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Radiochemical age verification for two deep-sea rockfishes : Sebastolobus altivelis and S. alascanus

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RADIOCHEMICAL AGE VERIFICATION FOR TWO DEEP-SEA ROCKFISHES

Sebastolobus altivelis and *S. alascanus*

A Thesis

Presented to

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Master of Science

By
Donna E. Kline

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ABSTRACT

Radiochemical Age Verification for Two Deep-Sea Rockfishes

Sebastolobus altivelis and S. alascanus

by

Donna E. Kline

Thornyhead rockfishes (*Sebastolobus altivelis* and *S. alascanus*) have been commercially harvested at an increasing rate off the west coast of the United States. Age estimates from otoliths indicate that both species are long-lived, potentially making the populations vulnerable to heavy fishing pressure. The purpose of this study was to verify longevity by quantitatively comparing growth patterns in otoliths with the radiochemical age of their cores. Growth increment patterns visible in transverse otolith sections from these two species were narrow, often irregular, and difficult to interpret, resulting in poor ageing precision. A technique that measures the radiochemical disequilibria between natural ^{210}Pb and ^{226}Ra in otolith cores was used to independently determine longevity. Levels of (^{210}Pb:^{226}Ra) disequilibria in otolith cores confirmed ages of at least 45 years for *S. altivelis* and 80 years for *S. alascanus*. This technique, however, is very sensitive to small variation or errors in ^{226}Ra measurements when ^{210}Pb levels reach approximately 75% of the equilibrium value. Ages over 80 years, estimated for *S. alascanus*, could not be confirmed due to variation in ^{226}Ra assays.

Sebastolobus altivelis (top) and *Sebastolobus alascanus* (bottom)

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PAGE

INTRODUCTION

Sebastolobus (family Scorpaenidae), known collectively as thornyheads, is a slope-dwelling rockfish genus endemic to the North Pacific and abundant along the west coast of the United States and Canada. Two species occur in the eastern Pacific, *Sebastolobus altivelis* and *S. alascanus*, and are important components of the commercial Pacific coast groundfish fishery. The two co-occur over much of their depth and distributional ranges, and are similar in behavior and morphology (Miller and Lea 1972; Eschmeyer *et al.* 1983). *Sebastolobus alascanus*, the shortspine thornyhead, inhabits depths of 90 to 1500 m from northern Baja California, Mexico to the Bering Sea (Phillips 1957; Berry and Perkins 1965; Miller and Lea 1972; Eschmeyer *et al.* 1983). The range of *S. altivelis*, the longspine thornyhead, is slightly more southerly, from the southern tip of Baja to the Aleutian Islands at depths between 400-1500 m (Miller and Lea 1972; Eschmeyer *et al.* 1983). *Sebastolobus alascanus* ontogenetically migrates down the slope, moving into deeper water with growth (Wakefield 1990, Jacobson and Vetter *in prep*). *Sebastolobus altivelis* does not ontogenetically migrate; all sizes can be found at all depths of occurrence (Wakefield 1990). Both species are demersal, living on soft substrates (Smith and Hamilton 1983; Wakefield 1990), where they are collected primarily by the commercial bottom-trawl fishery (Jacobson 1991; Ianelli *et al.* 1994).

Though eggs and larvae are nearly identical in size and appearance (Moser 1974, Matarese *et al.* 1989), and the two mature at about the same size (215-220 mm;

Jacobson 1990), *S. alascanus* grows larger, to a maximum of 800 mm total length, whereas *S. altivelis* reaches only 350 mm. Both have pelagic larvae and juveniles that dwell in the midwater for extended periods; *S. alascanus* for 14-15 months and *S. altivelis* for 18-20 months (Moser 1974). They settle to the bottom as large juveniles, *S. alascanus* at 22-27 mm in 90-100 m depths (Moser 1974; Straty 1987), and *S. altivelis* at 42-56 mm between 600 and 1200 m (Moser 1974; Wakefield 1990). Historically plentiful on the slope (Best 1964; Westrheim 1968; Smith and Hamilton 1983; Cross 1987), abundances for both species are greatest in the oxygen minimum zone between 600 and 1000 m (Pearcy *et al.* 1982; Wakefield 1990), where spawning individuals are predominantly found (Ianelli *et al.* 1994; Jacobson and Vetter *in prep*).

Deep-water fishes, such as thornyhead rockfishes, have been commercially harvested at increasing rates off the west coast of the United States. Thornyheads are targeted commercially as components of the Pacific deepwater (DW) complex which also includes sablefish (*Anoplopoma fimbria*) and Dover sole (*Microstomus pacificus*; Jacobson 1991). Thornyhead landings increased coastwide from less than 2,000 metric tons (mt) in 1981 to 10,000 mt in 1990 (Pacific Fisheries Management Council (PFMC) 1991). Originally managed solely as part of the DW complex, weekly trip limits were placed on the combined thornyhead component of the catch beginning in 1991, and the 1991-1994 average regulated catch was 8,500 mt (Ianelli *et al.* 1994). In 1990 the thornyheads ranked fifth in total commercial groundfish

landings on the west coast and in 1994 were third (PFMC 1994). In 1995, the two species will have separate catch limits. All sizes of both thornyhead species are marketable (Ianelli *et al.* 1994).

Fisheries management policies for these species are founded upon ages estimated from analyses of otolith growth increments (Jacobson 1991). Preliminary examination of transversely sectioned otoliths indicated that *S. alascanus* may commonly reach more than 80 years (y) and *S. altivelis* 35 y of age with maximum ages of 115 y and 45 y respectively (Jacobson 1991). However, these ages have not been validated. Population age structure, growth rates, age at maturity, and longevity, all essential components of a comprehensive management plan, have been based on preliminary estimates. Both species are probably long-lived, reproduce relatively late in life, therefore could be vulnerable to heavy fishing pressure.

Otolith interpretation requires a certain degree of subjectivity, and must be independently validated for each species and life history phase, across the age range for the species (Chilton and Beamish 1982; Beamish and McFarlane 1983; Campana *et al.* 1990). Thornyhead otolith growth increments are narrow, often irregular, and difficult to interpret, making substantiation doubly important. Validation, determining the accuracy of an ageing method, requires examination of known-age fish obtained through mark-tag-recapture methods or laboratory rearing (Ricker 1975; Beamish and McFarlane 1983; Geffen 1992). However, tag-recapture studies are impractical for fishes, such as the thornyheads, that inhabit deep water where the

live capture rate is low and recapture probability negligible, and laboratory-raised specimens are unavailable.

In the absence of satisfactory validation, it is important to employ a separate and independent ageing method, to see if both estimates yield similar results. Common techniques include comparison of growth increments among various hardparts from the same individuals, marginal increment analysis of otolith section edges by time of year, and size frequency analysis. For both *Sebastolobus* species, ages for the first two years have been verified through size frequency analysis (Moser 1974). After age class two, however, size frequency modes overlap to such an extent that peaks are indistinguishable, making it impossible to distinguish a year class further using this method. Hardpart comparison is useful during initial periods of maximum growth but increment deposition in scales and bones can slow, and even cease, when growth becomes asymptotic (Beamish and McFarlane 1987; Casselman 1990). Marginal increment analysis is difficult for these species because the growth increments are very narrow, making changes in pattern difficult to detect.

Researchers that have successfully verified age estimates for long-lived or deep-dwelling fish species have used otolith radiochemical ageing (Bennett *et al.* 1982; Campana *et al.* 1990; Fenton *et al.* 1991; Watters 1993; Kastelle *et al.* 1994; Stewart *et al.* 1995; Fenton and Short 1995). A well-recognized geochemical tool (DeMaster and Cochran 1977; Nozaki *et al.* 1977; Peng *et al.* 1979; Li *et al.* 1979; McKee *et al.* 1984; Coale and Bruland 1985, 1987), radiochemical disequilibria have been used to

age biogenically produced calcium carbonate minerals in coral skeletons (Moore and Krishnaswami 1972; Dodge and Thomson 1974), clam shells (Turekian *et al.* 1975; Turekian and Cochran 1981; Turekian *et al.* 1979, 1982, and 1983), crabs (Bennett and Turekian 1982), nautilus shells (Cochran *et al.* 1981; Cochran and Landman 1984), and pteropod and heteropod shells (Fabry and Delaney 1989), as well as fish otoliths.

Radiochemical age is determined by measuring the extent of disequilibrium between a naturally occurring parent/daughter radioactive pair within the biomineralized structure. When a radioactive parent/daughter pair, possessing different half-lives (and the parent's significantly exceeds that of the daughter's), are isolated in unequal proportions in a system where decay of the two can proceed undisturbed, without addition or removal, the two will eventually reach an equilibrium state where their rates of decay are equal (secular equilibrium). The time required to reach secular equilibrium depends on the half-life of the daughter radionuclide and is reached in approximately five to seven half-lives.

Uranium and thorium decay series radionuclides are particularly useful for biological studies because radium isotopes, ^{238}U and ^{232}Th daughter products and calcium analogues, are readily deposited within calcium carbonate structures as they grow. To measure time-based processes, researches of invertebrates have used the radioactive pairs (^{210}Po:^{210}Pb) which reaches secular equilibrium in 2 y and (^{228}Th:^{228}Ra) which reaches secular equilibrium in 10 y. In addition, the change in

(^{228}Ra:^{226}Ra) over time has been used chronomically to 30 y. Fish otoliths are composed of crystals of aragonitic calcium carbonate formed within an organic matrix (Degens *et al.* 1969; Lowenstam and Weiner 1989) and, like invertebrate structures, incorporate radium isotopes as they grow. Although the (^{228}Th:^{228}Ra) has been used successfully to determine age in short-lived fishes successfully (Smith *et al.* 1991), longevity estimates for many deep-water fishes, including the two thornyheads, exceed the useful time limits for the aforementioned isotope pairs.

The radioactive pair (^{210}Pb:^{226}Ra), effective as a chronometer to about 100 y, has been used successfully to verify ages for *Sebastes diploproa* (Bennett *et al.* 1982), *Sebastes mentella* (Campana *et al.* 1990), *Hoplostethus atlanticus* (Fenton *et al.* 1991), *Sebastes rufus* (Watters 1993), *Anoplopoma fimbria* (Kastelle *et al.* 1994), three tropical Lutjanids (Milton *et al.* 1995), and *Allocyttus verrucosus* (Stewart *et al.* 1995) and *Macruronus novaezelandiae* (Fenton and Short 1995). However, at least two studies (Welden *et al.* 1987; Fenton *et al.* 1990) have been unsuccessful in attempting to use radiochemical ageing in fish, citing violation of assumptions required for use of the technique and emphasizing that the assumptions should be tested for each species.

Three assumptions constrain the use of this technique: (1) uptake rate of both radionuclides must be constant in relation to mass increase in the otolith over time; (2) uptake rate of the parent radionuclide (^{226}Ra), must be significantly greater than that of the daughter (^{210}Pb); and (3) the system must be closed (i.e. no loss or gain

of either parent (^{226}Ra), daughter (^{210}Pb), or any intermediate decay products, can occur following initial deposition except through radioactive decay or ingrowth). The constant uptake requirement can be limited to the period of core formation when restricting the analyses to the oldest portion of the otolith by coring to remove exterior layers (Campana *et al.* 1990).

The purpose of this study was to confirm the longevity of two *Sebastolobus* species, and to assess the accuracy of otolith increments as indicators of their age. Specific objectives were: (1) to examine otolith section growth increments from a broad range of sizes to develop age and growth estimates for comparison with fishery data; (2) to assess the precision of age estimates both within and between readers and labs; (3) to test the assumption of constant mass increase over the period of core formation; (4) to measure the (^{210}Pb:^{226}Ra) in otolith cores from each species and compare radiochemical age to the otolith section growth increment count; and (5) to test the assumption of constant uptake rate by measuring the activities of ^{226}Ra in a series of weight-stratified samples.

METHODS

Collection

Sebastolobus altivelis and *S. alascanus* specimens were collected September 1991 during a National Marine Fisheries Southwest Fisheries Science Center (SWFSC)

groundfish survey cruise southwest of Santa Cruz, CA. Fish were collected from 100 m depth and along isobaths at 200 m intervals from 200 to 1400 m using a modified 75/90 Poly-Aberdeen bottom trawl with three-inch mesh net. Total length was measured to the nearest 1 mm. Sagittal otolith pairs were removed, rinsed in 70% ethanol, air dried, and stored in glass or polypropylene vials. Too many *S. altivelis* specimens were collected to process onboard. Unprocessed fish were frozen and returned to shore where otoliths were removed and treated identically. Additional *S. alascanus* specimens were collected from similar depths on a Moss Landing Marine Labs (MLML) cruise off the Farallon Islands near San Francisco, CA in October 1991 and additional *S. altivelis* were collected in October 1990, by otter trawl in Monterey Bay from 650 m. All fish from the MLML cruises were frozen and otoliths collected and processed on shore. Frozen specimens were not used in fish morphometric analyses except for the *S. altivelis* collected from the MLML cruise that were used for age analysis and radiochemistry. They were plotted separately. Remaining otoliths collected from frozen fish were weighed and pooled for bulk radium analyses.

Ageing

Right otoliths from both species were measured with calipers or an ocular micrometer to the nearest 0.1 mm in three dimensions; length, width, and thickness. They were weighed to the nearest 0.1 mg. A 0.5 mm thick transverse section encompassing the core was removed using a Buehler Isomet® low-speed saw with

two 0.25 mm spacers between two diamond blades (Cailliet *et al.* 1986; Secor *et al.* 1992). Sections were mounted on microscope slides and ground to approximately 0.3 mm thickness on a Buehler Ecomet® III grinding wheel with 400-800 grit aluminum carbide wet-dry grinding paper. Band pairs, representing a single growth increment, one opaque and one translucent, were counted at 50X magnification between the sulcus and the dorsal tip of the section (proximal to the brain *in vivo*) using established rockfish criteria (Chilton and Beamish 1982; PMFC 1984). The sections were viewed using both reflected and transmitted lighting. Unsectioned left otoliths from aged specimens and both otoliths from the remaining specimens were weighed to the nearest 0.1 mg and reserved for radiochemical assay.

Age precision analyses were conducted to assess the reproducibility of ages by different individuals and labs. Inter-reader precision was estimated using a randomly selected subsample of 50 sections for each species with increment counts ranging from 1 to 50. Increment counts were made independently by two separate readers from MLML and one from SWFSC. All counts were made at 50X magnification using either reflected or transmitted lighting, whichever the reader preferred. Increment counts were made also once at 50X using the Macintosh® image analysis program "Bony Parts" (Brittnacher and Botsford 1991) by an experienced operator. All readers used the same criteria to evaluate growth increments (Chilton and Beamish 1982; PFMC 1984). Percent agreement among all combinations of the four readings, average percent error (APE; Beamish and Fournier 1981), and coefficient

of variation (V) and index of precision (D; Chang 1982) were calculated. The Friedman test for a randomized blocks design with multiple comparisons (Zar 1995) was used to test for differences among the readings.

Age-specific precision for reader 1 was estimated using sections previously "aged" within ten-year groups. Each section was evaluated three times, without knowledge of prior counts, at 50X magnification under a combination of transmitted and reflected lighting. A minimum of one week separated counts. From these data, within reader percent agreement, APE, V, and D were calculated.

Reader 1 age estimates were used for all subsequent analyses, including VBGF analyses and comparisons with radiochemical measurements. The von Bertalanffy growth function (VBGF; $L_t=L_\infty(1-e^{-kt})$) was fitted to size at age data using the computer program FISHPARM (Prager *et al.* 1987). These data were compared to those developed from Oregon commercial catch data (Jacobson 1991).

Radiochemistry

^{226}Ra occurs naturally in seawater as a soluble radioactive decay product of ^{238}U (Fig. 1). ^{238}U and its daughters are transported to the sea via mechanical weathering processes from crustal rock. However, most of the ^{226}Ra in the ocean is supplied via remobilization at the sediment/water interface of the ocean floor (Chung and Craig 1973; Nozaki and Tsunogi 1976). ^{230}Th, a ^{238}U daughter and parent of ^{226}Ra, is extremely particle reactive (Coale and Bruland 1985), incorporating into sinking particulate matter as it passes through the water column. Once in the sediment,

^{230}Th decays to highly soluble ^{226}Ra which builds up in pore water and diffuses back to the ocean.

Radium, a group IIA element, is a biogeochemical analogue for calcium. Radium is taken up by fish through seawater during osmoregulation and food intake (Swanson 1985; Porntepkasemsan and Nevissi 1991), and metabolized similarly to calcium. The various isotopes of radium, as well as other group IIA elements, are incorporated into calcified tissues, and their organic components and associated tissues, through normal metabolic processes. ^{210}Pb is not a calcium analogue and is therefore, less likely to be deposited in calcified tissues. The high solubility of ^{226}Ra in seawater compared to its parent and daughter radio-isotopes, and radium's unique chemical similarity to calcium, allows the ^{226}Ra to be incorporated into fish otoliths unsupplemented and out of equilibrium with its decay products.

^{226}Ra decays within the otolith via five short-lived intermediate radionuclides (Fig. 1), to ^{210}Pb which is also radioactive, producing ^{210}Po. Through time, as both ^{226}Ra and ^{210}Pb decay, the ratio of the daughter (^{210}Pb) activity to that of the parent (^{226}Ra) increases since the daughter half-life is shorter than that of the parent. If undisturbed, the two will approach a state of equilibrium, where they decay at the same rate. The extent of the disequilibria between the two isotopes provides a measure of elapsed time since the ^{226}Ra was first incorporated.

Radiochemical age was determined for the two *Sebastolobus* species by measuring the specific activities of ^{210}Pb in otolith core samples and ^{226}Ra in whole

otolith samples, subsequently comparing the ratio of the two to that expected based on first-order-rate decay. Optimally, both ^{226}Ra and ^{210}Pb specific activities would be measured in a single otolith core, thus determining an individual specimen radiochemical age for comparison with band pair counts from the other otolith removed from the same fish. However, otoliths from these species are relatively small and activities of the two isotopes are low, less than 0.1 dpm/g (decay per minute per gram). Background radiation and analytical limitations of the currently available analytical techniques make statistically valid data impossible to collect from a single otolith. Therefore, otoliths with similar growth increment counts or of similar weight were pooled to provide enough material for the analyses. The coring technique developed by Campana *et al.* (1990) was used, with slight modifications. The otolith core (first five growth increments) was assumed to follow a linear mass growth model in keeping with the conditions required for use of this technique. This assumption was tested for *S. altivelis*, for which specimens were collected whose otoliths contained one to five band pairs. However, no *S. alascanus* otoliths were collected with five or fewer increments.

The three operational assumptions required when using radioisotope ageing techniques were tested when possible. ^{210}Pb uptake was assumed to be proportional to that of ^{226}Ra throughout the period of core formation and less than 20% of the ^{226}Ra uptake (Bennett *et al.*, 1982; Campana *et al.*, 1990; Kastelle 1991). Measured ratios were plotted against curves depicting the expected (^{210}Pb:^{226}Ra) ratio based on

three different proportional uptake rates (0, 0.1, and 0.2) to test the validity of this assumption. An additional test of this assumption was conducted by measuring the ^{210}Pb specific activity in the smallest otoliths available for each species (five growth increments for *S. altivelis*, 10-15 increments for *S. alascanus*).

The otolith was assumed to provide a closed radiochemical system, that no loss or addition of either isotope or the radiochemical intermediates occurred following deposition except through radioactive decay, an assumption supported by previous radiochemical verification and otolith microstructure studies (Simkiss 1974; Mugiya 1974; Campana 1983; Yoklavich and Boehlert 1987).

The third assumption was that ^{226}Ra was incorporated at a constant rate in proportion to otolith mass growth over the lifespan of the fish. As whole otoliths were used to measure the specific activity of ^{226}Ra for these two species, this assumption could not be ignored for ^{226}Ra. To test the assumption of constant uptake for *S. altivelis*, otolith samples were assembled into size groups for measurement of ^{226}Ra. However, similar analyses were not conducted for *S. alascanus* because of limited otolith material.

Sample Preparation

Coring

Core shapes approximated the size and shape of an otolith with five growth increments. *Sebastolobus altivelis* core dimensions were determined from measurements of otoliths containing five completed increments (length, width, and

thickness). *Sebastolobus alascanus* core width and height were estimated from measurements of the first five increments in a sample of 40 sections. The third dimension, core length, was determined by regressing otolith length with otolith weight for otoliths containing 5 to 12 increments. Cores were removed by grinding the exterior surfaces of the otolith on all sides to form a rounded oblong block, centered around the externally visible otolith nucleus (Campana *et al.* 1990, Kastelle *et al.* 1994). Grinding was accomplished by holding the otoliths on a Buehler Ecomet® III grinding wheel covered with 100-250 grit wet-dry grinding paper. Large *S. alascanus* otoliths were first embedded in L.R. White®, a histological mounting medium, and four cuts were made around the core with a Buehler Isomet® low-speed bone saw to remove excess material. These cores were then ground to the same dimensions as small whole otoliths.

Cleaning

Researchers that have successfully conducted radiochemical analyses of fish otoliths have emphasized that the low activities of the isotopes in the otolith require the use of clean techniques in sample preparation and extensive pretreatment to remove external contaminants (Campana *et al.* 1990; Fenton *et al.* 1990; Kastelle 1991). All radiochemical analyses were conducted using trace metal techniques and high purity reagents. Otolith samples were cleaned ultrasonically in 30% H_2O_2 and then repetitively with highly purified nitric acid and milli-Q purified, deionized water, to remove the surface layer which was exposed to handling and grinding. A

cleaning procedure (Fig. 2) was developed based on techniques used for trace level analyses on biogenic calcium carbonate by Linn (1988) and Fabry and Delaney (1989). Acid-cleaned glassware was used throughout and samples were kept dust-free at all times.

^{226}Ra Analysis Procedures

^{226}Ra specific activity was determined by measuring the decay rate of its first α-emitting daughter ^{222}Rn (Fig. 1). When ^{226}Ra is sealed in an air-tight container, ^{222}Rn reaches secular equilibrium (equal rate of decay) with ^{226}Ra quickly because ^{222}Rn's half-life is short (3.82 days) relative to that of ^{226}Ra (1622 y). A 30-day equilibration period (about seven half-lives) was used to ensure that secular equilibrium had been reached. The analyses were performed via emanation and collection of ^{222}Rn using a gas emanation and transfer system (Figs. 3a and 3b; Lucas 1957; Mackenzie *et al.* 1979; Smith and Walton 1980). Radon was stripped from the dissolved sample, trapped on activated carbon, and transferred to a counting cell where activity was determined by scintillation photon counting in a darkened chamber on a photomultiplier tube. Photon pulses recorded on a scaler were used to quantify the ^{222}Rn activity.

