LEAD-RADIUM DATING OF TWO DEEP-WATER FISHES FROM THE SOUTHERN HEMISPHERE, PATAGONIAN TOOTHFISH (*DISSOSTICHUS ELEGINOIDES*) AND ORANGE ROUGHY (*HOPLOSTETHUS ATLANTICUS*)

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ABSTRACT

Patagonian toothfish (*Dissostichus eleginoides*) or "Chilean sea bass" support a valuable and controversial fishery, but the life history is little known and longevity estimates range from ~20 to more than 40 or 50 yr. In this study, lead-radium dating provided validated age estimates from juveniles to older adults, supporting the use of otoliths as accurate indicators of age. The oldest age groups were near 30 yr, which provided support for age estimates exceeding 40 or 50 yr from grow zone counts in otolith sections. Hence, scale reading, which rarely exceeds 20 years, has the potential for age underestimation. Lead-radium dating revealed what may be minor differences in age interpretation between two facilities and findings may provide an age-validated opportunity for the CCAMLR Otolith Network to reassess otolith interpretations.

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Orange roughy (*Hoplostethus atlanticus*) support a major deep-sea fishery and stock assessments often depend on age analyses, but lifespan estimates range from ~20 to over 100 yr and validation of growth zone counts remained unresolved. An early application of lead-radium dating supported centenarian ages, but the findings were met with disbelief and some studies have attempted to discredit the technique and the long lifespan. In this study, an improved lead-radium dating technique used smaller samples than previously possible and circumvented assumptions that were previously necessary. Lead-radium dating of otolith cores, the first few years of growth, provided ratios that correlated well with the ingrowth curve. This provided robust support for age estimates from otolith thin sections. Use of radiometric ages as independent age estimates indicated the fish in the oldest group were at least 93 yr. Lead-radium dating has validated a centenarian lifespan for orange roughy.

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To date, radium-226 has been measured in otoliths of 39 fish species ranging from the northern Pacific and Atlantic Oceans to the Southern Ocean. In total, 367 reliable radium-226 measurements were made in 36 studies since the first lead-radium dating study on fish in 1982. The activity of radium-226 measurements ranged over 3 orders of magnitude (<0.001 to >1.0 dpm·g^{-1}). An analysis revealed ontogenetic differences in radium-226 uptake that may be attributed to changes in habitat or diet. Radiometric age from otolith core studies was used to describe a radium-226 uptake time-series for some species, which revealed interesting patterns over long periods. This synopsis provides information on the uptake of radium-226 to otoliths from an environmental perspective, which can be used as a basis for future studies.

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Keywords and phrases: Patagonian toothfish, Chilean sea bass, *Dissostichus eleginoides*, Nototheniidae, orange roughy, *Hoplostethus atlanticus*, Trachichthyidae, deep-sea fishes, deep-water fisheries, age estimation, age validation, longevity, lifespan, age and growth, lead-210, radium-226, lead-radium dating, radiometric dating, radiometry

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I dedicate this dissertation to those that fostered my interest for the natural wonders of this world as a child. My parents always supported my endeavors to discover more about nature through observational science by providing me with my first microscope, binoculars and chemistry set. My mother piqued my interests in nature and field sciences by introducing me to the enjoyment of identifying the kind of animal or plant that was before us. I am a birder for life because of the time we spent together working out the identity of local fauna. My Uncle Frank holds a special place in my history as the one that would always point to the resources that answered the questions I had about science and nature. I remember him showing up at the right time in my life with a telescope to show me the wonders of the universe and him providing me with books, some of which I still have today, that led me to a variety of personal studies as a naturalist and amateur astronomer. It is the broad spectrum of sciences that he introduced me to that has held my interest through to a professional and gratifying career in science and teaching.

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To the depths of sea and space…

Allen Hia Andrews

CHAPTER ONE

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GENERAL INTRODUCTION

One of the most recent technological developments in the science of fish age validation is the lead-radium dating technique. Its use is novel relative to the evolution of age determination of fishes because the chronological relationship is almost completely independent of fish growth characteristics, if the application is applied correctly and in the latest form of the art. For most studies that worked to prove an understanding and accurate quantification of the age and growth of fishes, an observation of some kind of change in the structure of fish with time is required. Validation of age is based on a timely observation of growth that is measureable and translatable into a growth rate, and this observation must be valid through ontogeny. Use of lead-radium dating provides a first opportunity in the history of age validation to determine the age of fish with no observation of growth because lead-radium dating relies solely on the law of radioactive decay. Given a closed system where radium-226 has been taken in and contained, it is certain that with sufficient time lead-210 will begin to appear in a process called ingrowth at a rate that is well defined. Comparable to a clock, the ingrowth of lead-210 from radium-226 functions as a natural chronometer. For fish ear bones, commonly known as otoliths, the structure provides a unique experimental opportunity to use this chronometer in the determination of age for fish where little or nothing is known.

Two well-known fishes were chosen for an application of lead-radium dating to determine age and longevity and to test hypotheses about the validity of procedures used to estimate age. Patagonian toothfish (*Dissostichus eleginoides*) and orange roughy (*Hoplostethus atlanticus*) were chosen as high profile animals that have demonstrated a crucial need for the determination of accurate, age-related life history characteristics because of overexploitation and significant changes to the fisheries. Each species is primarily a resident of the southern hemisphere where fisheries have provided boom-and-bust productivity on regional scales. Each has a history of age and longevity interpretation problems that stemmed from erroneous age estimation procedures, misinterpretation of age validation procedures, and application of age validation techniques that did not provide definitive answers.

1.1 History and importance of fish age validation

Age estimation of fish dates back several centuries with what appears to be the first documented opinion on the use of hard structures for age estimation made by Aristotle in 340-350 B.C. Stated in the context of rather odd statements about the edibility of senescent "old fishes," a translation of *Historia Animalia* revealed that Aristotle reported "The age of a scaly fish may be told by the size and the hardness of its scales" (Gotthelf 2002). It would not be until the late 1600s that any notion of this sort was reported and further investigated. With the advent of the microscope, an unlikely person by the name of Anthonie van Leeuwenhoek, a tradesman of Holland with no higher educational degrees and a deep curiosity for science, improved the optical quality of microscopes that he used. He proceeded to make a long series of microscopic investigations and may have been inspired by Robert Hooke's (1665) *Micrographia*. At some point in his investigations, he turned his microscope to fishes to determine the presence or absence of scales on a couple of fish species. The purpose of the scale investigations is reported as a concern for whether certain fishes could be eaten in a Biblical context; contrary to popular opinion, van Leeuwenhoek found that the skin of an eel (*Anguilla anguilla*) was covered with scales and reported on this relative to the commandment in Deuteronomy and Leviticus that the Jews may not eat fishes that do not have fins and scales.

Upon closer examination of scales, van Leeuwenhoek noticed circular markings in the scales and noted, "altho [sic] all the scales, are not just of the same shape, I have yet observed, in many of them, as I judged, the same number of circular lines. From whence I conclude that every year the scale encreased [sic] one circular line…" (van Leewenhoek 1685). The scale that he investigated was estimated to have come from a fish seven years old based on the ring count, assuming the scale contained a full record of the life of the eel;

however, it is now known that eel scales appear at age three and the eel in this instance may have been 10 to 11 years old (Frost 1945). The finding of this discrepancy, in addition to the great age potential of *Anguilla anguilla* later discovered (e.g. Poole and Reynolds 1998), is perhaps the first instance where age estimation was in need of age validation.

Perhaps the first case of what appeared to be fish age validation was the use of mark-recapture to provide an age to a fabled fish. A northern pike (*Esox lucius*), taken from a lake in Wurttemberg, Germany in 1497, was rumored to have been 19 feet (5.65 to 5.8 m) in length and weighing 350 to 550 pounds (148 to 247 kg) with a story that reportedly verified an age of at least 267 years at the time of its capture (Hederström 1759, Norman 1930, Craig 1995). It was a ring on its gill at capture that was reported to have inscribed upon it that the fish was captured and released by Emperor Frederick II in the year 1230, which led to the name it goes by today, "The Emperor's Pike" (Figure 1-1).

Figure 1-1. The Emperor's Pike, by an unknown artist of the 17th century, is housed at the Natural History Museum, London (NHML). From the placard at NHML, "The inscription reads: This is the biggness of the pike, which the emperor Frederick the second with his own hand, hath put the first time into a poole at Lautern; and hath marked him with this ring in the years 1230. Afterwards hee brought him to Heydelberg the 6 of November 1497. When hee beene in the poole 267 yeares."

The skeleton of this monster was preserved at the Cathedral of Mannheim, was later found to contain vertebrae from a number of fish, and is now known as the Mannheim Hoax; however, in the late 1600s it was this controversial story that fueled the interest and refutation of such a finding by Hans Hederström (Hederström 1759). This interesting story may have led to the first call for age validation in fishes using hard parts.

Hederström (1759) begins his argument of disbelief based in preconceived notions on the hierarchy of living things by stating, "Is it in agreement with the order established within the animal kingdom that nobler and more useful animals should have such a short span of life compared with that of the pike?" He follows, however, with a call for scrutiny and proof of age determination in fishes and posits that the vertebrae provide a means by which to do so. In his studies of ring counting of vertebrae, verification was performed by counting both sides of the same vertebrae as well as other vertebrae from within the same fish. The result of counting rings from vertebrae of a range of fish sizes led him to deduce that the ring count was related to changes in fish length, "… but I have always found the number of rings to be roughly proportionate to the size of the fish."

Hederström (1759) further noted that there was evidence for the loss of age information once a maximum size is reached; he ventured to assume, "… the number of the rings upon the vertebrae indicates the correct age of the fish only as long as it is still growing." He supports this perspective with the observation "[a]nd since presumably fishes, like other animals, can live a long time after they have attained full size, the age of the fish with a maximum number of rings is uncertain." But in properly taking all sides into consideration, he further considers the perceptions of those that would proclaim that fish grow until dead and would therefore always have an accurate representation of age in the vertebral rings. It is with this point that he points to caution and he puts forth the proposition "[w]hat is the truth in this respect can only be decided by experiences and observations which everybody with an opportunity to do so is invited to make."

It is this call for fish age validation that has been missed in many cases over the past several centuries, where improper investigations that made assumptions about age and growth have led to problems with the sustainability of fisheries. Along this line of thinking, it is interesting to note that Hederström further cautioned to those that fish to practice proper stewardship with the knowledge of age and reproduction by saying, "What should be the reason for our unreasonable and indefensible way of fishing, when we catch the fish in spawning time and with the mother kill 1000 lives of which every one [sic] within some years could be as good as the mother? And that we catch small fry of which 10 hardly suffice to still the hunger of one person, but of which one within some years could sate several?"

To place the Hederström (1759) paper in proper historical context for its insight, it should be noted that the article, as submitted by Hederström to the Royal Swedish Academy of Science, was forwarded by the Secretary of the Academy to the celebrated Carolus Linnaeus for review. In his letter recommending publication of the work, Linnaeus further stated "he himself never came to think of this possibility of working out the age of fishes." (Fishery Board of Sweden (1959), footnote in Hederström 1759 translation). It is these fundamental truths that ring true today and point to the importance of fish age validation.

Determination of fish age from scales came in various forms over the next 140 years with captive rearing and other attempts, and successes, to provide a temporal basis for the use of rings or circuli in scales. Some erroneously claimed that with the validation of a few annual rings in scale formation, accurate age could be inferred for all fishes using scales (Pell 1859). Broad application of such findings was further questioned with a reminder that age estimates need species specific validation and that some methods of validation need critical analysis before findings can be applied to all size and age classes (e.g. van Oosten 1923, 1929, 1941). An example of where problems arise is with scales and the first few years of growth; as stated previously for *Anguilla anguilla*, annual growth is not yet manifested as rings until later in life and circuli counts on adult fish required the addition of 3 years (Frost 1945). Similar to this observation, and likely more important in terms of understanding the life history characteristics of long lived fishes, was the determination that scale reading can underestimate age of the largest fish for a given species. In a number of cases, the annual formation of circuli in scales was confirmed for a series of age classes, typically with fish in the period of most rapid growth where scale rings can be easily elucidated. The findings for these years of well-defined growth led to conclusions about the validity of circuli counting for the largest fish; the unrecognized assumption was the extrapolation of the growth pattern to maximum age estimates and the determination of longevity with no accurate age determination for the largest fish. An example of this failed assumption was with whitefish (*Coregonus clupeaformis*), where circuli in scales were validated as accurate indicators of age for early growth, but were later determined to underestimate age by several decades (Barnes and Power 1984).

The shift from scales to otoliths (fish ear bones or ear stones) has been credited to Johannes Reibisch while working for the Commission for the Scientific Investigation of German Seas at Kiel (Jackson 2007), whom was frustrated with the lack of ring visibility in scales of plaice (*Pleuronectes platessa*). A well-illustrated paper was later published on the use of whole otoliths as a structure for age determination (Reibisch 1899). Numerous other studies were pursued with other skeletal structures (e.g. opercula, pectoral girdle, cleithra, and fin rays), many of which are still in use today as validated indicators of age for some species (e.g. Beamish and McFarlane 1987), but the otolith has taken center stage in the development of accurate age and growth parameters. Its use has become widely accepted for its utility and, as a result of its popularity, a namesake series of international symposia was created to share methodological and technological advances associated with otolith research (i.e. International Otolith Research and Application Symposium).

1.2 Modern age validation of fishes

Despite the appeal of otolith time-keeping qualities, it is with otoliths that many problems still exist in terms of invalid assumptions about the accuracy of age interpretations. Many have used a form of otolith age verification by comparing age estimates with those from scales or other hard parts supposedly to "validate" the use of otoliths as an accurate indicator of age. Actual age validation requires a temporal relationship and this was not established. As a result, a number of overexploited fishes have been reevaluated and revealed major discrepancies between age estimation procedures (Beamish 1979). It was revealed that methods like whole otolith ageing or surface ageing and the use of scale reading could provide age estimates that were far less than ages obtained from sectioned or broken and burned otoliths. It was this finding that brought forth once again the concept of age validation and that many researchers were responsible for making invalid assumptions about age estimations (Beamish and McFarlane 1983). Proving the accuracy of age determinations was the "forgotten requirement" and Beamish and McFarlane (1983) pointed to a common problem of relying too heavily on methods that should not have been extrapolated as age validation of the largest fish or applied to other related species. The survey of some 500 published scientific papers discovered that the application of age validation procedures was either being missed or misapplied. The call for validation of fish age estimates some 250 years ago by Hederström (1759) could not be more important in this day and age.

Age validation in fishes has become a science of its own. The development of numerous methods associated with various hard parts from fishes, and technologies to assist with the visualization and refinement of age determinations, has led to numerous age validation techniques (Campana 2001). Some methods rely on establishing a chronological relationship to early growth by measuring changes in otolith zones or fish length (i.e. marginal increment and length frequency analyses); however, these techniques require an extrapolation of the age and growth information to larger fish because of a loss of growth zone or year-class length resolution (Macdonald 1987). This is especially true with long-lived fishes (e.g. Mace et al. 1990, Ewing et al. 2007). Other methods rely on marking and recapturing older fish (e.g. oxytetracycline injection and/or tagging), but the techniques suffer from low returns (Hannah and Matteson 2007) and deep-water, physoclistic fishes usually have problems with survival upon return due to barotrauma. There was little hope for such applications to deep-water fishes until recent developments provided some promise for tagging deep-water species at depth or *in situ.* Use of underwater tagging equipment for captured rockfishes (*Sebastes* spp.) brought up to scuba depths, and off Iceland at submersible depths of around 500–800 m on redfish (*Sebastes mentella*), have shown promise (Starr et al. 2000, Sigurdsson et al. 2006); however, returns are still likely to be low.

A tool for validating the early growth of fishes is the use of daily growth increments (Panella 1971, Campana and Neilson 1985). The technique held promise for making reliable age estimates for tropical fishes where annual growth zones are either not visible or are poorly developed, but care must be taken with the interpretation of results. An example of a refined application to tropical fishes was with age determination for Hawaiian snapper or opakapaka (*Pristipomoides filamentosus*). Early growth was well documented and validated otolith growth rates were successful for the first few years of growth (Ralston and Miyamoto 1983, Radtke 1987, DeMartini et al. 1994), but age for the largest and oldest adults was still in question (Moffitt 2005). Ralston and Miyamoto (1983) developed a relationship called numerical integration of daily increment widths as a model for age prediction from otolith dimensions for larger fish. This led to a maximum reported age within the study of 18 years; however, this age has been treated in some cases as the maximum age for this species (e.g. Manooch III 1987). This was not the intent of the findings. Ralston and Miyamoto (1983) clearly stated, "Extrapolation… may be an unrealistic exercise and growth rates of large fish may in fact be overestimated." Application of the technique to larger fish was: 1) based on assumptions about otolith growth during adult stages; 2) not applied to the largest fish (>70 cm FL for the region); and 3) not adequately tested for the limitations of the technique at great ages (Morales-Nin 1988, Stevenson and Campana 1992).

The words of caution were confirmed for opakapaka with the application of a technique that is one of the most recent to evolve in the science of fish age validation. Advances in the use of both anthropogenic and naturally occurring radioactive proxies for age have proved useful as a means of providing independent age determinations for numerous fishes. The two primary techniques in use are bomb radiocarbon (^{14}C) and lead-radium dating (Panfili et al. 2002). For opakapaka, application of lead-radium dating provided an independent estimate that confirmed a life span significantly greater than suspected. An age of 52 years (42 to 64 years, 2 SE) was determined for a group of 70 - 75 cm FL fish (A.H. Andrews, unpublished data), a result which created more questions than answers for understanding the age structure and life history characteristics of opakapaka.

1.2.1 Bomb radiocarbon dating

Use of the bomb radiocarbon chronometer typically requires a series of individual otoliths for which the birth years, based on standardized growth-zone age estimates, range from a time prior to significant atmospheric testing of thermonuclear devices (pre-1957) to the post-bomb period (after ~1967). This approach utilizes the rise in radiocarbon from atmospheric testing, reported as $\Delta^{14}C$ in reference to a pre-bomb radiocarbon record, as a time specific marker for age validation. It is the agreement of the $\Delta^{14}C$ record from the species with age in question, with a reference $\Delta^{14}C$ time-series that becomes a form of age validation. Hence, the utility of this approach for determining age or lifespan is dependent upon the difference between the collection year and time of first rise in radiocarbon for the reference time series. Application of this technique to fish otoliths began with fishes in the southern hemisphere (Kalish 1993, Kalish 2001), followed by a series of studies in the northern hemisphere (e.g. Campana 1997, Kalish et al. 2001a).

The northeastern Pacific Ocean did not have a reference time series for bomb radiocarbon until two recent applications were made to fish with validated or known age. The first application of the bomb radiocarbon technique to rockfishes was a follow-up study to a lead-radium age validation study on yelloweye rockfish (Andrews et al. 2002). Because yelloweye rockfish could be aged with relatively high precision from otolith growth zone counts (CV = 4%) and lead-radium dating had provided support for the age estimation procedures, a series of yelloweye rockfish otoliths were used to establish a bomb radiocarbon chronometer for the northeastern Pacific Ocean (Kerr et al. 2004). The chronometer established by Kerr et al. (2004) was further corroborated by an independent study of known age juvenile Pacific halibut (*Hippoglossus stenolepis*) from various locations around the Gulf of Alaska (Piner and Wischniowski 2004). These records subsequently provided an independent chronometer for age validation of quillback (*S. maliger*; Kerr et al. 2005), bocaccio (*S. paucispinis*; Andrews et al. 2005), and canary (*S. pinniger*; Andrews et al. 2007) rockfishes. Using a rather basic approach utilizing the time of first rise in ^{14}C as a reference point, it can be said that from each of these rockfish studies that quillback live at least 43 ± 2 years, bocaccio to at least 37 ± 2 years, and canary can live to 44 ± 3 years. Other studies have made similar conclusions. For example, a minimum lifespan of 30 to 38 years was determined for the red snapper (*Lutjanus campechanus*) based on these principles (Baker and Wilson 2001b). In addition, age can also be determined by projecting measured radiocarbon levels back to a reference time series (Campana 1997, Andrews et al. 2005) or a series of samples with different collection years and ages can be selected to validate age estimation procedures for a range of age classes younger than the minimum lifespan (Piner and Wischniowski 2004). The latest approach has been an investigation of determining age estimation bias based on the offset of the data from the region of the rise in radiocarbon (Stewart and Piner 2007) and better describing the variability of the radiocarbon rise to better quantify the confidence in age estimates relative to the curve (Kastelle et al. 2008).

In most cases, the utility of this technique is limited to the otolith material that formed in the near surface waters, a region of the ocean that is well mixed with the atmosphere. Many fishes have an ontogenetic migration from shallow water to deep water; therefore, the material laid down in the otolith from life in deep water may not contain the bomb radiocarbon signal. This was demonstrated as a problem for deep-water fishes, and specific to the line of work presented here, there were problems with an application to orange roughy (*Hoplostethus atlanticus*) and Patagonian toothfish (*Dissostichus eleginoides*; Kalish 2001). This information is discussed in their respective chapters.

1.2.2 Lead-radium dating

Lead-radium dating is a geochronological technique that was used to date recent geological formations, such as igneous rock and accretionary carbonates (e.g. Condominesa and Rihs 2006). Use of this system as a chronometer relies on the decay of the relatively long-lived radioisotope radium-226 (^{226}Ra) to the relatively short-lived granddaughter product lead-210 (^{210}Pb). Because the half-life of radium-226 is much greater (1600 years) than lead-210 (22.26 years) the disequilibrium of the lead-radium system can function as a natural chronometer as lead-210 builds into equilibrium with radium-226. Once radium-226 is incorporated and isolated by some kind of structure (e.g. crystalline lattice), it is the ingrowth of lead-210 activity relative to radium-226 activity that provides a measure of time. In an ideal system there would be no exogenous source of lead-210 and the lead-radium ratio would increase purely from ingrowth. This ingrowth would exponentially approach a ratio of one, at which time the rate of lead-210 decay would be equal to the rate of lead-210 ingrowth from radium-226 (Figure 1-2).

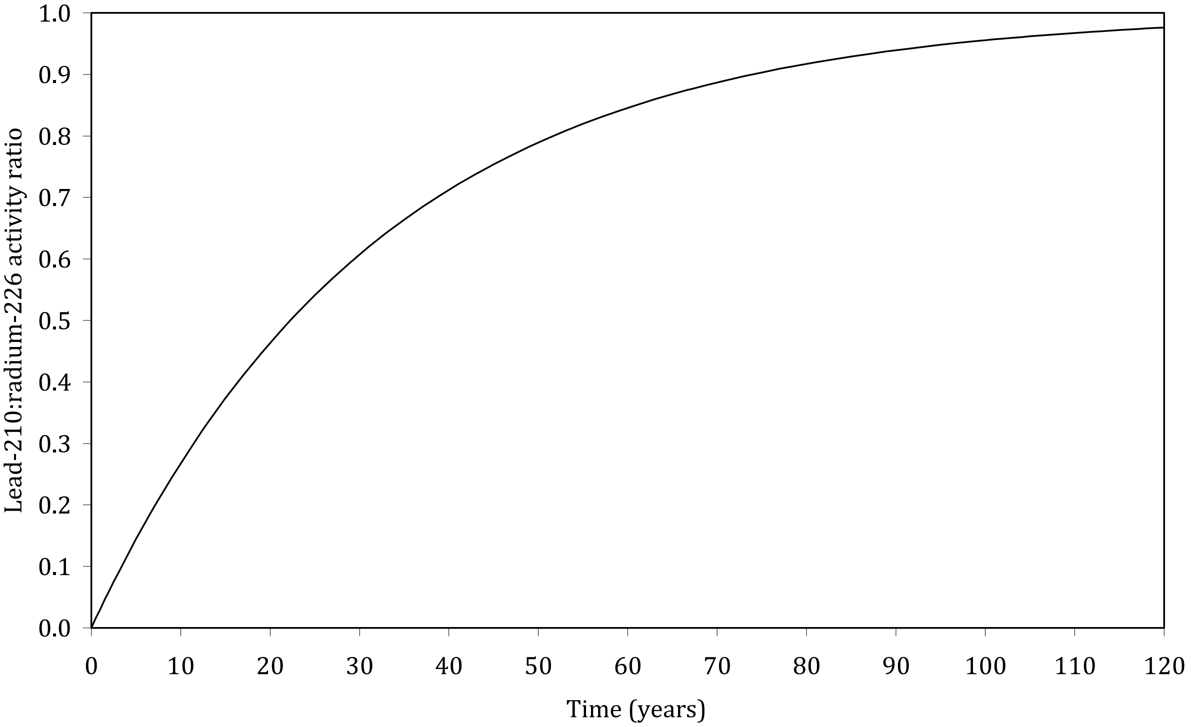

Figure 1-2. Ingrowth of lead-210 from radium-226 plotted over a period of 120 years, where the activity ratio approaches secular equilibrium or a ratio of 1.0.

This dynamic equilibrium is called secular equilibrium and is achieved to within 1% in a period of 156 years or 7 lead-210 half-lives. For fishes, lead-radium dating depends on the incorporation of naturally occurring radium-226 from the environment, where it is locked into the otolith matrix, and subsequently decays to lead-210. The otolith lead-radium system can be used as an independent estimate of age, as well as a form of age validation for age estimation methodologies (Smith et al. 1991, Panfili et al. 2002).

1.2.2.1 Background to lead-radium dating of fishes

The first application of this technique to fishes was performed on otoliths from redfish (*Sebastes diploproa*), a deep-water member of the family Scorpaenidae, from the Northwest Pacific Ocean (Bennett et al. 1982). In this study, it was necessary to: 1) pool whole otoliths for measurable lead-radium activities; 2) develop an otolith mass growth model to compensate for the lead-210:radium-226 ingrowth gradient that would exist from the core, the oldest material, to the exterior or youngest part of the otolith; 3) assume that uptake of radium-226 was constant relative to mass growth of the otolith; and 4) that the otolith remains closed to losses or gains of the lead-radium decay series. The requirements and assumptions necessary in this study were because of methodological limitations that have become more refined since this seminal application of lead-radium dating to fishes. Part of the reason for pooling whole otoliths was because of the detection limits of the radon emanation method for the determination of radium-226 activity (Mathieu 1977). Radium-226 activities were measured with relatively low precision for samples that were close to 1 g (range of 14% to 21% error, 1 sigma). Provided the assumptions stated above were valid, ages on the order of 80 years were supported over 20-30 year estimates from the whole otolith ring counting method. These findings provided the first indirect validation of the major discrepancy discovered with the transverse break and burn method on Pacific ocean perch (*S. alutus*) otoliths (Beamish 1979), assuming the otolith interpretation method could be applied to its congener.

A method that circumvented some of the problems associated with the circularity of developing a mass growth model was the use of extracted otolith core material for the determination of lead-210 activity (Campana et al. 1990). With this approach, compensation for the lead-210:radium-226 gradient was not necessary, except in the small portion of core material where the first few years of ingrowth were measured collectively. Eliminating the need for a mass growth model throughout the growth of the otolith reduced the uncertainties of lead-radium dating and provided a basis for increased confidence in its application to otoliths, but added another factor; numerous otolith cores were necessary from a given age group to provide measurable polonium-210 activity (used as a proxy for lead-210 in alpha-spectrometry). In this case, it was necessary to use 21 to 28 otolith cores for each age group, which was not previously a problem for older adults with large otoliths. The findings of the study provided an age validation of the break and burn method over whole otolith age estimates and supported a life span on the order of 65 to 75 years. In addition, the conformity of the measured lead-radium values from the age groups (ranging from 10 - 15 years to 60+ years) to the ingrowth curve provided additional support for the age estimation method through ontogeny.

Perhaps the most significant weakness that persisted with the improved approach introduced by Campana et al. (1990) was the necessity of determining radium-226 activity from massive, whole otolith samples. In the study, an average radium-226 activity was measured using the radon emanation method on five whole otolith samples (~13 g each) using radon emanation. A determination of radium-226 activity was made for each of the pooled otolith core samples, but imprecision and no significant differences relative to the larger and more precise measurements on whole otolith samples was cited as the reason for using an average radium-226 activity from the 5 whole otolith samples. Radium-226 activity was not reported from the individual samples, but an average value with a 6% error (1 sigma) was used to determine the lead-radium ratios. It is the necessary assumption that uptake of radium-226 is relatively constant throughout the formation of the otolith that continued to be a potential problem.

The potential problem of inconsistent uptake of radium-226 was exemplified in a study of blue grenadier (*Macruronus novaezelandiae*) otoliths (Fenton et al. 1990). It was determined from a series of whole otolith samples that uptake of radium-226 was more than 10 times greater in juvenile otoliths when compared to older adults, which was attributed to either habitat or metabolic affects. The blue grenadier is known to migrate from inshore/estuarine waters to deep water with increasing age, which could account for variation in uptake because some nearshore waters are known to contain higher levels of radium-226 (e.g. Hancock et al. 2000, Moore 2007). Because of this factor, age validation using lead-radium dating was deemed inconclusive, but values of radium-226 activity were determined using an alternate method, direct alpha-spectrometry. The limitations of this technique were represented by high error (range of 10% to 100% error for 1 sigma) from low sample sizes (~1 g each); the lowest error was associated with youngest age groups (7 to 30 whole otoliths) in which radium-226 activities were highest. A follow up study using otolith cores confirmed ontogenetic changes in radium-226 uptake, but provided marginal age determinations because of the high degree of uncertainty associated with the radium-226 assays (Fenton and Short 1995).

To address the question of variable radium-226 uptake and potentially verify consistency, a study on shortspine and longspine thornyhead rockfishes (*Sebastolobus alascanus* and *S. altivelis*) determined radium-226 activity from a series of low weight to high weight whole otoliths (presumably youngest to oldest) for *S. altivelis* (Kline 1996, Cailliet et al. 2001). Radium-226 activities were found to be relatively constant for this species, but a low number of otoliths precluded this kind of analysis for *S. alascanus*. In both cases it was necessary to pool very large numbers of whole otoliths to decrease the analytical uncertainty of radium-226 determination using the radon emanation method, with sample masses ranging from 10.6 to 30.6 g. Even though precision improved (range of 4% to 11% for 1 SE) the constant uptake assumption could not be directly addressed. Given the assumptions were met in this study, lead-radium dating of numerous age classes provided support for age estimates and age estimation procedures up to approximately 40 years for *S. altivelis* and up to approximately 80 years for *S. alascanus*.

