age determination of these fishes, it appears that they all are relatively long-lived. The bank rockfish reaches an age of at least 41 yr, based on radiometrics, but is estimated to reach 53 yr using otolith growth-zone counts (Watters, 1993; Cailliet et al., 1996). The two deeper-dwelling thornyheads get older, with radiometric analyses indicating the longevities of longspine and shortspine thornyheads to be at least 27 and 62 yr, respectively. For these two species, otolith growth-zone counts indicates that they reach 45 and 115 yr, respectively (Table 2). The radiometric estimates for bocaccio indicate a longevity of at least 24 yr, but the otolith ages suggest that bocaccio get much older, from 36–50 yr. It is important to remember that, even though commercial fisheries for the bank rockfish and thornyheads are relatively recent (past two decades or so), there might have been size-selective fishing mortality on all four of these species. Therefore, their historical longevities may have been even higher, and the northerly distribution of increasing age (Fig. 4) may be an artifact of regional fishing pressure.

4.2. Implications for management of deep-sea fisheries

With the collapse and closure of fisheries on the continental shelf, fishers are turning to deep-water fish stocks on the continental slope (Bergstad, 1995; Merrett and Haedrich, 1997). Along the Pacific coast, *C. acrolepis* (Pacific grenadier) is the target of a relatively new directed fishery off California and Oregon (Matsui et al., 1990; Andrews et al., 1999a). The fishery in Monterey Bay, California grew substantially from practically zero landings during 1992 to the fifth largest fishery during 1996 (900 tons; Leos, 1996; 1997; Andrews et al., 1999a). This is a dramatic example of what can happen when the fishing target shifts.

As early as 1959, Beverton and Holt (1959) proposed a relationship between longevity and natural mortality in fishes, and summarized what was known at that time about their growth characteristics. In this, and a later paper (Beverton, 1987), it was proposed that

Table 2

Longevities of selected long-lived marine fishes with information on age validation. Estimated longevity is based on some kind of growth-zone interpretation. Ages given in the age validation column are the minimum age that can be interpreted based on the age validation technique

Group or species	Estimated longevity	Age validation
Elasmobranchs (sharks and rays)		
<i>Rhizoprionodon</i> spp. (sharpnose sharks)	10 yr ^a	10 yr (MIA, Tag–recap) ^a
<i>Isurus oxyrinchus</i> (mako shark)	25 yr ^b	25 yr (MIA, Tag–recap) ^b
<i>Triakis semifasciatus</i> (leopard shark)	30 yr ^c	30 yr (OTC, edge analysis) ^c
<i>Squatina californica</i> (angel shark)	35 yr ^d	35 yr (Tag–recap) ^d
<i>Carcharodon carcharias</i> (white shark)	~50 yr ^e	13 yr (MIR) ^f
<i>Squalus acanthias</i> (spiny dogfish)	50–75 yr ^g	50–75 yr (OTC, Tag–recap) ^g
Sturgeon (fresh water/anadromous)		
<i>Acipenser oxyrinchus</i> (Atlantic sturgeon)	42 ^h –60 ⁱ yr	Juveniles (MIR and OTC) ^h
<i>Acipenser transmontanus</i> (white sturgeon)	104 yr ^j	Juveniles (OTC) ^j
Tarpon (tropical shallow water)		
<i>Megalops atlanticus</i> (Atlantic tarpon)	55 yr ^k	50 + years (radiometric) ^l
Skilfishes (deep slope)		
<i>Anoplopoma fimbria</i> (sablefish)	114 yr ^m	34 (radiometric) ⁿ , 65 (OTC) ^m
Grenadiers or rattails (deep slope)		
<i>Coryphaenoides acrolepis</i> (Pacific grenadier)	73 + years ^o	56 yr (radiometric) ^o
<i>Albatrossia pectoralis</i> (giant grenadier)	56 + years ^p	32 yr (radiometric) ^p
Rockfishes (nearshore to deep slope)		
<i>Sebastes paucispinis</i> (bocaccio rockfish)	36 ^q –50 yr ^r	24 yr (radiometric) ^r
<i>Sebastes rufus</i> (bank rockfish)*	53 yr st	41 yr (radiometric) ^l
<i>Sebastes</i> spp. (thornyheads)*	45 and 115 yr ^u	27 and 62 yr (radiometric) ^u
<i>Sebastes ruberrimus</i> * (yelloweye rockfish)	118 yr ^v	100 yr (prelim. radiometric) ^w
Seamount fishes (South Pacific Ocean)		
<i>Hoplostethus atlanticus</i> (orange roughy)	125 yr ^x	116–134 yr (radiometric) ^x
<i>Allocyttus verrucosus</i> (warted oreo)	130 yr ^y	120–140 yr ^y
<i>Epigonus telescopus</i> (black cardinal)	104 yr ^z	None

* Indicates information for species presented here.

^a Parsons (1985) and Simpendorfer (1993).

^b Pratt and Casey (1983).

^c Kusher et al. (1992).

^d Cailliet et al. (1992).

^e Calculation based on $\text{age}(\text{max}) = 5(\ln 2)/k$.

- ^f Cailliet et al. (1985) and Wintner and Cliff (1999).
- ^g McFarlane and Beamish (1987) and Tucker (1985).
- ^h Stevenson and Secor (2000).
- ⁱ Magnin (1964).
- ^j Rien and Beamesderfer (1994).
- ^k Crabtree et al. (1995).
- ^l Andrews et al. (2001).
- ^m Beamish and McFarlane (2000).
- ⁿ Kestelle et al. (1994).
- ^o Andrews et al. (1999a).
- ^p Burton (1999).
- ^q Chilton and Beamish (1982).
- ^r Andrews et al. (2000).
- ^s Cailliet et al. (1996).
- ^t Watters (1993).
- ^u Kline (1996).
- ^v K. Munk (ADFG), pers. comm.
- ^w A. Andrews, unpublished data.
- ^x Smith et al. (1995).
- ^y Stewart et al. (1995).
- ^z Tracey et al. (2000).

there were relationships between mortality, growth and metabolic rates, as well as phylogenetic implications. Both of these papers were stimulated by the need to better understand fish population dynamics, as determined by growth, maturation, and fecundity, relative to proposing effective fishery management principles.