Whole otoliths were pooled to form samples weighing at least 10 g. Larger samples provided more α- decays, which increased statistical precision and ensured that counts were greater than background and blank counts. Whole otoliths were used instead of cores for these analyses because the size of the otolith core was

small (30-40 mg) and the material required to achieve precision at the activities expected was large (10 g). It was assumed that ^{226}Ra:Ca ratios in whole otoliths are the same as in the cores (i.e. radium is incorporated in constant ratio to calcium over the life of the fish). To test this assumption, *S. altivelis* otoliths were pooled into weight categories of <40 mg, 40-65 mg, 85-100 mg, >100 mg and two additional samples of mixed weights from the excess otoliths. *Sebastolobus alascanus* otoliths were simply pooled into three mixed size samples due to the limited number available. After assembly, otolith samples were cleaned (Fig. 2). The samples were then dried to constant weight (at least 12 hours) in an oven at 60° C , and covered by an acid-cleaned watch glass. The otolith samples were reweighed and transferred to an acid-cleaned gas wash bottle and dissolved with 2.8N HNO_3. The samples required 6-10 mL/g for complete dissolution. The dissolution process produced large amounts of CO_2 gas rapidly with addition of only small amounts of acid. Also, presence of the otolith's organic matrix caused the formation of foamy bubbles. The acid, therefore, was added slowly and in small amounts to prevent sample loss due to bubble overflow. Use of weaker acid reduced bubble formation by slowing the reaction but required the addition of large volumes of liquid that required reduction before complete dissolution could be achieved. Using 2.8N HNO_3, one 30-gram sample required a full week to dissolve.

When the sample was completely dissolved, the solution was adjusted to 1M acidity, heated to boiling point to remove CO_2, and allowed to cool. The bottle was

then sealed by placing silicon grease around the ground glass edge of the gas-wash bottle lid and clamping off rubber tubing (also sealed with silicon grease) attached to the inlet and outlet tubes (Fig. 3a). ^{222}Rn is a noble gas and will escape unless trapped in an air tight container. The sample was left undisturbed for 30 days before analysis to allow the ^{222}Rn to build to equilibrium activity levels with ^{226}Ra.

At the completion of the 30-day build-in period, ^{222}Rn was extracted by bubbling helium through the liquid sample at a flow rate of 2.5-3.0 L/min for 15 minutes using a gas emanation system (Fig. 3a). Helium flow carried the radon gas through a scrubbing column (where CO_2, acid, and water vapor were removed) and into a U-shaped column filled with activated carbon and immersed in a dry ice/isopropanol bath at -57° C. The ^{222}Rn adsorbed onto the carbon at low temperature. The sample was monitored constantly during extraction to ensure that all elements of the system remained tightly sealed so that the sample did not at any time vent to the surrounding air. Helium was recycled through the system after passing through the carbon column so that the same helium recirculated throughout the 15-minute extraction period.

When extraction was complete, the column was transferred to a heating block where it was heated to 300°C (Fig. 3b). High temperature caused the ^{222}Rn to be released from the activated carbon. Helium flow was used again as a carrier to transfer the radon from the heated column into an evacuated Lucas scintillation cell (Lucas 1957). The Lucas cell was lined with a coating of silver activated zinc sulfide,

ZnS(Ag), which fluoresces when struck by a high-energy α-particle. Both the extraction and transfer systems were flushed ten times with clean helium immediately before and following an extraction to ensure no residual ^{222}Rn was in the system.

The cell was then placed in a darkened chamber on top of a photomultiplier tube attached to a high voltage power supply and the output routed to a scaler. Gross α-decays, in the form of fluorescent pulses, were recorded electronically. ^{222}Rn possesses two short-lived daughter nuclides (^{218}Po, half-life 3.05 min and ^{214}Po, half-life $1.6X10^{-4}$ sec) whose α-particle emissions are indistinguishable from those of ^{222}Rn using scintillation counting. The gross α-count is therefore approximately three times the decay rate of ^{222}Rn. Total counts were corrected for the two α-emitting daughter nuclides using a computer program that integrates the Bateman equation (Sarmiento *et al.* 1976; Mackenzie *et al.* 1979) predictions for all three nuclides over the counting period. This integral solution predicted the total number of α-decays expected for all three radioisotopes, based on 1 dpm ^{222}Rn, relative to the point when ^{222}Rn was extracted. The integral solution incorporated duration of the count and was based on the delay time from extraction to count initiation. The specific activity of a sample was calculated from one to four day α-counts using the Bateman integral solution and normalized per gram of sample using the following equation:

$$A_{^{222}Rn} = \frac{\frac{(\sum CNT - CNT_{BKG})}{(\alpha * EFF)} - BLK_{dpm}}{WEIGHT_{sample}}, \quad (1)$$

where:

$A_{^{222}Rn}$ = the specific activity of ^{222}Rn in the sample in dpm/g,

Σ CNT = total counts recorded within the count time,

CNT_{BKG} = counts due to system electronics, helium, and Lucas cell (cpm x Δt),

α = Bateman integral solution, expected counts resulting from decay of all three radioisotopes (^{222}Rn, ^{214}Po, and ^{218}Po) within the count time,

EFF = efficiency of the gas emanation system as determined through extraction from known activity NBS standards,

BLK_{dpm} = counts resulting from equivalent volume of dissolution acid and gas wash bottle, measured in dpm and corrected for background, and

$WEIGHT_{sample}$ = total weight of cleaned and dried otoliths prior to dissolution.

Uncertainty estimations followed the methods of Sarmiento *et al.* (1976):

$$\sigma^2_{A_{^{222}Rn}} = \left[\frac{1}{\alpha * EFF * W}\right]^2 \left[\frac{CNT * 3 * EFF}{BE}\right] + \left[\frac{\Delta t * \sigma_{BKG}}{\alpha * EFF * W}\right]^2 + \left[\frac{(\sum CNT - CNT_{BKG})\sigma_{EFF}}{\alpha * EFF^2 * W}\right]^2 + \left[\frac{\sigma_{BLK}}{W}\right]^2 + \left[\frac{\sigma_{W}}{W^2}\right]^2, \quad (2)$$

where:

$$BE = EFF \cdot EFF(1 \cdot EFF) \cdot EFF(1-EFF)^2, \quad (3)$$

and,

$\sigma^2_{A\text{-}222\text{-}Rn}$ =variance for the measured activity of ^{222}Rn,

α=Bateman integral solution with $A_{A\text{-}222\text{-}Rn}$ factored out,

W=sample weight,

Δt=duration of the count (min),

σ_{EFF}=standard deviation of the efficiency measurements,

σ_{BKG}=standard deviation of the background counts,

σ_{BLK}=standard deviation of the blank measurements,

σ_W=standard deviation of the sample weight measurements, and

$A^0_{222\text{-}Rn}$=total sample ^{222}Rn activity.

System background (CNT_{BKG}) is that portion of the registered counts which are due to random photon activity in the counting chamber (Lucas cell), helium, and dark current noise inherent to the photomultiplier tube. Background (cpm) was measured at least monthly by flushing the Lucas cell repeatedly, filling it with fresh helium, and counting in the same manner used for samples.

Blanks, measured in dpm, are that part of the count rate which is not due to the sample itself but is attributable to the container, reagent, and extraction/transfer system. There is some question whether the blank counts originate from the reagent or whether they represent ^{222}Rn production due to ^{226}Ra decay in the activated carbon of the column and the SiO_2 of the bottle. Very clean (double re-distilled) HNO_3 was used. Therefore, reagent contamination was a less likely source than the

carbon column and bottle (Biscayne *et al.* 1977). Therefore, blanks used in the calculations were based on a filled bottle of 1M reagent, processed identically to a sample, and were not based on the absolute amount of acid added. The mean of three blank preparations was subtracted from the sample activity before normalizing for sample weight.

Two extractions were made from each sample when possible. At least 30 days elapsed between extractions to allow ^{222}Rn to re-establish secular equilibrium with ^{226}Ra. A t-test (Zar 1995) was used to test for differences between two extractions from a single sample. The likelihood ratio X^2 test (Kastelle *et al.* 1994) was used to test for differences among samples.

^{210}Pb Analysis Procedures

^{210}Pb specific activity was computed from three-week counts of its α-emitting daughter ^{210}Po (Fig. 1) using Tennelec® TC-256 alpha spectrometer with silicon surface barrier detectors. Alpha chambers were connected to either a Tennelec® VC-5 multi-channel analyzer or Nucleus® personal computer analyzer. One series of four "age"-stratified samples was compiled by combining cored left otoliths from specimens whose right otoliths had been sectioned and increments counted. "Age" strata were: *S. altivelis* 2-5, 10-15, 20-25, 30+ years; *S. alascanus* 10-15, 20-25, 30-35, 40-45 years. In addition, two series of weight-stratified samples were compiled from "unaged" otoliths into the following categories: *S. altivelis* <40 mg, 65-85 mg, 110-125 mg, >140 mg; *S. alascanus* 50-100 mg, 170-190 mg, 260-280 mg, >320 mg.

Mean sample "ages" were extracted from an otolith weight/increment count curve developed from sectioned otoliths. One of the *S. alascanus* weight-stratified series of four samples was provided by the National Marine Fisheries Service Southwest Fisheries Science Center (SWFSC), La Jolla, CA. The SWFSC otoliths were collected from fish caught in Oregon waters November 1990. SWFSC provided an additional sample of 30 otoliths (and corresponding sections) from the oldest age group available (SWFSC mean count 80 $\pm$ 11) caught in September 1988. Only otoliths caught within a one month time period were pooled to simplify radiochemical corrections.

Pooled otolith samples were cleaned using the multi-step procedure in Fig. 2. They were dried to constant weight, transferred to a 125 mL beaker, and dissolved in 2.8N double redistilled HNO_3. The solution pH was adjusted to 0.5 using additional dissolution acid. Low-activity ^{208}Po yield tracer was added (0.125 mL, about 0.3 dpm) and a polished silver planchet held in a custom made teflon holder with mounted teflon stirrer-bar was placed in the digested sample. A small amount (about 50 mg) of ascorbic acid was added to reduce plating interference by iron. Ascorbic acid reduces plating interference by keeping iron in solution and inhibiting iron deposition on the silver planchet. Autodeposition was allowed to proceed on a hotplate-stirrer for 4-6 hours at 85-90°C (Figgins 1961; Flynn 1968). When plating was complete, planchets were removed, washed with milli-Q water, dried lightly, and then stored in air-tight polypropylene vials. The plated silver planchets were placed

in Tennelec® TC-256 alpha chambers with silicon surface barrier detectors connected to either a Tenelec® VC-5 multi-channel analyzer or Nucleus® personal computer analyzer. Alpha decays from the ^{210}Po and ^{208}Po were recorded for three weeks.

Before alpha counting, each detector was precisely calibrated to determine channel intervals of interest for each of the two isotopes, ^{208}Po and ^{210}Po. Standard activities of known isotopes were analyzed, determining energy-specific channels in each quadrant. Decay energies were regressed against channel numbers to calibrate the detectors. In addition, separate planchets plated with 10-15 dpm of each of the ^{208}Po and ^{210}Po isotopes were analyzed individually for short periods in each detector to verify the calibration. Both ^{208}Po and ^{210}Po emit α-particles of a single energy - 5.114 MeV for ^{208}Po and 5.305 MeV for ^{210}Po. Channels immediately around the peak of occurrence which registered counts were included in the region of interest because some particles are deflected, or slowed slightly, before striking the detector and register at slightly different energies. An example of a spectrum observed for otolith samples is illustrated in Fig. 4. Recorded α-particle emissions of the two isotopes registered as two distinct peaks on the spectrum. Integrated counts under the peak, less background and divided by the count interval, represented the activity (cpm) of that isotope on the planchet at the midpoint of the count. Detector backgrounds were measured between sample counts using clean silver planchets. The mean rate of two background counts, one before and one after a sample count, was used to adjust raw counts:

$$cpm = \frac{\sum counts_{interval} - (cpm_{bkg} * mins.counted)}{mins.counted}, \quad (4)$$

where:

cpm = counts per minute at the midpoint of the count (for either ^{208}Po or ^{210}Po),

$\Sigma counts_{interval}$ = total α-counts within the channel interval defined for the isotope,

cpm_{bkg} = rate of counts registered within the interval with a clean planchet in the chamber, and

mins. counted = duration of the count in minutes.

Corrections for chemical yield and detection efficiency for ^{210}Po were made using the known activity of ^{208}Po added before plating to calculate the activity of ^{210}Po at the midpoint of the count:

$$A_{M_{210}Po}(dpm) = A_{M_{208}Po} \left| \frac{cpm_{210_{Po}}}{cpm_{208_{Po}}} \right|, \quad (5)$$

where:

$A_{M\text{-}210\text{-}Po}$ (dpm) = activity of the ^{210}Po at the count midpoint,

$A_{M\text{-}208\text{-}Po}$ (dpm) = activity of ^{208}Po tracer at the count midpoint, and

cpm = measured count rate (counts per minute) of each isotope.

Individual reagents used for cleaning and/or dissolution were assessed for blank activity by plating three samples of each in the same manner that otolith samples were plated. Preparation blanks, consisting of blank L.R. White® blocks, were treated identically to actual samples. The mean of three preparation blanks was subtracted from the calculated ^{210}Po activity corrected to date of plating, and normalized per gram of sample material using the following formula:

$$A^{\circ}_{210_{Po}}(dpm/g) = \frac{\frac{A_{M_{210_{Po}}}}{e^{(-\lambda_{210_{Po}} * \Delta t)}} - Blank_{dpm}}{weight_{sample}}, \quad (6)$$

where:

$A^{\circ}_{210\text{-}Po}$ (dpm/g) = specific activity of ^{210}Po on the day of plating (also the activity of ^{210}Pb since they were assumed to be at secular equilibrium),

$\lambda_{210\text{-}Po}$ = decay constant for ^{210}Po (1.79 yr^{-1}), and

Δt = time between plating and the midpoint of the count.

^{210}Pb specific activity (in equilibrium with ^{210}Po) at the date of plating was corrected back to death using the first order rate decay equation for that isotope:

$$A_{210_{Pb_{death}}}(dpm/g) = \frac{A^{\circ}_{210_{Pb}}}{e^{(-\lambda_{210_{Pb}} * \Delta t)}}, \quad (7)$$

where:

$A_{210\text{-}Pb\text{-}death}$(dpm/g)=specific activity of ^{210}Pb in the otolith on the day of capture and thus death,

$\lambda_{210\text{-}Pb}$=the decay constant for ^{210}Pb (3.11×10^{-2} yr^{-1}), and

Δt=time between capture (death) and plating.

Counting uncertainties were based on total counts above background for both isotopes (Wang *et al.* 1975):

$$\sigma_{Sample_{^{210}Pb}} = A_{M_{^{210}Pb}} \sqrt{\left[\frac{(N_{^{208}Po})^{0.5}}{N_{^{208}Po}}\right]^2 + \left[\frac{(N_{^{210}Po})^{0.5}}{N_{^{210}Po}}\right]^2}, \quad (8)$$

where:

$\sigma_{Sample\text{-}210\text{-}Pb}$=standard deviation of the measured ^{210}Pb activity in the sample,

N=total number of counts registered under the peak for either ^{208}Po or ^{210}Po as indicated.

The total uncertainty in the activity of ^{210}Pb in each sample is estimated by computing sample variance which includes all potential sources of error:

$$\sigma^2_{A_{^{210}Pb}} = \left[\frac{\sigma_{Sample_{^{210}Pb}}}{W}\right]^2 + \left[\frac{\sigma_{bkg_{^{208}Po}}}{W}\right]^2 + \left[\frac{\sigma_{bkg_{^{208}Po}}}{W}\right]^2 + \left[\frac{\sigma_{blk}}{W}\right]^2 + \left[\frac{\sigma_{spike}}{W}\right]^2 + \left[\frac{A_{^{210}Pb}\sigma_W}{W^2}\right]^2, \quad (9)$$

where:

σ^2=total variance of the measured activity of ^{210}Pb,

σ_{bkg}=background error, either ^{210}Po or ^{208}Po, as indicated,

σ_{blk}=blank error,

$\sigma_{pipette}$ = pipette error,

σ_W = weighing error, and

W = sample weight.

Radiochemical ageing

A radiochemical ageing model incorporating linear otolith mass growth over the period of core formation (5 increments) and constant proportional radium uptake with subsequent first order rate decay (Campana *et al.*, 1990; Smith *et al.*, 1991) was used to predict expected (^{210}Pb:^{226}Ra) over the period 0-100 y. Measured sample isotopic ratios, (^{210}Pb:^{226}Ra), corrected to date of death (when increment deposition stopped) were plotted in relation to the mean growth increment count and to the predicted curves for R° (initial uptake ratio of ^{210}Pb:^{226}Ra) of 0, 0.1 and 0.2. The equations used to predict expected (^{210}Pb:^{226}Ra) as a function of time under these constraints were derived by Smith *et al.* (1991):

1) first five years:

$$\frac{A_{^{210}Pb}}{A_{^{226}Ra}} = 1-(1-R^{o})\frac{(1-e^{-\lambda T})}{\lambda T}, \qquad (10)$$

where:

$A_{Pb\text{-}210}/A_{Ra\text{-}226}$ = the ratio of the specific activity of the daughter radionuclide, ^{210}Pb, to that of the parent ^{226}Ra during the first five years of otolith growth,

R^0 = initial activity ratio of (^{210}Pb/^{226}Ra) at the time of deposition,

λ = decay constant for ^{210}Pb (3.114×10^{-2} yr^{-1}), and

T = 5 years, the period of core formation,

and 2) subsequent years:

$$\frac{A_{210Pb}}{A_{226Ra}} = (1 - e^{-\lambda(t-T)}) + \left[1-(1-R^{o})\left(\frac{1-e^{-\lambda T}}{\lambda T}\right)\right] e^{-\lambda(t-T)}, \tag{11}$$

where t = 5-100 years.

Uncertainty calculations again followed the methods of Wang *et al.* (1975):

$$\sigma_{\frac{210Pb}{226Ra}} = \frac{A_{210Pb}}{A_{226Ra}} \sqrt{\left(\frac{\sigma_{A_{210Pb}}}{A_{210Pb}}\right)^2 + \left(\frac{\sigma_{A_{226Ra}}}{A_{226Ra}}\right)^2}. \tag{12}$$

Since linear errors in activity ratios scale exponentially with age, radiochemical age uncertainties based on these values were estimated by calculating upper and lower limits using the 1σ errors on the individual activities:

$$Upper = \frac{A_{210Pb} + \sigma_{A_{210Pb}}}{A_{226Ra} - \sigma_{A_{226Ra}}} \qquad Mid = \frac{A_{210Pb}}{A_{226Ra}} \qquad Lower = \frac{A_{210Pb} - \sigma_{A_{210Pb}}}{A_{226Ra} + \sigma_{A_{226Ra}}}. \tag{13}$$

RESULTS

Morphometrics

A total of 409 *S. alascanus* was collected in trawls between 200 and 1400 m depths with none caught in 100 m trawls. The smallest fish caught was 115 mm total length (TL) and the largest was 846 mm (Fig. 5). The majority of the fish were 250-600 mm. Larvae and early juveniles spend their first 14-15 months in the midwater, therefore, were not sampled. Small benthic individuals (30-200 mm) were caught in very low numbers, as were fish greater than 600 mm.

The 208 *S. altivelis* specimens collected randomly onboard the SWFSC cruise ranged from 104-307 mm TL (Fig. 6). Other specimens used for otolith analyses were not included in the frequency plots because their selection was not random. They were chosen to represent the size range equally for comprehensive growth curve development. Most of the fish collected randomly ranged from 175-250 mm TL (range 87-305 mm, smallest 54 mm from the Monterey Submarine Canyon collection). Only three fish from this study exceeded 300 mm. Midwater larvae/juveniles were not sampled.

Sebastolobus alascanus otoliths weighed 22 to 597 mg. Otolith weight generally increased with total length (Fig. 7). Variation in otolith weight increased noticeably at fish lengths greater than 400 mm, requiring a log transformation of the data to remove heteroscedasticity. The best fit equation from a log transformed linear model (Chatterjee and Price 1977) was multiplicative ($p<0.001$).

Otoliths from 478 *S. altivelis* individuals were collected for growth increment analyses. Otolith weights ranged from 4.5 to 205.8 mg (Fig. 8), increasing with total length. Fish collected within the Monterey submarine canyon were included on the graph because they were aged. However, note that the TL differences observed are probably due to fish shrinkage resulting from freezing, therefore, these fish were excluded from curve fit analyses. Otolith weight variation increased less for *S. altivelis* than for *S. alascanus* but a residual plot indicated that data transformation was required to remove heteroscedasticity. The best fit equation was also multiplicative ($p<0.001$).

Age and Growth

A recognizable pattern of opaque and hyaline (translucent) rings was apparent in examination of otolith sections from both species. However, much irregularity was evident, which made interpretation difficult. Some growth increments were not as easily identified as others because they contained checks. Growth increments continued to form on all otolith surfaces except the distal face throughout otolith formation, increasing in height and length as well as thickness. Deposition occurred often in irregular widths and patterns but was most continuous and regular, though narrowest, on the side proximal to the brain *in vivo*, between the sulcus and the dorsal tip. Sections varied from clear and moderately easy to read, to disorganized, inconsistent, and indistinct.

Sebastolobus alascanus otoliths from the Santa Cruz collection contained 6 to 83 increments, and otoliths from the SWFSC sample contained 50 to 97 (SWFSC estimate 63-99) increments (Fig. 9). Number of growth increments increased with increasing otolith weight. More variation occurred in otoliths with higher increment numbers and otolith weight. The relationship is approximately linear to about 400 mg weight, though an increase in variation with increased increment count required log transformation of the data to remove heteroscedasticity. The best fit equation from a log transformed linear model was multiplicative (Fig. 9, $p<0.001$) though small sample size above 300 mg may obscure the true relationship.