Application of lead-radium dating to orange roughy was the first to provide independent radiometric support for a centenarian lifespan in fishes (Fenton et al. 1991). The study did not perform any growth zone derived age estimations, but instead sought independently to determine age for groups of fish with similar length and otolith weight. Whole otoliths were used for both lead-210 and radium-226 determinations and the number of otoliths ranged from 135 for the smallest length group to two or four for the largest length groups. The groups of otoliths were each used for an independent determination of lead-210 (via polonium-210), but a pooling of five groups ("younger group") and seven groups ("older group") was necessary to increase precision of radium-226 determinations. Each group (*ca*. 5.7 and 7.1 g sample weights, respectively) resulted in relatively consistent activities with an improved margin of error relative to the blue grenadier study (4.8% and 6.8% for 1 sigma). Although the precision of radium-226 determination was improved, the assumption of consistent radium-226 uptake remained a factor with potential implications. Because of the technological limitations at the time and the small size of juvenile orange roughy otoliths, application of lead-radium dating to whole otoliths for both lead-210 and radium-226 made it was necessary once again to apply a mass-growth model to account for the lead-radium gradient. In addition, all of the other assumptions remained and were largely unaddressed.

1.2.2.2 Lead-radium dating – improved application and its limitations

Increased sensitivity in the methods used to determine radium-226 activity has made it possible to reduce the sample size necessary to detect radium-226 in otolith material with increased precision and accuracy (Andrews et al. 1999b). As a result, the first few years of growth can now be extracted from the core of otoliths and analyzed for both lead-210 and radium-226; hence, there is no need for sample weight dependence in calculating age, nor the assumption that radium-226 uptake was constant (Andrews et al. 1999a, Campana 2001). In addition, advances in mass spectrometry have significantly reduced the error and processing time associated with the measurement of radium-226; hence, the determination of radium-226 is no longer the source of limitations and previously necessary assumptions. It is the determination of lead-210 activity (via alpha-spectrometry of polonium-210 by proxy) that has become the limiting factor for lead-radium dating (Andrews et al. 1999b). By using core material (the first few years of growth) for the measurement of both lead-210 and radium-226 activities from the same small sample, the problems associated with mass growth assumptions or variable uptake of radium-226 were largely circumvented (Kimura and Kastelle 1995). Even large differences in uptake during the earliest growth would have had little impact on radiometric age. Worst case scenario would be an offset of just a few years for cores of a few years because of the core-age compensated ingrowth curve (the assumption is the core has a relatively constant uptake of radium-226 relative to mass growth).

This technique works well as a tool for determining the validity of age interpretations that differ considerably, but its application is limited by relatively low age resolution from either 1) low lead-radium activity or 2) ages that approach the asymptotic portion of the ingrowth curve (approaching 100 years). The typical end result for this kind of study is that it provides 1) support for one age estimation technique over another and 2) an independent estimate of minimum lifespan.

An example of this kind of application was with age estimate comparisons for Pacific grenadier (*Coryphaenoides acrolepis*) in which age estimates for full sized fish ranged from six to greater than 60 years. Age estimated from scale ring counts were the source of six-year longevity estimates (Kulikova 1957), while a series of other studies using scales, vertebrae, and whole otoliths ranged up to 25 years (Brothers et al. 1976, Mulcahey et al. 1979, Wilson 1982). The most recent study using a simple transverse view (break-and-burn) of the otolith provided age estimates that exceeded 60 years (Matsui et al. 1990). Amongst these studies, lead-radium dating provided strong support for the break and burn method with a minimum radiometric age of 48 years (Andrews et al. 1999a). It can be concluded from the findings that Pacific grenadier age was underestimated by a factor of about 10 from scales and a factor of at least two with the other methods; age estimates using the break-and-burn method, coupled with an independent age estimation study using transverse sectioning (Andrews et al. 1999a), were the only methods supported by lead-radium dating. The findings provided a basis for refining the best age estimation method, but did not provide true age for any given fish. What can be concluded from the Pacific grenadier study is: 1) the lifespan is at least 48 years; 2) transverse views of the otoliths provide estimates that are suitable for accurate age determination and; 3) age was underestimated by the other techniques.

1.2.2.3 Lead-radium dating – factors affecting sample design

A couple of factors that are often misunderstood are the effects of radium-226 activity and sample size on radiometric age resolution. Campana (2001) cites an age precision of 25 to 50% as a general guideline, but this precision is occasionally misinterpreted as the minimum. Because radium-226 levels vary considerably between and often within species, and otolith mass growth is highly variable between species, the precision of lead-radium dating cannot be simply quantified. The factors that most seriously affect the application of lead-radium dating are the activity of radium-226 and the mass of the otolith within the first few years of growth. Simply put, the continuum of possibilities range from otoliths that are too small for extraction of core material (first few years of growth) combined with low radium-226, to large otoliths with high radium-226 activity. In addition, the estimated age must be taken into consideration because it is the ingrowth of lead-210 that is the limiting factor with the improved technique.

Small fish otoliths are probably the most common problem, which reduces the utility or precludes use of lead-radium dating. An example of this can be had from a pilot study that was performed with the blue mackerel (*Scomber australasicus*; Andrews 2008a). Otoliths from this species average 0.006 g for the smallest and youngest fish (estimated ages of 0-5 years old). Coring the first few years from adult otoliths would be a significant technical challenge and gathering enough material for measureable lead-radium data (assuming typical activity levels) would likely require close to 100 individuals. Hence, otolith mass-growth modeling was necessary to provide an opportunity for lead-radium dating. In a borderline application of lead-radium dating to the small otoliths of lookdown dory (*Cyttus traversi*), otolith cores were extracted using a micromilling machine (Tracey et al. 2007a). Two of the three age groups in this feasibility study were adult groups weighing approximately 0.22 g each and consisting of a remarkable 45 to 46 extracted cores for an average core mass of only 0.005 g.

The application of lead-radium dating to blue mackerel was based in the optimistic position that radium-226 activities would be higher than usual. However, the measured radium-226 activities were about average. The precision for radium-226 determinations was fairly high at approximately 3 to 5% (2 SE), but the results were inconclusive because the corresponding lead-210 determinations resulted in activity that was very low and near background levels; as a consequence, a high margin of error was determined (greater than 60%). The results from this scenario could not rule out whether the oldest age group (23 – 35 year group with an average estimated age of 26 years) was 26 years or younger, but could eliminate the possibility that the age of the group was much older than 26 yr; lead-210 activity would have become measurable and differentiable from background at about 50 years based on the measured radium-226 activity and sample mass.

In the case of bocaccio rockfish, otoliths from juveniles were much larger than other rockfishes and the first three years of growth amounted to approximately 0.11 g (Andrews et al. 2005). Given an approximate radium-226 activity based on other rockfish studies, there was optimism for an application of lead-radium dating to this difficult to age species. In the end, however, this species had some of the lowest radium-226 activities recorded with a range of 0.00871 to 0.0148 ± 1.5% dpm·g^{-1} (1 SE). Otolith groups consisted of 10 to 20 otolith cores, but the resultant lead-210 activity was almost too low to provide meaningful age estimates for the otolith groups. The result was that bocaccio could attain an age of at least 31 years based on the margin of measurement uncertainty.

An example of the other extreme for otolith size and lead-radium activity was with an application to both Atlantic tarpon (*Megalops atlanicus*; Andrews et al. 2001) and black cardinalfish (*Epigonus telescopus*; Andrews and Tracey 2007). In both cases the otolith material for juvenile fish was quite large and an analysis of the radium-226 activity provided higher activities than has been usual in the literature. For black cardinalfish, otoliths from juvenile fish were on the large end of the spectrum (approximately 0.1 g) and radium-226 activities reached relatively high levels (up to 0.179 ± 2.1% dpm·g^{-1}). For this study it was necessary to pool a small number of otoliths (7 to 12 otolith cores) for activities that were measured with relatively high precision. Atlantic tarpon otoliths had some of the highest radium-226 activities reported (up to 0.401 ± 1% dpm·g^{-1}) with rapid otolith growth for the first two years (approximately 0.1 g). These parameters made an accurate extraction feasible for the first two years of growth, leading to an unprecedented application of lead-radium dating to individual fish.

1.3 Research focus and thesis outline

The primary goal of this study was to apply lead-radium dating to two deep-water Southern Ocean fishes, namely orange roughy and Patagonian toothfish, to answer questions about age and growth. It is hypothesized that application of lead-radium dating to these fishes will provide age determinations that will support one age estimation scenario over another, precluding further consideration of inaccurate scenarios that differ by many years (e.g. decades). The overall hypothesis for this study is the following: Will the observations of slow growth and high longevity for orange roughy and Patagonian toothfish populations in the natural environment be supported by lead-radium dating?

Sub-hypotheses for Patagonian toothfish were:

1) Will age estimations made from otolith cross sections agree with age determined from measured lead-radium ratios by testing a series of replicated age groups (youngest to oldest)?

2) What will the minimum longevity be for Patagonian toothfish based on lead-radium dating of the oldest age group?

3) Can a critical analysis of other age estimation techniques be used to resolve questions about age estimate disparities (maximum age of approximately 20 years vs. more than 50 years)?

Sub-Hypotheses for orange roughy were:

1) Will age estimations made from otolith cross sections agree with age determined from measured lead-radium ratios by testing a series of age groups (youngest to oldest)?

2) What will the minimum longevity be for orange roughy based on the lead-radium dating of the oldest age group and can concerns about a wide disparity in estimated lifespan (approximately 30 years vs. more than 100 years) be put to rest?

3) Can a critical analysis of these findings, relative to other lead-radium dating discussions that have cast doubt on the technique, be used to provide support for the efficacy of lead-radium dating as tool for age determination in fishes?

This dissertation is divided into six chapters. The focus of the study is presented in the context of the history and importance of fish age validation studies, with a review of radiometric techniques focusing on lead-radium dating, were provided in this chapter (Chapter One). Chapter Two provides a brief description of the fishes studied in this dissertation and the general methodological and equipment details that were common between the two applications of lead-radium dating. Chapter Three and Chapter Four are full scientific papers on the application of lead-radium dating to each species with an analysis of the results: Chapter Three is entitled "Lead-radium dating of Patagonian toothfish (*Dissostichus eleginoides*), a long-lived denizen of deep southern oceans," and Chapter Four is entitled "Lead-radium dating of orange roughy (*Hoplostethus atlanticus*): validation of a centenarian lifespan." Chapter Five is an extensive research review and a first-look analysis of radium-226 in otoliths for all known studies to date. Chapter Six is a closing synopsis covering some recent insights on the life history of fishes and the importance of age-validated longevity.

CHAPTER TWO

✵

FISHES STUDIED AND GENERAL METHODS AND MATERIALS

In this section the two species examined using lead-radium dating, orange roughy and Patagonian toothfish, will be discussed briefly with the methodological and equipment details that were common between the two lead-radium dating applications. Only the details and circumstances that differ for the approach used for each species are specified in the methods sections of the respective chapters dealing with Patagonian toothfish (Chapter 3) and orange roughy (Chapter 4).

2.1. Patagonian toothfish

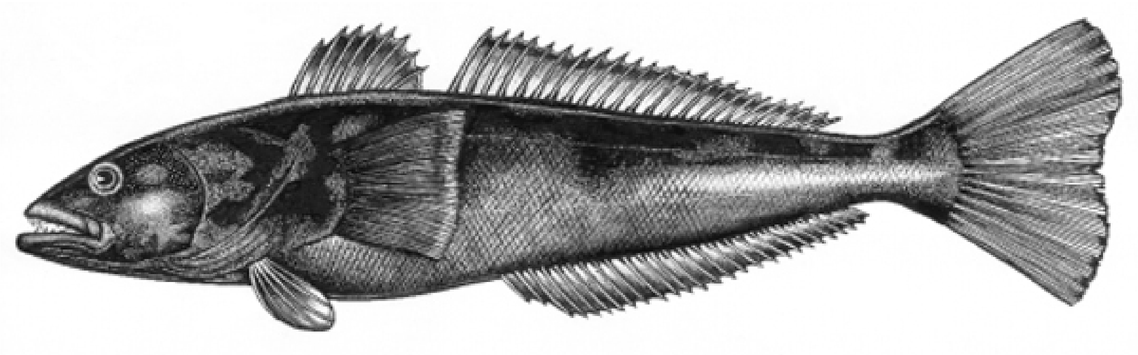

Figure 2-1. Illustration of Patagonian toothfish (*Dissostichus eleginoides*)

Bruce Mahalski (TRAFFIC)

Patagonian toothfish (*Dissostichus eleginoides*, Smitt 1898) is classified as members of the Family Nototheniidae, or cod icefishes, under the perciform suborder Notothenioidei (Figure 2-1; Dewitt et al. 1990). Notothenioid fishes are one of the most specious groups in the Southern Ocean, occupying principally benthic habitats, lacking swim bladders and feeding on the substrate (Eastman 1993). Specialized buoyancy adaptations allow the toothfishes, largest of the notothenioids, to inhabit the midwater as the largest piscine predators (Eastman 1985). Neutral buoyancy is achieved through density reduction with reduced scale and skeletal mineralization and muscular and subcutaneous lipid deposition (Eastman 1993). For the Patagonian toothfish, its distribution is typically confined to sub-Antarctic waters north of 55-60°S because of low temperatures south of the Antarctic convergence and its lack of antifreeze glycopeptides (Eastman 1990, Eastman 1993; Figure 2-2). They inhabit deep water with an ontogenetic movement from shelf to deep slope regions of Southern Ocean islands, seamounts and ridges at depths ranging from 50 to 3,850 m (Duhamel 1993, Miller 1993). It ranges furthest north on the continental slopes of South America along Chile to 20°S, and to Uruguay along Argentine Patagonia to 35°S, as well as island and seamount groups of the southern Indian Ocean (Yukhov 1972, Dewitt et al. 1990, Eastman 1993).

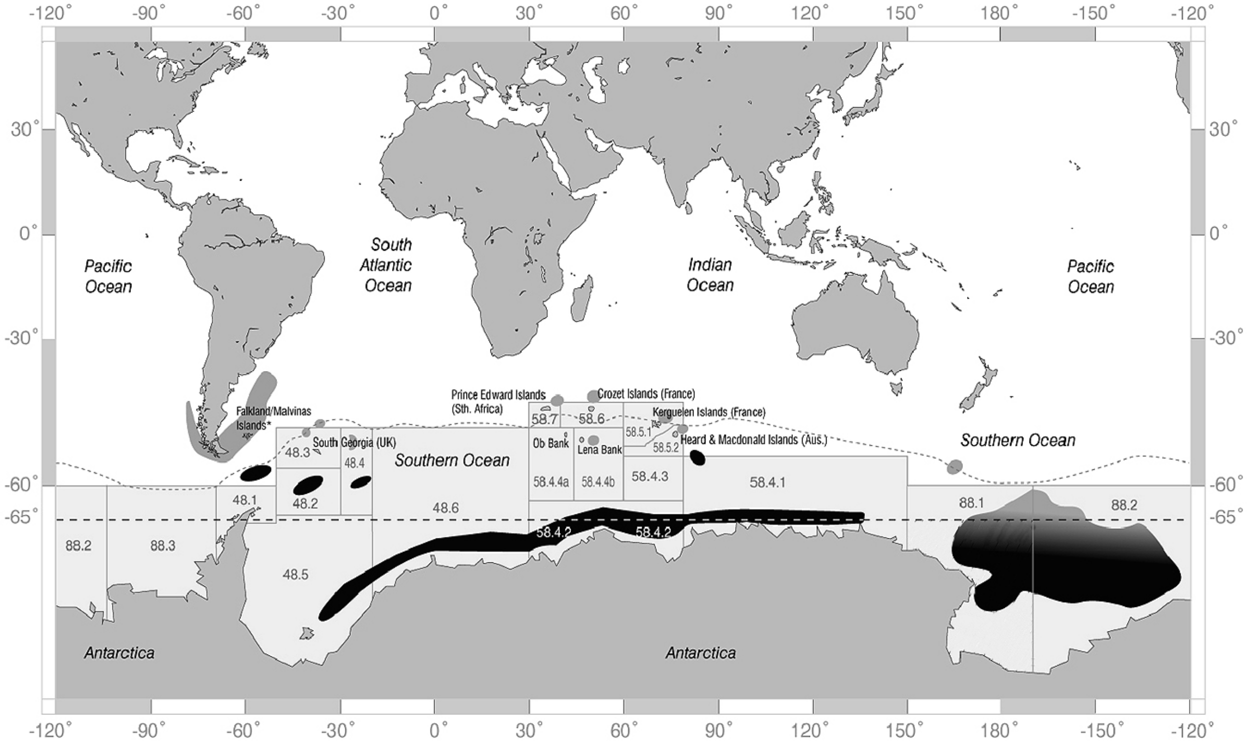

Figure 2-2. Approximate distribution of Patagonian (grey oceanic regions) and Antarctic (black oceanic regions) toothfishes (*Dissostichus eleginoides* and *D. mawsoni*). The knowledge of the distribution of each species is constantly changing as exploration for new fishing grounds progresses through the Southern Ocean (Watson et al. 2007). Many of the island slopes and ridges labeled here have considerably greater distributions. The dashed line is an approximate indication of where the Antarctic Convergence is located in the Southern Ocean. Shaded and numbered regions are CCAMLR Convention fishing areas and subareas. The map was sourced from Lack and Sant (2001) and a Briefing Document by TRAFFIC and WWF (October 2002).

Patagonian toothfish appear to spawn in deep water between May and September, but results are variable from region to region (Duhamel 1981, Evseenko et al. 1995, Agnew et al. 1999, Everson and Murray 1999). They produce large yolky eggs (~4 - 5 mm in diameter) that are dispersed to the pelagic environment and float in midwaters for up to three months (Evseenko et al. 1995). Fecundity ranges from approximately 50,000 to 500,000 eggs per individual and has been shown to increase with fish size and weight (Chikov and Melnikov 1990). Larvae that require more than a year to fully develop (Kock and Kellerman 1991, Everson et al. 1996), and juveniles are believed to remain pelagic for an additional year until they reach 15 - 20 cm TL (Des Clers et al. 1996). Patagonian toothfish appear to grow quickly to lengths near 75 - 100 cm TL in an estimated 6 - 12 years, at which time growth slows significantly with the onset of sexual maturity (Everson and Murray 1999, Horn 2002).

2.2 Orange roughy

Figure 2-3. Photograph of orange roughy (*Hoplostethus atlanticus*)

A. Blacklock (NIWA)

Orange roughy (*Hoplostethus atlanticus*, Collett 1889) is member of and odd group of fishes under the order Beryciformes (Figure 2-3). This group of marine fishes is covered by seven families, of which orange roughy is a member of Trachichthyidae, commonly known from various parts of the world as slimeheads or roughies (Nelson 2006). Orange roughy is probably best known from the southern hemisphere because of its well developed fisheries off New Zealand and Australia, but also well known in the Northern Atlantic (Figure 2-4). More recent fisheries have developed in various parts of the world with the discovery of orange roughy populations associated with slopes, seamounts and ridges off southern Africa and throughout the northern fringe of the Southern Ocean (Clark et al. 2007, Watson et al. 2007). Orange roughy is an opportunistic predator of temperate deep waters with a depth distribution ranging from approximately 180 m to over 1,800 m (Rosecchi et al. 1988, Sissenwine and Mace 2007). Temperature is thought to be an important factor in its distribution for some regions, but the range worldwide, especially in the northern Atlantic, is considerable (2°C to 11.2°C; Branch 2001, Lowrance et al. 2002, Kulka et al. 2003). A centralized depth distribution of spawning aggregations that is exploited by fisheries around the world lies between approximately 600 and 1,200 m for most of its distribution (Branch 2001).

Spawning is synchronous and for short periods in mid-winter in both hemispheres (Pankhurst 1988, Minto and Nolan 2006). Orange roughy produce large eggs (~2 mm) that are briefly planktonic and hatch near the bottom after 10 days, but little is known about juveniles. (Mace et al. 1990, Zeldis et al. 1995). Fecundity ranges between approximately 30,000 and 90,000 eggs per individual for the southern hemisphere, but has been recorded as high as 385,000 eggs per individual in the northeastern Atlantic (Pankhurst and Conroy 1987, Branch 2001, Minto and Nolan 2006). While Koslow et al. (1995) observed a decrease in fecundity after an estimated 60 years, Minto and Nolan (2006) determined that fecundity increased with age with a maximum at 122 years. Orange roughy grow slowly and reach sexual maturity at lengths near 30 - 40 cm SL in an estimated 22 - 40 years (Horn et al. 1998, Branch 2001).

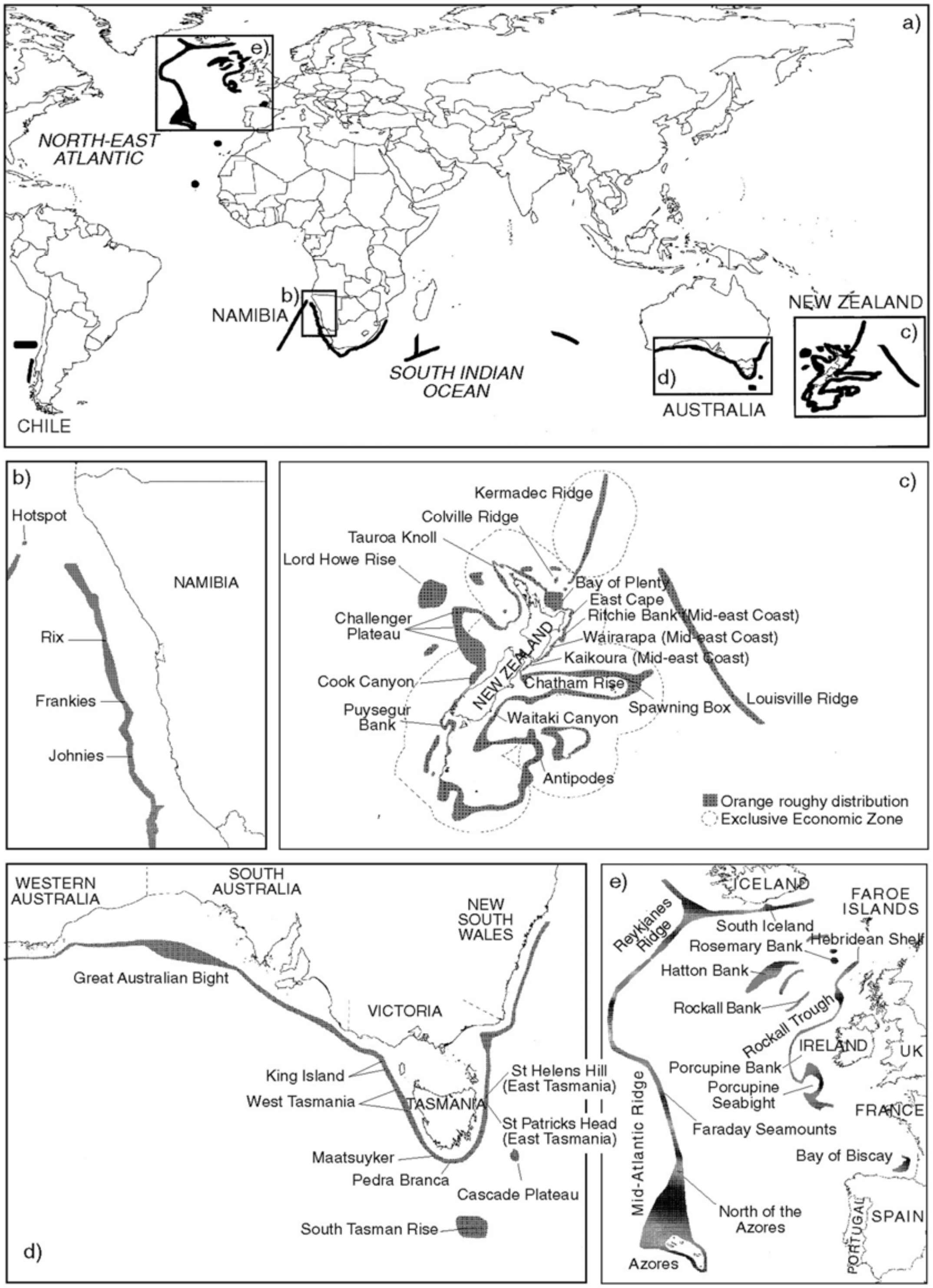

Figure 2-4. Shaded regions indicate the known and potential distribution of orange roughy from fisheries data, collections, and habitat-based estimations a) worldwide, with regional distributions for waters off b) Namibia, c) New Zealand, d) Australia, and e) in the Northeastern Atlantic. Map from Branch (2001) with permission to reproduce by T. Branch (University of Washington, Seattle, Washington, USA; personal communication).

2.3 Otolith preparation and treatment

The extraction of otolith core material differed considerably between the orange roughy study and the Patagonian toothfish study because of differences in otolith geometry. The details of core extractions are described in the methods section for each species in their respective chapters.

Trace-metal precautions were taken during sample cleaning and processing because naturally occurring levels of radium-226 and lead-210 found in otoliths are extremely low. Because the levels range from femtogram (10^{-15} g) for radium-226 to attogram (10^{-18} g) quantities for lead-210, there was a high potential for contamination from various sources. Contamination from lead-210 and polonium-210 were of primary concern because these isotopes are common in the environment. Acids used in the radiometric procedures were ultrapure, double distilled acid (GFS Chemicals®) and dilutions were performed using Millipore® filtered Milli-Q water (18 MΩ cm^{-1}).

Otolith samples were cleaned, dried, and weighed before dissolution in the following manner. Rough cleaning began with hydrating the otoliths in de-ionized water for several hours. Samples were rough cleaned first. Each was agitated by hand and rinsed three times with each of the following: (*i*) a mixture of de-ionized water and Micro® laboratory cleaner, (*ii*) de-ionized water, and (*iii*) Milli-Q water. Fine cleaning was performed by making sequential steps between agitation in four cleaning solutions with a Branson 2200 sonicator and a triple rinse with MQ water. The four cleaning solutions with agitation times were (*i*) Milli-Q water (10 min), (*ii*) 0.15 N HNO_3 (1 min), (*iii*) basic 1:1 mixture of 30% H_2O_2:0.4 N NaOH (10 min), (*iv*) Milli-Q water (10 min), and (*iv*) 0.15 N HNO_3 (3 times at 1 min). After the final rinse, samples were dried to constant weight overnight in an oven at 80°C, cooled in a desiccator, and weighed to ±0.0001 g. Dried and weighed samples were placed in acid-cleaned 100 mL Teflon® PFA griffin beakers. While on a hot plate at 80°C, 8 N HNO_3 was added dropwise to the otoliths in 0.5 - 1.0 mL aliquots until dissolved. The dissolved sample was dried, redissolved with 1 mL of 8 N HNO_3, and dried again. These steps were repeated 3 - 5 times. Before drying the fifth dissolution completely, 0.5 - 1 mL of 6 N HCl was added to form an aqua regia solution. This solution was dried, redissolved with 1 mL 6 N HCl, and dried again. Dissolution in 0.5 - 1 mL of 6 N HCl was repeated 5 times, which left the final sample in the desired chloride form. The repeated drying and dissolution enhanced the oxidation of otolin, an organic that may interfere with column chromatography or mass spectrometry.

2.3.1 Lead-210 determination

Lead-210 measurement from the dissolved sample was accomplished by daughter proxy with polonium-210. Under specific circumstances polonium-210 will auto-deposit from solution to silver for measurement using α-spectrometry (Flynn 1968). To ensure that all of the polonium-210 activity was the result of ingrowth from lead-210 and that secular equilibrium was achieved, all of the samples chosen had been collected many years prior to processing. Samples prepared for polonium-210 analysis were spiked with a yield tracer of polonium-208/209, which had been calibrated against NBS and geological standards. Spiked samples were dissolved in approximately 50 mL of 0.5N HCl on a hot plate (90°C). The polonium-210 and polonium-208/209 tracer were simultaneously auto-deposited onto a purified silver planchet (99.999%, A.F. Murphy Die and Machine Co.) held in a rotating Teflon holder over a 3-4 hour period (Flynn 1968). Silver planchets were analyzed for polonium activity using both ion implant detectors in either Ortec Octete® or Tennelec® TC 256 alpha-spectrometers. Counts were collected with a PC computer, interfaced with the alpha spectrometers via an Ethernet connection, with Maestro-32 software. The unknown polonium-210 sample activity of was calculated using basic isotope dilution principles. The error reported for these measurements represented those propagated for all known sources (pipetting error, yield-tracer uncertainty, etc.) and included basic count statistics (Wang et al. 1975). The sample remaining after polonium auto-deposition was dried and used for radium-226 analysis.

2.3.2 Radium-226 purification and determination

The separation of radium from calcium and barium is an important part of obtaining good radium ionization efficiency during thermal ionization mass spectrometry (TIMS). Because determination of radium via TIMS was prone to ionization suppression from interfering quantities of calcium and barium, use of inductively coupled plasma mass spectrometry (ICPMS) has been investigated. Since the development of this procedure, improvements in ICPMS have led to the use of multi-collector ICP-MS for the determination of radium-226 (Craig Lundstrom, University of Illinois-Urbana Champaign, personal communication). The margin of error with ICP-MS was slightly greater than TIMS, but the advantage was that the potential problem with signal suppression was no longer an issue.

Purification of radium from sample material was achieved by applying a three column, ion-exchange separation procedure (Andrews et al. 1999b). Elution characteristics for each column separation were determined using otolith samples and calcium and barium standards, where the collection intervals were previously optimized using flame atomic absorption spectrophotometry (commonly known as “flame AA”). Solid/solute distribution coefficients provided by the chromatography resin manufacturer were used to determine the acid strength necessary to achieve the greatest separation between radium, barium, and calcium. Based on these findings, an optimized ion-exchange separation procedure was developed and was quantified in Andrews et al. (1999b).

To determine radium-226 using isotope-dilution ICP-MS, the dissolved otolith sample was spiked gravimetrically with a radium-228 yield tracer. The radium-228 solution was prepared by separating radium-228 from its parent thorium-232 at University of California, Santa Cruz (Frank Tepley, Geological Sciences, University of California, Santa Cruz, personal communication). The yield tracer atomic ratio for radium-228 to radium-226 in solution was 0.72905 ± 0.227% (2 SE) as of April 1, 2004. The radium-228 spike solution was calibrated against NBS and geological standards. The spike was added to the sample after polonium plating, which avoided auto-deposition of thorium-228 and subsequent contamination of the α-detector from thorium-228 recoil (Sill and Olson 1970). In addition, thorium-228 decays at a similar energy to that of polonium-210, causing a problem with separation of counts for the region of interest in the measured MeV alpha-spectrum.