Leaman and Beamish (1984) noted that many species of bottom fishes have greater longevities than previously estimated, causing major changes in the management policies regulating their fisheries. They presented some of the advantages of longevity for fishes, including a long reproductive life, increased population stability, ability to persist in less than ideal habitats, and energy conservation. They also, however, presented evidence that age frequencies of fish populations could be deleteriously affected by fishing mortality, resulting in fewer of the older individuals, and an underestimate of longevity. In a later paper, Leaman (1991) demonstrated that some long-lived (50–100 yr) rockfishes (family Scorpaenidae) had limited phenotypic plasticity and therefore could not withstand heavy fishing mortality that could reduce their lifespan.

To date, there are 47 species of northeastern Pacific rockfishes (*Sebastes* spp.) with estimates of maximum age ranging from 12 to 205 yr (Table 1). As research techniques have improved and age estimate accuracy has increased, the estimated longevity of many of these species has increased over time. A prime example of increased longevity due to advances in age estimation techniques was described for the Pacific ocean perch (*S. alutus*; Beamish, 1979). Age estimates for this species, from microscopic analysis of the otolith surface, placed the maximum longevity at approximately 30 yr. However, sections taken from the same otoliths later increased this estimate to greater than 70 yr, and perhaps to 90 yr (Chilton and Beamish, 1982). The scenario is similar for many of the species listed (Leaman and Beamish, 1984), the most recent example being the rougheye rockfish (*S. aleutianus*) aged at 205 yr using traditional otolith readings, an increase of more than 50 yr over the previous estimate (Kristen Munk, ADFG, Juneau, AK, personal communication).

Because fishes in several different orders are long-lived, it appears that longevity is not

unique to deep-sea fishes (Table 2; see also Beverton, 1987). As can be seen from our cursory review of longevity studies, sharks and rays (elasmobranchs), sturgeons (Acipenseridae), tarpon (Megalopidae), skilfishes (Anoplopomatidae), grenadiers or rattails (Macrouridae), roughies (Berycidae), oreos (Oreosomatidae), cardinalfishes (Apogonidae), as well as rockfishes (Scorpaenidae), also are long-lived. However, some of these are generally deep-dwelling groups (Macrouridae, Oreosomatidae, etc.) and it would be interesting to know if the relationship between longevity and maximum depth in these groups is similar to the trend we found for the Scorpaenidae. It appears that those species in the family Macrouridae that occupy the outer shelf and upper slope tend to be smaller and have estimated maximum ages that are lower than deep slope and abyssal species (Middleton and Musick, 1986; Morales-Nin, 1990; Savvatimsky, 1994; Kelly et al., 1997; Andrews et al., 1999a). This is still an open question for other families and orders of fishes.

An additional factor that must be considered is the regional history of fisheries exploitation. Virgin stocks of fishes are probably very rare today (Craig, 1985), but may have a higher probability of existing further north because exploitation tends to be more logistically difficult and has not been happening as long as in regions further south. This is exemplified by the fact that many rockfishes were originally described from specimens taken in commercial catches as early as the mid-1800s. Thus, fishing pressure today may have reduced the longevity we now see for fishes taken in modern fishing practices (Robert Lea, CDFG, Monterey, California, personal communication; see also Leaman and Beamish, 1984; Craig, 1985; Leaman, 1991). This could mean that a species could have the potential to attain greater ages than the age estimates we now have, especially those which live in southern California waters, because it is possible that the oldest cohorts of the population have long since been removed from the population.

4.3. *Why do deeper-dwelling fishes live longer?*

4.3.1. *Environmental factors in the deep sea*

Our analysis indicates that the longevity of scorpaenid fishes are related to their depth and/or distribution (Fig. 4). These fishes occupy a diversity of habitats ranging from shallow, nearshore to deeper slope waters, from Baja California, Mexico to the Aleutian Islands, Alaska. Indeed, longevity in the genus *Sebastes* exponentially increased with maximum depth of occurrence. The two species of thornyheads, while also long-lived, occupy even deeper waters.

It is not known why deep-dwelling fishes might live longer. Thus, it is important to evaluate the environmental factors in deep water that might have selected for physiological adaptations leading to longer lives. It is well known that several environmental factors change with depth in the ocean (Childress, 1977; Siebenaller and Somero, 1982; 1989; Somero, 1992a,b; Childress, 1995). These include increasing pressure, decreasing temperature and light levels, and reduced food availability. In addition, at some depths there is an oxygen minimum zone, to which some organisms are physiologically adapted (Yang et al., 1992; Childress, 1995).

4.3.2. *Decreased metabolism and enzyme activities in deeper-dwelling organisms*

Early hypotheses suggested that deep-sea organisms have metabolic and biochemical

adaptations related to reduced temperatures and increased pressures (e.g. Childress, 1977). However, more recent studies indicate that these metabolic adaptations are not only influenced by temperature reduction and increased pressure, but by a combination of factors, including reduced oxygen, light and food levels (Torres and Somero, 1988a,b; Siebenaller and Somero, 1989; Somero, 1992a,b; Yang et al., 1992; Childress, 1995; Vetter et al., 1994; Vetter and Lynn, 1997). Although several papers proposed that deep-dwelling fishes would have increased body sizes and reduced metabolism, few have attempted to explore the relationship of these factors with increased longevities in deep-sea fishes (e.g. Beverton, 1987).