A similar relationship between otolith weight and number of growth increments was observed for *S. altivelis* (Fig. 10). Number of growth increments observed was 1 to 45. Variation increased slightly as the number of increments increased requiring transformation before curve fitting. The best fit equation from a log transformed linear model was multiplicative (Fig. 10, $p<0.001$). Sample sizes were small above 125 mg potentially obscuring the relationship past that point.

For the first five years, the relationship between *S. altivelis* otolith mass and increment number was linear ($y=5.46\ x+1.011$, $r^2=0.878$, $n=85$), supporting that assumption for radiochemical tests (Fig. 11). *Sebastolobus alascanus* specimens with less than six growth increments were not available for a similar analysis. However, linearity was assumed based on apparent linearity for the smallest range available, 6 to 13 increments ($y=0.089x\ +4.91$, $r^2=0.725$, $n=40$). Failure of this assumption,

however, could have contributed an additional source of error in radiochemical ageing calculations.

Five increment core dimensions for *S. alascanus* were 6.0 x 3.0 x 1.0 mm (mean [SD]: length=6.02 [regression], height=3.43 [0.15], and thickness=1.05 [0.06] mm; n=40). *Sebastolobus altivelis* otoliths were somewhat shorter in length but slightly greater in height and thickness than *S. alascanus*. Core dimensions for *S. altivelis* were 5.5 x 3.5 x 1.0 mm (mean [SD]: length=5.67 [0.34], height=3.70 [0.20], and thickness=1.15 [0.09] mm; n=25). In all cases dimensions were rounded down to provide a more conservative size estimate, therefore not diluting the ^{210}Pb specific activities with younger otolith material containing lesser ^{210}Pb activity.

Precision of growth increment counts was relatively low for *S. alascanus* (Fig. 12, Table 1). Growth increment counts differed by as much as 23 among the four different readers. Overall percent error among the four readings was 8.73%, and ranged from 6.35% to 14.8%. These translate to ageing errors of 0.64 to 1.48 y at 10 y of age to 5.08 to 11.84 y at 80 y. Percent errors were lowest (D=6.35%) between two readers from the same lab (readers 1 and 2), counts were within $\pm$5 increments more than 84% of the time. Percent error was greatest between readers 1 and 3 (D=14.8%), counts were within $\pm$5 only 54% of the time. The Macintosh readings were central among the four. The Macintosh readings were used as a control for multiple comparisons among the readings because that is the technique on which fishery information is based (Jacobson 1991). No differences were found

between readers 1, 2, and MAC ($X^2_{(0.05, 3)}$=7.815, 0.975<P<0.95); however, reader 3 increment counts were different from all other readings, and consistently lower. Reader 1 ages were used for von Bertalanffy analysis and radiochemical comparisons. The percent error between reader 1 and MAC was 7.79% and were within 5 increments 70.0% of the time. The 7.79% error translates to ageing errors of 0.78 y at 10 y of age to 6.2 y at 80 y of age.

Precision of increment counts was lower for *S. altivelis* than for *S. alascanus* (Fig. 13, Table 1). Growth increment counts differed by as much as 26 among the four readers. Overall percent error was 10.8%, and ranged from 8.25% to 18.4%. These translate to ageing errors of 0.83-1.84 y at 10 y of age to 3.3-7.36 y at 40 y. Percent errors were lowest (D=8.25%) between two readers from the same lab (readers 1 and 2), and counts were within $\pm$5 increments more than 85% of the time. Percent error was greatest between readers 3 and MAC (D=18.4%), and the counts were within $\pm$5 only 66% of the time. No difference was found between reader 2 and MAC ($X^2_{(0.05, 3)}$=7.815, 0.99<P<0.975); however, readers 1 and 3 was different and consistently lower. Reader 1 ages showed a 2 to 4-year bias toward younger ages than the MAC. Reader 1 ages were used for von Bertalanffy analysis and radiochemical comparisons. Percent error between reader 1 and MAC was 10.6% and were within 5 increments 86% of the time. The 7.79% error translates to ageing errors of 0.78 y at 10 y of age to 6.2 y at 80 y of age.

Sebastolobus alascanus was easier to age than *S. altivelis* as measured by the

lower average percent error (overall APE: 13.1 vs. 16.3) and coefficient of variation (overall V: 17.5 vs. 21.6) though the maximum number of increments observed was greater (Table 1). All combinations of readers resulted in errors lower for *S. alascanus* than *S. altivelis* with the exception of the reader 1-3 couple which was slightly higher.

Precision of within-reader 1 age-specific estimates decreased slightly with increasing age over the range 0 to 50 y for *S. alascanus* (Fig. 14, Table 2). Differences ranged from 0 to 10 y and percent error ranged from 2.72% to 3.18%. These translate to ageing errors of 0.17 y at 10 y of age to 1.46 y at 50 y. Agreement within five increments ranged from 88 to 100%. Reproducibility was highest for otoliths with fewer increments and lowest for those with the greater number of increments.

Reproducibility of age estimates was better for *S. altivelis* than for *S. alascanus*, though errors were slightly higher for *S. altivelis* (Fig. 15, Table 2). Percent errors ranged from 2.46% to 3.22% which translate to ageing errors of 0.15 y at 5 y of age to 0.97 y at 30 y. All counts agreed within ± 5 increments except those over 30 which agreed within ± 5 82.8% of the time. The maximum difference observed was 9 increments.

Von Bertalanffy growth function parameters (L_∞, t_0, and k) for *S. alascanus* indicated a significant growth model fit (Fig. 16; $r^2=0.896$). Asymptotic standard error estimates for L_∞, k, and t_0 were 72.9, 0.0024, and 1.14 respectively. The growth

coefficient (k) was very low (0.017), and the predicted asymptotic length (L_∞) was 945 mm, more than 100 mm larger than the largest fish caught. The number of large (>600 mm) and small (<150 mm) fish in the collection was small resulting in overestimation of L_∞ and underestimation of k.

Sebastolobus altivelis size classes were more equally represented. The von Bertalanffy growth model fit was highly significant (r^2=0.933) and the predicted curve strongly asymptotic (Fig. 17). The growth coefficient for *S. altivelis* was greater (k=0.072) than *S. alascanus*. The estimate for L_∞ was 301 mm, slightly below the maximum length caught of 305 mm. Asymptotic standard error estimates (Prager *et al.*f 1987) for L_∞, k, and t_0 were 37.9, 0.0028, and 0.211 respectively.

Radiochemistry

^{226}Ra analyses

The mean gas emanation system background was 0.047 $\pm$ 0.002 cpm (n=21, $\pm$1 SE). Mean system efficiency was 71.4% $\pm$ 1.4% (n=13, $\pm$ 1 SE) measured periodically between sample extractions using NBS calibrated standards, and did not vary significantly during the period this study was conducted. The mean activity of three preparation/system blanks, measured three times each was 0.077 $\pm$ 0.008 DPM ($\pm$1 SE). This rate translates to 4-5 counts per hour.

Duplicate extractions on ^{226}Ra samples did not differ (t-tests, P<0.001), however, sample rate was arbitrarily selected as the first extraction rate because two samples had only a single extraction. Sample rates were not statistically different (*S. altivelis* 0.75<P<0.90, *S. alascanus* 0.05<P<0.10) so a weighted mean rate (Zar 1995) was

used to calculate sample ratios. Mean ^{226}Ra activities for *S. altivelis* (0.045 dpm/g) and *S. alascanus* (0.042 dpm/g) were similar, though measurements for *S. altivelis* samples were more precise than for *S. alascanus* samples (Table 3). Individual ^{226}Ra measurements for *S. altivelis* were similar, 0.0425 to 0.0476 dpm/g, with no pattern of increase or decrease with increase in otolith size (and presumably age). Similar otolith weight-based analyses were not conducted for *S. alascanus*. However, two of the three samples had very similar specific activities whereas the third (S-17) was somewhat greater.

^{210}Pb analyses

Alpha spectrometer detector backgrounds were 10^{-4} to 10^{-3} cpm (0.4 to 6 counts per day) in the ^{208}Po and ^{210}Po regions of interest. Backgrounds in individual detectors remained nearly constant throughout the study. Individual reagent blank activities were not above background, however, preparation blanks were above background levels. ^{210}Po activity at the time of plating was corrected for preparation effects by subtracting the mean of three preparation blanks, 0.0038 $\pm$ 0.0006 dpm.

All otolith cores, with the possible exception of the four youngest *S. altivelis* samples, were sufficiently old when analyzed that ^{210}Po (half-life 138 days) and ^{210}Pb (half-life 22.3 y) were in secular equilibrium. The four young samples (which contained 2-6 annuli) were within 90% of the equilibrium value.

Otolith samples consistently contained a deficiency of ^{210}Pb activity in relation to ^{226}Ra activity with the exception of a single *S. altivelis* sample (T-17), that may have been contaminated. ^{210}Pb activity generally increased, and its deficiency relative to ^{226}Ra decreased with increasing otolith size and increment count for both species (Table 4). Activity of ^{210}Pb was 0.0045 to 0.0307 dpm/g for *S. altivelis* (T-17

0.0471 dpm/g) and 0.0054 to 0.0387 dpm/g for *S. alascanus*. Both types of samples, grouped by increment count and by weight, had comparable ^{210}Pb specific activities, though variation was considerable among similarly aged samples. *Sebastolobus altivelis* replicates indicated more variability than those for *S. alascanus*.

Radiochemical Age

Ratios of (^{210}Pb:^{226}Ra) for *Sebastolobus alascanus* (based on the mean species ^{226}Ra measurement) increased with increasing growth increment count, conforming closely to the predicted curve where $R^0=0$ (Fig. 18). Both types of samples, those assembled by growth increment count ("aged", open circles and squares) and those assembled by otolith weight (filled circles and squares), were near the curve. Five sample ratios fell above the $R^0=0$ predicted curve and all samples were within two standard deviations of the curve. The youngest sample, S-2, had a ^{210}Pb activity of 0.0054 $\pm$ 0.0020 dpm/g which placed it below the $R^0=0$ curve indicating minimal uptake at formation. Sample SO-1, containing the oldest available otoliths from SWFSC (large horizontal error bars indicate that a wide range of otolith ages were grouped in the sample), was estimated by reader 1 to have a mean age of 71.7 $\pm$ 12.1 y and is plotted accordingly. However, the estimate by SWFSC for this sample was 80.03 $\pm$ 11.02 y. Both estimates are within one standard deviation of each other and the curve.

Measured radionuclide activity ratios corresponded to predicted ratios for $R^0 < 0.2$

for *Sebastolobus altivelis* (Fig. 19). Ratios conformed most closely to the $R^0=0.1$ curve. The ^{210}Pb content of the youngest samples was slightly greater than would be expected if there were no initial uptake of ^{210}Pb, indicating an initial uptake rate between 0 and 10% of the ^{226}Ra level, though this may simply reflect previously measured ageing error. Samples of similarly aged *S. altivelis* had less precision than the *S. alascanus* samples. One *S. altivelis* sample ratio (T-17) had a measured activity ratio above unity. Contamination was suspected.

DISCUSSION

Age and Growth

Preliminary morphometric and ageing analyses indicated that both *Sebastolobus* species grow slowly and are long-lived, *S. alascanus* to about 100 y and *S. altivelis* to at least 45 y. However, imprecision due to structure variability and subjective evaluation generates uncertainty in age estimates. Growth increment patterns were difficult to interpret due to their irregularity and narrow dimensions. Additionally, the otoliths did not form in the pattern observed for other deep-sea fishes that are long-lived such as eastern Pacific rockfishes (*Sebastes* spp.: Beamish 1979; Bennett *et al.* 1982; Beamish and McFarlane 1987; Watters 1994), western Atlantic redfish (*Sebastes mentella*: ICES 1984), and the North Sea roundnose grenadier

(*Coryphaenoides rupestris*: Bergstad 1990). For those species, concentric $CaCO_3$ crystal deposition stops when the fish near asymptotic length, and subsequent deposition continues only on the medial surface, adjacent to the sulcus and proximal to the brain, causing the otolith to thicken but not lengthen or grow in height (Beamish 1979; Boehlert and Yoklavich 1984; Wilson and Boehlert 1990). This type of otolith growth generates a two-stage otolith mass growth model over the life of the fish (Bennett *et al.* 1982; Fenton *et al.* 1991). The *Sebastolobus* pattern, however, appears to follow a single-stage linear mass growth model, continuing to accrete material over most of the otolith and growing in length and height as well as thickness, throughout the fish's life. Otolith weight, therefore, appears to increase linearly throughout the life of the fish (Fig. 9 & 10), though small sample size in large otolith size classes may obscure the actual relationship.

Ageing precision was relatively poor for both species (Tables 1 and 2). The two thornyheads were comparable in difficulty of ageing, as measured by the coefficient of variation (V: Chang 1982), to sablefish, a species considered difficult to age (V = 12.9 ages 1-29 y; Kimura and Lyons 1991). Both were more difficult than Pacific Ocean perch (*Sebastes alutas*, V = 4.9 ages 1-78 y, 4.8 for 1-50 y), another scorpaenid of similar longevity.

Computation of VBGF parameters for *Sebastolobus alascanus* resulted in estimates of asymptotic total length that were well above the maximum observed length for fish in this study or observed by Jacobson (1991) (Table 5, Fig. 16). The

small sample size in the largest size classes resulted in overestimation of L_∞ and thus underestimation of k. The discrepancy between estimates from these data and from Jacobson (1991) may be attributed to under-representation of large individuals in this collection. Large individuals may be able to avoid the net as they are caught in greater numbers on longlines than by trawls (Cross 1987). However, the small number collected may simply reflect their low numbers in the population. The larger collection of Jacobson (1990), from Oregon commercial catches, was more representative of the population, resulting in better parameter estimates. However, age at length data from this collection were nearly identical with those of Jacobson (1990) and confidence intervals from the two predicted curves overlap. VBGF parameters were similar and discrepancies can be attributed primarily to sampling differences and not to significant differences in ageing criteria. Geographic growth differences, however, cannot be eliminated since the two collections represent discrete geographic areas. Additionally, the fish analyzed here were collected over a single three-day period of time, which may have introduced bias as well.

This collection contained more complete size class representation for *S. altivelis* than *S. alascanus*. All size classes, with the exception of larvae/midwater juveniles less than 50 mm, were represented for ageing analyses. In the initial random sample of *S. altivelis*, the 50-160 mm size class was under-represented compared to a larger collection from Pt. Sur, CA (Wakefield 1990), but the second size frequency peak corresponded closely to that of Wakefield (1990) at 180-220 mm. However,

Jacobson (1991) found the second size-frequency peak occurred at a larger size, 240-280 mm, for fish caught in Oregon and the predicted VBGF asymptotic size was slightly larger (Table 5, Fig. 17). Maximum sizes caught in the two areas also were different. Approximately 4-5% of the commercial Oregon samples were more than 300 mm TL (largest >330 mm), whereas none over 300 mm were caught off Pt. Sur and only three fish from this study exceeded 300 mm. However, age at length data were nearly identical for the two data sets and the variation is relatively high so that confidence intervals from the two curves overlap. The same potential geographic and sampling time biases may apply to *S. altivelis* as well as *S. alascanus*.

Age estimates indicated that *S. alascanus* ranks with some of the slowest growing fish (Beamish and McFarlane 1987; Mace *et al.* 1990; Fenton *et al.* 1991), and *S. altivelis*, though growing more quickly than its congener, also grows very slowly. Uncertainty in initial age estimates was marked, but radiochemical analyses strongly supported the otolith evidence. Longevities on the order of that observed for these two species are not uncommon in the Pacific groundfish fishery. Beamish and McFarlane (1987) provided a list of the maximum ages reported for commercially important groundfish off the west coast of Canada, in which 14 of the 23 listed were greater than 40 y old, eight of those were greater than 70 y, and two scorpaenids, *Sebastes borealis* and *Sebastes aleutianus*, reached 120 y and 140 y, respectively. Longevities for *Sebastolobus alascanus* and *Sebastolobus altivelis* of 80+ y and 45+ y are not inconceivable.

Fishes such as the thornyheads that live in deep water are subject to strenuous external conditions not commonly encountered in more shallow environments. Constant low temperatures, high external pressure, reduced light, and low food supply are all conditions that influence adaptive biochemical responses that select for low metabolic rates and slow growth in the deep-sea (Somero 1984; Seibenaller and Somero 1989). The four members of the Pacific deep-water (DW) complex have the added limitation of living and reproducing primarily within the oxygen minimum zone where oxygen levels available to support muscle activity and respiration are extremely low (Cailliet *et al.* 1988; Hunter *et al.* 1990; Jacobson and Vetter In prep). Evidence has shown that *Sebastolobus alascanus*, the shortspine thornyhead, is energy limited in its environment due to hypoxia (Smith and Brown 1983; Yang *et al.* 1992) and low food availability (Yang and Somero 1993), and muscle metabolic activity is reduced (Siebenaller and Somero 1978; Siebenaller and Somero 1982) supporting slow growth. Dover sole (*Microstomous pacificus)* possesses longevity similar to the thornyheads and has comparably low metabolic and growth rates (Hunter *et al.* 1990; Vetter *et al.* 1994).

Radiochemistry

Radiochemical ages determined here agreed very well, within analytical uncertainty, with otolith growth increment counts for both thornyhead species. However, the validity of using the radiochemical pair (^{210}Pb:^{226}Ra) to age fish otoliths has recently been challenged on the basis that the conditions and assumptions of the

technique may not be met (West and Gauldie 1994). Specifically, degassing of intermediate ^{222}Rn from the otolith, unknown sources and sinks of ^{210}Pb and ^{226}Ra, possible changes in the ratio accreted over the life of the fish, contamination by ^{210}Po, difficulty in obtaining otolith cores, and dependence on a mass growth-in-time model were all suggested as conditions that invalidate the application of disequilibrium techniques to fish age determination. Use of otolith cores eliminates the need to apply an otolith mass growth model when determining radiochemical age, and difficulty in obtaining the cores is dependent on otolith characteristics for each species as well as the determination of the investigator. Of course, sources and sinks of the two radionuclides are not definitively known but investigations such as these help to define them. The assumptions can and should be tested, where possible.

The requirement that both parent and daughter radionuclides (^{226}Ra and ^{210}Pb) are incorporated into the otolith at a constant rate over the lifespan of the fish was not met in the case of blue grenadier, *Macruronus novaezelandiae* (Fenton *et al.* 1990). ^{226}Ra specific activity declined with age in whole otoliths, thus violating the assumption of constant uptake for that nuclide. The change was attributed to a major habitat shift between the juvenile and adult stages. *Macruronus novaezelandiae* moves from inshore/estuarine areas as juveniles, where radium activity levels are relatively high (Levy and Moore 1985), to deep water offshore as adults where radium is comparatively low (Chung and Craig 1973; Chung 1976;

Cochran 1982b). A habitat shift also was implicated as a possible cause for the inability to age elasmobranch vertebrae radiochemically using ^{210}Pb (Welden *et al.* 1987). The two species with discrepancies move from shallow nearshore and estuarine pupping grounds to deeper offshore habitats as adults. The shift in habitat and/or a concomitant diet change were proposed as possible contributing factors in the highly variable ^{210}Pb content in vertebrae. The two thornyheads make a habitat shift from the midwater as larvae and juveniles to deep-sea demersal adults, requiring verification of the assumption of constant uptake.

The uptake rate of a radionuclide is not solely a function of the nuclide's concentration in the water, but also can be affected by water temperature, pH, salinity, and undefined biological factors (Rosenthal 1963; Polikarpov 1966). Radionuclide uptake also is not directly proportional to external concentration, and distribution within various organs and tissues in the fish's body varies with the tissue, its function, and the element (Rosenthal 1963; Pentreath 1979). Uptake of ^{45}Ca and ^{90}Sr, calcium analogues that are known constituents in $CaCO_3$ minerals and commonly found in fish otoliths (Mulligan 1987; Kalish 1991), can be inhibited by the presence of mineral salts, and thus increases in salinity (Rosenthal 1963; Jeffree and Simpson 1969). Temperature, pH, and salinity differences between the early estuarine and offshore adult habitats of both *Macruronus* and the two sharks, could have contributed to variation in radionuclide uptake either directly or indirectly due to influences on physiology (Kalish 1991). In addition, surface and inshore ^{210}Pb

levels vary significantly due to precipitation and runoff, possibly influencing uptake rates.

Though the two thornyhead species studied here make a habitat shift from midwater to deep-sea demersal, the change is not as significant radiochemically as the shift from estuary to deep-water observed in both studies with apparent violations (Welden *et al.* 1987; Fenton *et al.* 1990). Temperature, pH, and salinity differences are minor between the midwater habitat of larvae and juveniles and the demersal adult habitat. Also, though surface and midwater radium concentrations are measurably lower than benthic levels due to biological uptake (Shannon and Cherry 1971) and scavenging of its parent ^{230}Th (Nozaki and Tsunogai 1976; Coale and Bruland 1985), the difference is less than that between estuary and offshore demersal environments (Nozaki and Tsunogi 1976; Chung 1976; Levy and Moore 1985; Nozaki 1986). Nevertheless, the assumption of constant uptake was tested because whole otoliths were used to measure ^{226}Ra specific activity. The ^{210}Pb analyses were conducted on core material only. Therefore adherence to the assumption of constant uptake of that radionuclide was not required.

The constant uptake of ^{226}Ra in *S. altivelis* otoliths was tested through measurement of specific activity in samples containing otoliths of different weights (and presumably different ages). Sample activity measurements were relatively precise compared to other studies (Tables 3 and 6). Measured levels of ^{226}Ra are slightly lower in the midwater, where *Sebastolobus* larvae and juveniles remain for

one to two years, than benthic waters in the deep-sea habitat where adults live (Bruland *et al.* 1974). However, ^{226}Ra content in otoliths did not increase with increased otolith size, and age, as would be expected if uptake had increased with the habitat, and external concentration, change. The first 1.5 to 2 growth increments, at least 40% of the mass of otoliths less than 40 mg, were formed in the midwater. However, the ^{226}Ra specific activity in samples containing the smallest otoliths, was not significantly different from samples containing large otoliths. These data support the validity of the constant uptake assumption for *S. altivelis*, though the material was not available to conduct a similar test for *S. alascanus*. Early life history, however, is similar and it is not unreasonable to assume constant uptake for that species as well, though metabolic differences may make this conclusion problematic and could have contributed additional error to the radiochemical ages for *S. alascanus* (Seibenaller and Somero 1978; Seibenaller and Somero 1982).