The spiked sample was dried and examined to determine the next step in the separation procedure. If the residue was not white, the sample was redissolved with 1 mL of 8 N HNO_3 and dried. This was repeated until a white residue was obtained. Before the final drying was complete, an aqua regia transition to 6 N HCl was created by adding 1 mL of 6 N HCl. This solution was dried. Dissolution with 6 N HCl and drying was repeated three times to put the precipitate in chloride form for the first column separation. These steps were repeated as necessary until the precipitate was as white as possible as an indication the sample was clean of organics that may change elution characteristics.

2.3.2.1 Calcium removal: two column separation

The first column type was a 10 mL chromatography column with a 20 mL reservoir (Bio-Rad Laboratories, Econo-Pac 10 Column). Bio-Rad AG® 50W-X8 cation exchange resin and MQ water were added to the column in a rinsed slurry to reach 13 mL of settled resin. The settled resin bed was cleaned and conditioned by passing 100 mL of MQ water, followed by 20 mL 4 N HCl and 40 mL 6 N HCl, through the column. Conditioning of the resin bed causes the resin volume to shrink to approximately 10 mL with a length:width aspect ratio of 3.9. Prior to introduction to the column, the sample was redissolved in 5 mL of 6 N HCl over mild heat (50–60°C) covered with a watch glass. The 5 mL sample was cooled, loaded onto the column, allowed to settle into the resin. The beaker was rinsed with an additional 1 mL of 6 N HCl. Using the sample specific pipette tip, the rinse acid was introduced by allowing it to fully settle into the resin, prior to adding the remaining 34 mL of wash acid. Once the acid rinse settled into the resin, two 1 mL aliquots of 6 N HCl were added to begin the column wash and each of these aliquots was allowed to settle into the resin to push the sample into the column and prevent a mixing of sample into a larger volume. The column wash was allowed to settle into the resin and the collected eluant containing most of the calcium was discarded (40 mL). An acid-cleaned 100 mL Teflon® PFA griffin beaker was placed under the column to collect the radium/barium fraction (barium coelutes with radium for this resin). The radium fraction was collected in the next 80 mL of 6 N HCl added to the column. Portions were added that kept the reservoir full to maintain the flow rate (~1.5 $mL \cdot min^{-1}$). Once the 80 mL sample fraction was collected the beaker was placed on a hot plate at 80-90°C and taken to dryness overnight. The sample was never boiled and the heat was reduced when a crystalline residue began to form. While samples were drying, the same columns were cleaned and conditioned for a second sample pass, as in the first preparation, and the separation procedure was repeated. One exception was the introduction of the sample was in 1 mL of 6 N HCl to narrow the elution peaks reduce the tailing of calcium (discard of 40 mL and collection of 80 mL was maintained).

2.3.2.2 Barium removal: third column separation

The third column pass was performed with a custom made 150 µL microcolumn made of TFE heat-shrink tubing (6.35 mm ID) shrunk over a hand machined stainless steel die. Die dimensions were 6.35 mm (0.25 in.) in diameter by 57 mm (2.25 in.) in length for the reservoir which tapers down to 2.38 mm (0.094 in.) in diameter by 35 mm (1.38 in.) in length for the column volume. Enough tubing was used to create an 800 µL reservoir and a constricted tip with minimal dead volume. A frit made of porous polyethylene (2 mm thickness with 10 µm pore size) was cut and squeezed tightly down the column and into the tip. The acid-cleaned microcolumn was prepared for sample processing by adding slurry of Milli-Q water and 50–100 µm Sr® resin (EiChroM Industries, Darien, Illinois). For best results, the column was filled with Milli-Q water first and then the resin was added to the water and allowed to settle into the column to just below the taper of the reservoir. Cleaning and conditioning were performed by passing 1000 µL of Milli-Q water followed by 800 µL of 1.1 N HNO_3 through the column. The conditioned microcolumn contained 150 mL of Sr® resin and had a length:width aspect ratio of 13.1. To prepare a sample for introduction to the third column, the sample was dissolved with 100 µL of 8 N HNO_3. Droplets were swirled in the beaker bottom, gathered together, and dried at 90– 100°C. If the dried sample spot was not white, the sample was treated with an aqua regia solution of 10 – 30 µL of 8 N HNO_3 and 10 – 30 µL of 6 N HCl, dried at 90 – 100°C, and redissolved in 10

– 30 μL of 8 N HNO_3. The last two steps were repeated until the sample was as white as possible. The sample spot was redissolved with 50 μL of 1.1 N HNO_3 over mild heat (60 – 70°C), cooled, and added to the microcolumn with a 100 μL pipette. The sample was allowed to settle into the resin and then a beaker rinse of 50 μL 1.1 N HNO3 was added to the column. A column wash of 100 μL of 1.1 N HNO_3 was added and allowed to settle into the resin. The eluant (200 μL of 1.1 N HNO_3) was discarded. This volume was 50 μL less than reported in Andrews et al. (1999b) because radium recovery was greater with this shift in the collection interval. Radium elution was performed by adding 450 μL of 1.1 N HNO_3 to the column, while the barium remained on the column, and the sample fraction was collected in an acid cleaned 3 mL Teflon® PFA sample vial. The collected sample was then placed on a hot plate at 90 – 100°C and dried. If the spot was not clear and very small (0.5 mm diameter), an aqua regia solution of 1 drop of 8 N HNO_3 and 1 drop of 6 N HCl was added and dried at 90 – 100°C. These steps were repeated until the sample would not lighten or shrink any further. The sample spot was then redissolved two times in 1 drop of 6 N HCl and dried into the chloride form. Microcolumn cleaning was performed by passing 2000 μL of Milli-Q water and were stored upright in a vial of Milli-Q water.

The radium-226:radium-228 atom ratio measured using ICPMS was calculated as the mean (± 2 SE) of all the readings taken in the analysis with outlying values statistically eliminated by the analysis routine. Because atomic radium-226:radium-228 ratio detected using ICP-MS was equal to the unknown atomic ratio of the sample, the known number of atoms in the radium-228 spike can be used to determine the unknown number of radium-226 atoms. Hence, radium-226 activity was determined, after correcting for radium-226 contributed by the spike, by multiplying the number of radium-226 atoms by the radium-226 decay constant.

2.3.3 Lead-radium age determination

Radiometric age was determined from the measured lead-210 and radium-226 activities. Because the activities were measured using the same sample, the calculation was independent of sample mass. Radiometric age was calculated as follows using an equation derived from Smith et al. (1991) to compensate for the ingrowth gradient of lead-210:radium-226 in the otolith core,

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

where t_{age} was the radiometric age at the time of analysis, $A^{210}Pb$ was the lead-210 activity at time of analysis, $A^{226}Ra$ was the radium-226 activity measured using ICP-MS, R_0 was the activity ratio of lead-210: radium-226 initially incorporated, λ was the decay constant for lead-210 (ln(2)/22.26 yr), and T was the core age. Typically, an initial uptake ratio of $R_0 = 0.0$ was used based on the close agreement of the measured juvenile age group lead-radium ratio with the expected ingrowth curve; however, other studies have accounted for what appeared to be exogenous lead-210 (e.g. Kastelle and Forsberg 2002, Stransky et al. 2005). A radiometric age range, based on the analytical uncertainty, was calculated for each sample by using error propagation through to the final age determinations (2 SE). Calculated error included the standard sources of error (i.e. pipetting, spike and calibration uncertainties, etc.), alpha-counting statistics for lead-210 (e.g. Wang et al. 1975), and the ICP-MS analysis routine (Craig Lundstrom, personal communication).

A graphical comparison of the measured lead-210:radium-226 ratio for each age group with the expected ratio from ingrowth was plotted to illustrate any observed trends. To allow for comparison with estimated ages, radiometric age for each group was corrected for lead-210 ingrowth from the time of capture of the fish to the time of auto-deposition by subtracting the time elapsed between capture and plating. The specifics of statistical testing are discussed for each species individually because circumstances varied considerably.

CHAPTER THREE

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LEAD-RADIUM DATING OF PATAGONIAN TOOTHFISH (*DISSOSTICHUS ELEGINOIDES*), A LONG-LIVED DENIZEN OF DEEP SOUTHERN OCEANS

3.1 Introduction

Patagonian toothfish (*Dissostichus eleginoides*) are large pelagic predators of the Southern Ocean that support a major commercial fishery for which there are numerous concerns. Commonly known as "Chilean sea bass" on the international market, the fishery has become one of the most valuable and controversial in history (National Environmental Trust 2004, Knecht 2006). The fishery had a meager beginning in the 1980's and has become a major contributor to deep and remote fisheries (Clark et al. 2007, Watson et al. 2007). Some of the fishery is regulated within the Antarctic region by the Commission for Conservation of Antarctic Marine Living Resources (CCAMLR), but a considerable portion of the fishery lies outside the jurisdiction of CCAMLR and proper regulation is reliant on regional and international cooperation (e.g. Gonzalez et al. 2001, Miller et al. 2005, Wöhler et al. 2006). The most significant regulatory concerns for this fishery are with: 1) illegal, unreported, and unregulated (IUU) fishing; and 2) controlling the problems in such remote locations (Agnew 2000, Butterworth and Brandão 2005, Molenaar 2005, Lack 2008). Aside from finding a way to regulate fishing, the ecosystem this species inhabits is poorly understood. Regulatory measures must take into consideration the biodiversity of these locations within what has been termed an ecosystem evaluation framework, which includes the effect of fishing on habitat (Auster and Langton 1999, Pitcher et al. 2007). Further concern for this fishery is based in a lack of life history information coupled with extremely efficient fishing and rapid stock depletions (e.g. De Oliviera et al. 2006, Butterworth and Brandão 2005). A lack of information necessary to understand the life history of this species and a more informed populous and conservation community has led to notable movements like "Take a pass on Chilean sea bass."

Accurate age and growth information is essential for understanding life history information, and as a result it is one of the most important factors in establishing sustainable fisheries. The CCAMLR Working Group for Fish Stock Assessment (WG-FSA) has encouraged testing of age estimation procedures and to establish age structured models to understand the population dynamics of Patagonian toothfish. Current age and growth information for Patagonian toothfish is based on age estimation procedures that vary in terms of resultant age and growth characteristics, of which the validity of these estimates is not well known. To address this issue, a CCAMLR workshop on estimating age of Patagonian toothfish was held at the Center for Quantitative Fisheries Ecology (CQFE) at Old Dominion University in July 2001. Participants endorsed a common set of criteria for estimating age from otolith microstructure in transverse otolith sections and initiated the CCAMLR Otolith Network (CON) for the purpose of exchanging samples to ensure that age estimates were precise and comparable. As a result of this meeting, participants recommended that a high priority be given to validation of age estimates to ensure that age data used in examining population dynamics are accurate.

The earliest estimates of age and growth for Patagonian toothfish came from a study of fish collected off the Kerguelen and Crozet Islands in 1974 - 1976 (Hureau and Ozouf-Costaz 1980). A total of 69 specimens with a size range of 69 - 845 mm SL was retained from the collections for the purpose of investigating age estimation using scales and otoliths. Observations of estimated age were made using sectioned and broken-and-burned otoliths. Sections were deemed too difficult to read, but burned otoliths provided an easily recognizable nucleus surrounded by 7 to 8 annuli (rings) that were followed by more regular and narrower annuli. This transition in otolith growth occurred at approximately 380 mm SL, but it was noted that size at spawning was greater (55 to 60 cm; Kock 1976). Based on a comparison of age estimations between scales and otoliths, age estimates ranged from 1 to 21 years ($n \approx 46$). At a workshop in Cambridge University in 1979, there was consensus that use of scales as an indicator of age was valid because of the agreement between scales and otoliths; however, the findings had no chronological framework and the observations were made at a time when the validity of age estimates was based on broad assumptions that were widely accepted. The maximum estimated age of 21 years was similar to the maximum age of 22 years estimated by Zacharov and Frolkina (1976) using scale annuli counting; however, the size of the oldest fish for Hureau and Ozouf-Costaz (1980) was 84.5 cm SL, less than half the length of the 22 year old fish (186 cm SL) from Zacharov and Frolkina (1976). A difference in length of close to 100 cm for fish that differ by only one year in age is suggestive of problems with age estimation from a loss of growth zone information. More recently, Zhivov and Krivoruchko (1990) also used scale readings that provided estimates up to 22 years for fish up to 115 cm SL, which is an indication that scale reading was widely applied and accepted as valid.

In a study of Patagonian toothfish scale and otolith age reading, an attempt was made to establish which structure was more reliable for age determination (Cassia 1998). The comparison was made for age estimates from scales read with transmitted light and sectioned otoliths viewed with incident light. Some agreement was found between scale and otolith readings, but numerous otolith samples were removed from consideration because of poor growth zone visibility. The conclusion from the comparison, despite the methodological challenges for otolith reading, was that there were no differences between ages determined from either structure and that age could reach 24 years. This finding was contrary to a previous comparison that indicated scales gave estimates that were significantly lower than otoliths (Young et al. 1995). It was further concluded by Cassia (1998) that the annual formation of growth zones could not be validated within the study, but that anecdotal evidence cited for seasonal deposition of scale annuli (Young et al. 1992) and the findings of North (1988) provided validation for Patagonian toothfish. While North (1988) did confirm the annual periodicity of growth zone formation in otoliths, their findings were for other Antarctic fishes and did not include Patagonian toothfish. Cassia (1998) engaged in the same manner of thinking as Pell (1859) by making the assumption that findings for similar species were applicable to the species at hand. In addition, the age estimate comparisons made by Cassia (1998) did not preclude the possibility of age underestimation, yet the author's state that use of scales was "most appropriate for determining age… because it did not underestimate age" with no support for such a conclusion.

In contrast to Cassia (1998), a discrepancy was documented between age estimates from scales and sectioned otoliths of Patagonian toothfish (Ashford et al. 2001). The problems encountered with reading otolith sections in previous studies were remedied with the use of baked otoliths. Growth zones were enhanced in this process and sectioned otoliths were read with reflected light (Figure 3-1). Age differed by a factor of two with otolith section ages ranging up to ~40 years. The improved technique using baked otoliths, coupled with large differences in estimated age from scales, led to the conclusion that a thorough age validation study was necessary (Ashford et al. 2001).

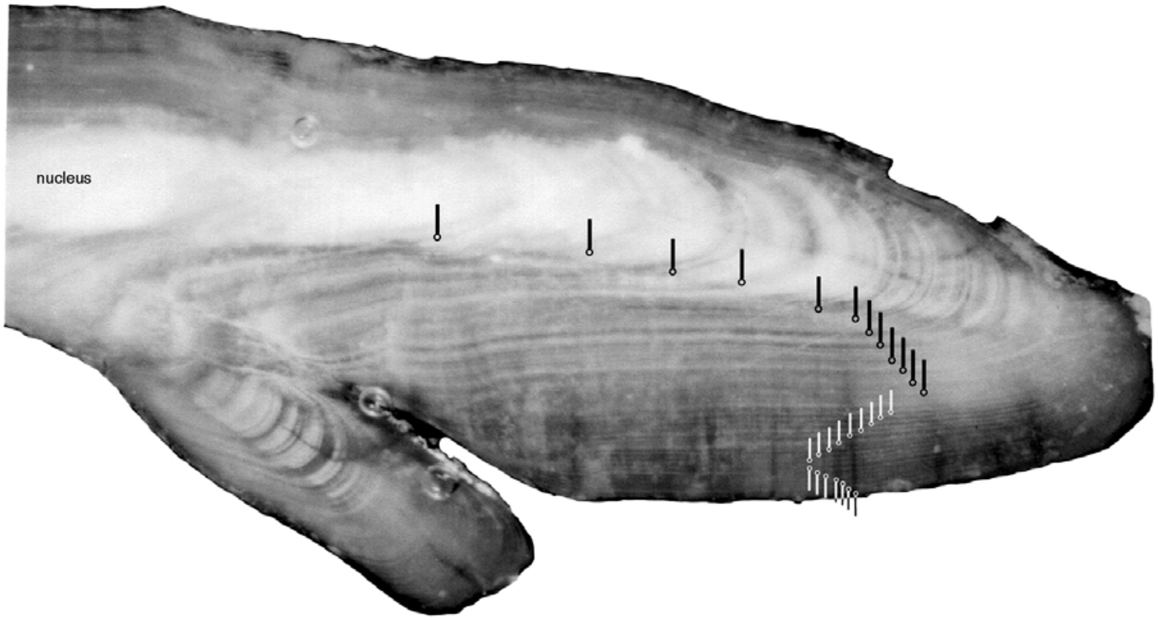

Figure 3-1. Example of a cross section for an otolith from a Patagonian toothfish (*Dissostichus eleginoides*) that was aged using the improved baked otolith method (from Ashford et al. 2001). This section was aged at 29 years, with the transition between growth patterns denoted by a change from black to white symbols.

Support for Patagonian toothfish age estimates and age estimation procedures have been provided to varying degrees in several age validation studies. An early application of bomb radiocarbon dating provided the first evidence for longevity exceeding 40 years (Kalish et al. 2001b). Application of marginal or edge analysis provided support for annual growth zone formation in the otoliths of Patagonian toothfish and the study provided age estimates that exceeded 50 years (Horn 2002). Early annual growth was quantified and validated by tracking changes in modal length frequencies of pre-recruit fish (Ashford et al. 2002). A tag-and-release program provided support for annual growth interpretation for 5 to 18 year old age classes using strontium chloride marking ($SrCl_2$; Krusic-Golub and Williams 2005). Each of these studies have provided key portions of information and evidence for differentiating age estimation procedures that are either consistent or inconsistent with these independent forms of age determination. Collectively, the studies performed to date provide support for accurate age estimation through the use of growth zone counts in transverse otolith cross sections; however, because of the limited scope of each study a more comprehensive validation study was recommended, and in some cases lead-radium dating was specifically suggested.

Application of lead-radium dating to fishes can provide two basic levels of support for determining the validity of age estimates; either one age estimation scenario is supported over another, precluding further consideration of the inaccurate scenario that usually differs by many years (in most cases decades); or age is not only supported by measured ratios, but an age estimation procedure is tested for accuracy and consistency through a series of age classes. In this study, lead-radium dating was applied to aged Patagonian toothfish otoliths in a series of age classes that were aged at two different facilities. The tested hypotheses were: 1) estimated age from growth zone counts is not different from lead-radium dating; 2) lead-radium dating between two age estimation facilities provides no difference in age; and 3) lead-radium dating supports longevity estimates exceeding maximum scale ages. These findings are also discussed in a critical analysis of other age estimation studies to resolve questions about the age estimate disparities in the literature.

3.2 Materials and Methods

In the initial stages of developing the lead-radium dating approach, a pilot study was performed on a small number of otoliths provided by Mark Belchier (British Antarctic Survey - South Georgia Project, Cambridge, United Kingdom). These otoliths were collected in 2000 and six whole otoliths were chosen from fish with a length range of 73 to 79 cm. Otolith weight was not available for these samples because each had some small portion of the otolith missing, but total sample mass was 0.8025 g for the cleaned whole otolith sample. Based on the measured lead-210 and radium-226 activity levels, the technical details of which are discussed later in this section, a radiometric age of 9 - 16 years was determined. This was similar to age estimated from a growth curve for the given fish lengths (~6 - 12 years; Horn 2002). Because the results from the pilot study were promising, a full analysis of a series of age groups (youngest to oldest) was pursued.

3.2.1 Otolith samples

For the comprehensive study, samples were collected from two sources to cover an age series that was similar between collections. The two agencies involved were the Center for Quantitative Fisheries Ecology (CQFE) at Old Dominion University in Virginia, USA and the Central Ageing Facility (CAF) at the Marine and Freshwater Resources Institute in Queenscliff, Victoria, Australia. For the age group sample series selected, each facility provided the whole otolith counterpart to the aged otolith for radiometric analyses.

3.2.2 Center for Quantitative Fisheries Ecology sample series

Otoliths were collected from the Kerguelen Plateau region in 1993, 1994, 1999, and 2000 and were previously aged by CQFE. These otoliths were made available for lead-radium dating to provide a basis for determining the accuracy of the age estimation protocol used by CQFE. An age frequency analysis was constructed for each of the collection years to best determine the number of otoliths available for the analyses. Age groups were determined based on the number of otoliths available for a given age or age range, while considering the potential number of replicates for each age group.

3.2.2.1 Preliminary sample design explorations

Prior to selecting age groups, the measured radium-226 activity from the BAS sample (0.026 dpm·g^{-1}) was used as a basis for the next set of samples. Based on this value, a trial sample size of approximately 0.5 g of cored material, the details of which are discussed later in this section, was estimated to provide detectible polonium-210 levels on the alpha spectrometer. As a trial run on replicated core otolith samples, a set of four 10 year old age groups were analyzed using a selected core size. Core size was chosen to represent a 1 - 2 year old otolith with dimensions of approximately 3 mm H x 5 mm L x 0.7 mm T and a weight of ~0.018 g for 24 - 27 otoliths, which amounted to approximately 0.40 - 0.47 g. Radium-226 levels were lower than anticipated at an average of 0.0178 dpm·g^{-1} for these samples and consequently, the polonium-210 activity from the trial samples was too low to be detected; activity was calculated at background levels (~1 count per day) at the alpha spectrometer. Core and sample sizes were increased considerably based on these results.

Sample size for the baseline juvenile samples (3-year-old age groups) was increased to over 1 gram to determine the low end of polonium-210 activity for the series of age groups. Upon examination of the otoliths it was noticed that otolith weight range was considerable (0.057 - 0.159 g) and that fish length followed suit. To potentially differentiate any age differences, the 3 year old age groups were split into 3 groups that weighed roughly the same, but ranged from low to high weight (CQFE 1A - 1C, Appendix 1a). All other age groups were randomly mixed for age group replicates and core size was determined from the 44 whole 3-year-old otoliths. Average dimensions for the 3-year-old otoliths were 5.5 mm H x 10 mm L x 1.3 mm T and a weight of 0.089 g. To be slightly conservative, coring dimensions of 5 mm H x 9 mm L x 1-1.2 mm T and a weight of ~0.07 g were targeted.

3.2.2.2 Sample series selection criteria

Selection and coring of age groups between the youngest and oldest otoliths was based on the availability of otoliths. The age frequency analysis revealed that the best collection year was 1999 in terms of the number of aged otoliths and the range of ages covered (Figure 3-2).

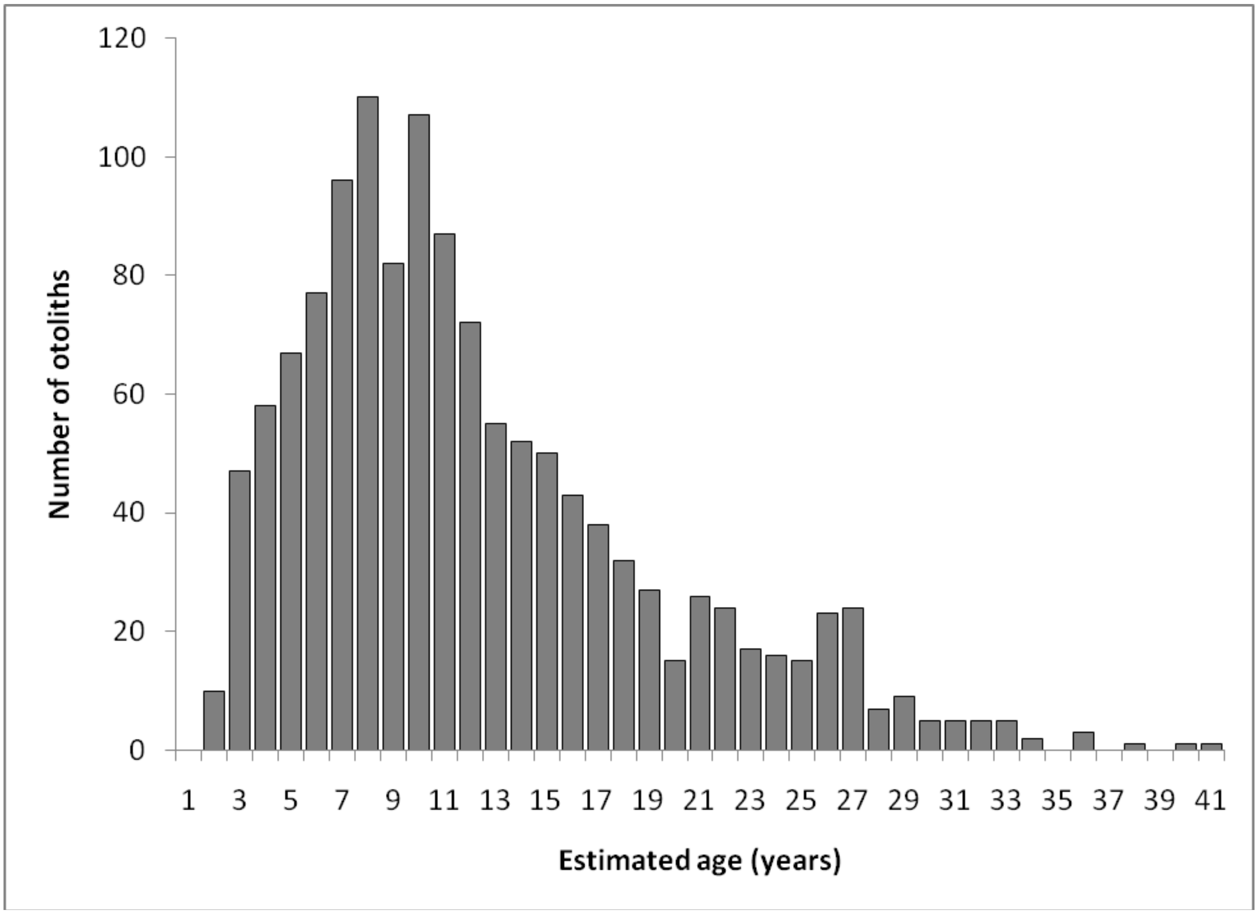

Figure 3-2. Age frequency histogram of Patagonian toothfish otoliths that were available from collections made in 1999 from the Kerguelen Plateau region. Age groups for radiometric analysis were selected from this distribution.

Four age groups, each with 3 randomized replicates, were chosen to cover evenly the age range. Age groups of 5 - 7, 11 - 12, 15 - 17, and 20 - 24 years were chosen with 24 to 36 otoliths per group (Appendix 1a). The oldest age groups were not replicated because of low age-class availability. Optimal composition of a few oldest aged groups, to address longevity from the samples available, was determined using the average measured radium-

226 activity (~0.0178 dpm·g^{-1}) and the estimated age of the oldest fish available. One age group (25 - 27 year) was chosen to include a large number of otoliths (n = 44) to reduce the error associated with polonium-210 counting and increase the precision of the final age determinations. The oldest age group possible covered the widest age range (28 - 34 years) to enable the pooling of enough otolith material (n = 28). Older groups were not possible due to low age class availability.

3.2.2.3 Central Ageing Facility sample series

Patagonian toothfish otoliths that were collected from the Heard Island region in 1990, 1992, 1993, and 1997 - 2003 were previously aged by CAF. These otoliths were made available for lead-radium dating to provide a basis for determining the accuracy of the age estimation protocol used by CAF and to compare lead-radium results between facilities. An age frequency histogram was constructed for each of the collection years to determine the number of otoliths available for the radiometric analyses. Age groups were determined based on the number of otoliths available for a given age or age range, while considering the potential number of replicates for each age group. Selection and coring of age groups between the youngest and oldest otoliths were based on the availability of otoliths. The age frequency analysis revealed that the best collection year was 2001 in terms of the number of aged otoliths and the range of ages covered (Figure 3-3).

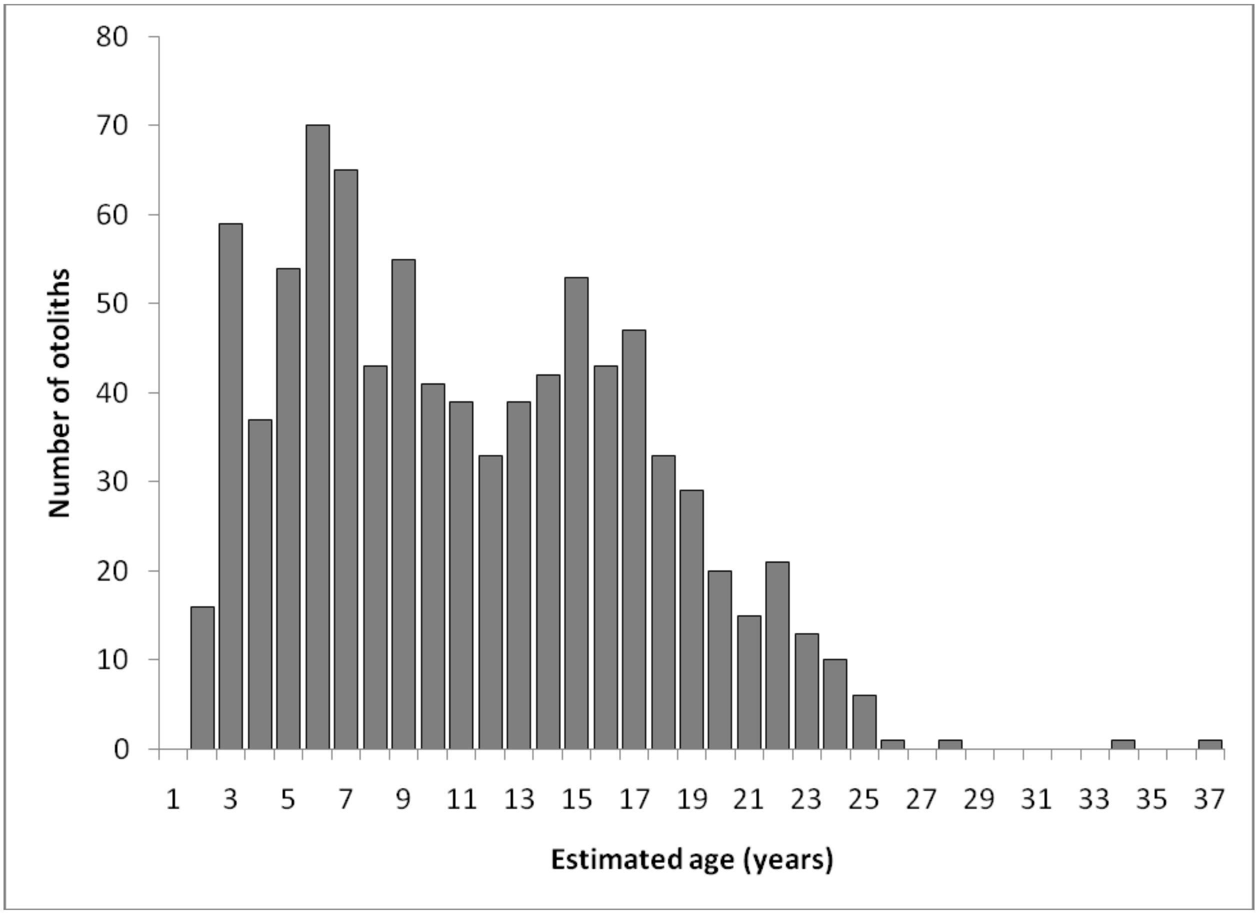

Figure 3-3. Age frequency histogram of Patagonian toothfish otoliths that were available from collections made in 2001 from the Heard Island region. Age groups for radiometric analysis were selected from this distribution.