There have been many studies concentrating on the effect of low temperature and high pressure on enzyme kinetics of deep-sea fishes, including some of those in this study (Siebenaller and Somero, 1978, 1982, 1989; Siebenaller et al., 1982; Siebenaller, 1983, 1984; Hennessey and Siebenaller, 1985; Vetter and Lynn, 1997). These studies have often noted metabolic rate reductions with increasing depth, both ontogenetically and between congeners occupying different depths. In both of the thornyhead species, the ontogenetic transition from pelagic to increasingly deeper benthic habitats result in a reduction in metabolism and enzymatic activities (Smith and Brown, 1983; Siebenaller, 1984). Also, as shown by Siebenaller and Somero (1982), the shallower species, *S. alascanus* (180–1524 m) had about twice the values of LDH, Lactate Dehydrogenase; PK, Pyruvate Kinase; MDH, Malate Dehydrogenase; CS, Citrate Synthase; and CPK (creatine phosphokinase) than the deeper-dwelling *S. altivelis* (550–1756 m).

Yang and Somero (1993) studied the difference in metabolic rates, blood oxygen affinity, and white muscle enzyme activities between the very shallow scorpionfish (*Scorpaena guttata*) and the deeper shortspine thornyhead. They found that oxygen consumption was higher for the shallow-dwelling scorpionfish, but blood oxygen affinity was higher for the deeper-dwelling thornyhead. In all cases, enzymatic activities (LDH, PK, MDH, and CS) were considerably higher for the shallow-dwelling scorpionfish. For flatfishes, Vetter et al. (1994) found similar results on metabolic adaptations and enzyme activity with depth of flatfishes (Dover sole, *Microstomus pacificus*; deep-Sea Sole, *Embassichthys bathybius*; *rex sole*, *Glyptocephalus* [= *Errex*] *zachirus*; and California halibut *Paralichthys californicus*).

Several studies have concentrated on reduced metabolism and growth in deep-sea fishes, mainly those in the meso- and bathypelagic region (Childress, 1977; Childress and Somero, 1979; Childress et al., 1980; Mauchline, 1988). In addition, Antarctic fishes also have metabolic and enzymic adaptations which decrease with increasing depth of occurrence, indicating that these metabolic reductions are the same as for temperate zone fishes (light, food location, food abundance, etc.), with pressure not playing much if any role in these depth-related reductions in oxygen consumption (Torres and Somero, 1988a,b). Hubold and Tomo (1989) found that the Antarctic silverfish (*Pleuragramma antarcticum*) had a low growth performance and the von Bertalanffy growth model for it predicted a maximum age of 21 yr for 245 mm TL fish.

In another study, Sullivan and Somero (1983) found increased LDH activity with increasing body size for the sablefish (*A. fimbria*), even though this species moves to deeper water as it grows larger. These higher LDH activities appear to reflect a general pattern of metabolic scaling, in which enzymes in white muscle associated with anaerobic

generation of ATP increase with body mass. However, in their study, a reduced ration size resulted in lower enzyme activities, indicating that food deprivation in the deep sea might reduce growth.

4.3.3. *Other biochemical changes in deep-sea fishes*

Many studies have investigated the enzymatic changes present in deep-sea organisms that facilitate life at low temperature and high pressures (Hochachka and Somero, 1984). The LDH situation is one, illustrating how pressure, in particular, is problematic for enzyme activities because Michaelis–Menton kinetics are adversely affected, and how deep-sea fishes have compensated. Deep-sea fishes most likely possess many modifications to their proteins, such as reduced enzymatic content which can reduce the costs of muscle production.

Another recent discovery about biochemical differences between shallow- and deep-living animals concerns the organic osmotic solute trimethylamine-*N*-oxide (TMAO). Gillett et al. (1997), Kelly and Yancey (1999), and Yancey and Siebenaller (1999) found that deep-sea organisms, including macrourid fishes, skates and decapod crustaceans, had higher TMAO levels in their tissues than shallow forms. Because TMAO is a powerful stabilizer of protein structure, these authors conjecture that high levels of TMAO in tissues of deep-living species may help to offset perturbation by elevated pressure of protein structure and function. Indeed, Fyfe-Johnson and Yancey (1998) reported that LDH of the deep-sea grenadier *Coryphaenoides leptolepis* was stabilized by TMAO under conditions of high pressure.

The effect of reduced protein damage at depth by elevated TMAO values on growth rates and longevities in deep-sea fishes is unknown. However, deep-sea fishes could have reduced energy costs needed for protein synthesis if elevated TMAO levels protect proteins from disruption by pressure, with the result that the half-lives of proteins are lengthened (George Somero, Hopkins Marine Station, personal communication).

4.3.4. *Reduced oxidative stress*

A question of particular and recent interest in marine fishes concerns the levels and effectiveness of their antioxidative mechanisms. Hill and Womersley (1993) reported on literature indicating that fluorescent age-pigments (FAS) accumulated with age in poikilothermic organisms. They proposed that differential expression of genes related to metabolic, antioxidant, or lysosomal enzymes could all potentially influence the rate of age pigment production. They also suggested that cold-water fishes might be susceptible to damage from free radical attack, if they did not compensate for this by consuming dietary antioxidants. Since deep-water fishes are among the longest-living vertebrates, they proposed that interactions of diet and peroxidative metabolism may be of great significance for them and discussed the possible evolutionary mechanisms involved.

Indeed, Rees et al. (1998) found that oxygen-detoxifying mechanisms may have provided excellent foundations for the emergence of many bioluminescent systems in deep-sea organisms. They proposed that the deep sea was an environment with reduced oxidative stress, and that the organisms colonizing this habitat most likely already had effective antioxidant mechanisms. They discovered that coelenterazine, a type of luciferin occurring in many marine bioluminescent groups, had strong antioxidative properties as it

is highly reactive with reactive oxygen species (ROS) such as the superoxide anion and peroxides. They suggested that its primary and original function was the detoxification of deleterious oxygen derivatives.