Porntepkasemsan and Nevissi (1990) have proposed that ^{226}Ra uptake may actually be driven more by a species' metabolic rate than by absolute concentration in the surrounding water. Benthic fish, with more sluggish metabolic rates, contained lower whole fish ^{226}Ra concentrations than did highly metabolic pelagic salmon. This is in contrast to the ^{226}Ra content of the water which is greater near the sediment than in surface water (Chung 1976). Pelagic species also contain seven to ten times greater concentrations of other uranium-series radionuclides in muscles, liver, and bone tissues than benthic species (Pentreath *et al.* 1979).

Reduction in metabolic rate reflects adaptations to the physiological and biological conditions of the deep sea (Somero 1984). Activities of enzymes related to energy metabolism are decreased in both *Sebastolobus* species (Seibenaller and Somero 1989), reflecting adaptations for reduced oxygen availability (Smith and Brown 1983; Yang *et al.* 1992) and food limitation (Yang and Somero 1993). Muscle enzymatic activities are three orders of magnitude greater in continuous swimming surface fishes, such as tunas, than in sluggish deep-sea fishes such as *Sebastolobus* (Somero 1984) and active deep-sea macrourids are six times greater (Smith and Brown 1983). Additionally, muscle enzyme activity correlates well with respiration rates (Smith and Brown 1983; Somero 1984) which are two to three times lesser in *Sebastolobus* than in the more active macrourids. Reduced metabolic characteristics are shared by Dover sole, another member of the DW complex (Hunter *et al.* 1990; Vetter *et al.* 1994). Reduction in growth rates reflect the low metabolic rates of these species.

Results from this study, and those from other radiochemical ageing studies, though limited to otoliths and not whole fish measurements as in Porntepkasemsan and Nevissi (1990), are consistent with a metabolic connection to uptake rate. Slow-growing, long lived *Sebastes*, *Sebastolobus*, *Hoplostethus*, and *Allocytus* species have an order of magnitude lower ^{226}Ra content in otoliths than does *Anoplopoma fimbria*, which is found in similar adult habitats but is a more active predator and a fast growing juvenile (Table 6; Cailliet *et al.* 1988; Boehlert and Yoklavich 1985). This

trend supports the metabolic theory, though data are still scarce and not conclusive. More measurements from active and/or pelagic species may further define any potential relationship between uptake rate and metabolism.

Among-sample ^{226}Ra variation has been a concern even in successful radiochemical ageing studies. Bennett *et al.* (1982) measured ^{226}Ra specific activity in one-gram samples of whole otoliths and found that the activity ranged from 0.042-0.054 dpm/g, noting that it was probably within the range of analytical uncertainty. They calculated radiochemical ages using individual ^{226}Ra measurements and mean values and found no difference in their conclusions using the two methods. Fenton *et al.* (1991) observed a weak trend in ^{226}Ra specific activities with age for *Hoplostethus atlanticus* which they attributed to decreasing total protein content with age in the otolith. Campana *et al.* (1990) mentioned that ^{226}Ra measurements in one-gram core samples and 13-g whole otolith samples were not different but they chose to use the mean of the five whole otolith samples in their calculations because they were more precise. Kastelle (1991) reported significant ^{226}Ra variation for *Anoplopoma fimbria* using only the first growth increment for otolith cores, though no trend with age was noted. However, *A. fimbria* is epipelagic for at least half of their first year and grow quickly during that stage (Boehlert and Yoklavich 1985), so high variability would not be unexpected since analyses were limited to only the first growth increment. ^{226}Ra measurements in this study were relatively precise for *S. altivelis*, varying less than 5% among the seven samples. *Sebastolobus alascanus*

^{226}Ra variation was double that observed for *S. altivelis*, but within the variation observed for other species (Bennett *et al.* 1982; Stewart *et al.* 1995).

High variance is an indication that individual fish uptake rate may vary substantially, especially when juveniles are epipelagic such as sablefish. It would be beneficial to our understanding radiochemical fish ages to assess individual variation by measuring ^{226}Ra in individual otoliths. Use of direct methods for measuring ^{226}Ra activities in small samples, such as the thermal ionization mass spectrometer (TIMS) should improve our understanding. A single *S. alascanus* sample containing eight otoliths has been analyzed using this technique resulting in an estimate of 0.0335 dpm/g ^{226}Ra (Allen Andrews, personal communication). This estimate is somewhat lower than those measured in this study but still within observed variation for other species.

Although differences in ^{226}Ra specific activity among individual samples of *S. alascanus* and *S. altivelis* were not large, the observed differences can result in very different age estimates (Fig. 20) for older samples. For example, estimates for sample SO-1, ^{210}Pb = 0.0387 $\pm$ 0.0021 dpm/g, range from approximately 50 y at Ra=0.0504 dpm/g, the highest measured rate, to more than 160 y at Ra=0.0387 dpm/g, the lowest. Even small variations or errors in radium measurement result in high ageing errors as the ^{210}Pb activity approaches 75% of the ^{226}Ra activity, the nature of an asymptotic curve. At lesser ^{210}Pb activity levels, however, ageing errors are small and confidence in the estimates are thus good. The ^{210}Pb trend with otolith

size, therefore, lends additional support to higher estimates.

The second assumption, that there is no source of daughter products except through radioactive decay of the parent, or that it is negligible compared to that of the parent (initial (^{210}Pb:^{226}Ra), R°, near zero), can be tested by measuring the ratio in the youngest otoliths available (Bennett *et al.* 1982). The uptake rate of the parent radionuclide (^{226}Ra), must be significantly greater than that of the daughter (^{210}Pb) so that we can distinguish between authigenic production and direct external uptake. In contrast to ^{226}Ra, ^{210}Pb levels are high in surface water, where it is supplied by radioactive decay of atmospheric ^{222}Rn (Nozaki *et al.* 1976), and depleted near the sediment, because it is highly particle reactive (Broecker and Peng 1982) and may adsorb onto resuspended sediment particles (Craig *et al.* 1973; Nozaki and Tsunogi 1976; Bacon *et al.* 1976; Chung 1987; Thompson and Turekian 1976). A midwater minima for ^{210}Pb occurs between 500 and 1000 m (Bacon *et al.* 1976), which corresponds to the larvae/juvenile habitat of both *Sebastolobus* species. ^{210}Pb is further depleted relative to radium with increasing depth, (^{210}Pb/^{226}Ra) averaging 0.1-0.39 in areas where surface productivity is high (Bruland *et al.* 1974; Thomson and Turekian 1976). Therefore, even if both were incorporated into the otolith with no physiological discrimination, the initial uptake ratio (R^0) would be low. Measurements for both *Sebastolobus* species produced results, consistent with other otolith studies, that estimate the initial uptake of ^{210}Pb is less than 20% of the ^{226}Ra uptake and likely 0 to 10%.

West and Gauldie (1994) suggested that ^{210}Po contamination in the otolith is an expected problem when using radiochemical ageing because the ^{210}Pb specific activity is determined by measuring ^{210}Po as a daughter proxy for ^{210}Pb. However, ^{210}Po has a very short half-life (138.4 days) and any allogenic content in the otolith core would have decayed away about two and one half years after deposition, leaving only authigenic production supported by ^{210}Pb decay. The youngest samples may have contained a small proportion of the allogenic ^{210}Po activity, but the combined ^{210}Po and ^{210}Pb allogenic contribution is reflected in the ^{210}Pb initial uptake estimate.

West and Gauldie (1994) also state that because ^{210}Po and ^{210}Pb are concentrated up the food chain, significant allogenic incorporation in the otolith is expected. Lead is concentrated relative to calcium up planktonic food webs (Swanson 1985). However, the atomic ratio of lead to calcium, and the concentration, decrease with increasing trophic level above the plankton (Michaels and Flegal 1990). West and Gauldie (1994) cite Heyraud and Cherry (1979) who reported significant ^{210}Pb levels in the liver of *Thunnus thunnus* as evidence supporting high lead uptake. However, fish accumulate radionuclides in different amounts in various organs and tissues, and the liver is the major area of concentration for uranium series radionuclides including ^{210}Po and probably ^{210}Pb also (Pentreath *et al.* 1979). Accumulation of high levels in one tissue does not mean high levels will accumulate in another. Wet weight ^{210}Po content is two orders of magnitude greater in liver than in bone or muscle of teleost fishes (Pentreath *et al.* 1979). Also, shallow water pelagic species

such as tunas had seven times greater levels in bone than did shallow water demersal species, and deep water species were highly variable but in the same range. These data also indicated a metabolic connection with radionuclide uptake rate. Nevertheless, reported ^{210}Pb activity levels in the liver of *Thunnus thunnus*, 0.044-0.067 dpm/g, cannot be considered unusually high as they are comparable to activities measured in otoliths of other species where the activity is directly attributable to ^{226}Ra decay (Table 6).

West and Gauldie (1994) refer to high lead levels in fish otoliths (Grady *et al.* 1989, *Scombromorus cavalla*) as evidence of high allogenic input. However, continuously-swimming *Scombromorus cavalla*, a mackerel, has a high metabolic rate. Relatively high ^{210}Pb levels would be expected, depending on the age of the fish, in accordance with the metabolic theory. Diffusion of ^{210}Pb and ^{210}Po is also mentioned as a possible allogenic source but is unlikely because of their high particle reactivity (Broecker and Peng 1982). Only allogenic incorporation at formation need be considered and data indicated that the level is sufficiently low to make the radiochemical ageing technique valid for these two *Sebastolobus* species.

Backgrounds and blanks are very important when applying low-level radioisotope counting techniques. Radioactivity in otoliths occurs at trace levels, therefore rigorous definition of blank sources and background activity levels is important. Reagent blank ^{210}Po activities for all chemicals and tracers and their combinations used in this study were not above background levels; however, total preparation

blanks (handling) were measurable. The mean of three preparation blanks was used to adjust measured activity rates. The mean blank value (0.038 $\pm$ 0.0006 dpm) measured here was lower than Fenton *et al.* (1990 & 1991) reported (0.0103 $\pm$ 0.0027 dpm), though they did not describe the basis for their measurement, but higher than others. Campana *et al.* (1990) reported 0.0005 dpm, and Bennett *et al.* (1982), and Kastelle *et al.* (1994) stated that their blanks were below background levels. Since plating of samples in this study was conducted over a period of several months, the actual variation in the preparation blank may have been greater than indicated from the three samples used to determine the mean blank. This might explain some of the variation among samples of similar ages.

Measured ^{222}Rn blanks in this study were roughly double that of Bennett *et al.* (1982) for the radon gas emanation system, though the much larger sample weight reduced the significance of the errors. Kastelle *et al.* (1994) measured no detectable blank using a slightly different form of gas emanation. Campana *et al.* (1991) did not report blanks or backgrounds for the gas emanation system used in that study. Efficiency of the system used here (71.4% $\pm$ 0.4) was somewhat lower than that reported in the literature for similar systems though it varied much less (ave 85% $\pm$ 5%, Sarmiento *et al.* 1976). It was higher than Kastelle *et al.* (1994) at 53.8 $\pm$ 1.5% (range 44.2-66.2%). The Fenton *et al.* (1990) and (1991) studies both indicated a significant radium blank of 0.0103 using direct alpha spectrometry.

The third assumption, that the system must be closed to losses or gains of either

parent (^{226}Ra), daughter (^{210}Pb), or any intermediate decay products (and including ^{210}Po) except through radioactive decay or ingrowth, is difficult to test. Welden *et al.* (1987) speculated that differences between shark vertebral growth increment counts and measured radiochemical age may have been influenced by violation of the closed system assumption as well as the assumption of constant uptake. Elasmobranch vertebrae have cartilage canals, and calcium reworking and ion exchange may occur in these species. Thus remobilization of ^{210}Pb or ^{210}Po may have contributed to observed discrepancies. Fish otoliths, however, are non-vascular and acellular (Simkiss 1974). Resorption/reworking has not been demonstrated for this structure (Simkiss 1974; Campana and Neilson 1985) and calcium incorporated is considered metabolically unavailable (Mugiya 1993). Studies using ^{45}Ca as a tracer indicated that once calcium is incorporated into the otolith it remains immobilized (Campana 1983; Yoklavich and Boehlert 1987).

West and Gauldie (1994) suggested that loss of ^{222}Rn due to recoil and subsequent diffusion out of the otolith is another potential source of error when using (^{210}Pb:^{226}Ra) disequilibria, citing data from Moraswka and Phillips (1993). Moraswka and Phillips (1993), however, discuss α-recoil and diffusion ranges for ^{222}Rn from rocks through air and water-filled pore spaces. Recoil distance and diffusion of ^{222}Rn in otolith material would not be similar to that of rocks because inter-crystalline spaces of otoliths are protein filled (otolin-Degens *et al.* 1969), not filled by either air or water. Ejection of a ^{222}Rn atom from the otolith crystal

through α-recoil would place it in the organic matrix. Sorption of ^{222}Rn to the organic material (Wong *et al.* 1992) would probably inhibit further diffusive movement out of the otolith. In any case, ^{222}Rn loss alone would lead to conservative age estimates, erring towards younger age estimates. Only the combination of both ^{222}Rn loss and high allogenic ^{210}Pb input would overestimate radiochemical ages. A growing number of studies in which (^{210}Pb:^{226}Ra) disequilibria correspond closely to estimated ages from otolith growth increment counts support the validity of using radioisotopes to age fish otoliths.

Fishery

Sebastolobus alascanus and *S. altivelis* are members of the DW complex, a major constituent of the Pacific groundfish fishery. They are both caught in large numbers by deep-water bottom trawl off northern California, Oregon, and Washington. Both species remain for long periods in the midwater, *S. alascanus* 14-15 months and *S. altivelis* 18-20 months (Moser 1974), and settle to the bottom as large juveniles. *Sebastolobus alascanus* settles in relatively shallow depths, about 100 m, and ontogenetically migrates down the slope, larger individuals being caught in deeper depths. *Sebastolobus altivelis* settles to the bottom throughout its depth range of 400-1500 m, grows to smaller sizes than *S. alascanus* but occurs in greater numbers, comprising the largest portion of the total thornyhead catch since 1990 (Ianelli *et al.* 1994). Size at 50% maturity for *Sebastolobus alascanus* is 220 mm which corresponds to an age of about 14 y (Jacobson 1990; Ianelli 1994). *Sebastolobus*

altivelis matures at 215 mm, also corresponding to about 14 years of age.

Fishes that live to old ages generally grow slowly and mature late in life. *Sebastolobus alascanus* and *S. altivelis* are both long-lived and mature late. Additionally, they are both available to the fishery before they mature. Though the two species mature at approximately the same size and age, *S. alascanus* continues to grow, though slowly, for many years afterwards whereas *S. altivelis* reaches asymptotic length shortly after attaining maturity. *Sebastolobus alascanus*' growth slows only gradually and over a longer time period than that of *S. altivelis*, resulting in larger sizes and older ages.

Current management regulations are based on data comparable to the longevities verified here. Ianelli (1994) produced models based on three different natural mortality rates for *S. alascanus* because of the uncertainty in maximum age for that species. Use of a model based on natural mortality of 0.05 to 0.07 corresponds most closely to longevity greater than 80 years, and is considered most appropriate based on the results of this study. Additionally, the maximum age of 45 y for *S. altivelis* with natural mortality 0.1 is appropriate.

Conclusions and Recommendations

The purpose of this study was to examine otolith patterns, and quantitatively compare the number of growth increments found in transverse cross-sections with radiochemical ageing of their combined mineralogical and biological components. Radiochemical ages agreed very closely with growth increment counts for both

species, confirming that counting otolith section growth increments, using currently established criteria, provides the most reliable age estimates for these species in spite of poor precision. Results confirm ages of at least 80 y for *S. alascanus* and 45 y for *S. altivelis*. Precision could be improved by using computer analytical tools such as the Macintosh® image analysis system used in this study where increment definition can be mechanically defined and much of the subjectivity and lack of repeatability associated with manual counts can be eliminated.

Radiochemical ageing has been criticized and its validity questioned because of strict assumptions required for use and our inability to test these assumptions. However, problems outlined are not insurmountable and collection of this information will enhance our understanding of the mechanics involved and potentially answer some of the questions raised. Results from this and other radiometric studies indicate that, when cautiously applied, radiochemical techniques can be applied with great success where other techniques are not feasible. Use of radiochemistry to age fish otoliths, however, must be considered carefully. Species life history must be examined closely to determine how best to apply a radiochemical verification technique.

Recommendations for further research: 1) more intensive ^{226}Ra analysis of a weight stratified sample series of *S. alascanus* would be beneficial to our understanding of potential variability in that species and clarify conclusions drawn about the assumption of constant ^{226}Ra uptake; 2) a comparative analysis of otolith

^{226}Ra content among species from various habitats and with different metabolic rates would help expand our knowledge of the mechanism of uptake of that nuclide.

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TABLE 1: Inter-reader ageing precision analyses results for two congeneric deep-sea rockfish, *Sebastolobus alascanus* and *S. altivelis*. MAC is Macintosh image analysis system used for fishery ageing of these species. Percent errors overall were higher for *S. altivelis* than for *S. alascanus*. Errors were lowest between two readers from the same lab and highest between readers 1 and 3 and the MAC readings were central among the four.

Increment Count	Percent Agreement			Average Percent Error	Coefficient of variation	Index of Precision
	+/- 1	+/- 2	+/- 5	APE (%)	V (%)	D (%)
S. alascanus						
All readers				13.1	17.5	8.73
Reader 1-2	45.7	60.9	84.8	6.35	8.98	6.35
Reader 1-3	22.0	34.0	54.0	14.8	20.9	14.8
Reader 2-3	23.9	30.4	63.0	14.0	19.8	14.0
Reader 1-MAC	36.0	52.0	70.0	7.79	11.01	7.79
Reader 2-MAC	28.3	43.5	76.1	8.26	11.7	8.26
Reader 3-MAC	28.0	36.0	58.0	13.8	19.5	13.8
S. altivelis						
All readers				16.3	21.6	10.8
Reader 1-2	41.5	58.5	85.4	8.25	11.7	8.25
Reader 1-3	24.0	42.0	70.0	14.6	20.7	14.6
Reader 2-3	26.8	36.6	58.5	17.2	24.3	17.2
Reader 1-MAC	22.0	46.0	86.0	10.6	15.0	10.6
Reader 2-MAC	31.7	48.8	78.1	10.5	14.9	10.5
Reader 3-MAC	18.0	36.0	66.0	18.4	26.1	18.4

TABLE 2: Reader 1 intra-reader age-specific precision analysis for *Sebastolobus alascanus* and *S. altivelis*. N is the number of otoliths aged in each group. Percent errors were consistent and low over the age ranges observed and increment counts were within ± 5 counts more than 80% of the time for all ages.

Increment Count		Percent Agreement			Average Percent Error	Coefficient of variation	Index of Precision
(N)		+/- 1	+/- 2	+/- 5	APE (%)	V (%)	D (%)
S. alascanus							
10-15	(25)	86.7	96.7	100	3.56	4.72	2.72
20-25	(38)	70.4	92.6	100	3.85	5.42	3.03
30-35	(35)	39.3	67.9	92.9	4.08	5.71	3.18
40-50	(26)	33.3	54.2	87.5	3.69	5.23	2.91
	AVE				3.80	5.27	2.96
S. altivelis							
0-5	(65)	93.3	100	-	3.88	5.04	2.91
10-15	(37)	90.0	100	-	3.44	4.46	2.58
20-25	(35)	51.7	79.3	100	3.21	4.27	2.46
30+	(47)	44.8	65.5	82.8	4.11	5.58	3.22
	AVE				3.66	4.84	2.83

TABLE 3: Mean and individual otolith sample ^{226}Ra specific activities for *Sebastolobus alascanus* and *S. altivelis*. Uncertainties are $\pm$ 1 standard error.