The same four age groups as with the CQFE sample series, each with 3 randomized replicates, were chosen to provide a statistically comparable data set. Age groups of 5 - 7, 11 - 12, 15 - 17, and 20 - 24 years were chosen with 22 - 32 otoliths per group (Appendix 1b). The youngest (3-year) age group was not processed because age differentiation would not be useful and the oldest age groups were not possible because of low age-class availability.

3.2.2.4 Technical details of coring

To extract the oldest part of the otolith from adult whole otoliths, a new procedure was developed that combined the use of hand grinding and micromilling. Whole otoliths were first flattened by grinding in the medial plane, on the proximal side of the otolith. The sulcal ridges were nearly removed by hand using a Buehler Ecomet III lapping wheel with 120 to 300-grit silicon-carbide, wet-dry paper. Grinding was halted once the apex of the sulcal groove was reached near the nucleus of the otolith. This stopping point was determined from examination of otolith cross sections as the point at which all otolith growth beyond the first few years was removed. Once the otolith met these specifications, the otolith was allowed to air dry overnight (wet from grinding) and was mounted to a glass microscope slide. The glass slides used were of a higher quality for a measured and consistent thickness, which was of importance in the extraction process because numerous otoliths needed to be processed and consistency would speed the process. The mounting medium used was medium viscosity Cytoseal®.

Mounted otoliths were ground down to the target thickness using the same lapping wheel process stated above, with a micrometer used to measure the thickness. Once the proper dimension was reached, a core was extracted from the medial section. Viewing with transmitted light on the New Wave Research micromilling machine provided well-defined zones that would be used to verify the target length and height determined from measurement of the juvenile otoliths. As stated previously, coring dimensions of 5 mm H x 9 mm L x 1-1.2 mm T and a weight of ~0.07 g were targeted with the micromilling machine. The extraction was performed by tapping out a series of holes through the section to the slide with a 0.5 mm Brasseler drill bit (no. 005). The pattern of holes was made to follow an outline of the 3-year target core. The core was released from the slide by soaking it in toluene for about an hour. Extracted cores were extracted quite successfully and very few samples were lost using this technique. Cores were allowed to air dry to remove the toluene that may have been absorbed by the otolith. Cores were cleaned and weighed to check for consistency with the target core weight. Toluene blanks were processed through the radiochemical assays to determine if there was any contamination and all was clean.

The final step was pooling of the extracted otolith cores into their respective age groups, cleaning and weighing to the nearest 0.1 mg, and application of lead-radium dating.

3.2.2.5 Radiochemical protocol

The detailed protocol describing sample preparation, chromatographic separation of radium-226 from barium and calcium, and analysis of radium-226 using mass spectrometry was given in Chapter 2. These procedures have not changed for this study, except for two aspects of the analysis: 1) radium recovery was improved by shifting the collection interval on the final chromatography column to begin after the first 200 µL (as opposed to after 250 µL); and 2) purified radium samples were analyzed using an multi-collector ICP-MS, which was less prone to ionization suppression from variable levels of barium.

3.2.2.6 Age comparisons

A two-factor ANOVA to examine differences within and between CQFE and CAF by having identical age group series and replicate number was to be applied to these data; however, the loss of samples and unequal availability of otoliths from each facility prevented this analysis. To best describe the similarities or differences between facilities, a regression of age estimated from growth zone counts and lead-radium dating was performed and compared with a line of agreement (1:1) using a *t*-test for slope and intercept. A test of the power to detect a Type II error (mistakenly accepting a false null hypothesis), as described for daily zones by Rice (1987), was considered, but its relevance was deemed uncertain because of other factors ignored by the *t*-test. Testing these data is a work in progress because statisticians have not been able to adequately address the: 1) unequal number of samples between facilities; 2) unequal replicate number within treatments; and 3) the changing error associated with each age determination from lead-radium ratios (increases as the ratio increases), the latter of which is a seriously confounding factor, if one wishes to consider all variability. For the sake of establishing patterns for observation of trends, age data were plotted with respect to each other and relative to a line of agreement (1:1). All data could be considered in this manner with a regression fitted to both CQFE and CAF age group data.

3.3 Results

Seventeen age groups from CQFE toothfish collections ranged in age from 3 years to 28-34 years with 3 sample replicates for each age group, except for the two oldest groups (Table 3-1). Fish length increased on average relative to age and ranged from 54.7 to 99.7 cm TL, but the range was considerable for some groups. Otolith weight increased as expected from an average of 0.068 g for the youngest group to 0.251 g for both of the oldest groups. Sexes were not separated because validation of age estimates was the focus of the analysis.

Table 3-1. Summary of characteristics for CQFE Patagonian toothfish samples processed in this study. Estimated age composition, fish length, and otolith weight information is summarized below. Sex ratio is given for this set of samples out of interest, but was not a factor in forming age groups. Age group replicates, selected randomly within the age class, are denoted with a number and lettering system.

Sample	Age group (yr)	Ave. length (cm TL)	Fish length range (SD, cm)	Ave. otolith weight (g)	Otolith weight range (g)	Sex ratio (M/F)
CQFE 1A	3	54.7	45 – 65 (4.4)	0.068 ± 0.008	0.057 – 0.082	14/6
CQFE 1B	3	62.2	58 – 69 (3.8)	0.091 ± 0.008	0.083 – 0.104	7/7
CQFE 1C	3	75.1	70 – 85 (4.9)	0.127 ± 0.018	0.103 – 0.159	5/5
CQFE 2A	5 – 7	73.7	53 – 89 (9.5)	0.121 ± 0.027	0.052 – 0.169	13/19
CQFE 2B	5 – 7	71.8	55 – 88 (7.9)	0.121 ± 0.025	0.081 – 0.184	17/16
CQFE 2C	5 – 7	68.0	50 – 91 (9.8)	0.105 ± 0.027	0.057 – 0.170	11/22
CQFE 3A	11 – 12	81.5	64 – 105 (8.4)	0.152 ± 0.043	0.105 – 0.266	15/11
CQFE 3B	11 – 12	82.7	63 – 104 (9.7)	0.149 ± 0.037	0.074 – 0.207	12/14
CQFE 3C	11 – 12	79.3	65 – 103 (8.6)	0.134 ± 0.024	0.098 – 0.215	10/17
CQFE 4A	15 – 17	89.9	68 – 122 (10.8)	0.184 ± 0.035	0.127 – 0.268	6/19
CQFE 4B	15 – 17	88.3	72 – 107 (9.7)	0.179 ± 0.032	0.126 – 0.232	11/12
CQFE 4C	15 – 17	89.1	72 – 115 (10.8)	0.179 ± 0.048	0.117 – 0.290	10/14
CQFE 5A	20 – 24	98.1	79 – 133 (11.4)	0.235 ± 0.048	0.162 – 0.356	23/12
CQFE 5B	20 – 24	96.2	75 – 126 (11.2)	0.224 ± 0.054	0.119 – 0.348	17/18
CQFE 5C	20 – 24	97.1	57 – 125 (12.9)	0.232 ± 0.043	0.172 – 0.348	21/15
CQFE 6A	25 - 27	97.4	78 – 119 (9.3)	0.251 ± 0.047	0.154 – 0.358	23/21
CQFE 7A	28 - 34	99.7	89 – 122 (7.3)	0.251 ± 0.048	0.173 – 0.372	14/14

Eleven age groups from CAF collections ranged in age from 5 - 7 years to 20 - 24 years, similar to the mid range for the CQFE age groups to allow for a comparison between facilities; however, otolith numbers were lacking for the 11 - 12 year age groups and only two replicates were possible (Table 3-2). Fish length increased on average relative to age and ranged from 53.4 to 125.9 cm TL, and fish were much larger than even the oldest CQFE age groups. Otolith weight increased as expected from an average of 0.070 g for one of the youngest groups to 0.278 g for one of the oldest groups, greater than the oldest CQFE age group and the range in otolith weight was also considerable. Sex was not recoded at the time of collection for most of the CAF fish used in this analysis.

Table 3-2. Summary of characteristics for CAF Patagonian toothfish samples processed in this study. Estimated age composition, fish length, and otolith weight information is summarized below. Sex ratio was not available for this set of samples. Age group replicates, selected randomly within the age class, are denoted with a number and lettering system.

Sample	Age group (yr)	Ave. length (cm TL)	Fish length range (SD, cm)	Ave. otolith weight (g)	Otolith weight range (SD, g)	Sex ratio (M/F)
CAF 2A	5 – 7	53.4	40.2 – 65.4 (6.1)	0.070 ± 0.015	0.045 – 0.093	N.A.
CAF 2B	5 – 7	57.0	41.8 – 78.2 (8.6)	0.082 ± 0.020	0.050 – 0.127	N.A.
CAF 2C	5 – 7	53.7	41.2 – 70.2 (7.0)	0.076 ± 0.023	0.029 – 0.153	N.A.
CAF 3A	11 – 12	85.0	69.3 – 103.2 (9.6)	0.147 ± 0.030	0.101 – 0.221	N.A.
CAF 3B	11 – 12	84.4	66.3 – 107.4 (9.3)	0.143 ± 0.027	0.099 – 0.214	N.A.
CAF 4A	15 – 17	103.4	78.8 – 127.1 (12.9)	0.199 ± 0.044	0.129 – 0.336	N.A.
CAF 4B	15 – 17	107.7	81.7 – 126.9 (11.5)	0.212 ± 0.044	0.129 – 0.315	N.A.
CAF 4C	15 – 17	100.9	84.2 – 125.7 (10.4)	0.200 ± 0.037	0.117 – 0.282	N.A.
CAF 5A	20 – 24	125.6	103.8 – 148.6 (14.8)	0.263 ± 0.045	0.180 – 0.365	N.A.
CAF 5B	20 – 24	124.8	88.5 – 159.0 (17.8)	0.263 ± 0.062	0.140 – 0.367	N.A.
CAF 5C	20 – 24	125.9	94.6 – 148.0 (14.1)	0.278 ± 0.058	0.174 – 0.411	N.A.

A visual representation of the notable differences between CQFE and CAF age groups for otolith weight versus fish length and estimated fish age provided some insight on collection differences. In general, there was a departure from agreement between otolith weight and fish length at approximately 0.15 g, after which CAF fish of similar otolith weight were on average larger than CQFE fish (Figure 3-4).

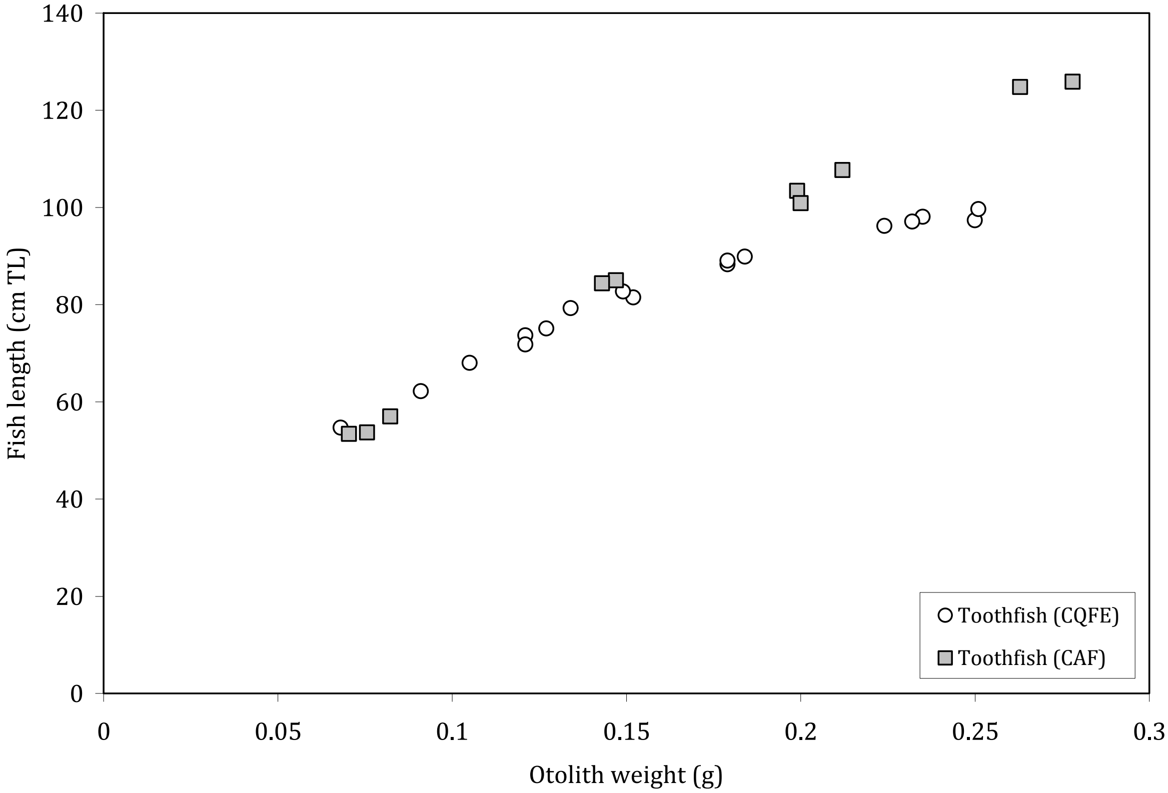

Figure 3-4. Illustration of the relationship between fish length and whole otolith weight for both CQFE and CAF collections, which may indicate there were differences in growth between regions.

For the CQFE age groups, the average estimated age of each group ranged from 3 to 30.4 years, with a time since capture between 5 and 6 years (Table 3-3). Age groups either consisted of whole juvenile otoliths (3-year age groups) or cored adult otoliths, the number of which ranged from 10 to 44. Sample weight ranged from 1.1027 to 2.6830 g and core weight was relatively consistent throughout the sample series at 0.048 ± 0.007 (SD); 3 year otoliths were not cored because of the close proximity to core size, but some were larger than expected (0.124 g average for heaviest 3-year age group) indicating coring was conservative.

Table 3-3. Summary of age and otolith coring characteristics for the CQFE Patagonian toothfish samples processed in this study. Time since capture for each group, required for correction of radiometric age, with the number of otoliths that were pooled into each sample, sample weight, and average cored otolith weight are listed to show consistency of coring. The 3-year age groups were whole otoliths and placed into progressively larger otolith groups; all other groups were randomly selected.

Sample	Age group (yr)	Average age (yr)	Time since capture (yr)	Number of otoliths	Sample weight (g)	Average core weight (g)
CQFE 1A	3	3	5.2	20	1.3175	0.066[1]
CQFE 1B	3	3	5.2	14	1.2509	0.089[1]
CQFE 1C	3	3	5.2	10	1.2396	0.124[1]
CQFE 2A	5 – 7	6.1	5.8	32	1.2941	0.040
CQFE 2B	5 – 7	6.2	5.8	33	1.2755	0.039
CQFE 2C	5 – 7	5.9	5.8	32	1.2847	0.040
CQFE 3A	11 – 12	11.6	5.4	26	1.2513	0.048
CQFE 3B	11 – 12	11.7	5.4	26	1.2052	0.046
CQFE 3C	11 – 12	11.4	5.4	27	1.1962	0.044
CQFE 4A	15 – 17	16.0	5.6	25	1.1685	0.047
CQFE 4B	15 – 17	15.7	5.6	24	1.1204	0.047
CQFE 4C	15 – 17	16.0	5.6	24	1.1027	0.046
CQFE 5A	20 – 24	21.9	5.6	35	1.7232	0.049
CQFE 5B	20 – 24	22.1	5.6	35	1.7831	0.051
CQFE 5C	20 – 24	22.1	5.6	36	1.9049	0.053
CQFE 6A	25 - 27	26.1	5.4	44	2.6830	0.061
CQFE 7A	28 - 34	30.4	5.4	28	1.6609	0.059

1. Whole juvenile otoliths.

For the CAF age groups, the average estimated age of each group ranged from 5.8 to 21.9 years, with a time since capture between 4 and 5 years (Table 3-4). Age groups either consisted of whole otoliths (5 - 7 year age groups were whole because they were unexpectedly small relative to the target core size previously established with CQFE otoliths) or cored adult otoliths, the number of which ranged from 22 to 32. Sample weight ranged from 1.1257 to 2.4226 g and core weight was relatively consistent throughout the sample series at 0.054 ± 0.002 (SD).

Table 3-4. Summary of age and otolith coring characteristics for the CAF Patagonian toothfish samples processed in this study. Time since capture for each group, required for correction of radiometric age, with the number of otoliths that were pooled into each sample, sample weight, and average cored otolith weight are listed to show consistency of coring. The 5 - 7 year age groups were whole otoliths and were randomly selected along with all other groups.

Sample	Age group (yr)	Average age (yr)	Time since capture (yr)	Number of otoliths	Sample weight (g)	Average core weight (g)
CAF 2A	5 – 7	5.8	4.4	32	2.1386	0.067[1]
CAF 2B	5 – 7	6.3	4.4	32	2.4226	0.076[1]
CAF 2C	5 – 7	5.8	4.4	32	2.2606	0.071[1]
CAF 3A	11 – 12	11.5	4.4	26	1.3409	0.052
CAF 3B	11 – 12	11.4	4.4	26	1.4697	0.057
CAF 4A	15 – 17	16.1	4.3	29	1.6135	0.056
CAF 4B	15 – 17	15.9	4.3	30	1.6328	0.054
CAF 4C	15 – 17	16.0	4.3	30	1.6342	0.055
CAF 5A	20 – 24	21.9	4.1	22	1.1257	0.051
CAF 5B	20 – 24	21.9	4.1	22	1.1608	0.053
CAF 5C	20 – 24	21.3	4.2	22	1.1593	0.053

1. Whole otoliths.

Radiometric measurements for each sample series resulted in measured lead-radium activities. For CQFE age groups, measured lead-210 activity increased with age as expected, given radium-226 was consistent among groups, and ranged from a low of 0.0034 ± 16.9% (2 SE) for one of the 3 year age groups to a high of 0.0124 ± 9.1% (2 SE) for the oldest age group (Table 3-5). Radium-226 activity was lower than usual for otolith material (see Chapter 1 for a review of radium-226 in otoliths) and ranged from 0.0124 ± 2.1% (2 SE) to 0.0221 ± 1.3% (2 SE) with a high degree of consistency (average = 0.0164 ± 0.0027 SD). The resultant lead-radium activity ratios for the sample series ranged as would be predicted by estimated age from near 0.2 for the youngest age group to greater than 0.6 for the oldest age groups.

Table 3-5. Radiometric results for CQFE Patagonian toothfish sample series. Listed are the estimated age range from growth zone counts and measured lead-210 (^{210}Pb) and radium-226 (^{226}Ra) activities for all samples. Two standard errors were expressed as an error percentage for the measured activities. Calculated activity ratios and their corresponding margin of error (based on error propagation and the delta method) are given to provide a 2 SE confidence interval.

Sample	Age group (yr)	^{210}Pb (dpm·g^{-1}) ± % error	^{226}Ra (dpm·g^{-1}) ± % error	^{210}Pb:^{226}Ra activity ratio	2 SE
CQFE 1A	3	0.0039 ± 15.8	0.0164 ± 2.4	0.240	0.043
CQFE 1B	3	0.0034 ± 16.9	0.0185 ± 1.6	0.184	0.033
CQFE 1C	3	0.0060 ± 12.8	0.0221 ± 1.3	0.271	0.038
CQFE 2A	5 – 7	0.0043 ± 14.4	0.0124 ± 2.1	0.348	0.056
CQFE 2B	5 – 7	0.0052 ± 16.7	0.0179 ± 2.0	0.290	0.053
CQFE 2C	5 – 7	0.0064 ± 11.4	0.0149 ± 2.6	0.432	0.059
CQFE 3A	11 – 12	0.0058 ± 13.4	0.0139 ± 2.4	0.417	0.064
CQFE 3B	11 – 12	0.0054 ± 13.4	0.0142 ± 1.6	0.377	0.056
CQFE 3C	11 – 12	0.0079 ± 10.1	0.0149 ± 2.0	0.526	0.062
CQFE 4A	15 – 17	0.0057 ± 16.1	0.0127 ± 4.2	0.448	0.087
CQFE 4B	15 – 17	0.0076 ± 11.9	0.0154 ± 2.4	0.493	0.069
CQFE 4C	15 – 17	0.0069 ± 13.1	0.0137 ± 2.0	0.503	0.074
CQFE 5A	20 – 24	0.0111 ± 8.5	0.0181 ± 3.7	0.611	0.072
CQFE 5B	20 – 24	0.0107 ± 8.0	0.0172 ± 2.7	0.621	0.065
CQFE 5C	20 – 24	0.0116 ± 7.8	0.0184 ± 2.1	0.630	0.061
CQFE 6A	25 - 27	0.0115 ± 8.4	0.0186 ± 2.4	0.621	0.066
CQFE 7A	28 - 34	0.0124 ± 9.1	0.0196 ± 1.7	0.636	0.068

Similar results were obtained for CAF age groups and measured lead-210 activity increased with age from a low of 0.0026 ± 19.8% (2 SE) for one of the 5 - 7 year age groups to a high of 0.0132 ± 8.5% (2 SE) for one of the oldest age groups (Table 3-6). Radium-226 not different on average than the activity measured for CQFE otoliths at 0.0165 ± 0.0014 SD and ranged from 0.0149 ± 2.0% (2 SE) to 0.0187 ± 5.7% (2 SE). Recovery of radium-226 from one sample was poor and unreliable; this sample (CAF 5A) could not be considered further. The resultant lead-radium activity ratios for the sample series ranged as was predicted by estimated age from near 0.2 for the youngest age group to greater than 0.6 for the oldest age groups.

Table 3-6. Radiometric results for CAF Patagonian toothfish sample series. Listed are the estimated age range from growth zone counts and measured lead-210 (^{210}Pb) and radium-226 (^{226}Ra) activities for all samples. Two standard errors were expressed as an error percentage for the measured activities. Calculated activity ratios and their corresponding margin of error (based on error propagation and the delta method) are given to provide a 2 SE confidence interval. Sample number CAF 5A suffered from poor radium-226 recovery and was not considered further.

Sample	Age group (yr)	^{210}Pb (dpm·g^{-1}) ± % error	^{226}Ra (dpm·g^{-1}) ± % error	^{210}Pb:^{226}Ra activity ratio	2 SE
CAF 2A	5 – 7	0.0026 ± 19.8	0.0149 ± 5.4	0.171	0.041
CAF 2B	5 – 7	0.0034 ± 15.0	0.0159 ± 6.8	0.213	0.043
CAF 2C	5 – 7	0.0034 ± 15.5	0.0187 ± 5.7	0.181	0.036
CAF 3A	11 – 12	0.0069 ± 11.1	0.0179 ± 4.5	0.387	0.058
CAF 3B	11 – 12	0.0067 ± 9.5	0.0186 ± 3.8	0.359	0.046
CAF 4A	15 – 17	0.0076 ± 8.3	0.0158 ± 3.1	0.478	0.053
CAF 4B	15 – 17	0.0081 ± 8.5	0.0161 ± 2.1	0.505	0.052
CAF 4C	15 – 17	0.0071 ± 9.6	0.0169 ± 2.2	0.418	0.048
CAF 5A	20 – 24	0.0132 ± 8.5	0.0038 ± 9.9[1]	N.A.	N.A.
CAF 5B	20 – 24	0.0089 ± 8.7	0.0149 ± 2.0	0.597	0.063
CAF 5C	20 – 24	0.0102 ± 8.8	0.0156 ± 6.4	0.654	0.094

1. Recovery was poor for this sample and it was removed from the analysis.

In general, agreement between estimated age and radiometric age was good for both CQFE and CAF age groups with no major departures from what was determined from growth zone counts. For the CQFE age groups, most radiometric ages were in agreement with estimated age and a few in the early to middle aged groups appear to be slightly older on average; age was underestimated from growth zone counts by a few years (Table 3-7). The maximum radiometric age was 28.5 years (23.0 - 35.4 year range) for the 28 - 34 year group.

Table 3-7. Summary of growth-zone ages and radiometric ages for CQFE Patagonian toothfish. Average growth-zone age is given for each age group with radiometric age, as calculated from the measured lead-210:radium-226 activity ratios, corrected for time since capture. Radiometric age range was based on the analytical uncertainty and error propagation (2 SE).

Sample	Age group (yr)	Average growth zone age (yr)	Radiometric age (yr)	Radiometric age range (yr)
CQFE 1A	3	3	5.1	3.4 – 7.1
CQFE 1B	3	3	2.8	1.5 – 4.2
CQFE 1C	3	3	6.5	4.9 – 8.2
CQFE 2A	5 – 7	6.1	9.5	6.8 – 12.5
CQFE 2B	5 – 7	6.2	6.7	4.4 – 9.4
CQFE 2C	5 – 7	5.9	13.9	10.8 – 17.6
CQFE 3A	11 – 12	11.6	13.4	10.1 – 17.4
CQFE 3B	11 – 12	11.7	11.3	8.5 – 14.4
CQFE 3C	11 – 12	11.4	20.0	16.1 – 24.7
CQFE 4A	15 – 17	16.0	15.0	10.3 – 21.1
CQFE 4B	15 – 17	15.7	17.8	13.7 – 22.7
CQFE 4C	15 – 17	16.0	18.4	13.9 – 23.8
CQFE 5A	20 – 24	21.9	26.3	20.9 – 33.4
CQFE 5B	20 – 24	22.1	27.1	22.1 – 33.5
CQFE 5C	20 – 24	22.1	27.9	23.0 – 34.0
CQFE 6A	25 - 27	26.1	27.2	22.1 – 33.7
CQFE 7A	28 - 34	30.4	28.5	23.0 – 35.4

For the CAF age groups, agreement was best for the middle-aged groups, with minor overestimation of age on average for the earliest groups, and minor underestimation of age for one of the oldest age groups (Table 3-8). The maximum radiometric age was 31.4 years (23.8 - 43.2 year range) for the 20 - 24 year group.

Table 3-8. Summary of growth-zone ages and radiometric ages for CAF Patagonian toothfish. Average growth-zone age is given for each age group with radiometric age, as calculated from the measured lead-210:radium-226 activity ratios, corrected for time since capture. Radiometric age range was based on the analytical uncertainty and error propagation (2 SE).

Sample	Age group (yr)	Average growth zone age (yr)	Radiometric age (yr)	Radiometric age range (yr)
CAF 2A	5 – 7	5.8	3.1	1.6 – 5.0
CAF 2B	5 – 7	6.3	4.8	3.1 – 6.9
CAF 2C	5 – 7	5.8	3.5	2.1 – 5.1
CAF 3A	11 – 12	11.5	12.8	10.0 – 16.3
CAF 3B	11 – 12	11.4	11.4	9.2 – 14.0
CAF 4A	15 – 17	16.1	18.1	15.0 – 21.8
CAF 4B	15 – 17	15.9	19.8	16.6 – 23.5
CAF 4C	15 – 17	16.0	14.6	12.1 – 17.5
CAF 5B	20 – 24	21.9	26.7	22.0 – 32.4
CAF 5C	20 – 24	21.3	31.4	23.8 – 43.2

Correspondence of the measured lead-radium ratios with the expected ingrowth curve indicated growth-zone derived age estimates were relatively precise and provided support for Patagonian toothfish age estimation procedures for both CQFE and CAF (Figure 3-5). For most of the samples from each facility the measured ratios fell within 2 SE of the expected ingrowth curve. Note that the age plotted is the total age of the sample, which are both growth zone counts plus the time since capture. Treating the radiometric age determinations as independent estimates of age, the results indicated otoliths in the oldest age group were at least 24 years old. The general conformity of the age data to the ingrowth curve provides strong support for age estimates exceeding this minimum using the same age estimation criteria.

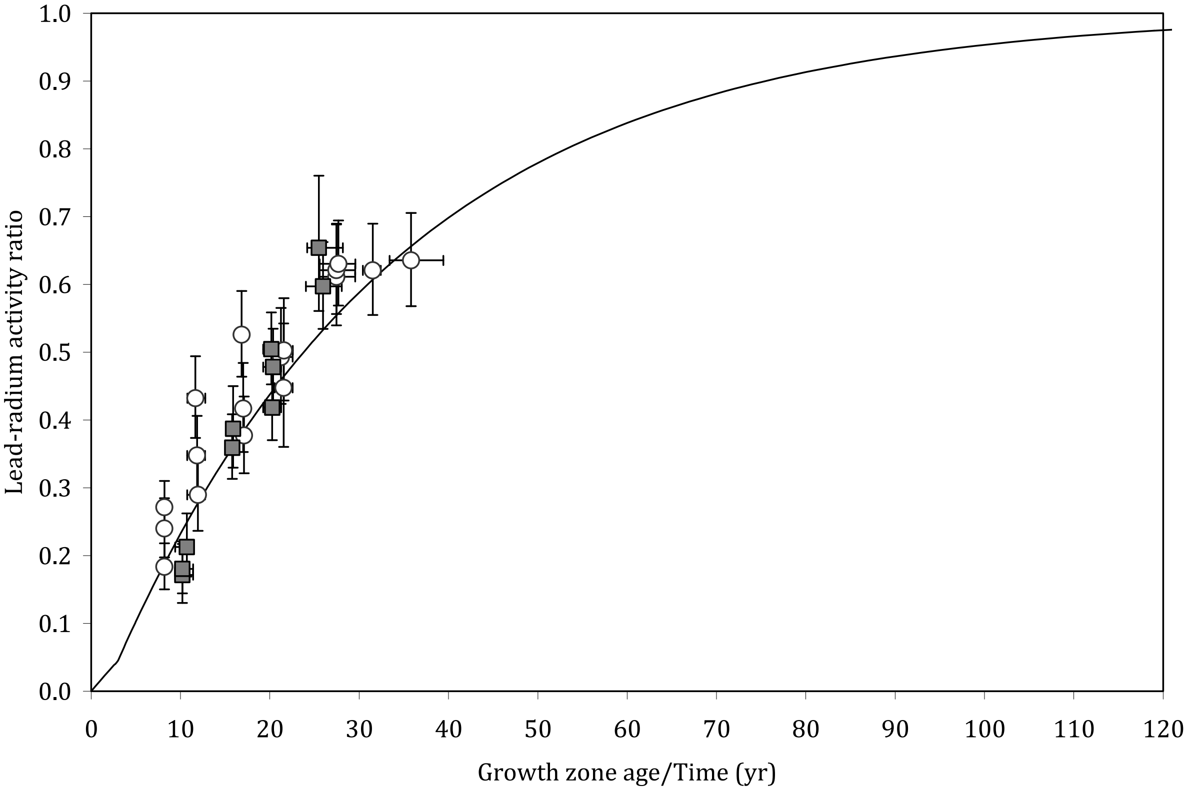

Figure 3-5. Plot of the measured lead-210:radium-226 ratios with respect to total sample age (growth-zone age plus the time since capture) for Patagonian toothfish samples processed for CQFE (open circles) and CAF (grey filled squares), plotted with the lead-210:radium-226 ingrowth curve. Horizontal error bars (some within the symbol size) represent the range of growth-zone age. The vertical error bars represent the analytical uncertainty associated with measuring lead-210 and radium-226 (2 SE).