Rees et al. (1998) also proposed that selection for antioxidative defense mechanisms may be decreased for deep-sea organisms-reduced light irradiance and lower oxygen levels reduce the exposure to oxidative stress. Because metabolic rates of deep-living species appear, in general, to be low, the production of ROS might be low as well, thus exposing them to less ROS damage.

Janssens et al. (2000) found a decrease in the ROS-detoxifying enzymes superoxide dismutase (SOD) and glutathione peroxidase (GPX) with increasing depth of occurrence of 16 species of mesopelagic and bathypelagic fishes. They suggested that the relatively low oxidative stress in the deep sea resulted in reduced antioxidative defenses that are used primarily against metabolically produced ROS. The amounts of catalase (CAT), however, did not vary with metabolic activity or depth, thus suggesting a different function. They found high levels of antioxidants in the bioluminescent organs, thus supporting the hypothesis generated by Rees et al. (1998). The levels of antioxidants in deep-dwelling, benthic fishes have not been studied and therefore, their influence on longevity is unknown. Because fewer deep-seabenthic fishes have well-developed bioluminescence, their antioxidant enzymes may not be as modified as those in midwater fishes.

4.4. Future directions

While this study has documented the tendency for deep-dwellings scorpaenid fishes to have long lives, we have only begun to suggest the mechanisms behind such extreme longevity. Our analysis of the literature on deep-sea fish adaptations indicates that a number of factors have resulted in their reduced metabolic rates. Of greatest potential relevance in this context is the fact that, for many species, there appears to be a reduced rate of oxygen consumption with depth, indicating that damage from ROS is likely to be lower. These two findings, plus the evidence in Rees et al. (1998) and Janssens et al. (2000), support the hypothesis that deep-sea fish longevity is related to their reduced metabolic rates. Our findings are at best correlative and will require experiments, such as those presented by Mangel and Abrahams (2001) on ferox trout and Reznick et al. (2001) on guppies to unravel the roles of food, predation, and other ecological factors in determining longevity in fishes. It is hoped that this heuristic analysis will stimulate biochemists and physiologists to concentrate their studies on the adaptations that deep-sea fishes may be using to increase their longevity.

Acknowledgements

Dr Kenneth Coale has consistently provided excellent advice on the application of radiogeochemical approaches to validating growth and longevity in fishes. For providing otoliths and assistance with otolith interpretation, we thank John Butler, Gerald Hoff, Bob Lauth, Bill Lenarz, Don Pearson, Mary Yoklavich, Milton Love, and Frank Henry. We thank Ken Bruland, Rob Frank, Ross Williams and Pete Holden for the use of analytical and counting equipment at the University of California at Santa Cruz. Bob Lea and Bob

Leos kindly provided information on fisheries. Kristen Munk supplied up-to-date estimates of longevity for many of the species of rockfishes reported in Table 2 and Fig. 4. Jason Cope provided many of the references on age determination and other aspects of the life histories of scorpaenid fishes and reviewed early drafts of the manuscript. George Somero kindly and efficiently read and reviewed our discussion, especially as it related to physiological adaptations of deep-sea fishes. We are grateful to Caleb Finch, Robert Ricklefs, and Steven Austad for bringing this interesting group of scientists together for the workshop that resulted in this series of papers. This research was funded by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, US Department of Commerce, under project numbers R/NP-1-20D, R/F-113, R/F-148, R/F-174 through the California State Resources Agency.

References

- Andrews, A.H., Cailliet, G.M., Coale, K.H., 1999a. Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. *Can. J. Fish. Aquat. Sci.* 56, 1339–1350.
- Andrews, A.H., Coale, K.H., Nowicki, J.L., Lundstrom, C., Palacz, Z., Burton, E.J., Cailliet, G.M., 1999b. Application of an ion-exchange separation technique and thermal ionization mass spectrometry to ^{226}Ra determination in otoliths for radiometric age determination of long-lived fishes. *Can. J. Fish. Aquat. Sci.* 56, 1329–1338.
- Andrews, A.H., Burton, E.J., Pearson, D., Cailliet, G.M., Coale, K.H., 2000a. Radiometric age validation of the bocaccio rockfish *Sebastes paucispinis*. Abstract: Western Groundfish Conference, Sitka, Alaska, April 24–28, p. 76.
- Andrews, A.H., Cordes, E., Heifetz, J., Cailliet, G.M., Coale, K.H., Somerton, D., Munk, K., Mahoney, M., 2000b. Age and growth of a deep-sea, habitat-forming octocorallian (*Primnoa* sp.) from the Gulf of Alaska, with radiometric age validation. Abstract: First International Symposium on Deep Sea Corals, Science and Conservation of Deep Sea Corals, Halifax, Nova Scotia, Canada, July 30–August 3, 2000, p. 11.
- Andrews, A.H., Burton, E.H., Coale, K.H., Cailliet, G.M., Crabtree, R.E., 2001. Application of radiometric age determination to the Atlantic tarpon *Megalops atlanticus*. *Fish. Bull.* (in press).
- Bagenal, T.B. (Ed.), 1974. *The Ageing of Fish*. Proceedings of an International Symposium. Surrey, England: Unwin Brothers Limited.
- Baker Jr., M.S., Wilson, C.A., VanGent, D.L., 2001. A test of the assumptions of the otolith radiometric aging technique with red snapper *Lutjanus campechanus* and red drum *Sciaenops ocellatus* from the northern Gulf of Mexico. *Can. J. Fish. Aquat. Sci.* (in press).
- Baker Jr., M.S., Wilson, C.A., VanGent, D.L., 2001. Radiometric validation of otolith section age estimates of red snapper *Lutjanus campechanus*, from the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* (in press).
- Beamish, R.J., 1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *J. Fish. Res. Board Can.* 36, 1395–1400.
- Beamish, R.J., McFarlane, G.A., 1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112, 735–743.
- Beamish, R.J., McFarlane, G.A., 2000. Reevaluation of the interpretation of annuli from otoliths of a long-lived fish *Anoplopoma fimbria*. *Fish. Res.* 46, 105–111.
- Bennett, J.T., Boehlert, G.W., Turekian, K.K., 1982. Confirmation on longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from $^{210}\text{Pb}/^{226}\text{Ra}$ measurements in otoliths. *Mar. Biol.* 71, 209–215.
- Bergstad, O.A., 1990. Distribution, population structure, growth and reproduction of the roundnose grenadier *Coryphaenoides rupestris* (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Mar. Biol.* 107, 25–39.
- Bergstad, O.A., 1995. Age determination of deep-water fishes: experiences, status and challenges for the future. In: Hopper, A.G. (Ed.). *Deep-Water Fisheries of the North Atlantic Oceanic Slope*. Kluwer, Netherlands, pp. 267–283.