SAMPLE	OTOLITH WEIGHT	SAMPLE WEIGHT (g)	^{226}Ra (dpm/g) $\pm 1\sigma$	MEAN ^{226}Ra (dpm/g) $\pm$ SE
Sebastolobus altivelis				0.045 $\pm$ 0.002
T-1	all sizes	10.639	0.0442 $\pm$ 0.0048	
T-2	<40 mg	11.085	0.0456 $\pm$ 0.0049	
T-6	85-100 mg	13.220	0.0476 $\pm$ 0.0043	
T-7	100-110 mg	11.263	0.0466 $\pm$ 0.0048	
T-20	40-65 mg	30.614	0.0441 $\pm$ 0.0034	
T-21	40-65 mg	30.509	0.0425 $\pm$ 0.0046	
T-23	all sizes	29.933	0.0475 $\pm$ 0.0038	
Sebastolobus alascanus				0.042 $\pm$ 0.002
S-15	all sizes	15.668	0.0387 $\pm$ 0.0033	
S-16	all sizes	15.631	0.0399 $\pm$ 0.0033	
S-17	all sizes	16.588	0.0504 $\pm$ 0.0040	

TABLE 4: ^{210}Pb activity and (^{210}Pb:^{226}Ra) for pooled otolith core samples from two deep-sea rockfishes, *Sebastolobus alascanus* and *S. altivelis*. Samples SO-1, SO-11, SO-12, SO-13, and SO-14 are cores provided by the Southwest Fisheries Science Center (SWFSC) from fish caught off Oregon. All other samples are from fish collected southwest of Santa Cruz, CA. N is the number of cores pooled to form samples weighing approximately 1 g (except T-2 (430) = 11.085 g used for both ^{210}Pb and ^{226}Ra analyses). Growth increment counts in parenthesis were derived from the increment count/otolith weight relationships (Figures 9 and 10). Others are mean counts from otoliths in the sample. Uncertainties are $\pm$ 1 standard deviation for all parameters. (*=suspected contamination)

SAMPLE (N)	INCREMENT COUNT	OTOLITH WEIGHT (mg)	^{210}Pb (dpm/g)	(^{210}Pb:^{226}Ra)	Radiochemical Age (y)
Sebastolobus altivelis					
T-2 (430)	(4.9 ± 1.1)	26.9 ± 7.5	.0072 ± .0008	.157 ± .017	8.0 (+0.8, -0.7)
T-3 (65)	(3.5 ± 0.9)	20.1 ± 4.1	.0049 ± .0017	.108 ± .038	6.2 (+1.5, -1.6)
T-4 (40)	(3.3 ± 0.9)	19.0 ± 4.2	.0067 ± .0023	.147 ± .051	7.7 (+2.1, -2.0)
T-5 (65)	4.3 ± 1.2	24.5 ± 7.8	.0045 ± .0014	.098 ± .030	5.8 (+3.7, -3.1)
T-22 (37)	12.3 ± 1.6	59.4 ± 9.1	.0168 ± .0032	.367 ± .071	17.2 (+4.4, -3.3)
T-9 (35)	(15.8 ± 1.6)	76.3 ± 5.1	.0158 ± .0028	.345 ± .061	16.1 (+3.7, -3.1)
T-10 (35)	(15.3 ± 2.2)	74.9 ± 5.9	.0119 ± .0041	.259 ± .091	12.2 (+4.6, -3.9)
T-13 (35)	(26.1 ± 4.0)	117.7 ± 4.4	.0187 ± .0030	.409 ± .066	19.4 (+4.5, -3.7)
T-14 (35)	(24.5 ± 4.3)	115.7 ± 3.4	.0234 ± .0023	.513 ± .052	25.7 (+4.5, -3.9)
T-15 (35)	23.6 ± 2.1	114.2 ± 13.1	.0176 ± .0045	.385 ± .098	18.2 (+6.3, -5.0)
T-16 (31)	(34.2 ± 3.7)	154.5 ± 10.6	.0307 ± .0055	.672 ± .122	38.4 (+17.9, -11.0)
T-17 (31)	(34.3 ± 4.0)	155.4 ± 11.8	.0471 ± .0052	1.029±.116*	inf
T-18 (32)	(34.1 ± 3.9)	151.0 ± 9.4	.0284 ± .0039	.620 ± .086	33.7 (+10.0, -7.3)
T-19 (47)	35.6 ± 4.9	147.8 ± 19.3	.0298 ± .0032	.652 ± .072	36.5 (+9.3, -6.9)
Sebastolobus alascanus					
S-2 (34)	(10.6 ± 3.4)	41.9 ± 20	.0054 ± .0020	.128 ± .049	6.9 (+2.1, -1.8)
S-3 (46)	13.0 ± 1.5	74.8 ± 13.7	.0115 ± .0027	.273 ± .064	12.8 (+3.4, -3.0)
S-7 (50)	(13.6 ± 1.7)	77.0 ± 13.6	.0161 ± .0025	.383 ± .061	18.5 (+3.7, -3.8)
SO-11 (46)	(13.4 ± 1.7)	73.5 ± 13.6	.0104 ± .0022	.248 ± .052	11.7 (+2.7, -2.4)
S-4 (38)	22.2 ± 1.8	154.0 ± 24.5	.0176 ± .0036	.418 ± .087	19.9 (+6.2, -4.9)
S-8 (34)	(27.5 ± 3.8)	185.5 ± 7.3	.0222 ± .0040	.530 ± .097	26.8 (+9.1, -6.7)
SO-12 (25)	(27.2 ± 3.8)	181.5 ± 11.6	.0254 ± .0031	.604 ± .075	32.3 (+8.8, -6.5)
S-5 (35)	32.3 ± 1.8	207.8 ± 30.4	.0269 ± .0032	.642 ± .078	35.5 (+10.4, -7.3)
SO-13 (26)	(40.5 ± 4.6)	263.4 ± 11.2	.0304 ± .0043	.723 ± .105	43.8 (+20.2, -11.6)
S-6 (26)	43.1 ± 2.3	262.7 ± 20.2	.0282 ± .0038	.673 ± .094	38.4 (+14.1,-9.2)
S-9 (24)	(43.3 ± 3.8)	277.0 ± 9.3	.0286 ± .0059	.681 ± .142	39.3 (+23.9,-12.8)
S-10 (28)	(50.0 ± 8.4)	354.5 ± 76	.0328 ± .0037	.780 ± .091	51.3 (+23.8,-12.9)
SO-14 (24)	(58.6 ± 5.2)	376.3 ± 34.5	.0347 ± .0046	.827 ± .113	59.0 (+52.7, -18.2)
SO-1 (30)	71.7 ± 12.0	423.4 ± 35.1	.0387 ± .0022	.922 ± .060	84.8 (inf, -22.6)

TABLE 5: Comparison of von Bertalanffy growth [$L_t = L_\infty(1-e^{-kt})$] parameters developed for *Sebastolobus alascanus* and *S. altivelis* from this study and from fishery data. Fish from Jacobson (1990) were collected off Oregon. Errors are $\pm$ 1 asymptotic standard error. Values of L_∞ and k for *S. alascanus* are over and underestimated respectively due to low sample size in the largest and smallest size classes.

PARAMETER	THIS STUDY	JACOBSON (1991)
Sebastolobus alascanus		
L_∞	945.0 ± 72.9	871.9 ± 33.0
k	.0169 ± .0024	.0145 ± .0010
t_o	-5.53 ± 1.14	-6.05 ± .78
Sebastolobus altivelis		
L_∞	300.6 ± 37.9	338.6 ± 12.3
k	.0720 ± .0028	.0585 ± .0057
t_o	-1.90 ± .21	-0.38 ± .56

TABLE 6: Results of radiochemical ageing studies for deep water fishes. The growth coefficient (k) was determined from the fit of the von Bertalanffy growth function [$L_t = L_\infty(1-e^{-kt})$]. ^{226}Ra values are mean specific activities with observed range of values measured.

SPECIES	k	PROJECTED MAXIMUM AGE	^{226}Ra (dpm/g)	Range	REFERENCE
Sebastes diploproa		>80 y	0.043 ± 0.004	0.033 to 0.054	Bennett *et al.* (1982)
Sebastes mentella		>75 y	0.033 ± 0.002	not reported	Campana *et al.* (1990)
Hoplostethus atlanticus	0.044	>100 y	0.0522 ± 0.0036 and 0.0625 ± 0.0030	not reported	Fenton *et al.* (1991)
Sebastes rufus	0.041	>50 y	0.072 ± 0.003	0.0700 to 0.0734	Watters (1994)
Anoplopoma fimbria		>50 y	0.414 ± 0.050	0.288 to 0.517	Kastelle *et al.* (1994)
Sebastolobus alascanus	0.017	>80 y	0.042 ± 0.002	0.039 to 0.0504	This study
Sebastolobus altivelis	0.072	>45 y	0.045 ± 0.002	0.043 to 0.048	This study
Allocytus verrucosus	0.056	>100 y	0.0530 ± 0.009	0.0391 to 0.0694	Stewart *et al.* (1995)
Macruronus novaezelandiae		>20 y	0.022 ± 0.004	0.0179 to 0.0290	Fenton and Short (1995)

FIGURE 1: Decay series for ^{238}U. α=radioactive decay through emission of an alpha particle, and ß=radioactive decay through emission of a beta particle.

Uranium-238 Decay Series

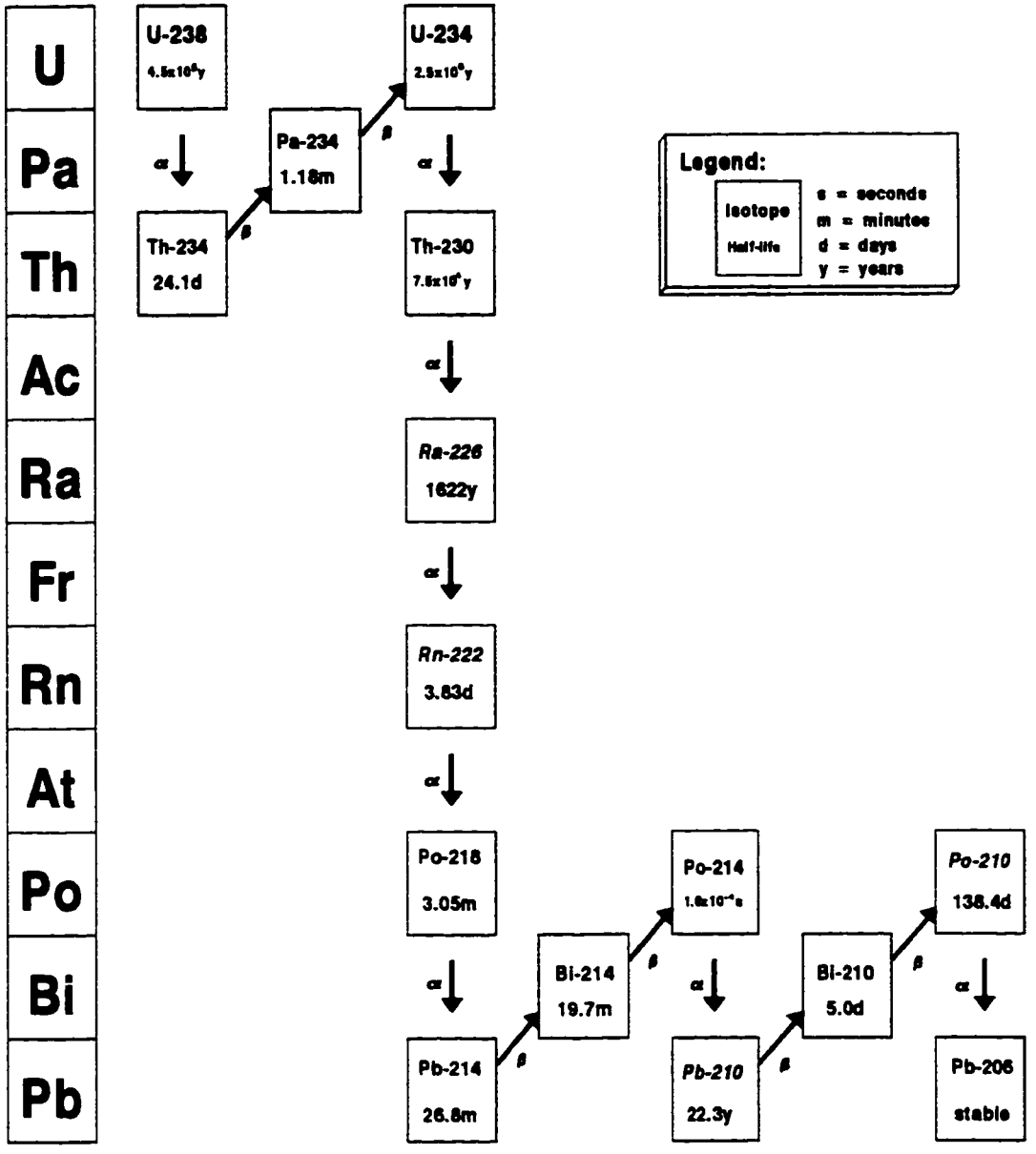


FIGURE 2: Otolith cleaning protocol for low-level radiochemical analyses. The protocol was developed to remove surface contaminants and an external layer of the otolith/core surface which had been exposed to handling.

OTOLITH CLEANING PROTOCOL

ROUGH CLEANING

↓

*Rinse 3X with deionized water/micro
*Rinse 3X with deionized water
*Rinse 3X with milli-Q water

↓

Transfer to acid-cleaned beaker

↓

FINE CLEANING

↓

*10 min in milli-Q water with ultrasound
*1 min in 0.15N HNO_3 with ultrasound
*10 min 30% H_2O_2/NaOH (pH 10) with ultrasound

↓

*Rinse 3X with milli-Q water

↓

*1 min in 0.15N HNO_3 with ultrasound
*5 min in milli-Q water with ultrasound
*5 min in milli-Q water
*Rinse 3X @ 30 secs with 0.001N HNO_3 with ultrasound

↓

*Rinse 3X with milli-Q water

↓

*Dry 12 hrs in oven covered with watch glass
*Weigh and transfer to new acid-cleaned beaker or gas wash bottle

FIGURE 3a: Diagram of the extraction board component of the gas emanation system used to extract ^{222}Rn from dissolved otolith samples. An otolith sample is represented in the foreground in a gas wash bottle.

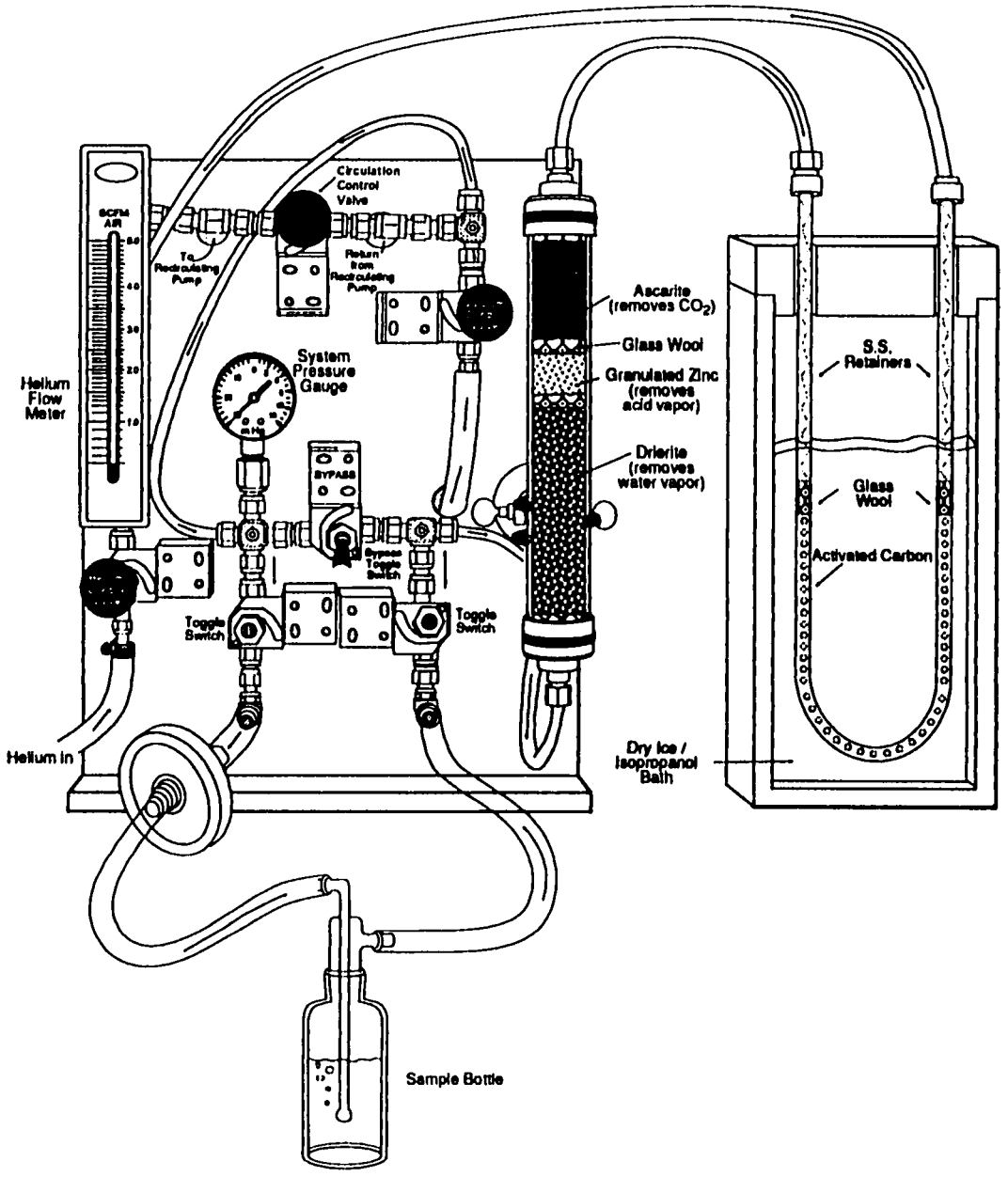

Circulation Control Valve
To Recirculating Pump
Return from Recirculating Pump
SCFM AIR
Helium Flow Meter
System Pressure Gauge
BYPASS
Bypass Toggle Switch
Toggle Switch
Toggle Switch
Helium In
Ascarite (removes CO_2)
Glass Wool
Granulated Zinc (removes acid vapor)
Drierite (removes water vapor)
S.S. Retainers
Glass Wool
Activated Carbon
Dry Ice / Isopropanol Bath
Sample Bottle

FIGURE 3b: Diagram of the transfer board, column heating system, and Lucas cell components of the gas emanation system used to extract ^{222}Rn from dissolved otolith samples.

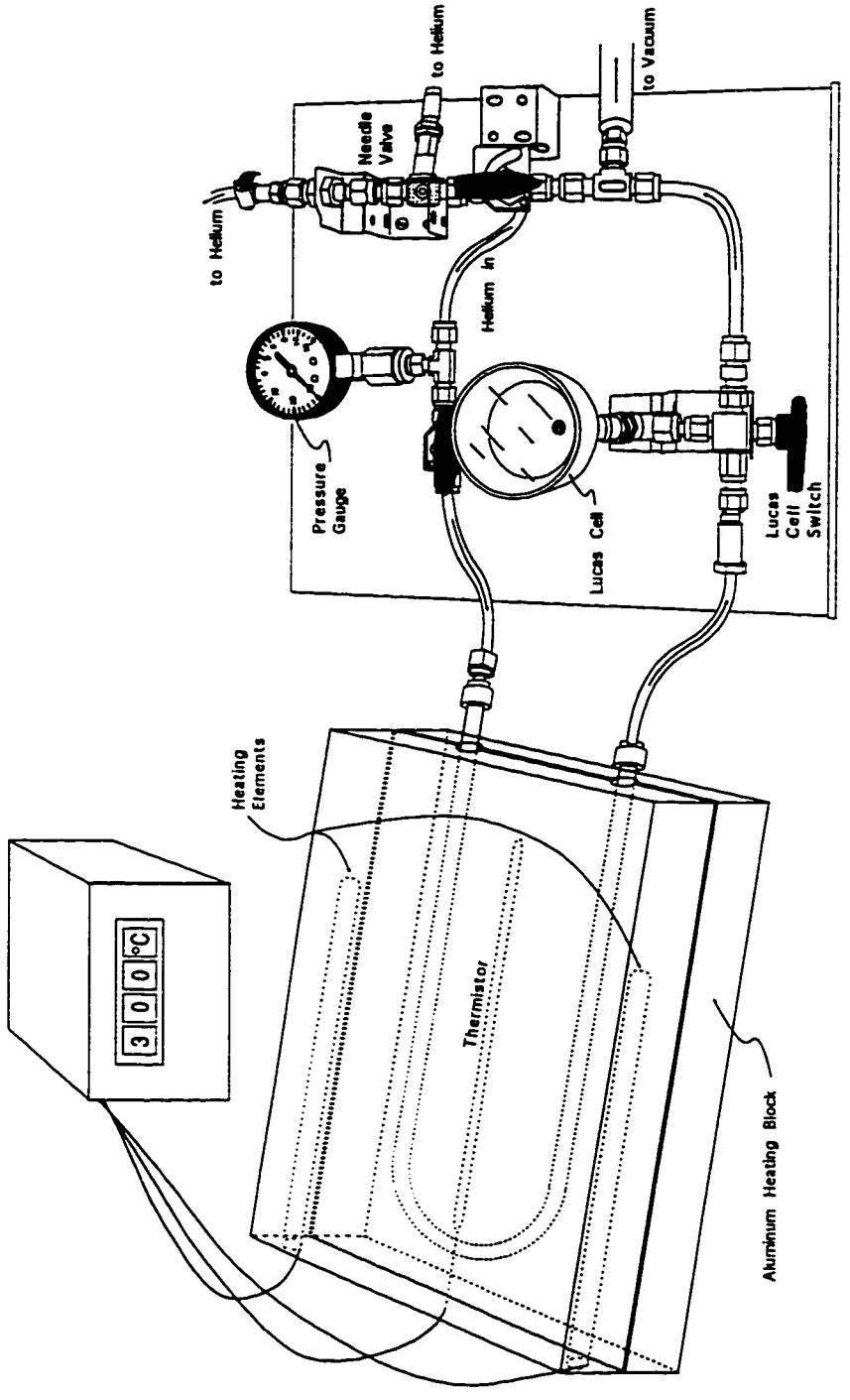

to Helium
Needle Valve
to Helium
to Vacuum
Helium In
Pressure Gauge
Lucas Cell
Lucas Cell Switch
Heating Elements
Thermistor
Aluminum Heating Block
300°C

FIGURE 4: Example of a typical alpha spectra from a three-week count of a spiked one gram otolith sample before correction for background. The ^{208}Po peak (region of interest, ROI, channels 165-176) indicates counts recorded from approximately 0.3 dpm yield tracer. The ^{210}Po peak (ROI channels 205-212) represents α-decays from ^{210}Po in the otoliths.