An age agreement plot allowed for direct comparison of average growth zone age for the age groups with radiometric age (Figure 3-6). Correlation between the two ageing methods was best for CQFE with a slope of the regression that was close to 1.0 (regression slope = 0.955), indicating there was agreement between the methods ($R^2 = 0.884$). A *t*-test for slope differences indicated the regression slope was not different from 1.0 ($t_{(\text{slope})} = 0.504$, $t_{0.05(2),16} = 2.120$, $P > 0.5$); however, an offset of just a few years on average is noticeable for the elevation of the regression relative to the line of agreement. A *t*-test for differences in the elevation or intercept of the regression relative to the line of agreement revealed there was a significant difference ($t_{(\text{intercept})} = 2.305$, $t_{0.05(2),16} = 2.120$, $0.05 > P > 0.02$).

For CAF age estimation, the agreement was not as good with a slope that deviated considerably from a line of agreement (slope = 1.55). A *t*-test indicated the regression slope and intercept were both different from a line of agreement ($t_{(\text{slope})} = 4.335$, $t_{0.05(2),9} = 2.262$, $0.002 > P > 0.001$; $t_{(\text{intercept})} = 3.191$, $t_{0.05(2),9} = 2.262$, $0.02 > P > 0.01$). Specifically, age from growth-zone counts was overestimated by a few years for the 5-7 year age groups and underestimated for the 20 - 24 year age groups.

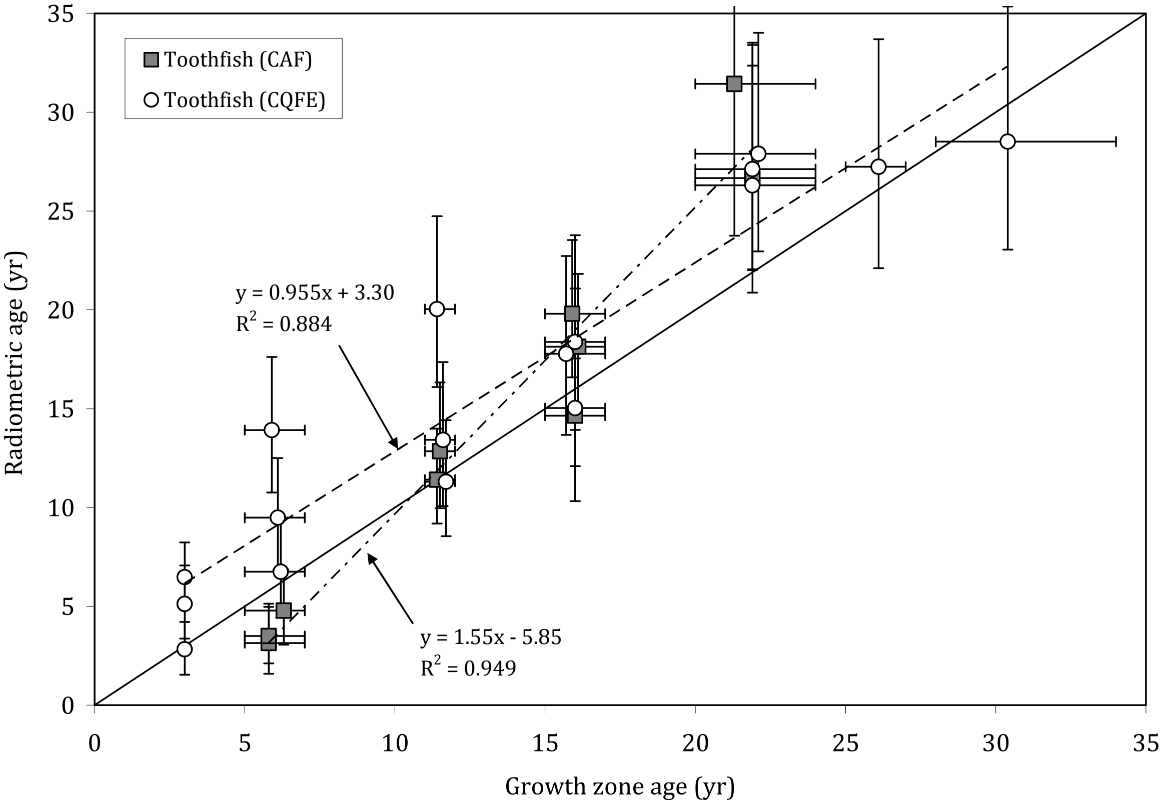

Figure 3-6. Patagonian toothfish age agreement plot of growth-zone derived age estimates *vs.* radiometric age estimates (corrected to time of capture), plotted with a line of agreement for comparison. The fine dashed line represents a regression of CQFE samples and the wide dashed line represents a regression of CAF samples for radiometric age vs. growth zone age. These trends were analyzed for agreement or disagreement relative to the line of agreement. Horizontal error bars (some within the symbol size) represent the range of growth-zone age. The vertical error bars represent the analytical uncertainty associated with measuring lead-210 and radium-226, and its calculated age (2 SE).

3.4 Discussion

Lead-radium dating provided valid age determinations for a range of Patagonian toothfish age classes in a trend that supported the use of otoliths as accurate indicators of age. Despite minor differences in age estimation procedures between CQFE and CAF facilities, differences that should be investigated and corrected, the general trend was in support of the criteria developed for age estimation from growth zone counting in baked and sectioned otoliths (Ashford et al. 2001). The radiometric age of the fish used in the oldest age groups was 28.5 years (23.0 – 35.4, 2 SE) for the Kerguelen region and 31.4 years (23.8 – 43.2, 2 SE) for the Heard Island region. While lead-radium dating was not possible for the oldest age estimates because of low sample availability, the age estimates made by Ashford et al. (2001) that approached or exceeded 40 years using the criteria were supported by lead-radium dating.

It is not likely that scale reading is accurate for the largest fish and probably underestimates the age of the oldest fish. While a minimum age of 23.0 to 23.8 years can be determined from the lower limit of the 2 SE distributions for the oldest age groups, these values were slightly older than most of the previous maximum scale age estimates of 21 - 24 years (Zacharov and Frolkina 1976, Hureau and Ozouf-Costaz 1980, Zhivov and Krivoruchko 1990, Cassia 1998). In addition, it is likely that individual fish in these groups were older because the lower limit was from a sampling distribution of means where 28 and 44 fish made up each experimental unit. Because radiometric age determinations indicate it is unlikely that the maximum age is in the low 20s, it recommended that scale circuli counting be used with caution at ages approaching 20 years.

Otolith cross section age estimates were accurate on average to within a few years of radiometric age for all age groups. The minor differences noted can be used to drive collaborative efforts to refine age estimation criteria among and within facilities. In a recent CON report, an age reader comparison revealed differences between CQFE and CAF that were exemplified by the lead-radium results for the oldest age groups; CAF tended to age fish older than CQFE at the 20 to 30 year level (Ashford et al. 2003). Lead-radium dating has provided an opportunity for CON to reassess otolith section interpretations based on valid age determinations and to develop age validated otolith reference sets for use in establishing an international age reading standard for Patagonian toothfish.

Lead-radium dating in this study provided support for the findings of other Patagonian toothfish age validation studies. Application of bomb radiocarbon dating provided the first evidence for accurate age determination using otolith thin sections (Kalish et al. 2001b). Data provided in the study were complicated by a high degree of variability in radiocarbon measurements relative to an expected rise in radiocarbon. From the findings of Kalish et al. (2001b), it can be stated that the maximum age of Patagonian toothfish used in that study were at least 40 to 41 years old based on a few key otoliths that show a clear indication that pre-bomb $\Delta^{14}C$ levels were recorded in the otolith core material. However, these results were complicated by 1) regional and depth related differences in the oceanographic $\Delta^{14}C$ signal; and 2) otolith age reader bias, which were discussed as plausible reasons for the variability by Kalish et al. (2001b).

While the findings provided a good basis for validation of age, further support was necessary because of the complications and the lead-radium dating from this study corroborate the findings of Kalish et al. (2001b). For young to middle age classes, application of modal length frequencies, edge analysis, and tag-and-release provided additional support for annual growth zone formation in the otoliths of Patagonian toothfish, but an extrapolation (to lesser or greater degrees) was required for older age classes (Ashford et al. 2002, Horn 2002, Krusic-Golub and Williams 2005). The comprehensive nature of the age group series used for lead-radium dating provides the missing link for age validation across these age classes.

Despite the relatively close proximity of the Kerguelen and Heard Island populations, there appeared to be a difference in the growth rate of fishes between these regions. Perhaps a difference in the formation of growth increment structure in the otolith, due to differing growth rates, is a reason for slightly different age interpretations. However, there is no way to account for differences between the collections relative to sex because sex was not recorded for most CAF samples.

While most of the replicate age groups were clustered in terms of radiometric age, there were a couple of notable outliers that might be explained by other factors (i.e. CQFE 2C and 3C). Age was unexpectedly high relative to the age determined for the other two members of the age groups. An analysis of potential factors (i.e. sex ratio, whole otolith weight, fish length) for anomalous individual fish or range of values provided no outstanding reason for the inconsistent results. The reason for the anomalous age determinations would not be expected because samples were randomly selected within the age groups. Furthermore, lead-210 activity for each of these samples was slightly greater than what would be expected from the relatively consistent radium-226 uptake in the otolith core samples. Because the radium-226 levels are some of the lowest ever recorded from fish otoliths (see Chapter 5), the resultant lead-210 activity will be consequently low for young age groups. This places sample counting close to background count levels. While background count levels, as well as contribution from blanks, are carefully accounted for and subtracted from the raw counts, it is possible that some unaccounted for factor led to more background or blank contribution to the counts for these samples. A drastically different value may allow for the elimination of these age groups from describing the age trends; however, these values were not different enough to remove them from the analysis.

3.5 Conclusions

Application of lead-radium dating to Patagonian toothfish was a success across numerous age classes and provided support for age estimation procedures using transverse otolith cross sections. Estimated age from growth zone counts was not different from lead-radium ages for CQFE, with what appears to be a bias of a few years for CAF and there may be differences between the two age estimation facilities. While differences appear to be statistically significant, the differences in age estimations were relatively minor and likely correctable in terms of otolith growth zone interpretation. These findings provide CON with an age-validated opportunity to develop a refined age estimation criteria and otolith reference sets for international standardization of the age estimation criteria. Because lead-radium dating indicated that Patagonian toothfish can live for more than 24 years, which provided support for the age estimation procedures that came up with longevity near 40 years, it is recommended that the use of scales is conservative and limited to age estimates much less 20 years.

CHAPTER FOUR

✵

LEAD-RADIUM DATING OF ORANGE ROUGHY (*HOPLOSTETHUS ATLANTICUS*): VALIDATION OF A CENTENARIAN LIFESPAN

4.1 Introduction

Orange roughy (*Hoplostethus atlanticus*) is a member of the family Trachichthyidae and is a deepwater commercially important fishery species in regions that range from New Zealand (Clark 1999, 2001) and Australia (Bax et al. 2005) to southwest Africa (Boyer et al. 2001) and the North Atlantic (Large and Bergstad 2006). Branch (2001) provided an overview of global orange roughy fisheries, and more recently Sissenwine and Mace (2007) reviewed the sustainable management of deepwater fisheries, including a case study of orange roughy fisheries. The development of deepwater fisheries has been relatively recent, with the first major orange roughy fisheries developing off New Zealand in the late 1970's, followed by Australia in the mid-1980's, smaller fisheries in the North-eastern Atlantic Ocean in the early 1990's, and fisheries off Namibia, Chile, and the Southern Indian Ocean through the mid to late 1990's (Branch 2001, Bax et al. 2005, Japp and James 2005, Large and Bergstad 2005, Sissenwine and Mace 2007). Similar to other deepwater species, orange roughy fisheries have proved difficult to manage sustainably; some tended to support a boom and bust fishery, in which much of the catch occurred in the first few years of the fishery, followed by substantial catch rate declines with increased effort, culminating in the fishery being effectively closed or abandoned (Branch 2001, Clark et al. 2007, Sissenwine and Mace 2007).

The most well developed and productive orange roughy fisheries in the world have been from the waters off New Zealand (Branch 2001). Of these, the largest fishery has been situated on the Chatham Rise, where annual catch levels of around 40,000 t were reached in the late 1980s, but by 2007–08 these were reduced to about 10,500 t following a series of Total Allowable Commercial Catch (TACC) reductions; however, in recent years there has been growing concern that this catch level will not be sustainable (Sissenwine and Mace 2007, Ministry of Fisheries 2008). A similar scenario was realized for orange roughy fisheries off Australia, where catch quotas were reduced over time (Bax et al. 2005), until in 2006 the species was declared threatened by the Australian Department of Environment and Heritage, and all but the Cascade fishery were closed. An approach that was thought to be conservative was applied to one of the most recent orange roughy fisheries to develop, off Namibia, with the hope of establishing a basis for sustainability. The fishery appears to have suffered quickly from over-exploitation (Boyer et al. 2001, Butterworth and Brandão 2005); however, hypotheses such as an intermittent aggregation for spawning are also being considered as an explanation for changes observed in the fishery (McAllister and Kirchner 2001, Oelofsen and Staby 2001).

Whilst major efforts have gone into managing orange roughy fisheries, after three decades of exploitation almost all stocks have been fished down substantially, and concerns are continually being raised about sustainability (Clark et al. 2007, Sissenwine and Mace 2007). The problem usually seems to be a high vulnerability of orange roughy to fishing, combined with rapid development of the fishery, such that substantial amounts are caught before management is introduced (Clark 2001, Lack et al. 2003, Morato and Clark 2007). For stocks where the accumulated biomass has now been fished-down, the sustainability of the fishery will be dependent upon stock productivity. The productivity of orange roughy stocks is believed to be especially low, but remains poorly understood (Francis and Clark 2005, Sissenwine and Mace 2007).

In most stock assessments, productivity is determined using ageing analyses to estimate growth, age at maturity, longevity and rate of natural mortality, and recruitment variability (Clark 2001, Francis and Clark 2005). Whilst there is growing confidence in current age interpretations of deepwater fish species, and in proposed mechanisms for how some may attain high longevity (Cailliet et al. 2001), many age estimates are based solely on sagittal otolith growth zone counts. In some cases, the lack of a convincing age validation associated with these counts has lead to the age interpretations being questioned; the orange roughy, believed to live to ages over 100 years, has been one of the most debated (Gauldie and Cremer 1998, Branch 2001).

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

The most recent estimations of orange roughy age have utilized growth zone counts from longitudinal thin sections of sagittal otoliths, and made the assumption that the zone counts represent age (Tracey and Horn 1999). The resolution of growth zones in older otoliths has proven difficult, and the zone counts can have high uncertainty (Figure 4-1). There may also have been some between-facility bias in zone counting interpretation (Francis 2006). While the general consensus in the international community is that orange roughy is a slow growing and long-lived species, the continued argument that they are actually short lived and fast growing, combined with limited nature of age validation studies to date, has highlighted the need for further and conclusive age validation.

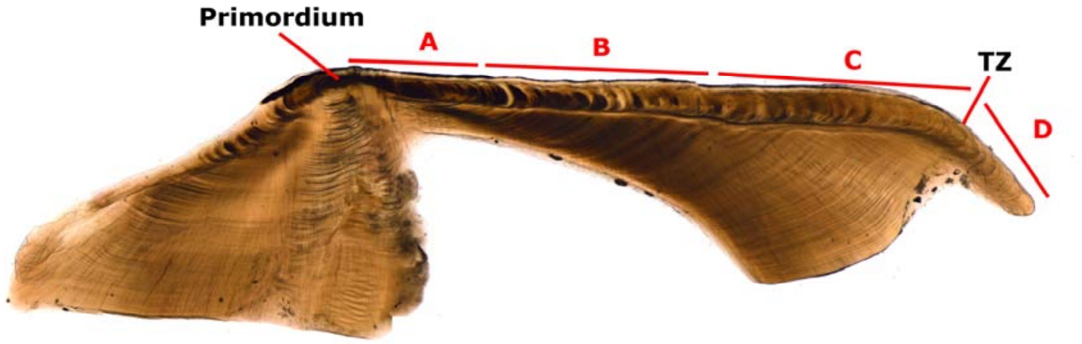

Figure 4-1. Cross section of orange roughy (Hoplostethus atlanticus) otolith using the methods described in Tracey and Horn (1999). Image labels morphological features and the region of zone counts; A) juvenile, B) adolescent, C) pre-transition and D) post-transition. TZ denotes the position of the transition zone, which can be a problematic location in the counting procedure (Image from Tracey et al. 2007).

The age validation techniques that have been applied to deepwater fishes range widely in efficacy and precision (Campana 2001). Some techniques rely on establishing a temporal context to early growth by measuring changes in otolith zones or fish length; for instance, marginal increment analysis and length frequency analysis have been applied to orange roughy (Mace et al. 1990, Tracey and Horn 1999). The disadvantage of these techniques is that is it necessary to extrapolate the findings to provide support for older ages because of a loss of growth zone or length mode resolution. Other age validation methods rely on marking and recapturing older fish (e.g. oxytetracycline injection and tagging), but recovery of deepwater fishes is time consuming and the survival rates are likely to be low (Campana 2001). The potential for more successful tagging of deepwater fishes in the future has been raised by the development of equipment for in situ tagging, which has been used for redfish (*Sebastes mentella*) off Iceland at depths of around 500–800 m (Sigurdsson et al. 2006). Advances in the use of radioactive proxies for age have provided opportunities for independent age determination of deepwater fishes, and the primary techniques currently in use are bomb-radiocarbon ($\Delta^{14}C$) and lead-radium dating, both of which can work well either independently or together (e.g. Andrews et al. 2007). However, for orange roughy bomb radiocarbon dating is unsuitable because the species lacks an epipelagic phase in its life cycle, a requirement if the timing of the influx of bomb radiocarbon is to provide an accurate temporal marker (Kalish 2001).

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

Increased sensitivity in the techniques used to determine radium-226 activity has made it possible to reduce the sample size necessary to detect radium-226 in otolith material, with increased precision and accuracy. As a result, the first few years of growth can now be extracted from the core of orange roughy otoliths and analyzed for both lead-210 and radium-226; hence, there is no need for sample weight dependence in calculating age, nor the assumption that radium-226 uptake was constant (Andrews et al. 1999a, Campana 2001). In addition, advances in mass spectrometry have significantly reduced the error and processing time associated with the measurement of radium-226, now making the measurement of lead-210 the limiting factor in lead-radium dating (Andrews et al. 1999b). By using the same small sample of core material (the first few years of growth) for the measurement of both lead-210 and radium-226 activities, the problems associated with mass growth assumptions or variable uptake of radium-226 are largely circumvented (Campana et al. 1990, Kimura and Kastelle 1995).

The aim of this study was to answer questions about the validity of centenarian age estimates for orange roughy. Will age estimations made from otolith cross sections agree with age determined from measured lead-radium ratios by testing a series of age groups (youngest to oldest)? What will the minimum longevity be for orange roughy based on the lead-radium dating of the oldest age group and can concerns about a wide disparity in estimated lifespan (approximately 30 years vs. more than 100 years) be put to rest? Can a critical analysis of these findings, relative to other lead-radium dating discussions that have cast doubt on the technique, be used to provide support for the efficacy of lead-radium dating as tool for age determination in fishes?

4.2 Materials and Methods

Samples used in this study were from archival collections that were previously aged from growth zone counts using longitudinal thin sections. The sister otolith from the aged fish was available for radiometric analyses and age groups were selected to for the best possible coverage of the age range. In the feasibility study, older collections aged by NIWA were used, but as an alternative to a lack of sample for older age groups, otoliths collected by the Seafood Industry Council (SeaFic) and aged by Central Ageing Facility (CAF), Australia were also used for lead-radium dating. The number of otoliths required for orange roughy age groups was based on lead-radium information determined from a feasibility study (Andrews and Tracey 2003). Orange roughy otoliths were selected to form a range of age groups from regions off the north island of New Zealand (Figure 4-2).

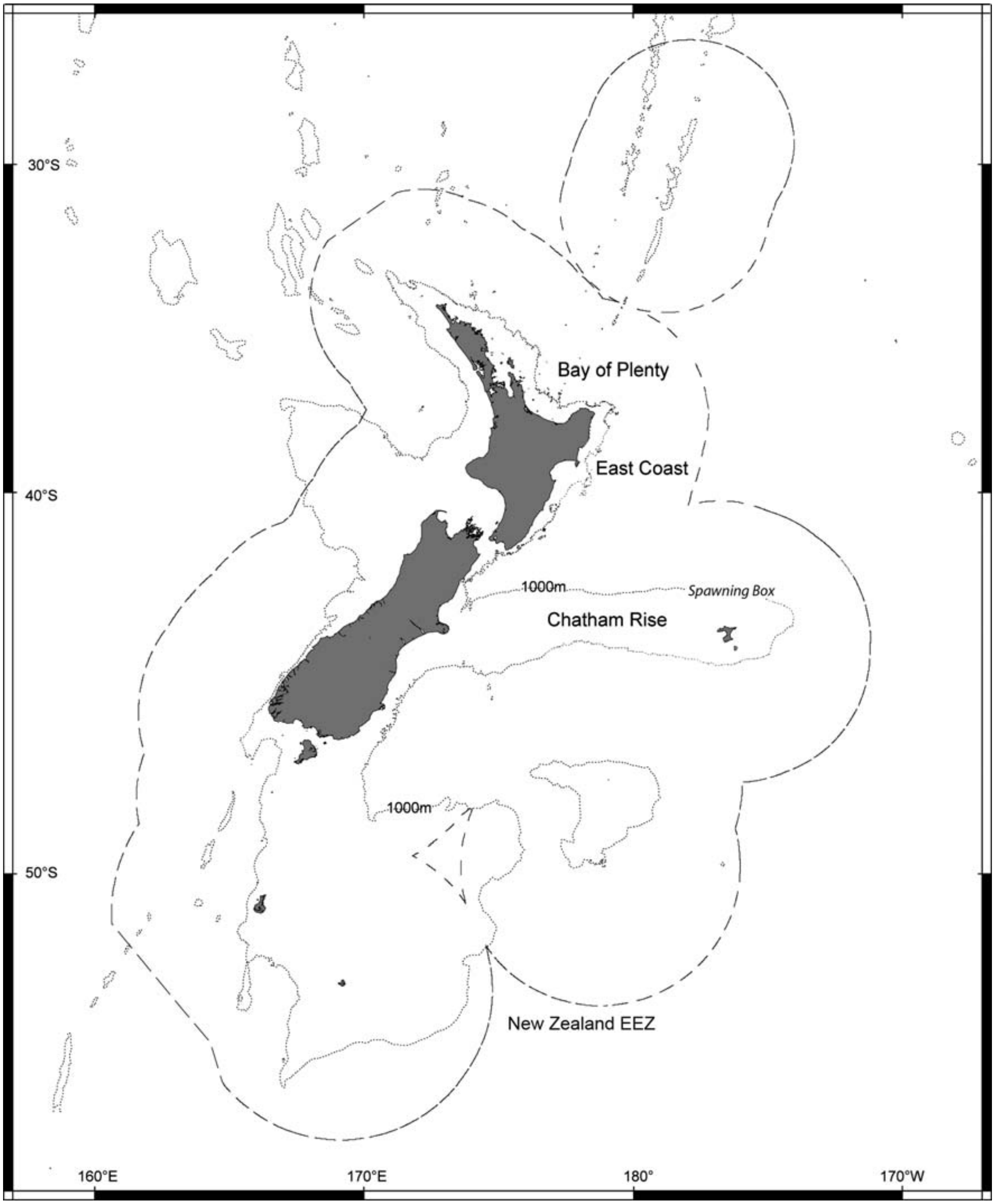

Figure 4-2. New Zealand with its diverse regional bathymetry denoted by a 1,000 m contour line. The New Zealand Exclusive Economic Zone (EEZ) is traced with the dashed line. Otoliths from orange roughy used for lead-radium dating were from the labeled regions. (Image modified from NIWA)

In the feasibility study, whole juvenile otoliths collected from the northwestern region of Chatham Rise in 1989 were selected to provide a low age group (group 0 - 2 yr). Additional otoliths used in the adult samples were from other Chatham Rise regions and Bay of Plenty collected in 1984 (group 34 - 38 yr), 1990 (group 61 - 71 yr), and 1996 (group 70 - 81 yr). The follow up age group series was composed by making use of the feasibility study results; core size and lead-radium activity information was used to determine the composition of the six pooled adult otolith samples. The additional age groups considered for analysis in this study were aimed at filling in the older age groups (Appendix 2). Otoliths for these samples came from four regions (Spawning Box, northeastern and northwestern Chatham Rise, and the middle East Coast) and all were collected in 2002 and 2003. Age groups were filled with otoliths from these regions and resulted in the following age groups: 25 – 30 yr (ORH 1), 40 – 45 yr (ORH 2), 60 – 69 yr (ORH 3), 70 – 80 yr (ORH 4), 81 – 88 yr (ORH 5), 90 - 108 yr (ORH 6). Samples from Spawning Box contributed exclusively to ORH 1 and 2, and composed part of ORH 3 with East Coast samples. The oldest age groups (ORH 4, 5, 6) consisted of otolith samples from all regions.

4.2.1 Sample preparation and processing

All otoliths used in this study were ground down by hand on a Buehler Ecomet III lapping wheel with 120 to 320-grit wet-dry silicon-carbide paper to the dimensions and weight of an otolith with a target estimated age, with the exception of the 0 – 2 year group that were processed whole. Hand grinding was chosen for this study over the use of a micromilling machine primarily to follow the method used in the feasibility study and also because of the ease at which each species could be cored. All cores were individually measured and weighed for consistency. Samples were cleaned of any adhering contamination, the details of which were described in Chapter 2.

Based on the dimensions and weight of 4 yr whole otoliths from several samples made available for the feasibility study, and from information on juvenile otolith weight data available from Mace et al. (1990), a target core sample size of 5.5L x 2.5W x 0.8D mm weighing approximately 0.012 g was removed from adult otoliths at the apex of the otolith, where it is known that the youngest material located. This was achieved by grinding away the proximal surfaces of the whole otolith down to the apex or juvenile otolith portion of the otolith, which could easily be identified visually; the result was a core that looked very similar to a juvenile otolith in shape (pyramidal) and size. It was ascertained from the feasibility study that dimensions alone were not enough to be certain the core was not heavier than targeted size because the average weight of cored otoliths was higher than expected (~0.024g). To correct for this in this study, each core was ground down using otolith weight and visual observations of growth structure and zone patterns as a guide; regrinding was a common result once the dimensions were met because the weight was greater than expected. A weight of just under 0.02 g was targeted to avoid the loss of too much material and to allow for mass loss during the cleaning process (typically 3-5%). The weight of the cleaned cores and pooled otolith age groups were measured to the nearest 0.1 mg.

4.2.2 Radiochemical protocol

A detailed protocol describing sample preparation, chromatographic separation of radium-226 from barium and calcium, and analysis of radium-226 using mass spectrometry is given in Chapter 2. These procedures have not changed for this study, save two aspects of the analysis; 1) radium recovery was improved by shifting the collection interval on the final chromatography column to begin after the first 200 µL (as opposed to after 250 µL), and 2) purified radium samples were analyzed using an improved ICP-MS technique, which is less prone to ionization suppression (Craig Lundstrom, University of Illinois-Urbana, Champagne, unpublished data).

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

4.3 Results

The six age groups ORH 1 to ORH 6 covered a range of pre-recruitment juveniles to old adults, and consisted of groups of 13 to 32 individual otolith cores, with an age group sample weight of 0.227 to 0.464 g (Table 4-1). The mean core weight was consistent and close to the target weight of a 4-year-old otolith (~0.12 g). The results from three of the four feasibility study age groups were added to provide more lead-radium dating results, but a sample that experienced accidental loss of radium-228 tracer during the spike addition process (61 – 71 yr group) was not included (Andrews and Tracey 2003). Sample weight for the feasibility study ranged from a very low weight for the juvenile sample (0.040g) to the highest group weight (0.842g). Mean core weights for the feasibility study were slightly higher because they were extracted in the exploratory phase of the overall study.

Table 4-1. Summary of characteristics for the orange roughy samples processed in this study and the previous feasibility study. Estimated age composition and average time since capture for each group, with resultant pooled sample number and weight are given. An average core weight for each otolith in each sample is given to show consistency of coring.

Sample	Age group (yr)	Average age (yr)	Time since capture (yr)	Number of otoliths	Sample weight (g)	Average core weight (g)
ORH 1	25 – 30	28	2.7	31	0.426	0.0137
ORH 2	40 – 45	42	2.7	32	0.464	0.0145
ORH 3	60 – 69	65	3.0	24	0.402	0.0168
ORH 4	70 – 80	74	3.1	26	0.339	0.0130
ORH 5	81 – 88	85	2.9	14	0.242	0.0173
ORH 6	90 – 108	98	2.7	13	0.227	0.0175
Feasibility	0 – 2	2	13.3	9	0.040	0.0044
Study	34 – 38	36	18.7	37	0.842	0.0228
	61 – 71[1]	66	12.7	20	0.474	0.0237
	70 – 81	76	7.0	28	0.701	0.0250

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

The activity of lead-210 and radium-226 was measured for all samples (Table 4-2). The activity of lead-210 was relatively inconsistent with increasing age, as would be expected for samples with consistent radium-226 levels; however, the variable activity of radium-226 compensated for what would have been a random age distribution, the result being a steady increase in the lead-210:radium-226 activity ratio with increasing estimated age. It is interesting to note that the measurable activities from the extraordinarily small sample juvenile sample were possible because the activity of radium-226 was relatively high and the overall age (time since collection plus average age) was 14 years. The range of sample contribution of radium-226 to the measured radium ratios using ICP-MS was calculated as 9 to 72% based on the known radium-228 spike ratio at the time of processing, which accounted for some of the differences in measurement precision.