- Beverton, R.H., 1987. Longevity in fish: some ecological and evolutionary considerations. In: Woodhead, A.D., Thompson, K.H. (Eds.). *Evolution of Longevity in Animals: a Comparative Approach*. Plenum press, New York, pp. 161–186.
- Beverton, R.J.H., Holt, S.J., 1959. A review of the life span and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: Wolstenholme, G.E.W., O'Connor, M. (Eds.). *The Life Span of Animals*. CIBA Foundation Colloquia on Ageing, vol. 5. Little, Brown and Co, Boston.
- Bloeser, J.A., 1999. Diminishing returns: The status of west coast rockfish. Pacific Marine Conservation Council.
- Brennan, J.S., Cailliet, G.M., 1989. Comparative age-determination techniques for white sturgeon in California. *Trans. Am. Fish. Soc.* 118, 296–310.
- Brennan, J.S., Cailliet, G.M., 1991. Age determination and validation studies of white sturgeon, *Acipenser transmontanus*, in California. In: Williot, P. (Ed.). *Acipenser: Actes Du Premier Colloque International Sur L'esturgeon*. CEMAGREF Publ, pp. 209–234.
- Burton, E.J., 1999. Radiometric age determination of the giant grenadier (*Albatrossia pectoralis*) using ^{210}Pb : ^{226}Ra disequilibria, MS thesis, San Francisco State University.
- Burton, E.J., Andrews, A.H., Coale, K.H., Cailliet, G.M., 1999. Application of radiometric age determination to three long-lived fishes using ^{210}Pb : ^{226}Ra disequilibria in calcified structures: a review. *Am. Fish. Soc. Symp.* 23, 77–87.
- Butler, J.L., Jacobson, L.D., Barnes, J.T., Moser, H.G., Collins, R., 1999. Stock assessment of cowcod. In: Pacific Fishery Management Council, Status of the Pacific Coast Groundfish Fishery Through 1999 and Recommended Acceptable Biological Catches for 2000. Appendix: Stock Assessments. Pacific Fishery Management Council: Portland, Oregon.
- Cailliet, G.M., 1990. Elasmobranch age determination and verification: an updated review. In: W.S. Pratt Jr., S.H. Gruber, T. Taniuchi (Eds.), *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*. NOAA Tech. Rep. NMFS 90, pp. 157–165.
- Cailliet, G.M., Natanson, L.J., Welden, B.A., Ebert, D.A., 1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. *Soc. Calif. Acad. Sci. Mem.* 9, 49–60.
- Cailliet, G.M., Love, M.S., Ebeling, A.W., Fishes, A., 1986. *Fishes: a Field and Laboratory Manual on Their Structure, Identification and Natural History*. Wadsworth Publ, Belmont, CA.
- Cailliet, G.M., Mollet, H.F., Pittinger, G.G., Bedford, D., Natanson, L.J., 1992. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. *Aust. J. Mar. Freshw. Res.* 43, 1313–1330.
- Cailliet, G.M., Botsford, L.W., Brittnacher, J.G., Ford, G., Matsubayashi, M., King, A., Watters, D.L., Kope, R.G., 1996. Development of a computer-aided age determination system: evaluation based on otoliths of bank rockfish off California. *Trans. Am. Fish. Soc.* 125, 874–888.
- Campana, S.E., Zwaenburg, K.C.T., Smith, J.N., 1990. ^{210}Pb / ^{226}Ra determination of longevity in redbfish. *Can. J. Fish. Aquat. Sci.* 47, 163–165.
- Casillas, E., Crockett, L., deReynier, Y., Glock, J., Helvey, M., Meyer, B., Schmitt, C., Yoklavich, M., Bailey, A., Chao, B., Johnson, B., Pepperell, T., 1998. *Essential Fish Habitat West Coast Groundfish Appendix*, National Marine Fisheries Service, Seattle, Washington, Located at website <http://www.nwr.noaa.gov/1sustfish/efhappendix/page1.html>.
- Childress, J.J., 1977. Physiological approaches to the biology of midwater organisms. In: Anderson, N.R., Zahuranec, B.J. (Eds.). *Oceanic Sound Scattering Prediction*. Plenum, New York, pp. 301–324.
- Childress, J.J., 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals?. *Trends Ecol. Evol.* 10, 30–36.
- Childress, J.J., Somero, G.N., 1979. Depth-related enzymic activities in muscle, brain and heart of deep-living pelagic marine teleosts. *Mar. Biol.* 52, 272–283.
- Childress, J.J., Taylor, S.M., Cailliet, G.M., Price, M.H., 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off southern California. *Mar. Biol.* 61, 27–40.
- Chilton, D.E., Beamish, R.J., 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. *Can. Spec. Publ. Fish. Aquat. Sci.* 60, 102.
- Cohen, A.S., O'Nions, R.K., 1991. Precise determination of femptogram quantities of radium by thermal ionization mass spectrometry. *Anal. Chem.* 63, 2705–2708.
- Cowart, J.B., Burnett, W.C., 1994. The distribution of uranium and thorium decay-series radionuclides in the environment B. A review. *J. Environ. Qual.* 23, 651–662.