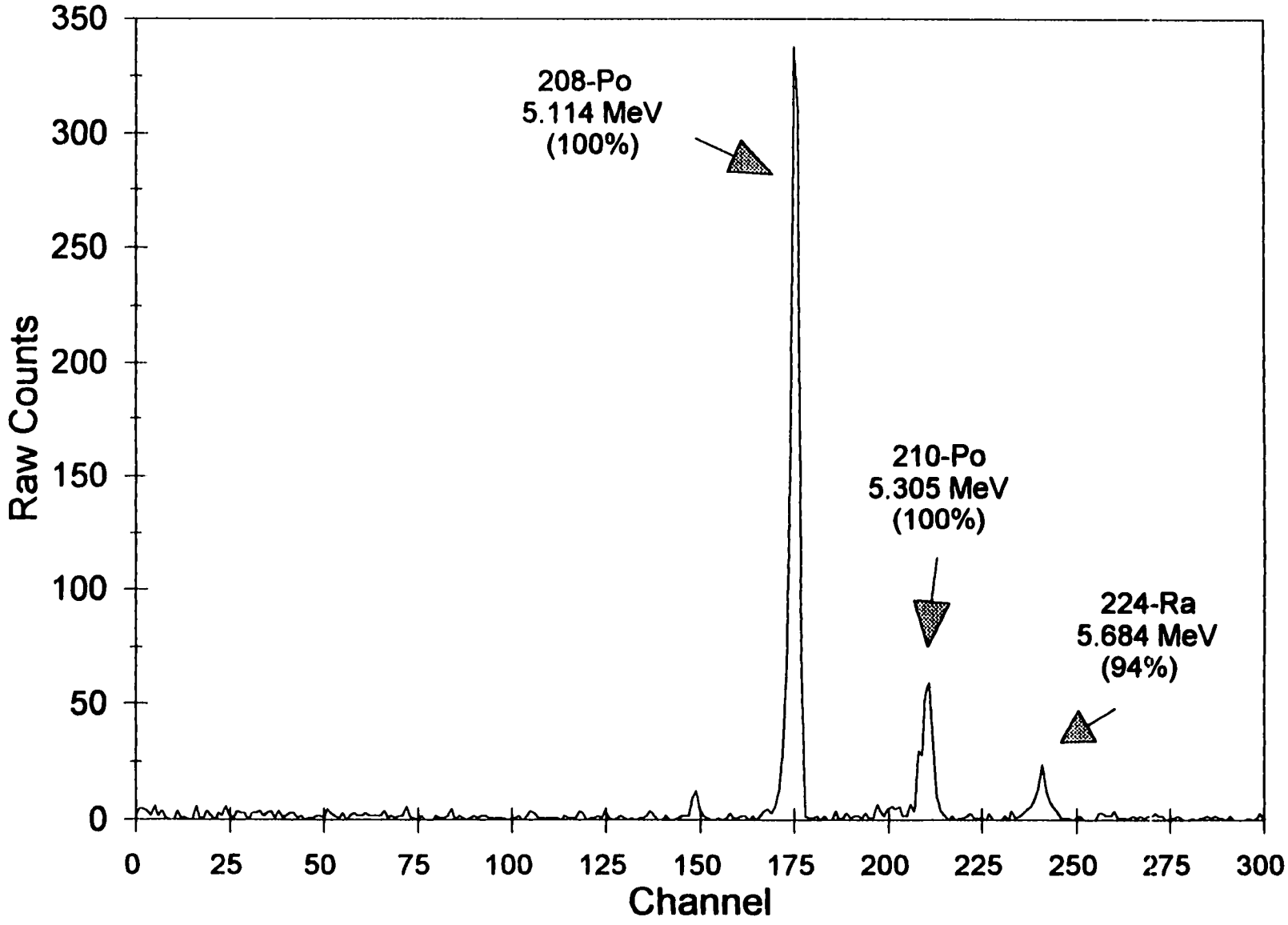

208-Po
5.114 MeV
(100%)
210-Po
5.305 MeV
(100%)
224-Ra
5.684 MeV
(94%)
Raw Counts
Channel
0
50
100
150
200
250
300
350
0
25
50
75
100
125
150
175
200
225
250
275
300

FIGURE 5: Length frequency of *Sebastolobus alascanus* specimens collected from 200-1200 m in bottom trawls conducted southwest of Santa Cruz, CA, September 1991.

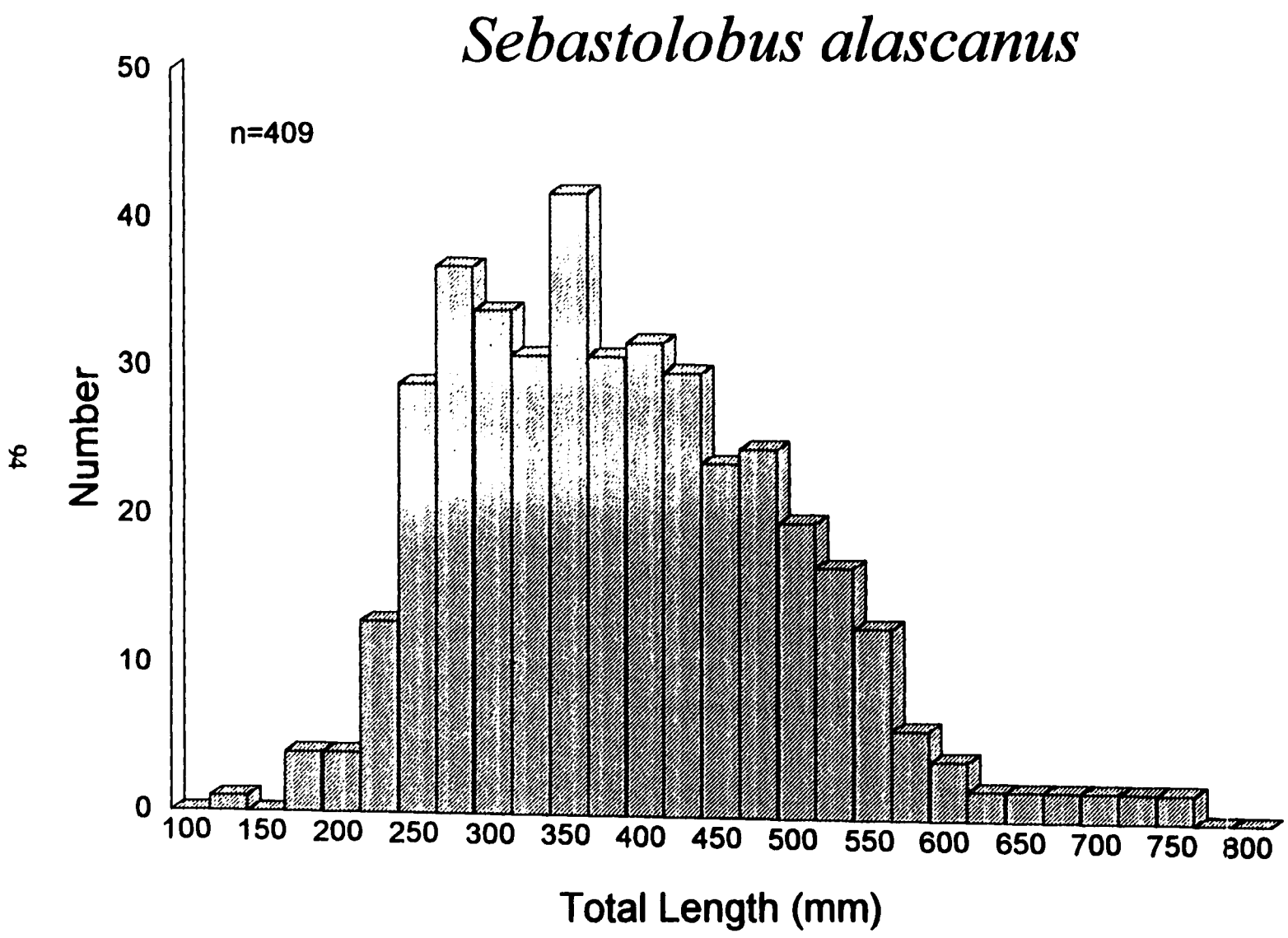

Sebastolobus alascanus
n=409
Number
50
40
30
20
10
0
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
Total Length (mm)

FIGURE 6: Length frequency of *Sebastolobus altivelis* specimens collected from 400-1200 m in bottom trawls conducted southwest of Santa Cruz, CA, September 1991. Data represent only those fish processed onboard.

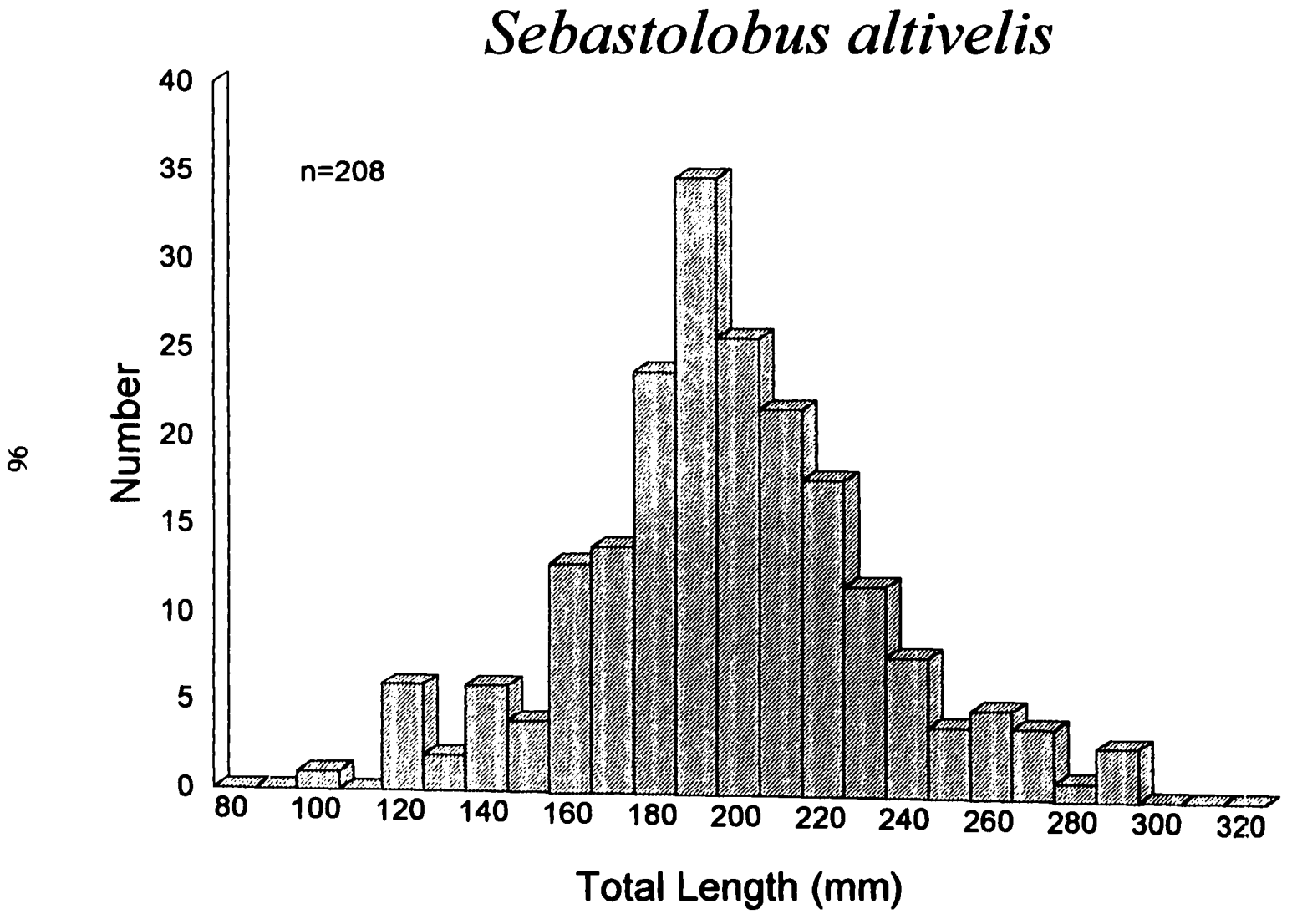

Sebastolobus altivelis
n=208
Number
0
5
10
15
20
25
30
35
40
80
100
120
140
160
180
200
220
240
260
280
300
320
Total Length (mm)

FIGURE 7: Relationship of sagittal otolith weight to fish total length for *Sebastolobus alascanus* (circles are fish from the Santa Cruz collection and squares are Oregon samples).

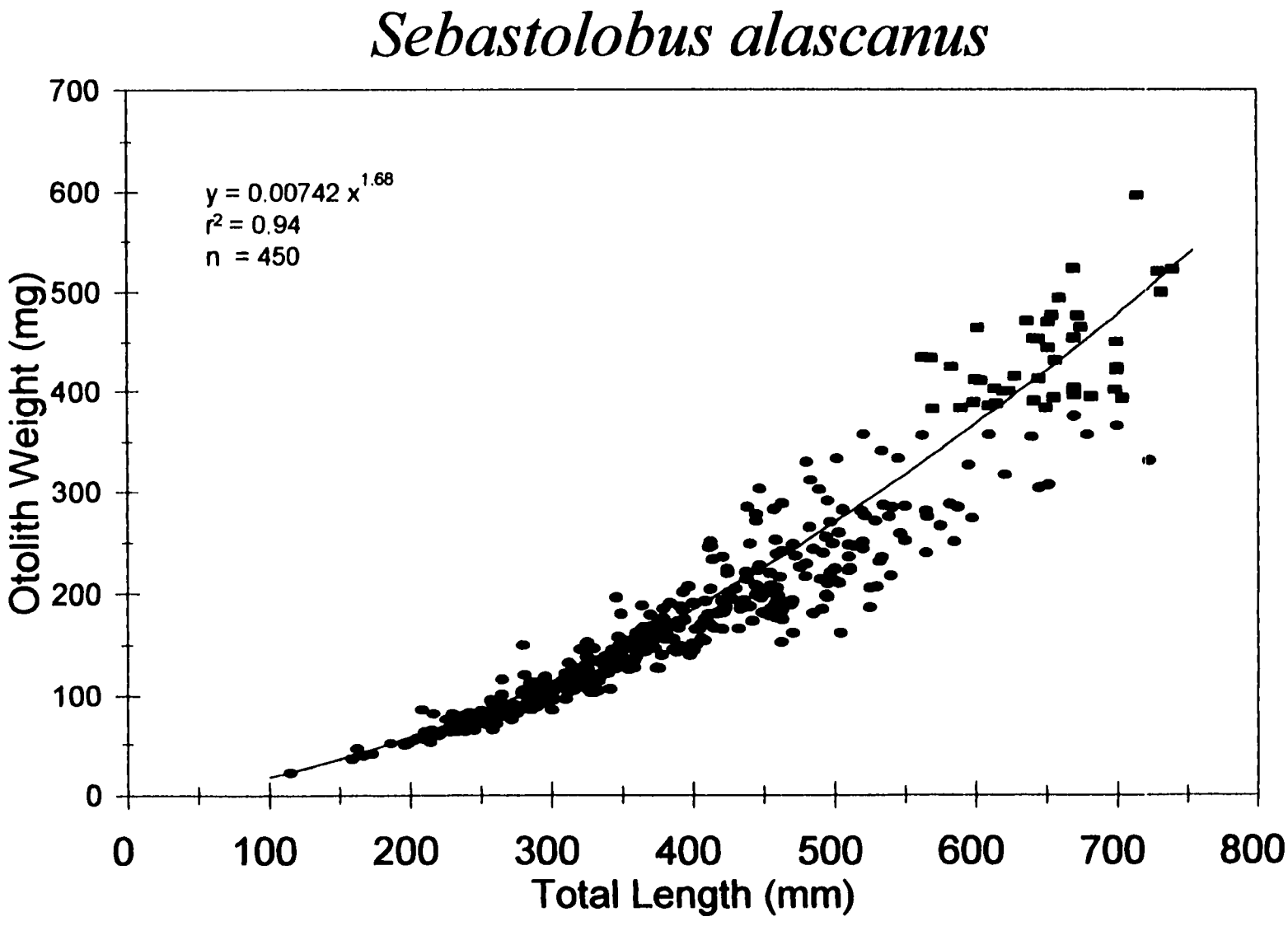

Sebastolobus alascanus
y = 0.00742 x^1.68
r² = 0.94
n = 450
Otolith Weight (mg)
0
100
200
300
400
500
600
700
0
100
200
300
400
500
600
700
800
Total Length (mm)

FIGURE 8: Relationship of sagittal otolith weight to fish total length for *Sebastolobus altivelis* from the Santa Cruz collection (circles). Fish collected in the Monterey submarine canyon (squares) and subsequently frozen were not included in the best fit analysis.

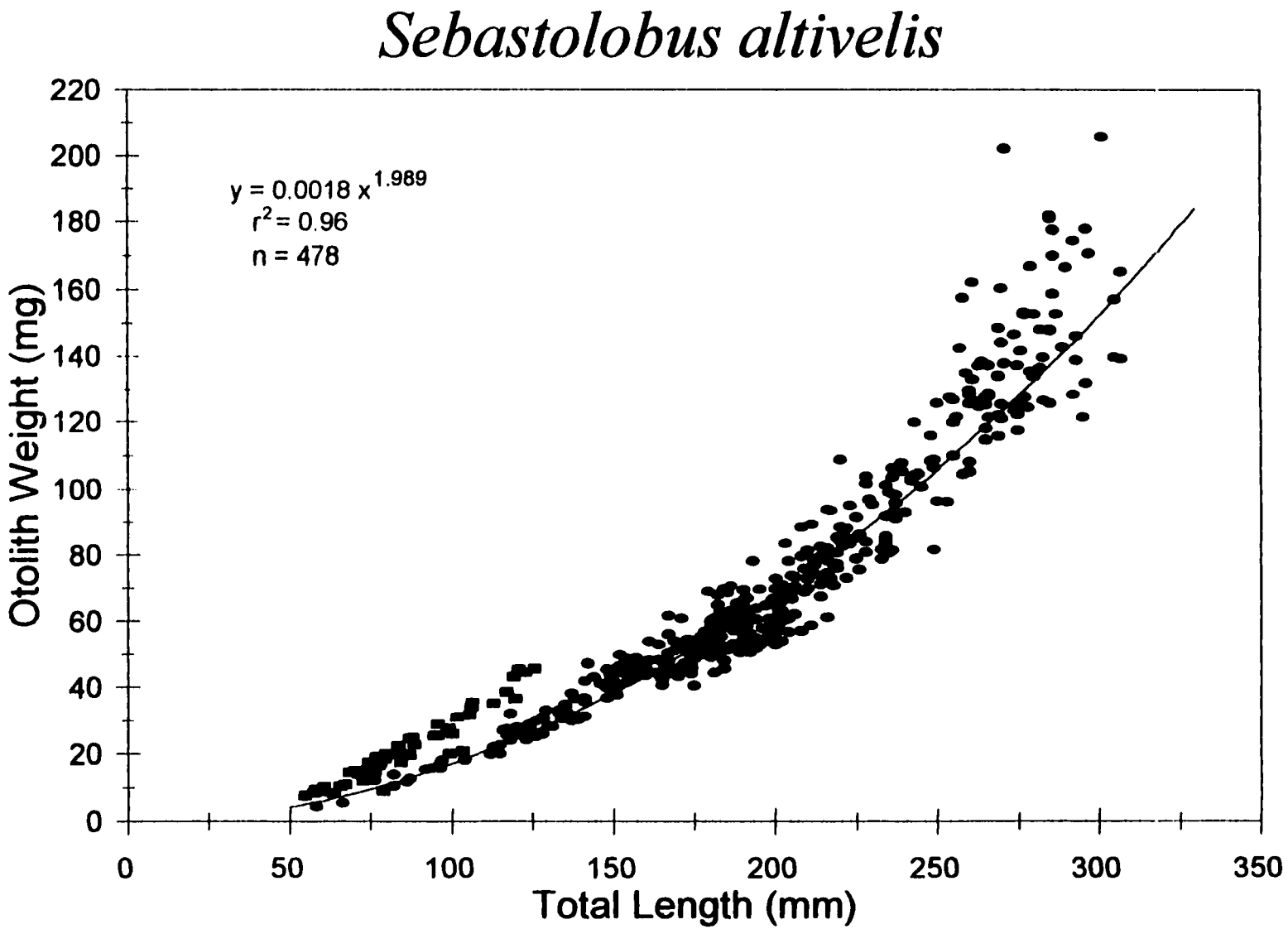

Sebastolobus altivelis
y = 0.0018 x^1.989
r^2 = 0.96
n = 478
Otolith Weight (mg)
Total Length (mm)
0
20
40
60
80
100
120
140
160
180
200
220
0
50
100
150
200
250
300
350

FIGURE 9: Relationship of otolith weight to number of growth increments visible in transverse sections of sagittal otoliths from *Sebastolobus alascanus* (circles = Santa Cruz collection, squares = Oregon samples).

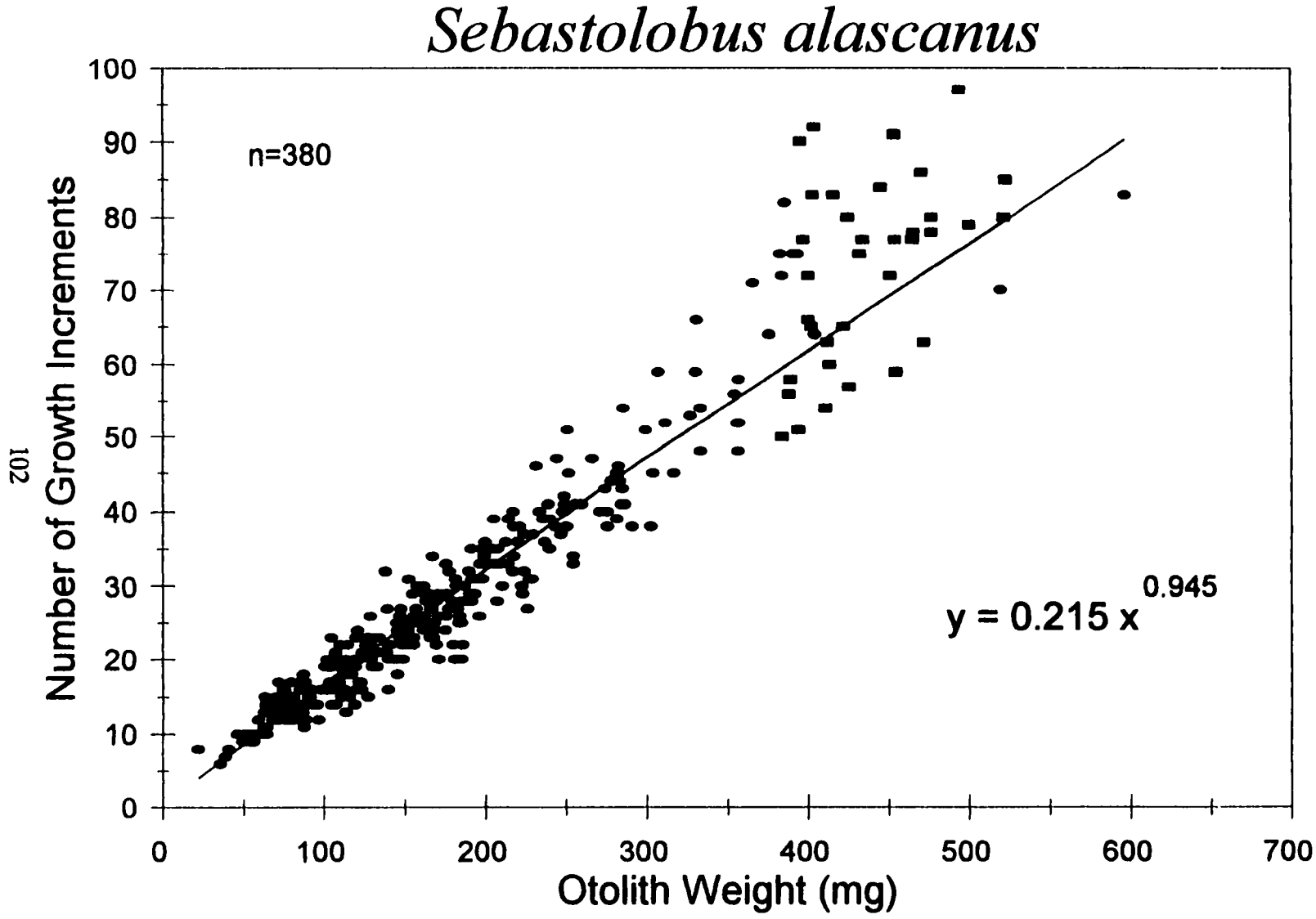

Sebastolobus alascanus
n=380
y = 0.215 x 0.945
Number of Growth Increments
Otolith Weight (mg)
0
10
20
30
40
50
60
70
80
90
100
0
100
200
300
400
500
600
700

FIGURE 10: Relationship of otolith weight to number of growth increments visible in transverse sections of sagittal otoliths from *Sebastolobus altivelis* specimens.