Table 4-2. Radiometric results for orange roughy. Listed are the estimated age range from growth-zone counts and measured lead-210 and radium-226 activities for all samples. Two standard errors were expressed as an error percentage for the measured activities. Calculated activity ratios and their corresponding margin of error (based on error propagation and the delta method) are given to provide a 95% confidence interval.

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

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

The estimated age of the samples from the growth zone counts were similar to the radiometric ages determined from the measured lead-210:radium-226 activity ratios

(Table 4-3). There was considerable agreement for the sample series, with one age group not in agreement (Feasibility study age group 34 – 38 yr) based on the margin of error from lead-radium dating (2 SE). This sample was aged lower using lead-radium dating than the estimate from growth zone counts.

Table 4-3. Summary of growth-zone ages and radiometric ages for orange roughy. Average growth-zone age (with 2 SE of the age group mean) is given with radiometric age, calculated from the measured lead-210:radium-226 activity ratios and corrected for time since capture. Radiometric age range was based on the analytical uncertainty and error propagation (2 SE).

Sample	Age group (yr)	Average growth zone age (yr)	Radiometric age (yr)	Radiometric age range (yr)
ORH 1	25 - 30	28 (0.5)	24	22 – 27
ORH 2	40 - 45	42 (0.7)	48	42 – 55
ORH 3	60 - 69	65 (1.0)	66	55 – 82
ORH 4	70 - 80	74 (1.1)	79	63 – 113
ORH 5	81 - 88	85 (1.4)	83	57 – undefined
ORH 6	90 - 108	98 (3.0)	undefined	93 – undefined
Feasibility	0 – 2	2 (0)	1	0 – 3
Study	34 – 38	36 (0.3)	29	24 – 34
	70 – 81	76 (1.4)	83	61 – undefined

Correspondence of the measured lead-210:radium-226 ratios with the expected ingrowth curve indicated growth-zone derived age estimates were accurate (Table 4-4), within a level of uncertainty that increases with age, and provides support for orange roughy age estimation procedures (Figure 4-2). This plot is only possible for total sample age (age from growth zone counts plus the time since capture). For all but two of the samples the measured ratio fell within 2 SE of the expected ingrowth curve. The youngest sample (total sample age of about 14 yr) was in close agreement with the expected ratio, indicating the effect of exogenous lead-210 was low or negligible. This was the basis for choosing an initial uptake ratio (R_0) equal to zero. Treating the radiometric age determinations as independent estimates of age, using core material and making no assumptions with regard to otolith growth, the results indicated otoliths in the oldest age group were at least 93 years old (Figure 4-3).

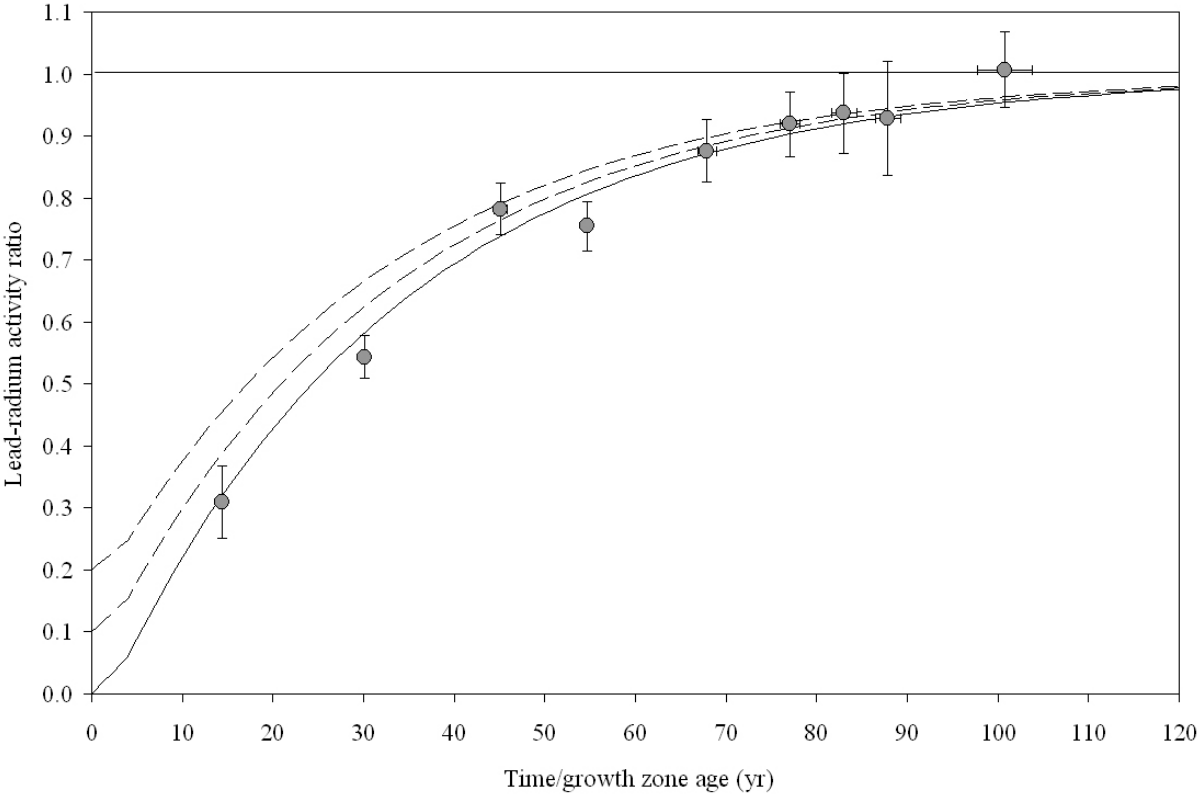

Figure 4-3. Plot of the measured lead-210:radium-226 ratios with respect to total sample age (growth-zone age plus the time since capture) for orange roughy samples, plotted with lead-210:radium-226 ingrowth curves representing no initial uptake of lead-210 (solid line) and an initial uptake of 0.1 and 0.2 as an indication of what the affect might be for a measureable contribution to the ratio. Horizontal error bars (some within the symbol size) represent 2 SE for the mean growth-zone age. The vertical error bars represent the analytical uncertainty associated with measuring lead-210 and radium-226 (2 SE).

An age agreement plot allowed for direct comparison of average growth zone age for the age groups with radiometric age (Figure 4-4). Age data were plotted with respect to each other and relative to a line of agreement (1:1). All data could be considered in this manner, except one data point (ORH 6) with a measured ratio that narrowly exceeded 1.0 (1.0067;

undefined age with a lower limit of 0.9461 or 93 years). Correlation between the two ageing methods was good (R^2 = 0.979). The slope of the regression was close to 1.0 (regression slope = 1.08), indicating there was general agreement between the methods; however, this finding does not take into consideration the change in radiometric age uncertainty as the measured lead-210:radium-226 activity ratio increases.

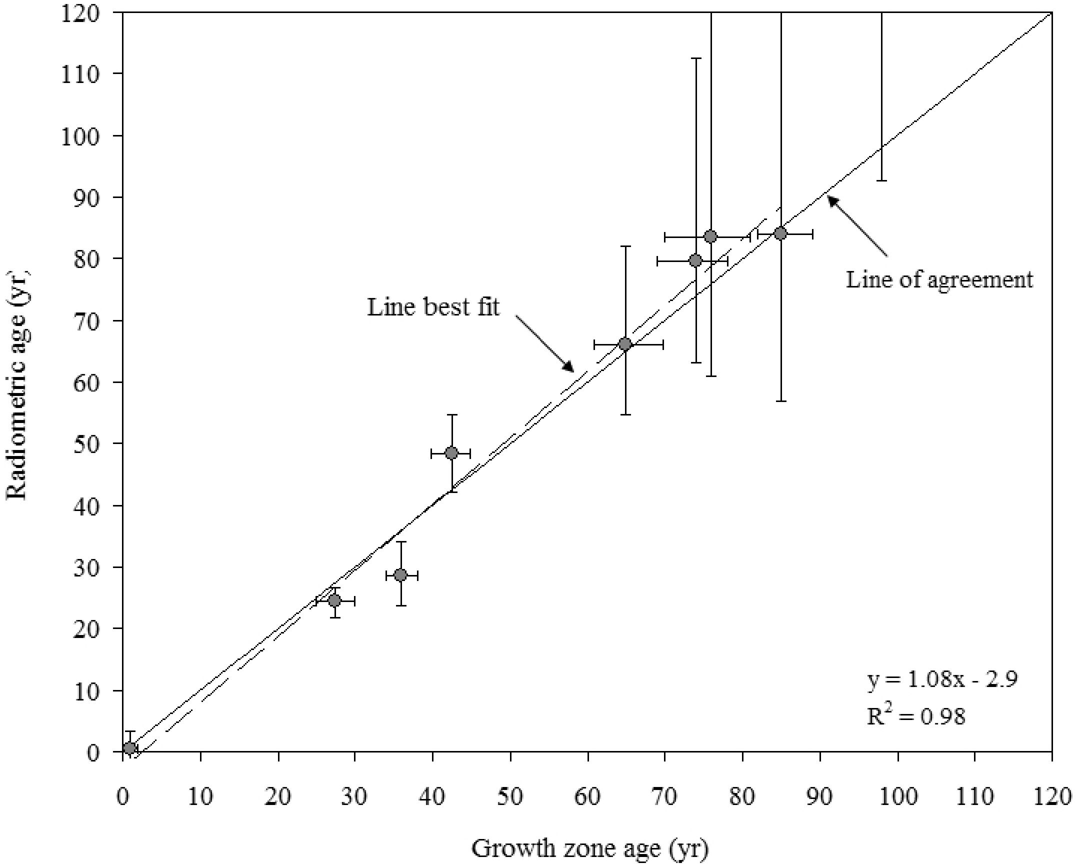

Figure 4-4. Orange roughy age agreement plot of growth zone derived age estimates versus radiometric age estimates (corrected to time of capture), plotted with a line of agreement for comparison. The dashed line represents a regression of radiometric age *vs*. estimated or growth zone age, which provided a representation of the trend in age agreement. Horizontal error bars (some within the symbol size) represent 2 SE for the age group mean. The vertical error bars represent the analytical uncertainty associated with measuring lead-210 and radium-226 (2 SE). Error bars that meet the upper margin exceeded a ratio of 1.0 are undefined in terms of radiometric age. The lower limit of the oldest group is represented by the lower portion of the error bar (93 yr) because the measured ratio is undefined (1.0067).

4.4 Discussion

The application of lead-radium dating to orange roughy otolith cores was successful with good agreement between the mean age from growth zone counts and the lead-radium technique. Use of otolith core material avoided potential problems associated with the application of otolith mass-growth models and provided the most accurate age determinations to date for orange roughy. No difference was found between age estimation techniques and the findings provided refined support for age estimates that exceed 100 years; however, uncertainty in radiometric age increased as lead-radium ratios approached one. Independent of age estimation procedures, lead-radium dating in this study provided support for a centenarian lifespan.

The uncertainty in orange roughy otolith zone counts remains a problematic area. Recent analyses have examined the consistency of age estimations, particularly those made between facilities in New Zealand and Australia (Francis 2006). As a result of a potential bias identified between institutes, a workshop was held between New Zealand, Australia, and Chile (Tracey et al. 2007b), to review the ageing protocols. Substantial progress to improve the consistency of zone counts was made at this workshop, but a high variability in zone count age estimates remains likely. It must be noted that the error bars on the growth zone age estimates shown in figures 4.2 and 4.3 describe the variability of age estimates within each sample group, and therefore do not include any age estimation uncertainty. Including this uncertainty would have inflated the error bars, but it would not have changed the overall conclusion because of the close 1:1 agreement between the mean growth zone and radiometric age estimates. The between-institute bias in growth zone counts was of the order of 10% (Francis 2006), which is also small enough that it would not have changed conclusions about orange roughy longevity.

Examination of otolith margin growth and length frequencies provided the first temporal evidence for a lifespan greater than 50 years, but this estimate was based on an extrapolation of trends observed with small fish to the largest fish (Mace et al. 1990). Further support for this finding came from one of the earliest applications of lead-radium dating to fishes (Fenton et al. 1991), and shortly thereafter with an application of radiocarbon dating (Kalish et al. 2001b). While radiocarbon dating (not to be confused with bomb radiocarbon dating) also provided support for a centenarian lifespan with rough age estimates that were complicated by other factors, lead-radium dating was the first to begin to provide more concrete evidence.

The seminal radiometric study on orange roughy by Fenton et al. (1991) used pooled whole otolith samples and an approach that made it necessary to make some educated assumptions about several unknowns. The study did not perform any growth zone derived age estimations, but instead sought to determine age independently for groups of fish with similar length and otolith weight. For the method to work there could be little or no: 1) between-individual variability in otolith-mass growth rate; and 2) variability in radium-226 uptake throughout the growth of the otolith. In addition to these factors, there were important assumptions about the very nature of the lead-radium dating technique; the otolith needed to be a closed system to the 1) ingrowth of lead-210 from radium-226 with no loss of radium-226 daughter products; and 2) incorporation of exogenous sources of the decay series radionuclides (not from the decay of incorporated radium-226). Within these assumptions the most conceivable problems were with the 1) potential loss of radon-222 (daughter product of radium-226 and a noble gas); and 2) incorporation of exogenous lead-210 or polonium-210 (used as a proxy for lead-210 in alpha-spectrometry). These concerns could not be thoroughly addressed at the time Fenton et al. (1991) performed the analyses on orange roughy otoliths, but the findings of this and other more recent studies have provided support for the assumptions that were necessary, and in some cases the assumptions have been tested directly.

A series of papers that typically focused on discrediting the high age determinations for orange roughy focused on the testing the veracity of lead-radium dating by working to address the assumptions necessary for the study performed by Fenton et al. (1991). In a perspective paper, West and Gauldie (1994) argued that there were uncontrollable errors that invalidated the technique for fish age estimation, but provided a series of observations and conclusions that failed to consider equally viable explanations that would not discredit lead-radium dating. In an attempt to measure loss of radon-222 from orange roughy otoliths, Gauldie and Cremer (1998) used bismuth-214 as a radioactive proxy for radon-

222 loss; however, the results of the study openly recognized anomalous experimental results that indicated the technique was functioning near detection limits and that equipment may have been faulty. Regardless of these rather significant observations, negative bismuth-214 activities (not a valid measure in nuclear sciences) were used to establish a weak trend that implied radon-222 loss was measured. To argue for inclusion of the negative values they stated, "However in the interests of showing all of the data the anomalous results are reported here and included in the analysis." Nevertheless, Gauldie and Cremer (1998) concluded from rather dubious results that loss of radon-222 was a problem for lead-radium dating and that these findings invalidated old ages. The inconclusive quality of the Gauldie and Cremer (1998) study was reiterated in a follow up application that reported a loss of 26-28% (Gauldie and Cremer 2000), but these findings were inconsistent with determinations made in this and other studies. Furthermore, the authors cited evidence that supported the conclusions (e.g. incomplete concepts from a report by Whitehead and Ditchburn (1996)), but a prior publication by Whitehead and Ditchburn (1995) that: 1) specifically addressed radon-222 diffusion from orange roughy otoliths; and 2) provided evidence to support a long lifespan was ignored (i.e. Gauldie and Cremer 1998, 2000, Gauldie and Romanek 1998).

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

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

Another scenario to consider with regard to loss of radon-222 is the potential affect on the measured lead-radium ratio as age approaches 100 years. In a study performed on yelloweye rockfish (*Sebastes ruberrimus*), otolith cores provided measured lead-radium ratios that were very close to secular equilibrium (Andrews et al. 2002). If radon-222 loss was a problem, secular equilibrium would not and could not be attained. It is at approximately 99 years that secular equilibrium was approached to within 95% for the ingrowth model used in the present study (core age of 4 years). Provided there was a radon-222 loss on the order of 25% for the oldest orange roughy age group (90-108 yr with an average age 98 yr), the measured ratio (1.0067, 2 SE low of 0.9461) would have been much lower (approximately 0.675) with a radiometric age of no more than 30 to 40 years. In addition, none of the samples analyzed in this study, as well as other studies (e.g. Andrews et al. 2002), would have exceeded this ratio. The findings presented here for orange roughy support the hypothesis that loss of radon-222 was not a significant factor in the determination of age from lead-radium dating.

The potential problem of radium-226 uptake variability was largely circumvented with the use of otolith cores (Campana et al. 1990), but detection limits for radium-226 combined with the small otolith core size for orange roughy precluded an analysis of otolith core material by Fenton et al. (1991). Whilst it is possible that otoliths with consistent radium-226 levels were measured in the whole otolith study, more support was necessary to alleviate concerns about this assumption. Based on a comprehensive synopsis, radium-226 uptake can vary considerably with a range of approximately 0.05 to 0.2 dpm·g^{-1} (Table 4-4); however, the present study provided support that radium-226 activity levels can also be relatively consistent among the core samples of a given size (average radium-226 = 0.0740 ± 0.0053 dpm·g^{-1}, n = 9). The notable exception was the whole juvenile age group (0.209 ± 0.011 dpm·g^{-1}), but this group consisted of otoliths that much smaller by about 3 to 5 times. This finding implies that within the first 2 years of growth radium-226 uptake may be greater. The reason for this finding is unknown, but may be attributed to differences in habitat or diet. Relatively high variability of radium-226 activities measured in other studies reinforce the hypothesis that uptake can vary and that mass-growth rate models using an average radium-226 activity provide radiometric ages that should have greater uncertainty than assumed. Whilst the radiometric ages in this study support those of Fenton et al. (1991), this study also places emphasis on the necessity for sample specific lead-radium measurements to avoid radium-226 uptake assumptions (Francis 2003).

Table 4-4. Summary of the study characteristics and radium-226 results for five orange roughy studies. Whole otoliths in this study refer to juvenile otoliths that were already smaller than coring size and weight. It is unclear what kind of sample was used in the analyses of Whitehead and Ditchburn (1996); they cite successive dissolutions from the same whole otolith sample and seven size fractions of 1-4 otoliths each (0.5 – 1 g), but also mention an 8 g sample.

	Technique	Sample type	Otolith number	Sample weight (g)	^{226}Ra activity (dpm·g^{-1})	Error (%)
This study	TIMS or ICP-MS	Whole & cores	9 – 37	0.040 – 0.842	0.0599 – 0.209	2.2 – 5.4
Allain and Lorance (2000)[1]	alpha-spectrometry	Whole	2 - 20	0.40 – 3.83	0.055 – 0.071	6.7 – 12.7
Gauldie and Cremer (1998)[2]	gamma-spectrometry	Whole	16 - 51	4.2 – 5.6	0.073 – 0.106	0.1 – 0.9[3]
Whitehead & Ditchburn (1996)	alpha-spectrometry	Whole	Not specified	~8	0.0560 – 0.137	5.5 – 7
Fenton et al. (1991)	alpha-spectrometry	Whole	28 – 315	6.06 – 6.793	0.0522 – 0.0625	5 – 7

[1] Unpublished data provided by personal communication with P. Lorance.

[2] Unpublished data from an absent Table 1 in Gauldie and Cremer (1998), later supplied by personal communication with R.W. Gauldie.

[3] The error associated with these measurements is statistically suspect given the radium-226 activities, sample masses, and a 48 hour experimental count time.

In an age and growth study of northeast Atlantic orange roughy lead-radium dating was applied to whole otoliths following a technique similar to Fenton et al. (1991), but the results were considered somewhat inconclusive (Allain and Lorance 2000). In the study, age estimates were made using whole and thin-sectioned otoliths, which indicated there was a high degree of age estimate departure beginning at approximately 40 years. This was similar to the classical plot discovered for Pacific ocean perch (*Sebastes alutus*; Beamish 1979), indicating there were differences in age on the order of decades between whole otolith and thin section ageing. Allain and Lorance (2000) did not consider the lead-radium results as conclusive because of low age resolution and indistinct results (P. Lorance, personal communication). Use of successive dissolutions on one otolith provided similar results to the findings of Whitehead and Ditchburn (1996). Each dissolution study was performed assuming the core material (youngest) was at the center of the otolith and that successive acid dissolutions would provide greater and greater lead-210 activities; however, both studies reveal anomalous distributions of lead-210 from this kind of study and properly concluded that the growth of the otolith was not concentric (Whitehead and Ditchburn 1996, P. Lorance, personal communication). The findings in this regard from Whitehead and Ditchburn (1996) have been cited as support for the argument that lead-radium dating cannot be applied to otolith material (Gauldie and Cremer 1998, 2000), yet the observable reason for the anomalous results was invalid assumptions about otolith growth geometry.

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

A centenarian lifespan is an indication that the sustainability of orange roughy fisheries may be challenged when taking into consideration concerns about the importance of maintaining size and age structure. Recent work has raised questions about the effect of fishing down age structure (Berkeley et al. 2004b), especially for species that may exhibit highly episodic recruitment (Longhurst 2002). To date, there is almost no information on orange roughy recruitment variability (Francis and Clark 2005). Management concerns for orange roughy may stem from a recent study on the use of lifetime egg production as an indicator of population persistence (O'Farrell and Botsford 2005). This study provided a means of assessing the impact of removing the largest, oldest and most fecund individuals of rockfishes (genus *Sebastes*). Furthermore, recent findings for black rockfish (*Sebastes melanops*) indicated the progeny of older females were better equipped for survival than from younger females (Berkeley et al. 2004a). Truncating the population age structure through size-selective fishing may exacerbate the problem by removing not only the most fecund individuals, but also potentially the producers of progeny that have the greatest chance of survival (O'Farrell and Botsford 2006a). With these factors in mind, the rather prognostic paper by Pankhurst and Conroy (1987) describing the bestowal strategy of orange roughy (maximizing reproductive investment in a small number of offspring) begs further consideration and research for the affects of fishing-down size and age structure. Validation of a centenarian lifespan for orange roughy is a call to not only better understand its life history, but to understand how the unknown complexities of its life history affect long-term sustainability as a fishery. The high longevity and low fecundity of orange roughy is an indication that the fishery has a low sustainable yield.

4.5 Conclusions

The findings of Fenton et al. (1991) were later examined in detail and found to be more robust than originally thought. Based on reasonable assumptions that were supported by orange roughy growth data (Smith et al. 1995), the radiometric data presented by Fenton et al. (1991) supported a maximum age that exceeded 84 years based on an analysis by Francis (1995). The present study circumvented assumptions that were previously necessary and provided additional support for accurate age estimates using thin otolith sections.

The question of whether orange roughy age estimates from otolith cross sections agree with lead-radium dating was well addressed by the series of age groups ranging from youngest to oldest. It is clear that precision for age estimation procedures is a work in progress (Francis 2006, Tracey et al. 2007b); however, the general agreement of radiometric age for each age group with increasing estimated age provided support for procedures used to by CAF. Independent of age estimation procedures, lead-radium dating indicated orange roughy have a minimum longevity of at least 93 years. It is likely that individual fish in these groups were older because this lower limit of 93 years is from a sampling distribution of means where 13 fish made up the experimental unit. The critical analysis of these findings, relative to other lead-radium dating discussions that have cast doubt on the technique, have provided strong support for the efficacy of lead-radium dating as tool for age determination in fishes. It is certain in these terms that the wide disparity in estimated lifespan, ranging historically from approximately 20 years to more than 100 years, can be resolved finally with a high degree of certainty. Lead-radium dating of otolith core material has validated a centenarian lifespan for orange roughy.

CHAPTER FIVE

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RADIUM-226 IN OTOLITHS: SYNOPSIS AND REVIEW

Application of lead-radium dating to numerous species from various habitats all over the world has given rise to an interesting and complex database for radium-226 in otoliths that has never been comprehensively reviewed. The intent of this chapter is to synthesize all measurements of radium-226 from otoliths and to organize it to allow for the development of analysis criteria and potential patterns that may assist with future works.

Measurement of radium-226 in otolith material began with the first application of lead-radium dating to the otoliths of splitnose rockfish (*S. diploproa*; Bennett et al. 1982), and since then number of application has increased to more than 40 species. Applications were largely to deep-sea fishes because other age validation techniques were not possible or were of limited application for logistical and technical reasons. For other more nearshore species, the difficulty of reading growth zone counts in otoliths was the reason for lead-radium dating.

Measurement of radium-226 in otoliths of marine fishes ranges from the northern Pacific and Atlantic Oceans to the Southern Ocean. Most of the work was from the northern Pacific Ocean with 20 species covered in 16 papers (Appendices 3 and 4). From these papers, there were 142 separate radium-226 measurements from otolith material, making it the most extensive record with papers dating from 1982 to the present. The waters around Australia and New Zealand have the second greatest number of species and papers covering 13 species in 12 papers, and producing 116 radium-226 measurements (Appendices 5 - 7). From the northern Atlantic Ocean and Gulf of Mexico there were six species and six papers producing a total of 64 radium-226 measurements (Appendices 8 and 9). The Southern Ocean is the most recent region to provide radium-226 measurements from otoliths and just two species in two papers provided a rather extensive data set from 45 otolith samples (Appendix 10). In total, there have been 326 reliable measurements of radium-226 in otoliths from 42 different fish species since the first application of lead-radium dating to fishes in 1982.

From the reported values to date, a general observation can be made about the range of radium-226 activity in otolith material and it can cover approximately three orders of magnitude. Values measured to date have ranged from near 0.001 $dpm\cdot g^{-1}$ to values exceeding 1.0 $dpm\cdot g^{-1}$ and an analysis of these data may seem straightforward. However, before research can be made regarding patterns between and within regions and species, consideration must be made for the diversity of sample composition from the numerous and varying experimental designs. There were basically three types of otolith samples among all studies to date: 1) whole juvenile otoliths; 2) cored adult otoliths; and 3) whole adult otoliths. Whole juvenile otoliths were separated from whole adult otoliths because they can be given special consideration in some studies. These otoliths can represent a more specific time period and may provide information on changes in early uptake of radium-226 when compared with otolith cores. Whole adult otoliths represent an average uptake through the period of growth to the age that is represented by the sample. Cored otoliths can represent a short period of uptake that can be dated back to when the fish were youngest (usually juvenile state); this scenario may provide a unique record of radium-226 uptake overtime, but there are additional considerations that will be discussed later.

Radium-226 information from early lead-radium studies was limited because measured activities were from whole otoliths, a necessity due to detection limits for the techniques available at the time. The feasibility of lead-radium dating for a given species was limited by one significant assumption; uptake of radium-226 needed to be in constant proportion to otolith mass growth through ontogeny. Provided this was true, either a mass growth model could be applied or otolith core material could be used in a radiometric age determination study. In one of the earliest studies, an inconsistent ontogenetic uptake of radium-226 was demonstrated and lead-radium dating was not successful for blue grenadier (M*acruronus novaezelandiae*; Fenton et al. 1990). In other applications, the consistency of radium-226 uptake was demonstrated in a creative manner by measuring activity from a series of whole otolith samples that ranged from younger (small otoliths/fish) to older (large otoliths/fish). Bennett et al. (1982) provided support for this assumption by measuring radium-226 in a series of four samples that ranged in age from 1-2 years to over 80 years in terms of estimated age. Uptake was consistent within the margin of error for the radium-226 assay at the time and a reasonably successful validation of age was made for splitnose rockfish.

Some of the highest radium-226 activities were recorded from otoliths that were known to form as juveniles living in continental nearshore waters. Otoliths from fish taken in the Gulf of Mexico (red snapper (*Lutjanus campechanus*), red drum (*Sciaenops ocellatus*), and Atlantic tarpon (*Megalops atlanticus*)) and the Bay of Carpentaria, Australia (three snapper species (*L. erythopterus*, *L. malabaricus*, and *L. sabae*), have all provided some of the highest radium-226 activities (Milton et al. 1995, Andrews et al. 2001, Baker et al. 2001 a and b). For red snapper and red drum taken near Louisiana and Alabama, whole juvenile or cored adult otoliths provided the highest levels for each species, ranging up to 0.9754 $\text{dpm}\cdot\text{g}^{-1}$ and 1.140 $\text{dpm}\cdot\text{g}^{-1}$, respectively. Whole juvenile and cored adult otoliths from Atlantic tarpon taken near Florida provided activities that covered a considerable range of uptake and varied by a factor of ten (0.0440 to 0.4010 $\text{dpm}\cdot\text{g}^{-1}$). Red snapper had an uptake that varied by a factor of approximately four, but precision was low; however, this case may provide evidence that it is important to compare samples with consistent otolith mass, or formational period. For this sample series, the activity of radium-226 decreased as average otolith/core weight increased, providing an indication there were changes in uptake during these early years of growth (Figure 5-1). This trend was further reinforced with the addition of radium-226 values for whole otolith samples (Baker et al. 2001a). It is important to note that the uncertainty associated with the cored otolith measurements was relatively high (Baker et al. 2001b), but the trend follows in relation to whole otolith analyses in a similar study on whole otoliths with greater precision (Baker et al. 2001a).

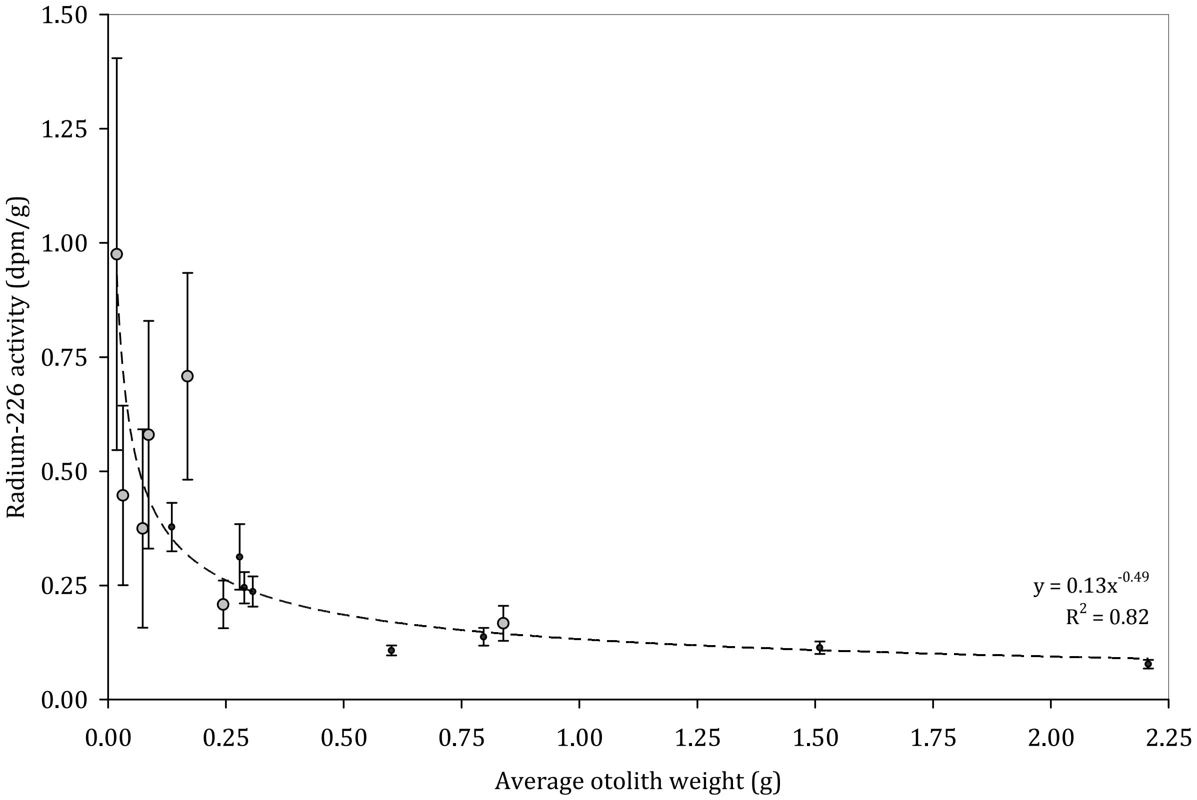

Figure 5-1. A trend in the levels of radium-226 were documented for both whole (black dot) and cored (grey filled circle) otoliths of red snapper (*Lutjanus campechanus*). The differences were measured in a series of experiments working to age this species and document radon-222 loss (data from Baker et al. 2001a and b), which have been synthesized here. Changes with increasing otolith weight appear to document an ontogenetic change in radium-226 uptake, especially within the very earliest growth. The lowest otolith weight group was whole juvenile otoliths and the additional five groups were cored to the first few years of growth with increasing core size. The curve was fitted to these data to provide visual assistance for the observed trend, but it is possible that the amplitude of the early growth uptake is an artifact of analytical uncertainty.