- Crabtree, R.E., Cyr, E.C., Dean, J.M., 1995. Age and growth of tarpon, *Megalops atlanticus*, from South Florida waters. *Fish. Bull.* 93, 619–628.
- Craig, J.F., 1985. Aging in fish. *Can. J. Zool.* 63, 1–8.
- Fenton, G.E., Short, S.A., 1992. Fish age validation by radiometric analysis of otoliths. *Aust. J. Mar. Freshw. Res.* 43, 913–922.
- Fenton, G.E., Ritz, D.A., Short, S.A., 1990. $^{210}\text{Pb}/^{226}\text{Ra}$ disequilibria in otoliths of blue grenadier, *Macruronus novaezelandiae*: problems associated with radiometric ageing. *Aust. J. Mar. Freshw. Res.* 41, 467–473.
- Flynn, W.W., 1968. The determination of low levels of polonium-210 in environmental materials. *Anal. Chim. Acta* 43, 221–227.
- Fossum, P., Kalish, J., Moksness, E. (Eds.), 2000. Second International Symposium on Fish Otolith Research & Application, Bergen, Norway, 20–25 June 1999, *Fisheries Res. (Special Issue)* 46.
- Fyfe-Johnson, A.L., Yancey, P.H., 1998. Pressure inhibition of deep-sea grenadier lactate dehydrogenase and counteractions by trimethylamine oxide. Abstract, *Am. Zool.*, 38, 120A.
- Gillett, M.B., Suko, J.R., Santoso, F.O., Yancey, P.H., 1997. Elevated levels of trimethylamine oxide in muscles of deep-sea gadiform teleosts: a high-pressure adaptation?. *J. Exp. Zool.* 279, 386–391.
- Hennessey Jr., J.P., Siebenaller, J.F., 1985. Pressure inactivation of tetrameric lactate dehydrogenase homologues of confamilial deep-living fishes. *J. Comp. Physiol. B* 155, 647–652.
- Hill, K.T., Womersley, C.Z., 1993. Interactive effects of some environmental and physiological variables on fluorescent age pigment accumulation in brain and heart tissues of an aquatic poikilotherm. *Environ. Biol. Fishes* 37, 397–405.
- Hochachka, P.W., Somero, G.N., 1984. *Biochemical Adaptations*. Princeton University, New Jersey.
- Hubold, G., Tomo, A.P., 1989. Age and growth of Antarctic silverfish *Pleuragramma antarcticum* Boulenger, 1902, from the southern Weddell Sea and Antarctic Peninsula. *Polar. Biol.* 9, 205–212.
- Ivanovich, M., 1992. The phenomenon of radioactivity. In: Ivanovich, M., Harmon, R.S. (Eds.). *Uranium-series Disequilibrium: Applications to Earth, Marine, and Environmental Sciences*. 2nd ed.. Oxford University Press, New York, pp. 1–33 (pp. 1–33).
- Janssens, B., Childress, J.J., Bagnet, F., Reese, J.F., 2000. Reduced enzymatic antioxidative defense in deep-sea fish. *J. Exp. Biol.* 203, 3717–3725.
- Kastelle, C.R., Kimura, D.K., Nevissi, A.E., Gunderson, D.R., 1994. Using Pb-210/Ra-226 disequilibria for sablefish, *Anoplopoma fimbria*, age validation. *Fish. Bull.* 92, 292–301.
- Kastelle, C.R., Kimura, D.K., Jay, S.R., 2000. Using $^{210}\text{Pb}/^{226}\text{Ra}$ disequilibrium to validate conventional ages in scorpaenids (genera *Sebastes* and *Sebastolobus*). *Fish. Res.* 46, 299–312.
- Kelly, R.H., Yancey, P.H., 1999. High contents of trimethylamine oxide correlating with depth in deep-sea teleost fishes, skates, and decapod crustaceans. *Biol. Bull.* 196, 18–25.
- Kelly, C.J., Connolly, P.L., Bracken, J.J., 1997. Age estimation, growth, maturity and distribution of the round-nose grenadier from the Rockall trough. *J. Fish. Biol.* 50, 1–17.
- Kimura, D.K., Kastelle, C.R., 1995. Perspectives on the relationship between otolith growth and the conversion of isotope activity ratios to fish ages. *Can. J. Fish. Aquat. Sci.* 52, 2296–2303.
- Kline, D.E., 1996. Radiochemical age verification for deep-sea rockfishes *Sebastolobus altivelis* and *S. alascanus*. MS thesis, San Jose State University.
- Kramer, D.E., O'Connell, V.M., 1995. Guide to northeast Pacific rockfishes genera *Sebastes* and *Sebastolobus*. Alaska Sea Grant Marine Advisory Bulletin, No. 25, 1–75, Alaska: University of Alaska Fairbanks.
- Kusher, D.I., Smith, S.E., Cailliet, G.M., 1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, from central California. *Environ. Biol. Fishes* 35 (2), 187–203.
- Leaman, B.M., 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environ. Biol. Fishes* 30, 253–271.
- Leaman, B.M., Beamish, R.J., 1984. Ecological and management implications of longevity in some northeast Pacific groundfishes. *Int. North Pac. Fish. Comm. Bull.* 42, 85–97.
- Leos, B. (Ed.), 1996. Monterey Bay commercial fisheries report: an annual newsletter to the commercial fishing industry. California Department of Fish and Game No. 7, Monterey, California.
- Leos, B. (Ed.), 1997. Monterey Bay commercial fisheries report: an annual newsletter to the commercial fishing industry. California Department of Fish and Game No. 8, Monterey, California.
- Love, M.S., 1978. Aspects of the life history of the olive rockfish (*Sebastes serranoides*). PhD thesis, University of California Santa Barbara.