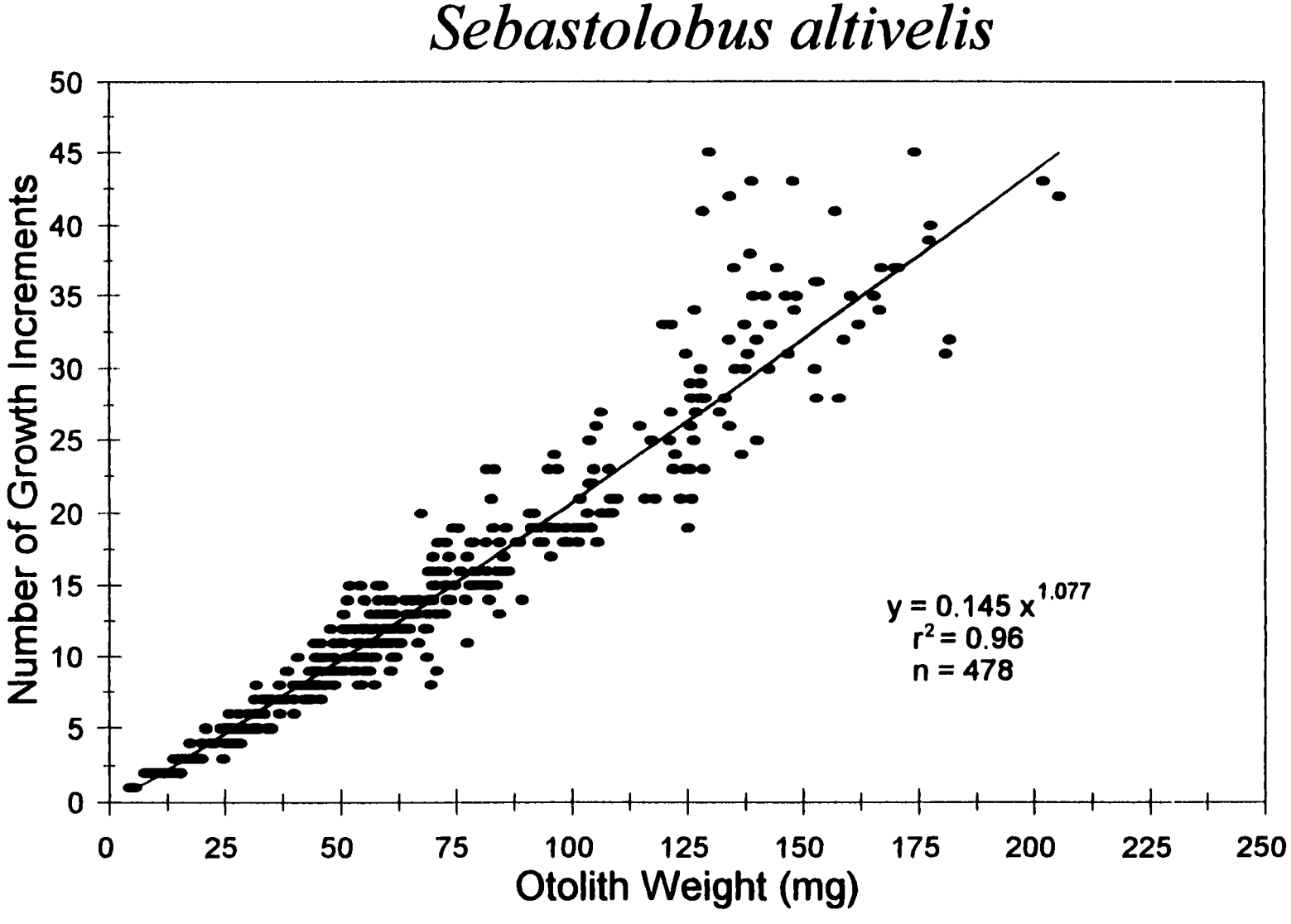

Sebastolobus altivelis
Number of Growth Increments
Otolith Weight (mg)
0
5
10
15
20
25
30
35
40
45
50
0
25
50
75
100
125
150
175
200
225
250
y = 0.145 x^1.077
r^2 = 0.96
n = 478

FIGURE 11: Regression of the first five *Sebastolobus altivelis* otolith growth increments versus otolith weight indicating that otolith mass increases proportionately over the period of core formation ($y=5.46x+1.011$, $r^2=0.878$, $n=85$). These data confirm the linear mass increase assumption required for use of the radiochemical ageing technique for this species.

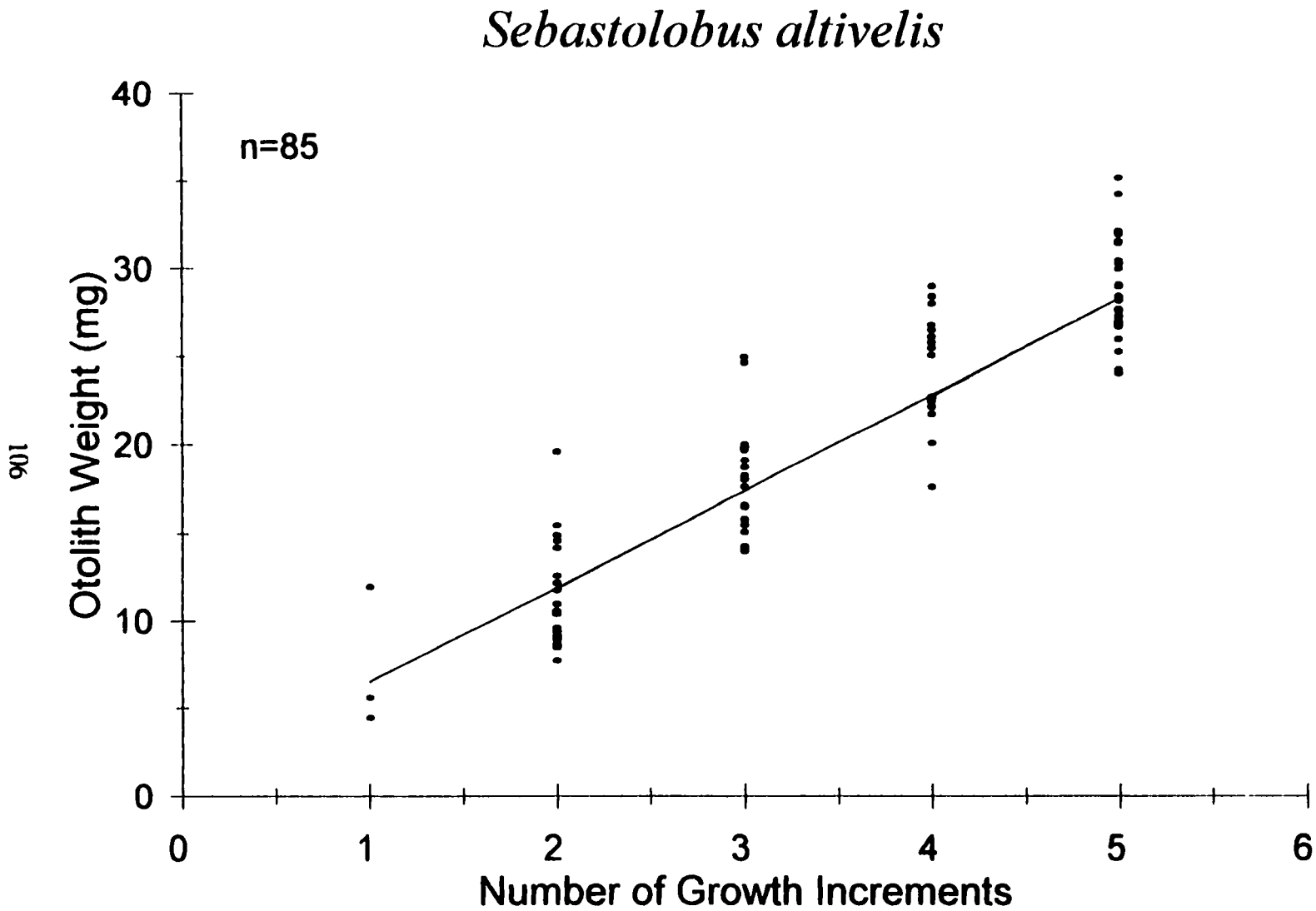
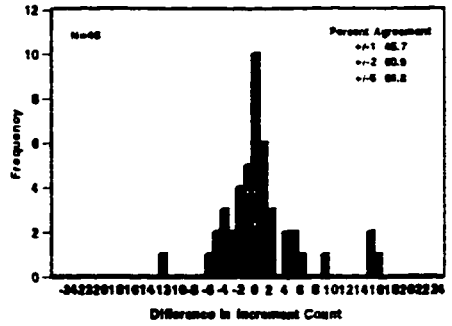

Sebastolobus altivelis
n=85
Otolith Weight (mg)
0
10
20
30
40
0
1
2
3
4
5
6
Number of Growth Increments

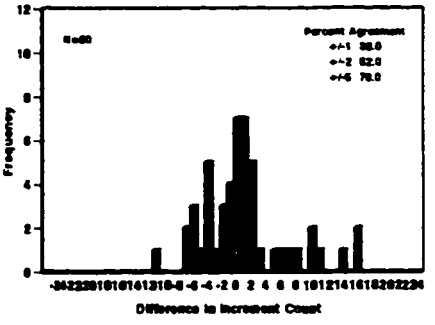
FIGURE 12: Precision of inter-reader age estimates for 50 randomly selected *Sebastolobus alascanus* otolith sections. MAC is the MacIntosh image analysis system.

Sebastolobus alascanus

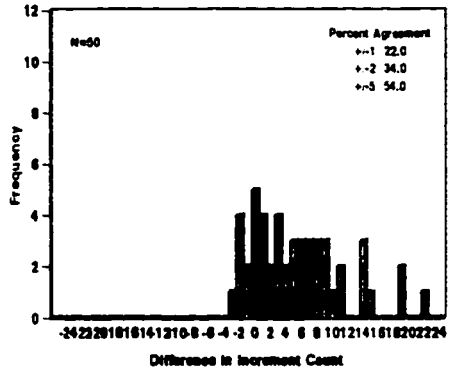
BETWEEN READERS 1-2



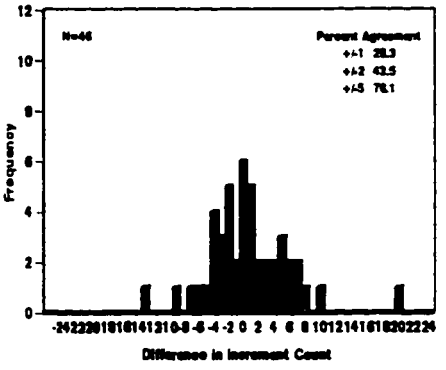
BETWEEN READERS 1-MAC



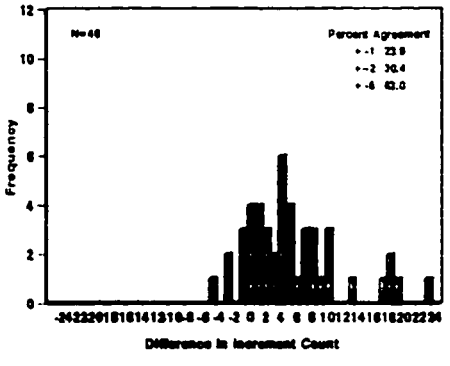
BETWEEN READERS 1-3



BETWEEN READERS 2-MAC



BETWEEN READERS 2-3



BETWEEN READERS 3-MAC

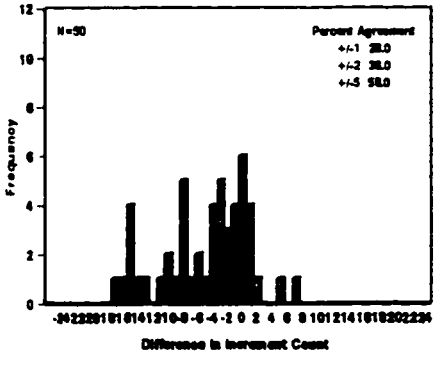
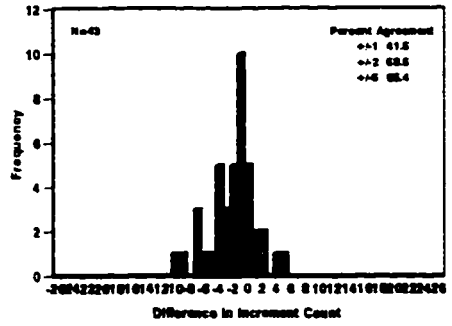


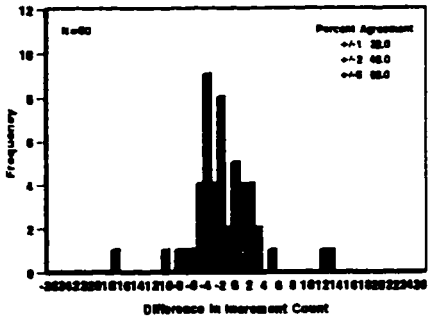
FIGURE 13: Precision of inter-reader age estimates for 50 randomly selected *Sebastolobus altivelis* otolith sections. MAC is the MacIntosh (MAC) image analysis program.

Sebastolobus altivelis

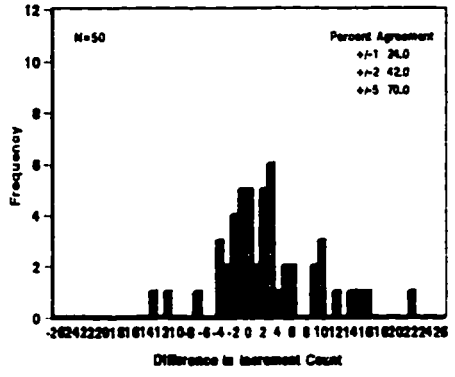
BETWEEN READERS 1-2



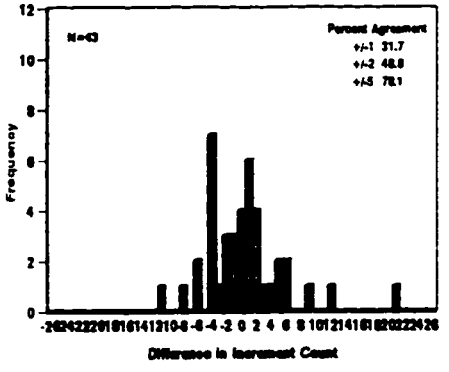
BETWEEN READERS 1-MAC



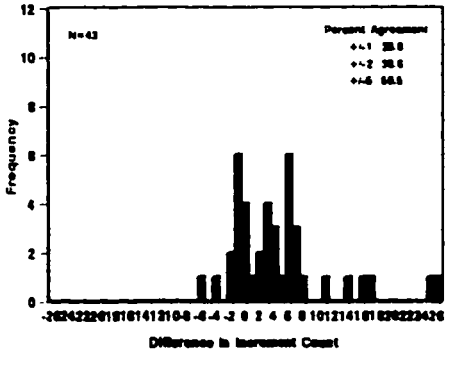
BETWEEN READERS 1-3



BETWEEN READERS 2-MAC



BETWEEN READERS 2-3



BETWEEN READERS 3-MAC

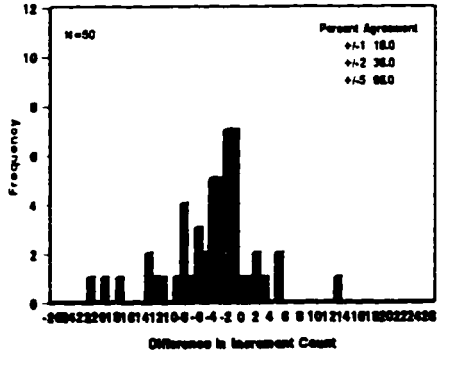
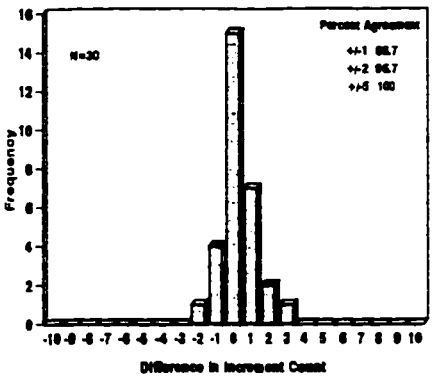


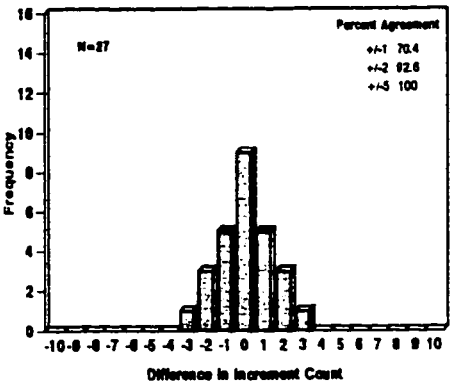
FIGURE 14: Reader 1 intra-reader age-specific precision analysis for *Sebastolobus alascanus* otoliths.

Sebastolobus alascanus

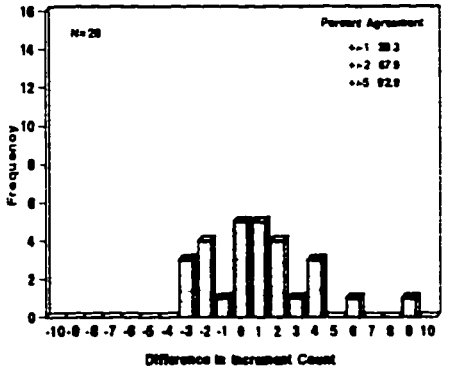
WITHIN READER 10-15



WITHIN READER 20-25



WITHIN READER 30-35



WITHIN READER 40-50

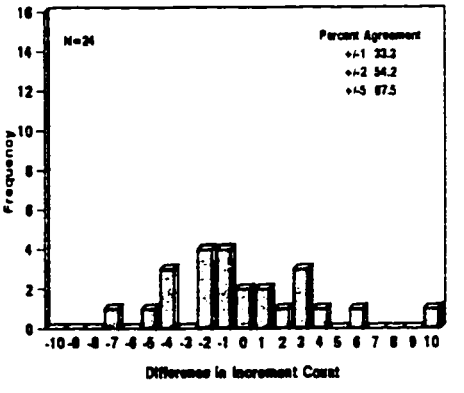
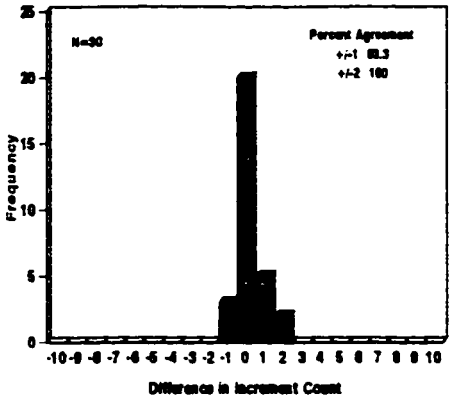


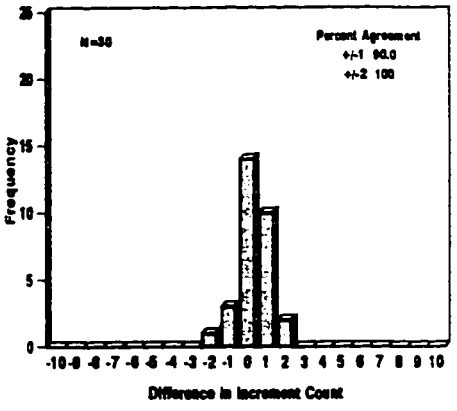
FIGURE 15: Reader 1 intra-reader age-specific precision analysis for *Sebastolobus altivelis* otoliths.

Sebastolobus altivelis

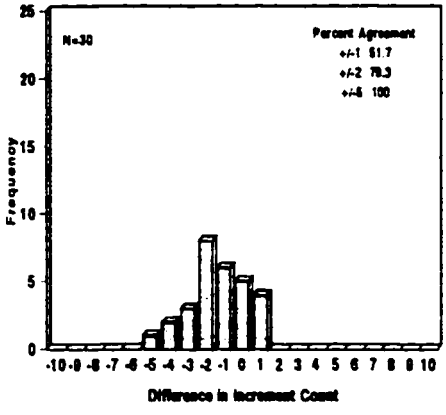
WITHIN READER 0-5



WITHIN READER 10-15



WITHIN READER 20-25



WITHIN READER 30+

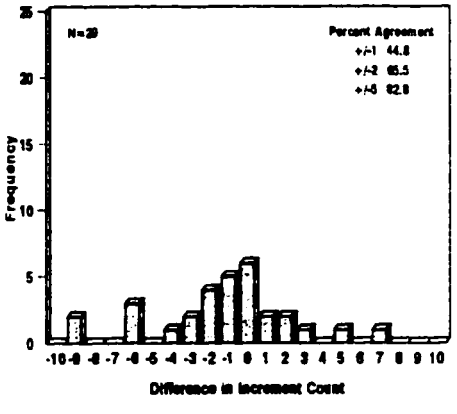


FIGURE 16: Von Bertalanffy growth curve [$L_t = L_\infty(1-e^{-kt})$] and parameters for *Sebastolobus alascanus* specimens collected southwest of Santa Cruz, CA. (Standard errors are: L_∞ = 72.9; k = 0.0024; and t_o = 1.14.)