The estimated age for the red snapper sample series was from 0.4 yr for the juvenile sample to 3 yr for the largest otolith cores; average otolith weights for the series of four samples differed by a factor of 13. Whole otoliths ranged from and estimated 2 yr to about 30 yr. In contrast, average otolith-core mass for Atlantic tarpon was very consistent and differed by a factor of only 1.7. For some of the Atlantic tarpon samples, the measurements were made for individual otolith cores. Because the cores were easily extracted in the study, we can assume the consistency of coring (accurately extracted based on numerous measurement and observational factors that were personally observed) is an indication that similar time periods in the life of this species were analyzed. The lack of a relationship between otolith-core mass and radium-226 activity provided evidence that actual differences in uptake occurred for this species during this early growth period (Figure 5-2).

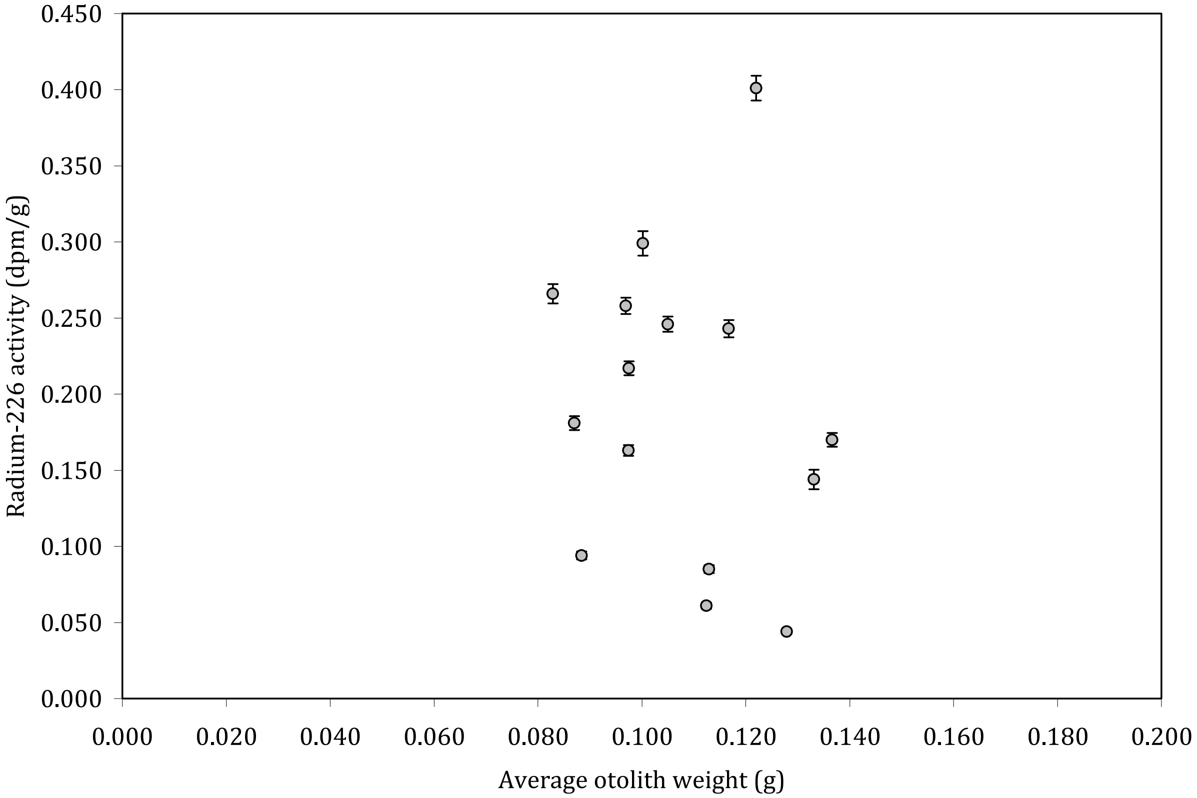

Figure 5-2. Consistency, and presumably accuracy, of coring provided evidence that there was an inconsistent uptake of radium-226 for the first two years of growth for Atlantic tarpon (*Megalops atlanticus*). Because coring was precise and extractions were performed carefully, the differences in radium-226 (dpm·g^{-1} ± 2 SE) may be attributed to environmental differences during this short period of formation (~2 years).

This observation can be explained by the early exposure of larvae to a pelagic environment, lower in radium-226 than inshore for the Florida region (Fanning et al. 1982), and a subsequent migration to highly variable inshore waters as a juvenile (Zale and Merrifield 1989). The study from the Bay of Carpentaria in northern Australia provided moderately high radium-226 levels (above 0.2 dpm·g^{-1}), but levels also covered a considerable range (down to 0.0460 dpm·g^{-1}). No apparent pattern in ontogenetic uptake could be discerned from this series of samples and may indicate there are complicated oceanographic or life history patterns for this region or group of fishes; variable ontogenetic uptake may be explained by highly variable levels of environmental radium-226.

An unexpected source for some of the highest radium-226 activities recorded from otoliths came from a few studies of pelagic fishes off Australia and New Zealand. An early report on radiometric age determination of three oreo dory species (Family: Oreosomatidae) taken off southern Australia provided the highest recorded radium-226 value to date (1.3409 ± 0.0603 dpm·g^{-1}; Fenton 1996). This sample is one of a series of whole otolith samples in an application to smooth oreo (*Pseudocyttus maculatus*) where uptake of radium-226 activity was opposite to the trend observed for some nearshore fishes (e.g. Figure 5-1); the measured values increased by a factor of five with fish size, as well as age according to lead-radium dating in the study. In the same study, black oreo (*Allocyttus niger*) otoliths provided a similar trend at lower radium-226 levels and spiky oreo (*Neocyttus rhomboidalis*) provided otoliths with relatively high radium-226 (up to 0.8966 ± 0.0395 dpm·g^{-1}) with a poorly defined trend that may indicate a decrease in radium-226 uptake with increasing fish size and age. It is interesting to note that despite the inconsistent uptake of radium-226 through ontogeny, lead-radium ratios measured for each species increased as expected with increasing fish size; robust support was provided for a longevity of approximately 50 years for smooth oreo and centenarian longevity for spiky and black oreo (*Allocyttus niger*; a species with intermediate radium-226 values).

The differences in ontogenetic uptake of radium-226 may reflect movement between two water masses associated with the Antarctic Convergence. Radium-226 levels south of Australia differ between these regions to a depth of approximately 1500 m by up to a factor of two (Ku et al. 1970). For smooth oreo, uptake of radium-226 may be related to life stages and location. It was noted that juvenile records were almost exclusively from mid-water trawls near the surface, south of the Antarctic Convergence in waters lower in radium-226. As adults smooth oreo move to deep slopes north of the Antarctic Convergence, waters greater in radium-226 concentration and more closely associated with the sea floor, as a benthopelagic predator (James et al. 1988). It is uncertain to what extent radium-226 sources (environment, diet, or metabolism) are responsible for such differences, but the correspondence of radium-226 between life stages and locations provides a reasonable explanation for this observation.

Otoliths from three pelagic species taken off New Zealand provided relatively high radium-226 activities (>0.2 dpm·g^{-1}) and for each species the highest values were from whole juvenile otoliths. Blue mackerel (*Scomber australasicus*) otoliths showed an early uptake of radium-226 that was more than twice the activity of whole adult otoliths, indicating the uptake of radium-226 was at least 10 times lower later in life (Andrews 2008a). Larvae for this species are known to settle inshore and near the bottom prior to transitioning to a more pelagic life (Manning et al. 2007). Whole juvenile otolith samples also provided the highest radium-226 activities for both orange roughy (*Hoplostethus atlanticus*) and black cardinalfish (*Epigonus telescopus*). Orange roughy is considered a bathypelagic species with a depth distribution ranging from approximately 180 m to over 1,800 m (Sissenwine and Mace 2007). Little is known about the depth distribution of juveniles, but there is evidence that they remain deep, relatively localized and pelagic before settling out as an adult (Rosecchi et al. 1988, Thresher and Proctor 2007). Black cardinalfish is considered a bathydemersal species with a depth distribution ranging from approximately 300 m to 1,100 m (Tracey et al. 2000), but juveniles may settle out quickly in deep, slope habitats near the bottom, in water hundreds of meters deep (Matthew Dunn, NIWA, New Zealand, personal communication).

Perhaps one of the more thought-provoking discoveries from this analysis of radium-226 data was the temporal distribution of radium-226 levels for orange roughy and black cardinalfish. When considering the consistency of otolith coring and radiometric age determinations for the age groups of each species, it is possible to observe consistency or variation of radium-226 uptake over time for this region. The consistency of coring was best for black cardinalfish (0.1003 ± 0.0035 dpm·g^{-1}, SD), with slightly greater variation for orange roughy coring (0.0176 ± 0.0043 dpm·g^{-1}, SD). Relative to the juvenile samples used as a baseline determination of lead-radium values, extracted otolith cores were considerably larger in size and mass, but radium-226 activities were lower (Figure 5-3).

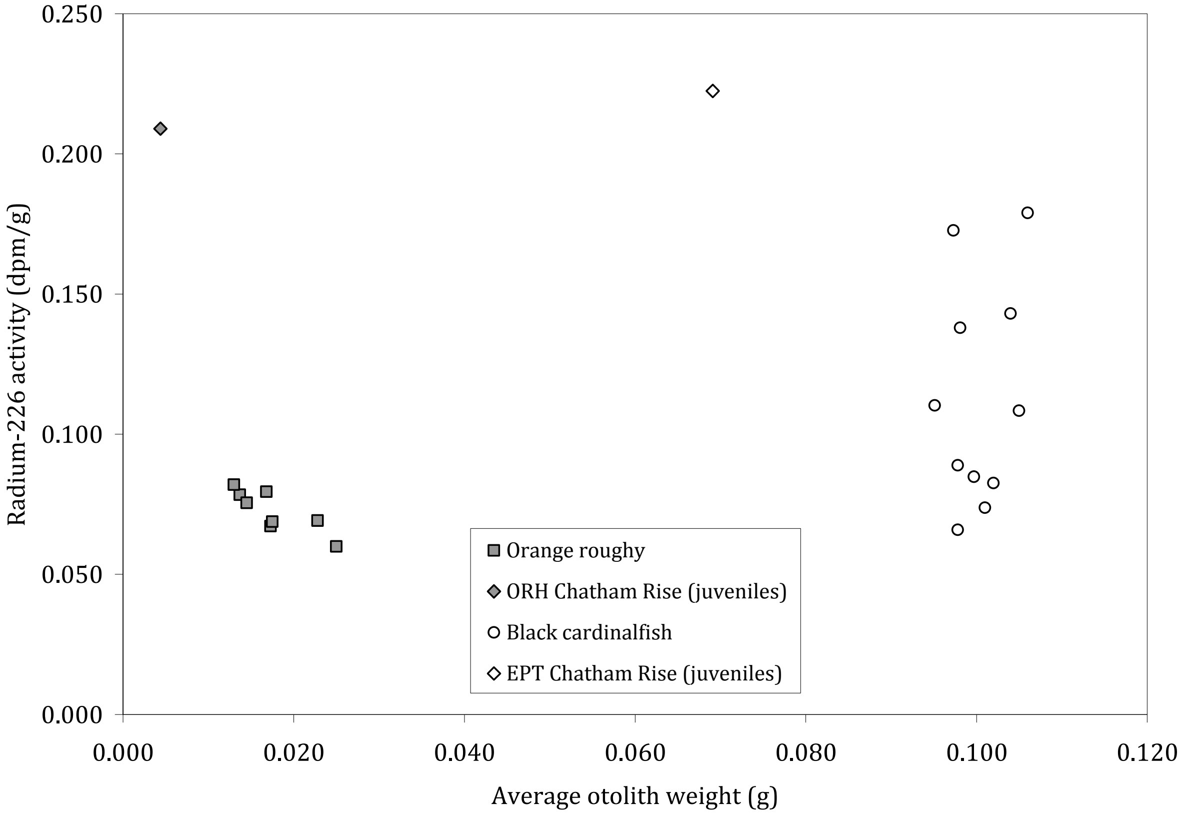

Figure 5-3 Coring consistency for both orange roughy (*Hoplostethus atlanticus*) and black cardinalfish (*Epigonus telescopus*) relative to measured radium-226 activities. In addition, juvenile whole otoliths are plotted to demonstrate the elevated uptake in even the earliest otolith.

While this demonstrates there were differences in uptake during the early years of growth, the figure also illustrates that relative to the consistent core size (4 years for orange roughy and 5 years for black cardinalfish) there were real differences in uptake among the age groups for black cardinalfish during the five-year formational period. The average uptake of radium-226 was relatively consistent for four year otolith cores from orange roughy age groups (0.0726 ± 0.0075 dpm·g^{-1}), but the nature of uptake for five year otolith cores from black cardinalfish age groups was highly variable (0.1134 ± 0.0394 dpm·g^{-1}). Given radiometric age and the relative uncertainty with each age determination (2 SE), a range of potential years of formation were determined for each measured radium-226 value (Figure 5-4).

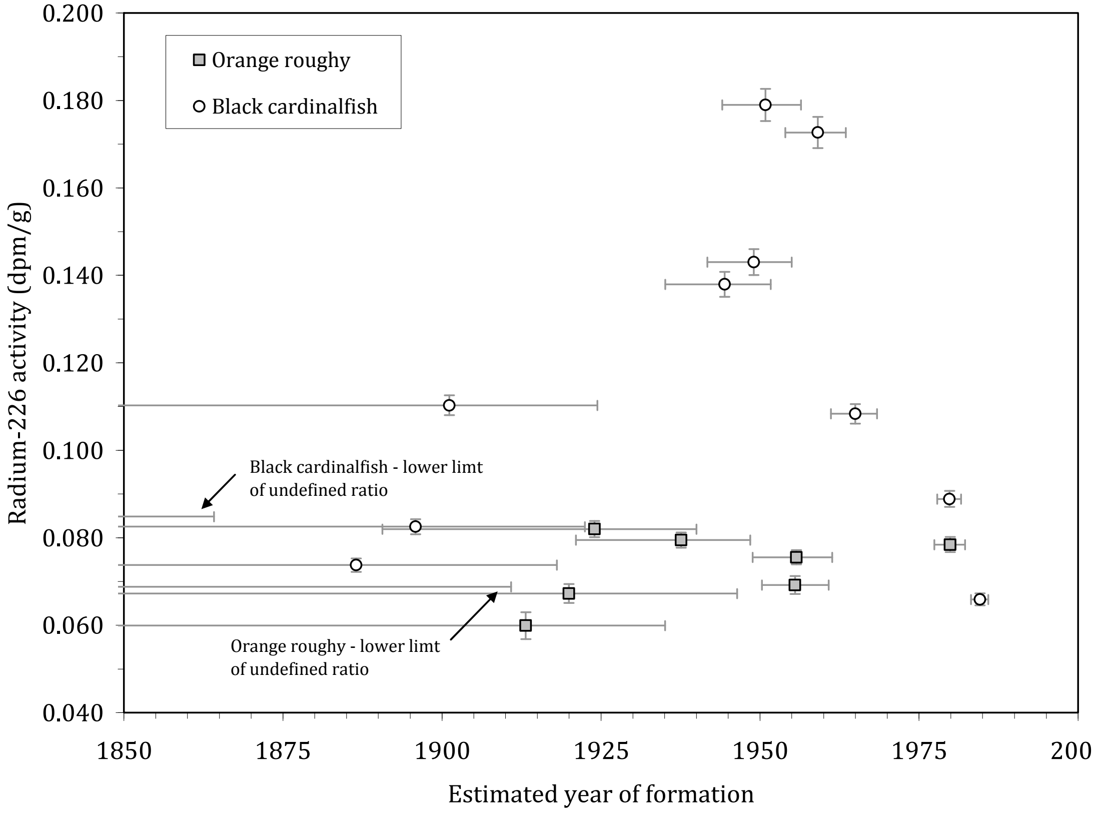

Figure 5-4. Changes in uptake of radium-226 over time for the first few years of growth were documented for black cardinalfish, but were not observed from orange roughy otolith cores. Estimated year of formation was based on lead-radium age determinations and only the lower limit of the measured ratio age was defined for two of the plotted samples noted in the figure (data from Andrews and Tracey 2007).

Figure 5-4 provides an indication that uptake of radium-226 was relatively consistent for orange roughy over a period of more than 100 years, but was inconsistent for black cardinalfish with a marked peak between the years of approximately 1935 and 1965. The reason for the increase in uptake is purely speculative, but may be related to changes in water chemistry, diet or both. Because the juvenile otolith sample provides evidence of an elevated uptake in the earliest years (Figure 5-3), it is possible that these age groups continued to reside in this water mass or fed on a similar diet for a more protracted period. An additional consideration that may be more plausible is related to deep advective flow in the form of seeps (e.g. Grindlay and Moore 2006). Either seeps could provide a long period flux of radium-226 rich waters or there was a regional association for this series of year-classes for black cardinalfish. Differing depth and habitat distributions between juvenile black cardinalfish and juvenile orange roughy may have contributed to the reason orange roughy did not show a similar response during that period.

In the northeastern Pacific Ocean, radium-226 measurements have now been made for a diversity of fishes. Aside from Bennett et al. (1982), the earliest application of lead-radium dating for this region was to sablefish (*Anoplopoma fimbria*) where radium-226 activities remain the highest yet measured from the region (up to 0.5170 ± 0.0212 $\text{dpm}\cdot\text{g}^{-1}$; Kastelle et al. 1994). Juvenile whole otoliths for this species were the lowest in the core sample series at approximately half the maximum value. The opposite was demonstrated for otoliths from Pacific grenadier (*Coryphaenoides acrolepis*); whole juvenile otoliths provided the highest radium-226 activity for this species. The average otolith/core mass provided evidence for a gradual decrease in radium-226 activity through the early growth of this species (Figure 5-5).

Whole juvenile otoliths were much smaller than two subsequent otolith sets that were cored at different times, the latter of which was greater to increase sample mass for analytical reasons (0.014 – 0.021 g and 0.033 – 0.035 g). Note that the whole adult otolith that was analyzed for radium-226 out of interest provided further evidence that the decreased uptake continued through ontogeny for a large adult (0.641 g otolith).

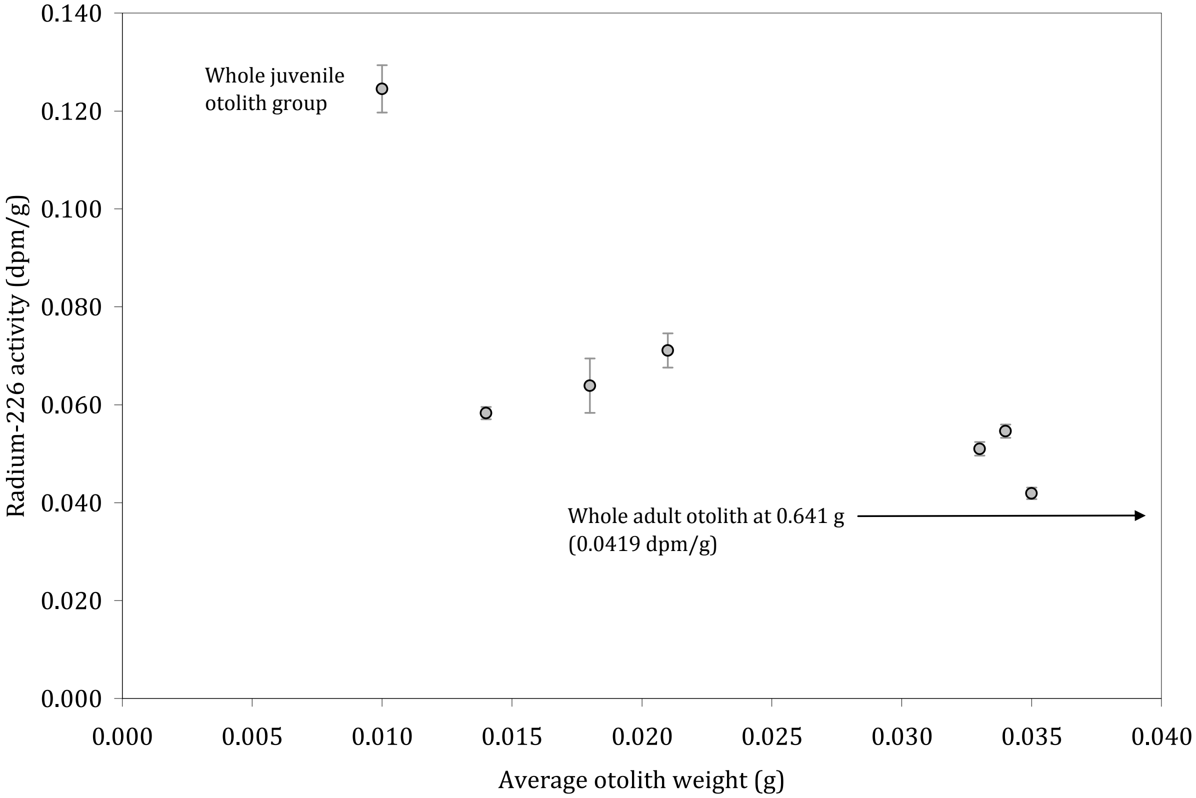

Figure 5-5. An otolith series from the deep-water Pacific grenadier (*Coryphaenoides acrolepis*) provided a similar trend to that of red snapper from the Gulf of Mexico; however, the life history for Pacific grenadier is very different (data from Andrews et al. 1999a).

The Pacific grenadier is regionally similar in distribution and depth to sablefish, but there are differences in ontogenetic habitat selection that may account for the observed differences in radium-226 uptake. Juvenile Pacific grenadier tend to remain deep, well below the thermocline (>300 m), and settle out quickly to the upper continental slope, whereas juvenile sablefish can be found inshore and at the surface. The surface water of the Pacific Ocean has been measured as one of the lowest open ocean radium-226 values, yet the deep water from the northeast Pacific Ocean increases considerably to some of the highest measured values (Chung 1976, Broecker and Peng 1982). Movement of sablefish from surface waters to depth and a close association with the benthos may explain the reversed relationship, an ontogenetic increase in radium-226 uptake. Pacific grenadier remain deep, become quickly associated with the deep benthos, and become increasingly benthopelagic through ontogeny. This life history pattern may explain early radium-226 values that are elevated, leading to reduced uptake as the species spends more time exposed to deep pelagic water.

Members of the Family Scorpaenidae (*Sebastes* spp. and *Sebastolobus* spp.) have been the most studied in terms of lead-radium dating with 14 species providing radium-226 measurements. For the northeastern Pacific Ocean 12 of the 20 species studied from this region were Scorpaenids. The range of average radium-226 uptake for these species is considerable and ranges from a low of 0.0116 ± 0.0018 (SD) dpm·g^{-1} for bocaccio (*S. paucispinis*) to a variable high of 0.1212 ± 0.0211 dpm·g^{-1} (SD) for northern rockfish (*S. polyspinis*). From minimum to maximum for Scorpaenids in this region, radium-226 uptake covers more than an order of magnitude (0.0087 to 0.1430 dpm·g^{-1}). By applying the same approach shown above for two New Zealand fishes, a temporal distribution of radium-226 uptake over time can be illustrated for Scorpaenids of the northeastern Pacific Ocean (Figure 5-6).

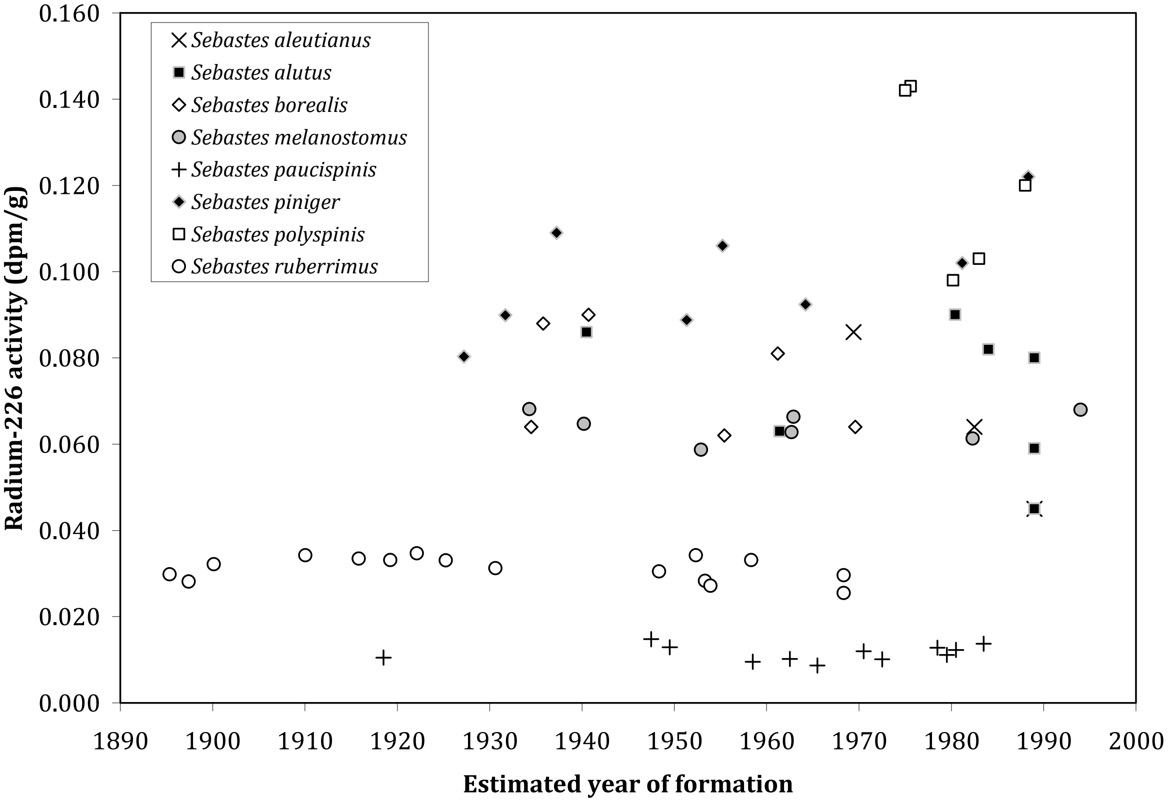

Figure 5-6. Plotted is the temporal distribution of radium-226 uptake for the juvenile otolith (extracted cores) from eight rockfishes (only cored otolith studies were selected for this analysis). The estimated year of formation was based on the radiometric ages determined in each study (see Appendices 3 and 4); the radiometric age error is not plotted for clarity, but it must be kept in mind the uncertainty for the estimated year of formation increases with time (data from Kastelle et al. 2000, Andrews et al. 2002, 2005, 2007)

In this figure, only juvenile and cored otolith measurements were considered and an assumption had to be made about coring consistency for some species (Kastelle et al. 2000). One of the longest records of radium-226 uptake was from yelloweye rockfish (*S. ruberrimus*) dating back to over 100 years ago. The degree of consistency over time for radium-226 uptake is remarkable (0.0312 ± 0.0027 dpm·g^{-1}) and a similar level of consistency can be observed for a few others that were plotted. Some species exhibit a relatively wide ranging uptake, but the coring consistency could not be accounted for in some studies and variable radium-226 activities may be an artifact of small differences in average core weight, as was demonstrated previously in this chapter as a potential complication for other species when making this kind of comparison.

Between members of the scorpaenids that have been studied to date, radium-226 uptake is highly variable for fishes of the northeastern Pacific Ocean, and seemingly consistent and relatively low for the northern Atlantic Ocean. This observation is consistent with measurements made for radium-226 levels in each oceanographic region, where the northern Atlantic is much lower in radium-226 at depth than the northeastern Pacific Ocean (Broecker et al. 1967, Broecker and Peng 1982). Surface waters of both open ocean areas are similar with markedly low radium-226 (typically less than 0.1 dpm·kg^{-1}), but differ greatly with increasing depth; northeast Pacific bottom water has some of the highest recorded levels of all ocean basins (some exceeding 0.4 dpm·kg^{-1}; Chung 1974, Broecker and Peng 1982). Movement throughout the water column in the northern Atlantic would provide little in terms of variability of environmentally available radium-226, where as the northeastern Pacific Ocean provides numerous environmental scenarios; however, an exception to this observation comes from a measurement made on very small juvenile otoliths from *Sebastes* sp., in which radium-226 uptake was three times greater that larger juvenile otoliths and adult otolith cores (Stransky et al. 2005).

When considering other species from the north Pacific in general, all are distributed between the extremes shown so far, with the highest values measured from sablefish. The lowest radium-226 values from Pacific halibut were similar to bocaccio rockfish. The highest values for rockfishes were from northern rockfish and were similar, albeit slightly lower, to Alaskan pollock. The disparity between radium-226 levels in seawater for this region may highlight differences or similarities within and between species as fish move to and from surface and deep waters. Highlighted for the north Pacific is a couple of samples made from the Hawaiian Islands; measurements made in a feasibility study currently underway for the opakapaka (*Pristipomoides filamentous*) revealed relatively low radium-226 (0.0311 ± 0.0072 dpm·g^{-1}; Andrews 2008b). This would be expected because the near surface waters of the Hawaiian Islands are located in the midst of the relatively depleted north Pacific surface water (Broecker and Peng 1982).