- Love, M.S., Johnson, K., 1998. Aspects of the life histories of grass rockfish, *Sebastes rastrelliger* and brown rock fish, *S. auriculatus*, from southern California. *Fish. Bull.* 87, 100–109.
- Love, M.S., Caselle, J.E., Herbinson, K., 1998. Declines in nearshore rockfish recruitment and population in the southern California Bight as measured by impingement rates in coastal electrical power generating stations. *Fish. Bull.* 96 (3), 492–501.
- Mace, P.M., Fenaughty, J.M., Coburn, R.P., Doonan, I.J., 1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the North Chatham Rise. *N. Z. J. Mar. Freshw. Res.* 24, 105–119.
- Magnin, E., 1964. Croissance en longueur de trios esturgeons d’Amérique du Nord: *Acipenser oxyrinchus* Mitchill, *Acipenser fulvescens* Rafinesque et *Acipenser brevirostris* Le Sueur. *Verh. Int. Verein. Limnol.* 15, 968–974.
- Mangel, M., Abrahams, M.V., 2001. Age and longevity in fish, with consideration of the ferox trout. *Exp. Gerontol.* 36.
- Matsui, T., Kato, S., Smith, S.E., 1990. Biology and potential use of Pacific grenadier, *Coryphaenoides acrolepis*, off California. *Mar. Fish Rev.* 52, 1–17.
- Mauchline, J., 1988. Growth and breeding of meso- and bathypelagic organisms of the Rockall Trough, north-eastern Atlantic Ocean and evidence of seasonality. *Mar. Biol.* 98, 387–393.
- McFarlane, G.A., Beamish, R.J., 1987. Validation of the dorsal spine method of age determination for spiny dogfish. In: Summerfelt, R.C., Hall, G.E. (Eds.). *The Age and Growth of Fish*. Iowa State University Press, Ames, IA.
- McFarlane, G.A., Beamish, R.J., 1995. Validation of the otolith cross-section method of age determination for sablefish (*Anoplopoma fimbria*) using oxytetracycline. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.). *Recent Developments in Fish Otolith Research*. Belle W. Baruch Library in Marine Science Number 19 University of South Carolina Press, South Carolina, pp. 319–329.
- Merrett, N.R., Haedrich, R.L., 1997. *Deep-Sea Demersal Fish and Fisheries*. Chapman & Hall, London.
- Middleton, R.W., Musick, J.A., 1986. Abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area. *Fish. Bull.* 84 (1), 35–62.
- Miller, D.J., Lea, R.N., 1972. Guide to the coastal marine fishes of California. *Calif. Dept. Fish. Game, Fish. Bull.* 157, 1–235.
- Moore, J.A., 1999. Deep-sea finfish fisheries: lessons from history. *Fisheries* 24 (7), 16–21.
- Moore, J.A., Mace, P.M., 1999. Challenges and prospects for deep-sea finfish fisheries. *Fisheries* 24 (7), 22–23.
- Morales-Nin, B., 1990. A first attempt determining growth patterns of some Mediterranean deep-sea fishes. *Sci. Mar.* 54, 241–248.
- Parsons, G., 1985. Growth and age estimation of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*: a comparison of techniques. *Copeia* 1985 (1), 80–85.
- Pratt Jr., H.L., Casey, J.G., 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. *Can. J. Fish. Aquat. Sci.* 40, 1944–1975.
- Probst, R.T., Cooper, E.L., 1954. Age, growth, and production of the lake sturgeon (*Acipenser fulvescens*) in the Lake Winnebago region, Wisconsin. *Trans. Am. Fish. Soc.* 84, 207–227.
- Rees, J.-F., De Wergifosse, B., Noiset, O., Dubuisson, M., Janssens, B., Thompson, E.M., 1998. The origins of marine bioluminescence: turning oxygendefence mechanisms into deep-sea communication tools. *J. Exp. Biol.* 201, 1211–1221.
- Reilly, P.N., Wilson-Vandenberg, D., Lea, R.N., Wilson, C., Sullivan, M., 1994. *Recreational angler’s guide to the common nearshore fishes of Northern and Central California*. Calif. Dept. Fish. Game, Marine Resources Leaflet.
- Reznick, D., Buckwalter, G., Groff, J., Elder, D., 2001. The evolution of senescence in natural populations of guppies (*Poecilia reticulata*): a comparative approach. *Exp. Gerontol.* 36, 791–812.
- Rien, T.A., Beamesderfer, R.C., 1994. Accuracy and precision of white sturgeon age estimates from pectoral fin rays. *Trans. Am. Fish. Soc.* 123, 255–265.
- Savvatimsky, P.I., 1994. Age structure of roughhead grenadier (*Macrourus berglax*) in the Northwest Atlantic. *NAFO Sci. Council Studies* 20, 53–64.
- Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), 1995. *Recent Developments in Fish Otolith Research*. Belle W., Baruch Library in Marine Science Number 19. South Carolina: University of South Carolina Press.
- Shaw, F.R., 1999. Life history of four species of rockfish (Genus *Sebastes*). PhD thesis, University of Washington.