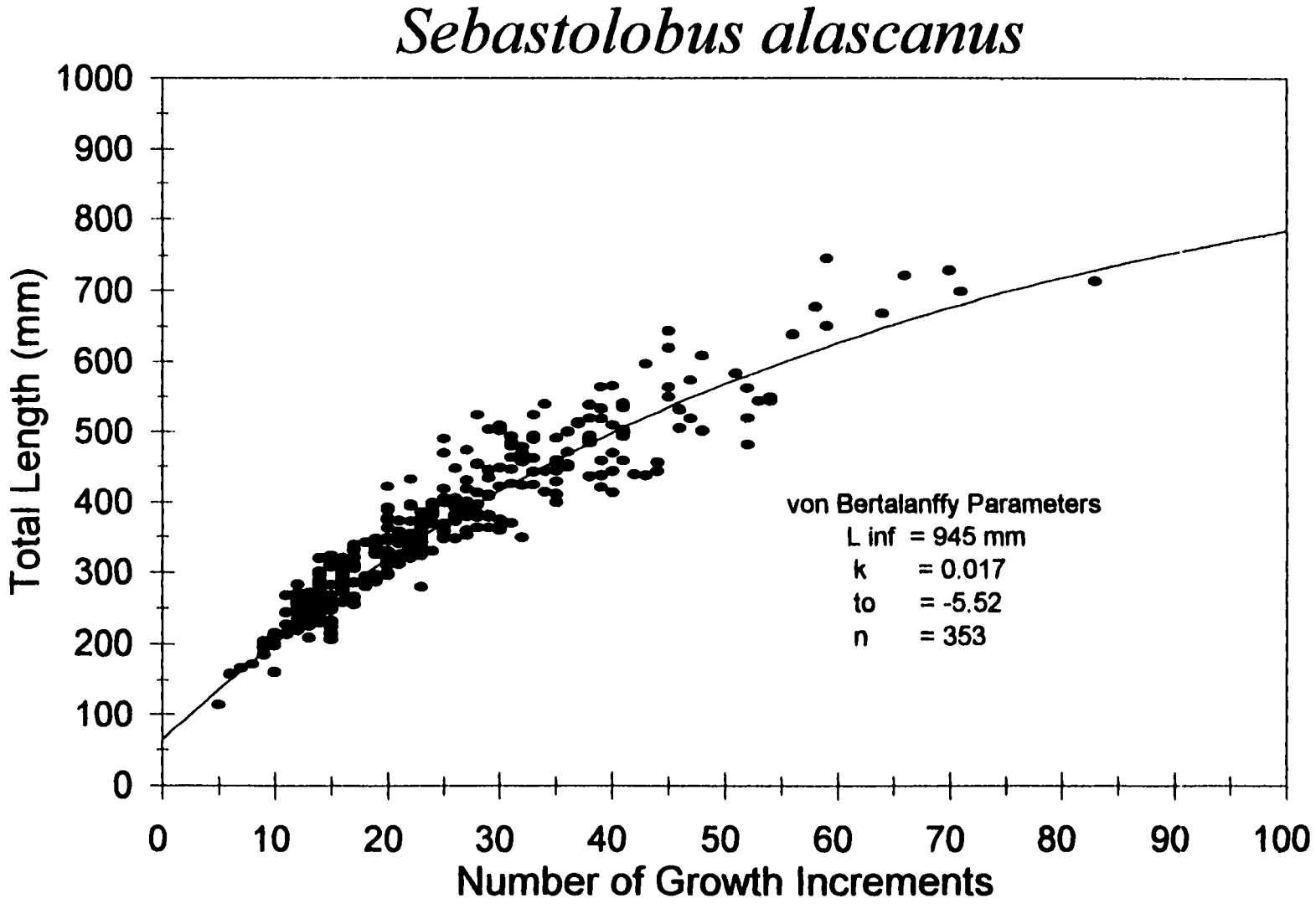

Sebastolobus alascanus
Total Length (mm)
1000
900
800
700
600
500
400
300
200
100
0
0
10
20
30
40
50
60
70
80
90
100
Number of Growth Increments
von Bertalanffy Parameters
L inf = 945 mm
k = 0.017
to = -5.52
n = 353

FIGURE 17: Von Bertalanffy growth curve [$L_t=L_\infty(1-e^{-kt})$] and parameters for *Sebastolobus altivelis* specimens collected southwest of Santa Cruz, CA. (Standard errors are: L_∞ = 37.9; k = 0.0028; and t_o = 0.211.)

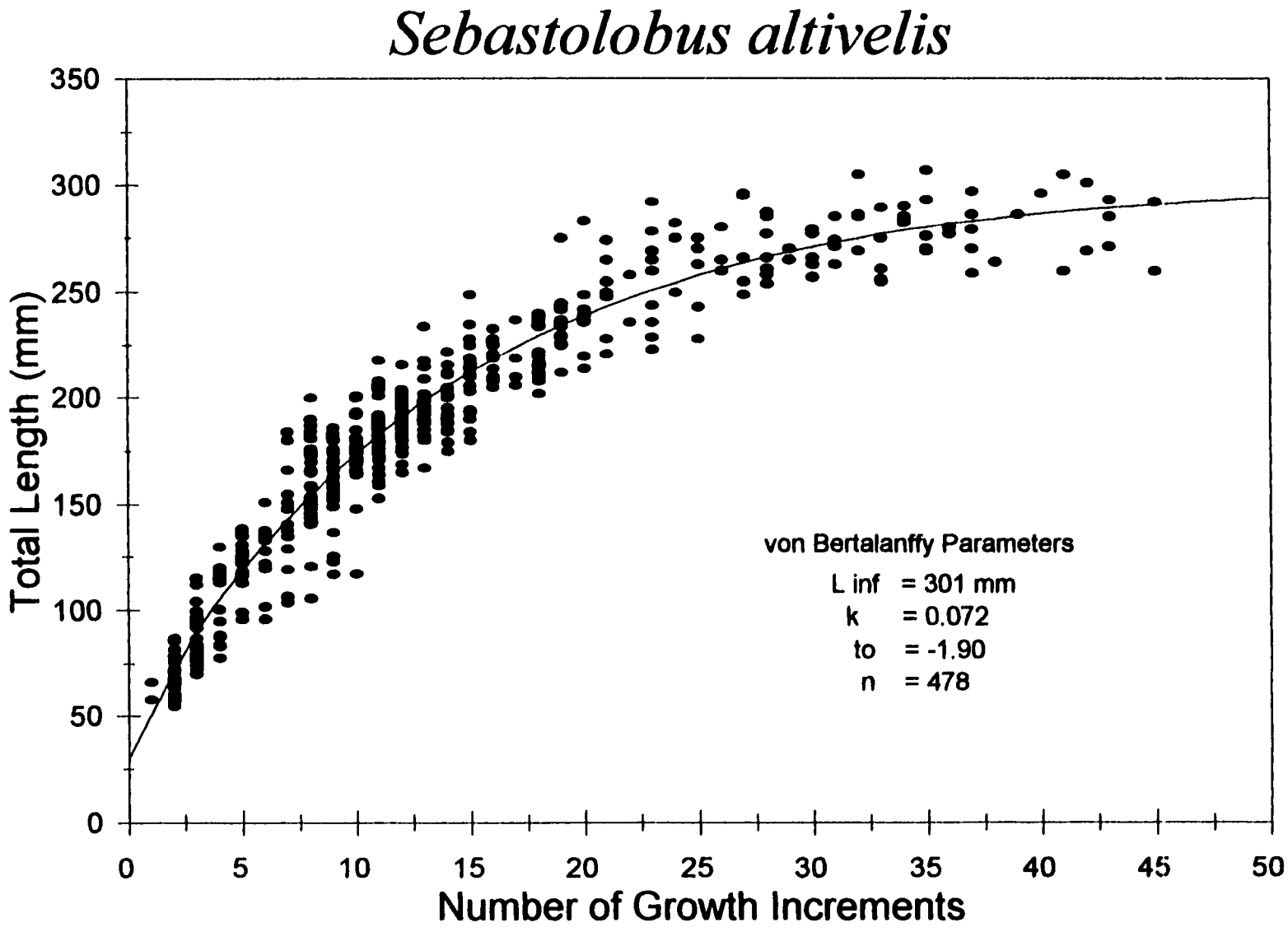

Sebastolobus altivelis
Total Length (mm)
Number of Growth Increments
0
50
100
150
200
250
300
350
0
5
10
15
20
25
30
35
40
45
50
von Bertalanffy Parameters
L inf = 301 mm
k = 0.072
to = -1.90
n = 478

FIGURE 18: Observed (^{210}Pb:^{226}Ra) and expected curves for pooled otolith core samples from *Sebastolobus alascanus* collected from two locations off the west coast of the United States. Expected curves represent initial uptake ratios (R^0) of 0 (solid line), 0.1 (dashed line), and 0.2 (dotted line). Squares are mean growth increment counts (time; one increment = one year) for the otoliths in the sample (■MLML - Santa Cruz, CA; □ SWFSC - Oregon) plotted against measured radiochemical ratios. Circles are samples pooled by weight with increment counts extracted from the otolith weight/increment count curve (Figure 9; •MLML - Santa Cruz, CA; ○ SWFSC - Oregon) plotted against measured radiochemical ratios. Vertical error bars represent counting uncertainty ($\pm$1 standard deviation) and horizontal bars represent increment count variation within the sample ($\pm$1 standard deviation).

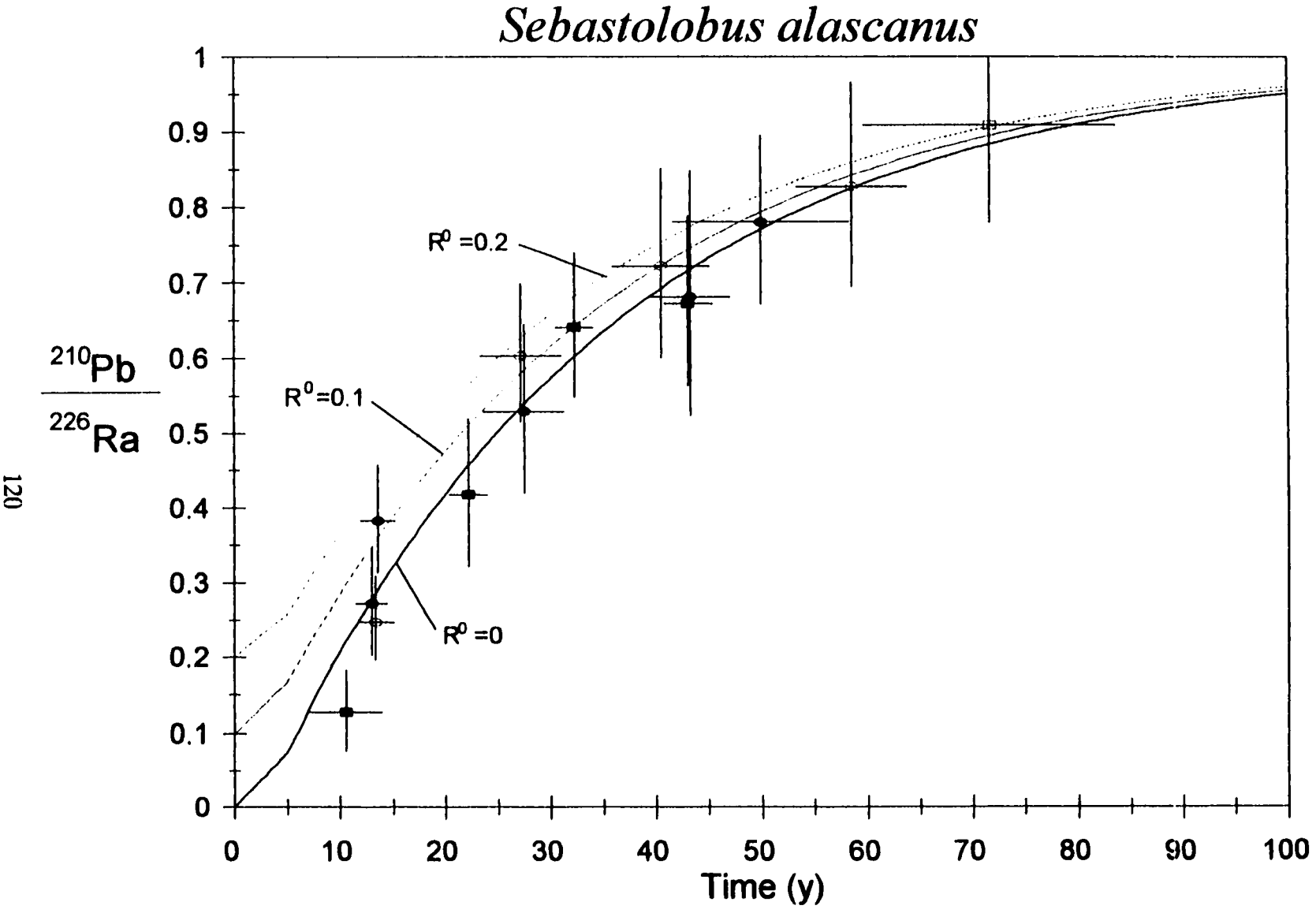

Sebastolobus alascanus
$\frac{^{210}Pb}{^{226}Ra}$
R⁰ =0.2
R⁰=0.1
R⁰ =0
Time (y)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70
80
90
100

FIGURE 19: Observed (^{210}Pb:^{226}Ra) for pooled otolith core samples from *Sebastolobus altivelis* specimens. Squares are ages derived from growth increment counts for the otoliths in the sample and circles are derived from the otolith weight/increment count curve (Figure 10). See figure 18 for details.

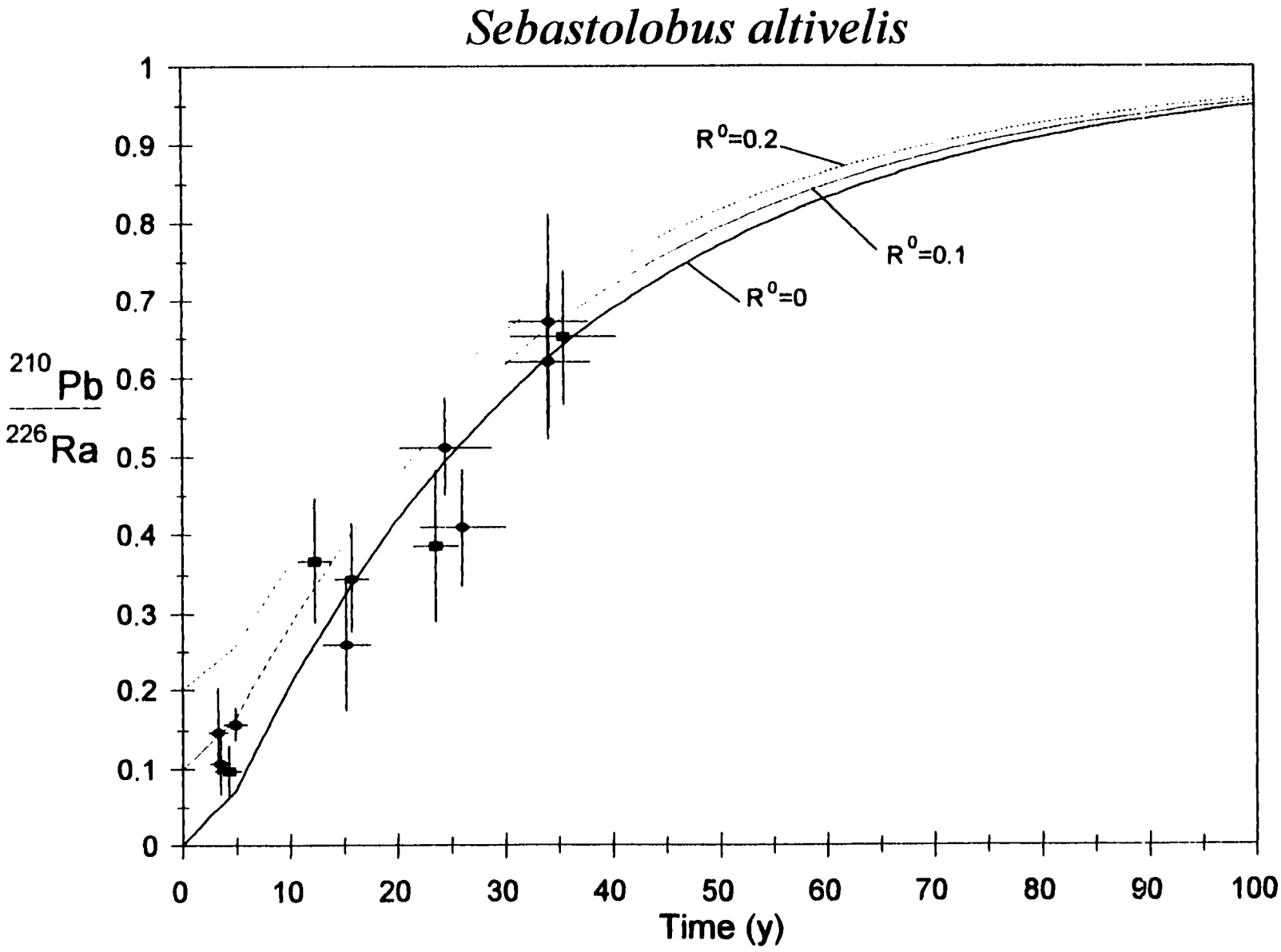
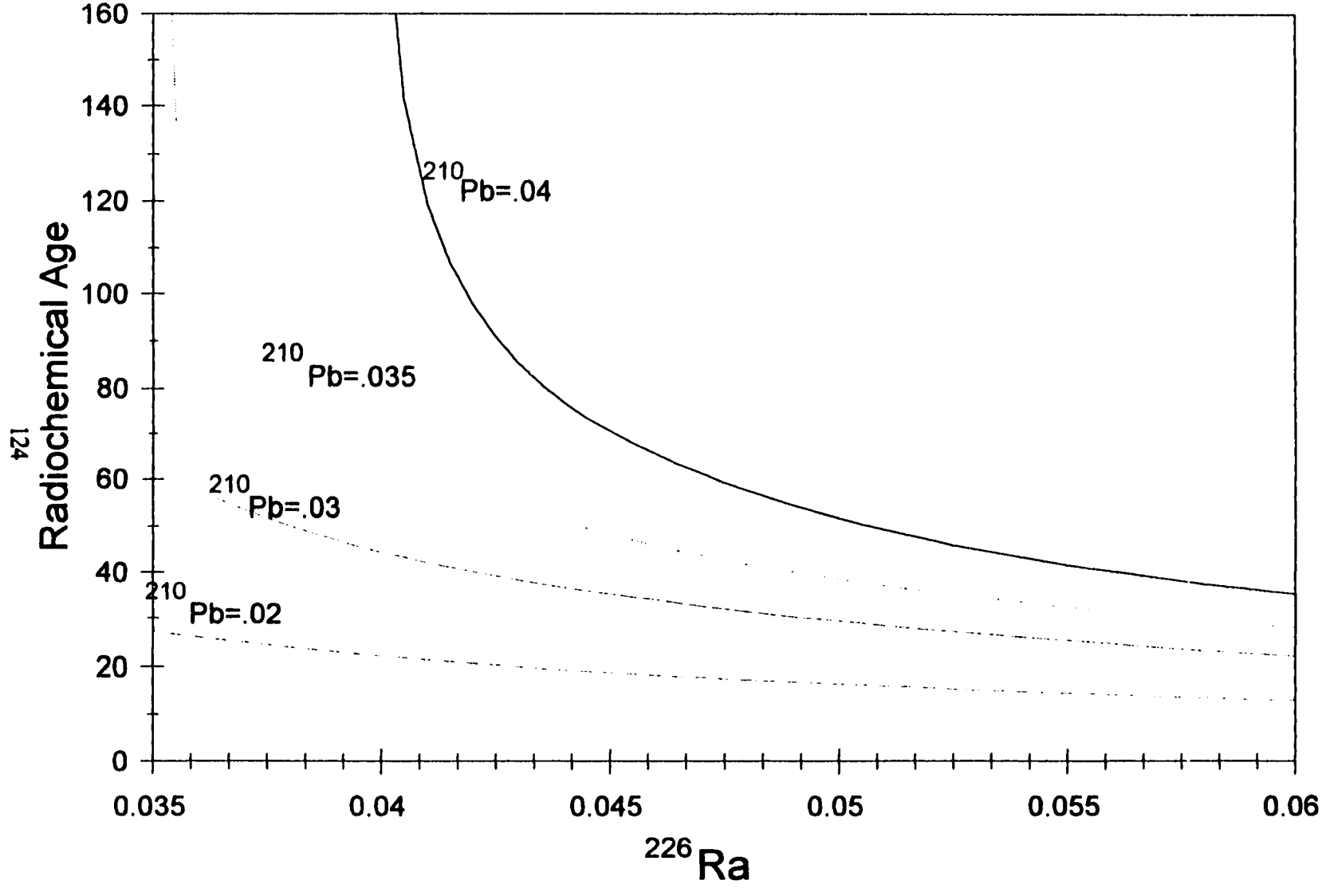

Sebastolobus altivelis
$^{210}Pb/^{226}Ra$
R^0=0.2
R^0=0.1
R^0=0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70
80
90
100
Time (y)

FIGURE 20: Predicted radiochemical age for indicated ^{210}Pb specific activities for a range of ^{226}Ra values. As ^{210}Pb specific activity approaches 75% of the ^{226}Ra specific activity, ageing error increases dramatically. At high ^{210}Pb levels, small variations/errors in ^{226}Ra measurement result in potentially large ageing errors.


160
140
120
100
80
60
40
20
0
Radiochemical Age
124
210Pb=.04
210Pb=.035
210Pb=.03
210Pb=.02
0.035
0.04
0.045
0.05
0.055
0.06
226Ra