- Siebenaller, J.F., 1983. The pH-dependence of the effects of hydrostatic pressure on the M₄-lactate dehydrogenase homologs of scorpaenid fishes. *Mar. Biol. Lett.* 4, 233–243.
- Siebenaller, J.F., 1984. Analysis of the biochemical consequences of ontogenetic vertical migration in a deep-living teleost fish. *Physiol. Zool.* 57, 598–608.
- Siebenaller, J.F., Somero, G.N., 1978. Pressure-adaptive differences in lactate dehydrogenases of congeneric fishes living at different depths. *Science* 201, 255–257.
- Siebenaller, J.F., Somero, G.N., 1982. The maintenance of different enzyme activity levels in congeneric fishes living at different depths. *Physiol. Zool.* 55 (2), 171–179.
- Siebenaller, J.F., Somero, G.N., 1989. Biochemical adaptation to the deep sea. *Crit. Rev. Aquat. Sci.* 1 (1), 1–25.
- Siebenaller, J.F., Somero, G.N., Haedrich, R.L., 1982. Biochemical characteristics of macrourid fishes differing in their depths of distribution. *Biol. Bull.* 163, 240–249.
- Simpfendorfer, C.A., 1993. Age and growth of the Australian sharpnose shark *Rhizoprionodon taylori*, from north Queensland, Australia. *Environ. Biol. Fishes* 36, 233–241.
- Smith Jr., K.I., Brown, N.O., 1983. Oxygen consumption of pelagic juveniles and demersal adults of the deep-sea fish *Sebastes altivelis* measured at depth. *Mar. Biol.* 76, 325–332.
- Smith, J.N., Nelson, R., Campana, S.E., 1991. The use of Pb-210/Ra-226 and Th-228/Ra-228 disequilibria in the ageing of otoliths of marine fish. In: Kershaw, P.J., Woodhead, D.S. (Eds.). *Radionuclides in the Study of Marine Processes*. Elsevier, New York, pp. 350–359.
- Smith, D.C., Fenton, G.E., Robertson, S.G., Short, S.A., 1995. Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Can. J. Fish. Aquat. Sci.* 52, 391–401.
- Somero, G.N., 1992. Adaptations to high hydrostatic pressure. *Annu. Rev. Physiol.* 54, 557–577.
- Somero, G.N., 1992. Biochemical ecology of deep-sea animals. *Experientia* 48, 537–543.
- Stevenson, J.T., Secor, D.H., 2000. Age determination and growth of Hudson River Atlantic sturgeon, *Acipenser oxyrinchus*. *Fish. Bull.* 97, 153–166.
- Stewart, B.D., Fenton, G.E., Smith, D.C., Short, S.A., 1995. Validation of otolith-increment age estimates for a deepwater fish species, the wartyeoreo *Allocyttus verrucosus*, by radiometric analysis. *Mar. Biol.* 123, 29–38.
- Sullivan, K.M., Somero, G.N., 1983. Size- and diet-related variations in enzymic activity and tissue composition in the sablefish *Anoplopoma fimbria*. *Biol. Bull.* 164, 315–326.
- Torres, J.J., Somero, G.N., 1988. Metabolism, enzymic activities and cold adaptation in Antarctic mesopelagic fishes. *Mar. Biol.* 98, 169–180.
- Torres, J.J., Somero, G.N., 1988. Vertical distribution and metabolism in Antarctic mesopelagic fishes. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 90 (3), 521–528.
- Tracey, D.M., George, K., Gilbert, D.J., 2000. Estimation of age, growth, and mortality parameters of black cardinalfish (*Epigonus telescopus*) in QMA 2 (east coast North Island). *New Zeal Fisheries Assessment Report* 2000/27.
- Tucker, R., 1985. Age validation studies on the spines of the spurdog (*Squalus acanthias*) using tetracycline. *J. Mar. Biol. Assoc. UK* 65, 641–651.
- Vetter, R.D., Lynn, E.A., 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastes*): paradigms revisited. *Mar. Ecol. Prog. Ser.* 155, 173–188.
- Vetter, R.D., Lynn, E.A., Garza, M., Costa, A.S., 1994. Depth zonation and metabolic adaptation in Dover sole, *Microstomus pacificus*, and other deep-living flatfishes: factors that affect the sole. *Mar. Biol.* 120, 145–159.
- Watters, D.L., 1993. Age determination and confirmation from otoliths of the bank rockfish, *Sebastes rufus* (Scorpaenidae). MS thesis, San Jose State University.
- Welden, B.A., Cailliet, G.M., Flegal, A.R., 1987. Comparison of radiometric with vertebral band age estimates in four California elasmobranchs. In: Summerfelt, R.C., Hall, G.E. (Eds.). *The Age and Growth of Fish*. The Iowa State University Press, Ames, IA, pp. 301–315.
- Williams, T., Bedford, B.C., 1974. The use of otoliths for age determination. In: Bagenal, T.B. (Ed.). *The Ageing of Fish*, Proceedings of an International Symposium. Unwin Brothers Limited, Surrey, England, pp. 114–123.
- Wilson, C.D., Boehlert, G.W., 1990. The effects of different otolith ageing techniques on estimates of growth and mortality for the splitnose rockfish, *Sebastes diploproa*, and canary rockfish, *S. pinniger*. *Calif. Fish. Game* 76 (3), 146–160.
- Wilson, M.T., Brown, A., Andrews, A., 2000. Growth of the axial rod of a sea pen, *Halipteris* sp. Abstract: First

- International Symposium on Deep Sea Corals, Science and Conservation of Deep Sea Corals, Halifax, Nova Scotia, Canada, July 30–August 3, 2000, p. 39.
- Wintner, S.P., Cliff, G., 1999. Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. *Fish. Bull.* 97 (1), 153–169.
- Yancey, P.H., Siebenaller, J.F., 1999. Trimethylamine oxide stabilizes teleost and mammalian lactate dehydrogenases against inactivation by hydrostatic pressure and trypsinolysis. *J. Exp. Biol.* 202, 3597–3603.
- Yang, T.-H., Somero, G.N., 1993. Effects of feeding and food deprivation on oxygen consumption, muscle protein concentration and activities of energy metabolism enzymes in muscle and brain of shallow-living (*Scorpaena guttata*) and deep-living (*Sebastolobus alascanus*) scorpaenid fishes. *J. Exp. Biol.* 181, 213–232.
- Yang, T.-H., Lai, N.C., Graham, J.B., Somero, G.N., 1992. Respiratory, blood, and heart enzymatic adaptations of *Sebastolobus alascanus* (Scorpaenidae; Teleostei) to the oxygen minimum zone: a comparative study. *Biol. Bull.* 183, 490–499.
- Zaitlin, J.A., 1986. Geographical variation in the life history of *Sebastes chrysomelas*. MA thesis, San Francisco State University.