For the Southern Ocean there are but two species that have been studied for lead-radium dating, Patagonian and Antarctic toothfishes (*Dissostichus eleginoides* (Chapter 3) and *D. mawsoni* (Brooks 2008); Appendix 10). The data series from otolith cores for these species provided an indication that uptake for the first few years of growth of each species were relatively consistent over several decades. For the Kerguelen and Heard Island regions, uptake was consistent and did not differ; however, differences between toothfishes were significant relative to the means (0.0166 ± 0.0078 vs. 0.0233 ± 0.0016 dpm·g^{-1} (2 SE); *t*-test, P < 0.001). The single sample of whole otoliths from South Georgia, analyzed as part of a feasibility study, was closer to the Antarctic toothfish in terms of activity (0.0258 ± 0.003 dpm·g^{-1}), but the average otolith weight was much greater than the cored otoliths used in the follow up study and likely represents more years of growth and uptake. Overall, the radium-226 activities were low with minor variations; a small drop in uptake appears to have occurred for Patagonian toothfish in the Kerguelen region for a period of about 10 years centered on the mid 1980s (Figure 5-7).

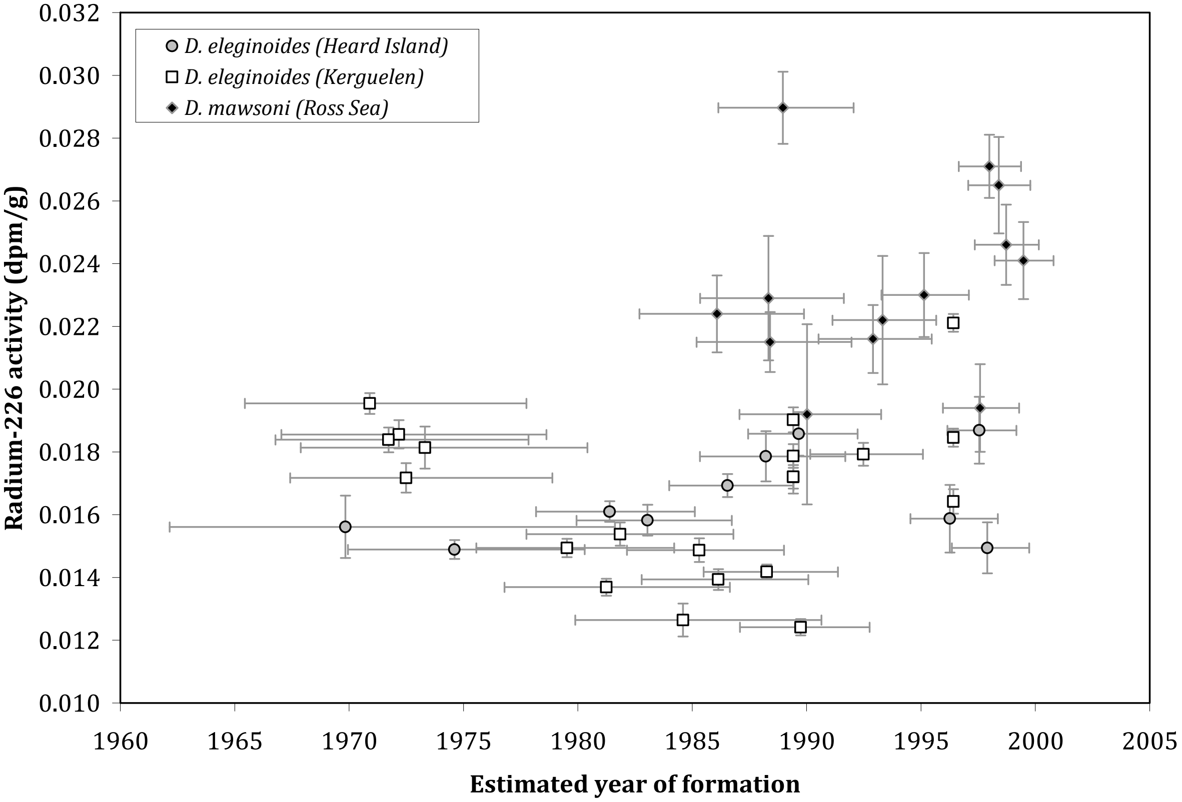

Figure 5-7. Plotted is the temporal distribution of radium-226 uptake for the juvenile otolith (core) from both toothfishes and three regions. The estimated year of formation was based on the radiometric ages determined in each study (see Appendix 10).

Radium-226 measurements in seawater from south of the Antarctic Convergence are remarkably consistent and are lacking depleted surface waters (Ku and Lin 1976). Radium-226 in deep Antarctic waters like the Ross Sea increases moderately and attains levels that are toward the middle of the range known for the world's oceans (~0.20 dpm·kg^{-1}; Broecker and Peng 1982). Recent measurements taken from the Kerguelen and Heard Island region provided more detail on radium-226 levels for the region; environmental radium-226 was about 25% lower than regions like the Ross Sea (van Beek et al. 2008). This minor difference could account for the significant difference measured between Antarctic toothfish from the Ross Sea and Patagonian toothfish from the Kerguelen Plateau and Heard Island region (difference of approximately 29% on average).

Studies have shown that uptake of calcium from either food sources or through respiration pathways can vary considerably, but the consensus is that most of the calcium, and presumably radium-226, comes from over the gills (e.g. Simkiss 1974). This may be a good general rule, but variations within and between species may be a function of both water chemistry and diet; more information is necessary to properly attribute the differences in radium-226 uptake. It is certain, however, that variation in ocean chemistry plays a significant role. A close proximity to nearshore environments and deep water sediments provides a tangible explanation for some of the highest radium-226 activities (e.g. Cochran 1980, Moore 1996, Grindlay and Moore 2006), but elevated levels measured from juveniles of pelagic species indicate there may be other factors involved and diet or metabolic rates may provide some answers. In addition, the finding that numerous species seem to exhibit a reduction in the rate of uptake in just the first few years of growth provides support for a dietary or metabolic connection.

Radium-226 concentrations determined for an array of marine food web organisms revealed a wide range of potential values (Cherry and Shannon 1974), with phytoplankton providing some of the greatest values and highest concentration factors (e.g. Szabo 1967, Shannon and Cherry 1971, Porntepkasemsan and Nevissi 1990, Tinker 1997). It is possible that the larval and earliest juvenile, feeding largely on phytoplankton, could take in radium-226 enriched food sources during this growth period leading to an unexpected enrichment of otolith radium-226. This concept may be well represented by the measurements made on very small juvenile otoliths from *Sebastes* sp. in the north Atlantic where radium-226 uptake was greatest in relatively depleted waters (Stransky et al. 2005).

Another possible exemplification of this scenario comes from an early lead-radium study on bocaccio rockfish; the activity of radium-226 in otolith material was determined to be one of the lowest values for fishes of the northeastern Pacific Ocean. Further consideration of bocaccio life history relative to radium-226 availability may provide some answers as to why this is the case. Bocaccio are known to remain pelagic for long periods, have been recorded as one of the fastest growing rockfishes, and become piscivorous early in life (Love et al. 2002). Juveniles settle out in nearshore waters, but remain in near surface waters for long periods where radium-226 levels would be relatively low. If water chemistry and diet both play a significant role in the uptake of radium-226 to the otolith, then both trophic and respiratory pathways for radium-226 to enter bocaccio metabolism would be depleted; it would be expected that bocaccio have some of the lowest radium-226 levels in their otoliths.

CHAPTER SIX

✵

A SYNOPSIS OF RECENT INSIGHTS ON THE IMPORTANCE OF AGE-VALIDATED LONGEVITY

Many marine fisheries throughout the world have been reported as overexploited and the impact of human activity extensive (Pauly et al. 2003, Halpern et al. 2008). Because many fisheries target apex predators, it appears that fishing activities may have influenced the relative abundance of predatory fishes in some marine ecosystems (Pauly 1995, Worm et al. 2005). In some cases, the balance of some major ecosystems may have been seriously altered (Pauly et al. 1998, 2002, Christensen et al. 2003, Frank et al. 2005). There is much disagreement about the extent and causes of these fishery declines (Walters 2003, Myers and Worm 2003, 2005, Hutchings and Reynolds 2004, Safina et al. 2005, Sibert et al. 2006, Hilborn 2007), but it is certain that many nearshore fisheries have suffered to the extent that fishing effort has moved further offshore and into deeper water (Gordon 2001, Haedrich et al. 2001, Roberts 2002, Clark et al. 2007). Despite lessons that might be learned from the overexploitation of nearshore fishes, deep-water fisheries have proceeded to extensive levels of exploitation on fishes that are even more vulnerable because of life history traits that can handle only minimal fishing pressure (e.g. Francis and Clark 2005).

Fishery modeling and management practices have primarily focused on stock assessments that use estimates of maximum (MSY) or optimum (OSY) sustainable yield in terms of biomass in an attempt to determine the level of exploitation or sustainability of a given fishery (Hilborn and Walters 1992, Berkeley 2006). In some cases, age composition has been taken into consideration, but age-structured analyses often make major assumptions about age-driven biological quantities. Because population age-structure is often poorly understood, the dynamic parameters that are important must be modeled or fixed (e.g. Methot 1990, Millar and Methot 2002, Brandão and Butterworth 2005). Stock assessments are now commonly performed, but the concept of sustainability is still very much in question (Millar and Methot 2002, Beamish et al. 2006, Longhurst 2006).

Fishing practices have fished down the size structure, and presumably age composition, of many fisheries (Pauly et al. 1998, Harvey et al. 2006). Perhaps the most severe impact was to fisheries with a long-lived age structure, for which the potential longevity of the species may never be known. In nearshore environments along the west coast of the United States, rockfish landings showed evidence of significant downward shifts in size composition (Mason 1998). This kind of change may affect a fishery in deleterious ways; five of the most significant points that have gained attention in recent literature are further discussed here.

First, fishing pressure can cause a loss of genetic diversity (heterozygosity) by removing successful age classes and overlapping generations (e.g. Hauser et al. 2002). This factor could be especially significant for long-lived fishes with episodic recruitment and a localized distribution. Localized gene flow that was described for Patagonian toothfish (Appleyard et al. 2002, Rogers et al. 2006), which was further supported with otolith elemental analyses (Ashford et al. 2007), would make this species susceptible to localized depletions. Orange roughy does not appear to suffer from fishing induced heterozygosity (Smith and Benson 1997), likely because of broad population distributions evidenced by considerable homogeneity over great distances (Elliott and Ward 1992). Stockley et al. (2005) demonstrated that the deep-sea blackspot seabream (*Pagellus bogaraveo*), which became a target in recent years because of nearshore stock depletions, exhibited low genetic diversity. This was attributed to a small and localized population that was susceptible to overfishing.

An additional consideration for the blackspot seabream fishery is the lack of age validation for this species. The age structure of the localized population may have played a significant role in the stock depletion. Recovery and sustainability efforts need to consider age validation as part of the approach. Age and growth for blackspot seabream was estimated using scales and whole otoliths and the range in estimated longevity is considerable (8 to 20 years; Chilari et al. 2006). Longevity remains unvalidated and underestimation of age is a distinct possibility when considering the revelations of modern techniques. As has been the case with numerous other fisheries, regional regulations stipulate a minimum landing size but do not address the size or age at first maturity (Chilari et al. 2006). Because of the population response to fishing pressure, it is possible that an unexpectedly high longevity may mean productivity is low; as result, recovery and sustainability may be difficult to achieve.

Second, fisheries that focus on removing the largest individuals can rapidly favor slower-growing and earlier-maturing fishes, as was determined for a recently exploited population of banded morwong (*Cheilodactylus spectabilis*; Ziegler et al. 2007). This species was age-validated to at least 40 years and may approach 100 years in age (Ewing et al. 2007), making localized populations susceptible to a severe loss of age structure. A study of recent fishery related changes to the population structure of two groups of redfish (*Sebastes mentella*) revealed: 1) a significant shift of maturity to smaller and younger fish; and 2) a reduction in the age-length and size-weight relationships (Novikov et al. 2006). These heritable differences in yield and life-history traits may have long term affects from selective fishing, which is exemplified by the heavily exploited northern cod stocks (*Gadus morhua*; Hutchings 2004, Olsen et al. 2004), and points to the third significant point.

Third, there can also be long-term ecological and evolutionary implications of targeted removal of the largest and oldest fish. This kind of fishing pressure can result in a "dynamic tug-of-war between natural and harvest selection" (Edeline et al. 2007), leading to long-term changes for size and age at first reproduction and size and age specific reproductive output (Conover and Munch 2002, de Roos et al. 2006, Walsh et al. 2006, Jorgensen et al. 2007). Other long-term ecological and evolutionary implications can be related to the "bet-hedging adaptation" that has been demonstrated for some long-lived rockfishes; reproductive effort for larger and older females is shifted to a different time interval from younger fish, which increases the chances of larvae encountering favorable conditions (Sogard et al. 2008). Loss of age structure for populations of fishes that are adapted to decadal changes in the environment may have detrimental affects to future recruitment success.

Fourth, there can be ecosystem effects that can be manifested as a loss of top carnivores and changes in trophic relationships of ecosystems (Frank et al. 2005, Scheffer et al. 2005, Worm et al. 2005). One management technique that may alleviate this problem on a local scale is the implementation of Marine Protected Areas (MPAs; National Research Council 2001). This conservative approach is being seriously considered in many places and was implemented in numerous places around the world, especially along the west coast of the United States (Parker et al. 2000). However, one of the biggest issues facing MPAs is evaluating the efficacy of MPAs for species of concern. Many implementations have not taken life history characteristics into consideration (Berkeley 2006). Understanding the residential nature of species of concern and their age-validated life history characteristics is of paramount importance to the successful designation, maintenance and monitoring of MPAs.

Fifth, removal of the largest fish would cause a reduction in lifetime production for individuals of the population, leaving productivity to reduced life spans. This factor was measured by O'Farrell and Botsford (2005, 2006a and b) as lifetime egg production (LEP) and by Harvey (2005) as age-specific egg production in rockfishes (Genus *Sebastes*; Family Scorpaenidae). Where this factor becomes significant is with increases in egg production with larger and older fish. A summary of size-specific fecundity for rockfishes demonstrated that larger, and presumably older, rockfishes typically produced more offspring (Phillips 1964, Gunderson et al. 1980, Love et al. 1990, 2002), and it appears that some fishes may continue to reproduce through ontogeny with no evidence of senescence (Cailliet et al. 2001, de Bruin et al. 2004). In addition to this scenario, production and survivorship of larvae from well-adapted or "fit" adults, those that have survived the test of time, may be reduced as the number of older fish is reduced. In concert with factors associated with egg production, an unanticipated factor recently discovered for some rockfishes was that larger females were not only more fecund, but produced larvae more capable of survival (Berkeley et al. 2004 a and b, Bobko and Berkeley 2004, Berkeley 2006, Sogard et al. 2008). Therefore, modeling and management of fisheries that focus on catching the largest fish must be investigated for maternal-age-dependent increase in larval survival. For fishes with this life history approach, accurate age and growth characteristics are required and some form of size and age structure maintenance should be part of the management strategy.

An examination of lifetime reproductive output for three rockfishes with different age, growth, and habitat characteristics (bocaccio, canary, and yelloweye rockfishes), can be used to demonstrate differences in reproductive output relative to longevity. These species were chosen because age was validated and longevity estimates were supported. Bocaccio have a reported maximum estimated age of approximately 50 years (Love et al. 2002), and the species was validated to at least 37 years using bomb radiocarbon dating (Andrews et al. 2005, Piner et al. 2006). Canary rockfish have a reported maximum age of 84 years (Munk 2001), and the species was validated to at least 44 years with bomb radiocarbon dating and at least 54 years with lead-radium dating (Piner et al. 2005, Andrews et al. 2007). Yelloweye rockfish have one of the highest longevity estimates at 118 years (Munk 2001), with support from lead-radium dating to approximately 100 years (Andrews et al. 2002). Given these maximum ages, and knowing the age at maturity for bocaccio, canary and yelloweye rockfishes (approximately 7, 8, and 19 years, respectively), and the number of productive years for the potential lifespan can be calculated. Bocaccio, canary and yelloweye rockfishes would have approximately 30 to 43 years, 46 to 76 years, and 81 to 99 years, respectively, for production. The longer-lived and deeper-dwelling canary and yelloweye rockfishes could have far more reproductive years, relative the shallower-living and shorter-lived bocaccio rockfish. It is relatively straightforward to predict that targeting the largest fish would have a deleterious impact on lifetime production, especially for bocaccio because of there is less time to contribute back to the population. In addition, coupling lifetime production potential with increasing fecundity with size and age provides a scenario for conservation the largest and oldest individuals.

Relative to these recent insights on the importance of validated age and longevity, it is important to note out that age validated species were not used. O'Farrell and Botsford (2005, 2006a and b) assumed that size classes represented age classes to demonstrate the effect of size-selective fishing on LEP. Similar studies on rockfishes by Harvey (2005) and Harvey et al. (2006) made similar assumptions. Therefore, it is suggested the hypothesis about age-specific relationships be tested on age-validated species.

6.1 Conclusions

The affect of heavy exploitation of larger, and potentially older, size classes can truncate the number of reproductive years, thereby reducing the viability of populations and creating unstable population dynamics (Anderson et al. 2008). Because age structure is often not well understood, it is of paramount importance that some form of validation or support be given for age estimation procedures, and ultimately estimates of longevity. Given accurate age and growth parameters, lifetime fecundity becomes an important factor in understanding and predicting population dynamics. This concept was well demonstrated in a demographic study of the shortbelly rockfish (*Sebastes jordani*), where weight-specific fecundity was calculated and used in a larval production method to determine population biomass estimates (Ralston et al. 2003).

Much remains that is unknown for Patagonian toothfish and orange roughy with regard to the recent perceptions on the importance of age-validated longevity in the sustainability of these fisheries. Age and growth was estimated for Patagonian toothfish with the purpose of gaining a better understanding of not only age and growth, but providing a basis for calculating rates of age-specific survival and mortality, and estimates of age-specific fecundity (Ashford et al. 2005). The age validation study presented in this dissertation (Chapter 3) provides a valuable step in meeting these objectives.

The age and growth of orange roughy remains as a complicated issue because of its extreme longevity and the high degree of difficulty in estimating age from growth zone counts (Tracey and Horn 1999, Francis 2006). Its reproductive strategy of bestowal, maximizing investment in a smaller number of offspring (Pankhurst and Conroy 1987), combined with its validated centenarian longevity (Fenton et al. 1991, Smith et al. 1995, see Chapter 4), make orange roughy of particular concern under any kind of fishing pressure (Francis and Clark 2005).

The recent perceptions on the importance of maintaining size and age structure has caused some authors to contend that it may be necessary in some fisheries to “leave the big ones” (Birkeland and Dayton 2005). It is a combination of age structure (leave the big ones), life-time egg production (greater productivity), and genetic diversity (potential enhanced survivorship) that beg for proper management practices that take these factors into consideration, in concert with establishing age-validated life-history characteristics and longevity. It may be, however, that sustainability is unachievable for some species (Longhurst 2002, 2006), and this is especially true when age-specific life history traits are unknown or extreme.

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APPENDICES

Appendix 1a. List of CQFE Patagonian toothfish samples used in the radiometric analyses with the details of each fish listed for consideration. Some reference numbers are meant for those using the system. Collection date was provided in the dd/mm/yy format.

Patagonian toothfish
3 yr group (CQFE 1A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	37	231	22/08/99	49	NA	0.057	F	3
		40	245	23/08/99	58	NA	0.059	M	3
		37	250	22/08/99	51	NA	0.059	F	3
		40	259	23/08/99	54	NA	0.06	M	3
		40	252	23/08/99	56	NA	0.061	M	3
		67	293	01/09/99	55	NA	0.061	M	3
		40	257	23/08/99	51	NA	0.062	M	3
		61	192	30/08/99	56	NA	0.066	M	3
		37	207	22/08/99	57	NA	0.067	M	3
		40	234	23/08/99	54	NA	0.067	M	3
		34	211	21/08/99	52	NA	0.069	M	3
		40	226	23/08/99	59	NA	0.07	F	3
		88	133	08/09/99	56	NA	0.071	M	3
		37	228	22/08/99	55	NA	0.071	M	3
		40	238	23/08/99	53	NA	0.073	F	3
	N. Pride	18	820	24/03/99	51	1	0.066	M	3
		2	472	07/03/99	45	NA	0.077	F	3
		7	518	12/03/99	61	2	0.079	M	3
		10	515	16/03/99	56	2	0.082	M	3
		23	803	30/03/99	65	3	0.082	F	3

Patagonian toothfish 3 yr group (CQFE 1B)									
Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	67	294	01/09/99	58	NA	0.083	M	3
		57	310	28/08/99	61	NA	0.083	M	3
		66	158	01/09/99	60	NA	0.088	F	3
		75	286	04/09/99	66	NA	0.088	F	3
		34	230	21/08/99	56	NA	0.09	F	3
		110	14	17/09/99	67	NA	0.094	F	3
		61	313	30/08/99	69	NA	0.101	M	3
		88	134	08/09/99	63	NA	0.103	M	3
		57	326	28/08/99	58	NA	0.104	M	3
	N. Pride	18	776	24/03/99	66	3	0.096	M	3
		6	427	11/03/99	61	3	0.1	F	3
		3	541	08/03/99	60	4.5	0.083	F	3
		20	687	27/03/99	64	2.5	0.085	F	3
		8	369	13/03/99	62	3	0.086	M	3

Patagonian toothfish
3 yr group (CQFE 1C)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	88	132	08/09/99	74	NA	0.123	M	3
		64	302	31/08/99	85	NA	0.159	F	3
	N. Pride	3	558	08/03/99	73	5	0.103	M	3
		3	371	08/03/99	70	5	0.109	M	3
		24	799	31/03/99	71	4	0.117	M	3
		14	661	20/03/99	70	4	0.118	M	3
		18	744	24/03/99	80	5	0.123	F	3
		8	362	13/03/99	78	4.5	0.125	F	3
		3	514	08/03/99	77	4.5	0.132	F	3
		25	419	01/06/99	73	6.5	0.158	F	3

Patagonian toothfish
5-7 yr group (CQFE 2A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	75	282	04/09/99	59	NA	0.066	M	5
		66	189	01/09/99	64	NA	0.112	F	5
		81	93	06/09/99	72	NA	0.123	M	5
		92	82	09/09/99	81	NA	0.136	M	5
		92	104	09/09/99	77	NA	0.141	F	5
		57	298	28/08/99	71	NA	0.091	M	6
		114	67	18/09/99	70	NA	0.098	F	6
		113	39	18/09/99	71	NA	0.107	F	6
		67	267	01/09/99	75	NA	0.118	M	6
		61	314	30/08/99	78	NA	0.146	M	6
		34	209	21/08/99	53	NA	0.052	M	7
		106	48	16/09/99	66	NA	0.104	F	7
		75	300	04/09/99	68	NA	0.109	M	7
		105	44	15/09/99	77	NA	0.133	F	7
		64	295	31/08/99	83	NA	0.164	F	7
	N. Pride	18	675	24/03/99	63	3.5	0.070	M	5
		12	512	18/03/99	69	4	0.100	F	5
		26	343	02/04/99	88	6	0.112	F	5
		18	783	24/03/99	67	3.5	0.112	M	5
		10	407	16/03/99	56	2.5	0.073	F	6
		8	367	13/03/99	76	4.5	0.121	F	6
		22	706	29/03/99	70	6	0.128	M	6
		20	731	27/03/99	76	4.5	0.130	F	6
		7	544	12/03/99	86	7	0.131	F	6
		15	415	21/03/99	88	8.5	0.147	F	6
		12	808	18/03/99	84	6	0.169	F	6
		9	773	14/03/99	65	3	0.101	M	7
		14	527	20/03/99	75	4.5	0.116	F	7
		9	740	14/03/99	71	6.5	0.132	F	7
		23	720	30/03/99	85	6	0.141	M	7
		9	758	14/03/99	84	6	0.156	F	7
		9	498	14/03/99	89	7	0.159	F	7

Patagonian toothfish
5-7 yr group (CQFE 2B)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	34	205	21/08/99	55	NA	0.081	M	5
		67	170	01/09/99	74	NA	0.122	F	5
		57	296	28/08/99	67	NA	0.125	M	5
		92	142	09/09/99	85	NA	0.184	M	5
		60	256	23/08/99	59	NA	0.085	M	6
		37	218	22/08/99	67	NA	0.092	F	6
		57	320	28/08/99	62	NA	0.094	M	6
		61	309	30/08/99	66	NA	0.110	F	6
		110	1	17/09/99	73	NA	0.126	F	6
		75	283	04/09/99	79	NA	0.138	F	6
		57	329	28/08/99	63	NA	0.093	M	7
		64	297	31/08/99	73	NA	0.095	F	7
		67	264	01/09/99	71	NA	0.105	F	7
		66	325	01/09/99	68	NA	0.108	M	7
		110	24	17/09/99	74	NA	0.119	F	7
		61	327	30/08/99	73	NA	0.137	M	7
		110	22	17/09/99	76	NA	0.143	M	7
		81	113	06/09/99	85	NA	0.160	F	7
	N. Pride	6	467	11/03/99	69	4	0.098	M	5
		22	771	29/03/99	74	4	0.110	F	5
		18	686	24/03/99	66	3	0.111	M	5
		9	511	14/03/99	70	4.5	0.118	M	5
		3	409	08/03/99	67	4	0.123	M	5
		18	735	24/03/99	72	4	0.096	M	6
		16	524	20/03/99	77	5	0.125	F	6
		17	772	23/03/99	79	5	0.133	F	6
		11	805	17/03/99	79	5.5	0.151	M	6
		12	785	18/03/99	60	2.5	0.082	M	7
		18	770	24/03/99	66	2	0.098	F	7
		22	705	29/03/99	73	3.5	0.121	M	7
		20	723	27/03/99	88	5	0.124	F	7
		18	815	24/03/99	85	6	0.137	F	7
		11	339	17/03/99	76	5	0.170	F	7

Patagonian toothfish
5-7 yr group (CQFE 2C)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	34	210	21/08/99	50	NA	0.057	M	5
		34	147	21/08/99	55	NA	0.073	F	5
		67	183	01/09/99	61	NA	0.078	M	5
		57	201	28/08/99	57	NA	0.085	F	5
		75	152	04/09/99	63	NA	0.086	M	5
		105	42	15/09/99	71	NA	0.107	F	5
		66	157	01/09/99	74	NA	0.108	M	5
		85	129	07/09/99	74	NA	0.110	F	5
		110	2	17/09/99	77	NA	0.120	M	5
		110	5	17/09/99	77	NA	0.121	F	5
		67	277	01/09/99	53	NA	0.065	M	6
		67	182	01/09/99	63	NA	0.080	F	6
		57	316	28/08/99	56	NA	0.081	F	6
		67	263	01/09/99	65	NA	0.084	F	6
		75	287	04/09/99	60	NA	0.085	M	6
		40	240	23/08/99	60	NA	0.089	M	6
		75	150	04/09/99	67	NA	0.111	F	6
		67	291	01/09/99	67	NA	0.114	F	6
		105	30	15/09/99	69	NA	0.098	F	7
		106	57	16/09/99	67	NA	0.102	M	7
		81	122	06/09//99	71	NA	0.102	F	7
		85	123	07/09/99	72	NA	0.111	M	7
		110	17	17/09/99	80	NA	0.124	F	7
	N. Pride	3	504	08/03/99	67	3	0.100	F	5
		22	802	29/03/99	91	8	0.169	M	5
		6	445	11/03/99	57	2.5	0.078	F	6
		14	381	20/03/99	64	2.5	0.088	F	6
		12	726	18/03/99	72	4	0.102	F	6
		19	608	25/03/99	75	4	0.135	F	6
		7	585	12/03/99	70	5	0.106	F	7
		7	359	12/03/99	83	6	0.150	F	7
		17	662	23/03/99	87	6	0.170	F	7

Patagonian toothfish
11-12 yr group (CQFE 3A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	81	90	06/09/99	80	NA	0.105	F	11
		105	33	15/09/99	64	NA	0.110	M	11
		81	83	06/09/99	75	NA	0.127	M	11
		88	114	08/09/99	82	NA	0.132	F	11
		92	166	09/09/99	70	NA	0.114	M	12
		92	141	09/09/99	73	NA	0.118	M	12
		61	308	30/08/99	69	NA	0.125	M	12
		92	140	09/09/99	80	NA	0.156	M	12
		64	151	31/08/99	86	NA	0.214	F	12
	N. Pride	14	822	20/03/99	73	4	0.109	M	11
		3	494	08/03/99	78	4.5	0.110	F	11
		20	778	27/03/99	86	5.5	0.110	F	11
		18	617	24/03/99	80	4.5	0.129	F	11
		15	393	21/03/99	79	5.5	0.142	M	11
		8	402	13/03/99	86	7.5	0.142	M	11
		14	645	20/03/99	83	6.5	0.147	F	11
		6	387	09/03/99	80	6.5	0.122	M	12
		11	357	17/03/99	80	6	0.123	M	12
		23	711	30/03/99	83	5	0.126	F	12
		9	813	14/03/99	89	7	0.139	F	12
		7	530	12/03/99	85	7	0.161	M	12
		6	698	11/03/99	81	6.5	0.164	M	12
		19	632	25/03/99	88	7.5	0.197	F	12
		7	358	12/03/99	88	8	0.209	M	12
		8	443	13/03/99	105	11.5	0.209	M	12
		6	428	09/03/99	95	11	0.266	F	12

Patagonian toothfish
11-12 yr group (CQFE 3B)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	106	50	16/09/99	77	NA	0.117	F	11
		75	190	04/09/99	78	NA	0.117	M	11
		85	206	07/09/99	77	NA	0.121	F	11
		81	265	06/09/99	85	NA	0.121	F	11
		110	7	17/09/99	83	NA	0.133	F	11
		88	70	08/09/99	91	NA	0.143	F	11
		110	4	17/09/99	63	NA	0.074	F	12
		81	111	06/09/99	73	NA	0.114	M	12
		66	186	01/09/99	74	NA	0.122	M	12
		88	86	08/09/99	76	NA	0.127	F	12
		88	98	08/09/99	84	NA	0.132	M	12
		81	74	06/09/99	74	NA	0.133	M	12
		81	89	06/09/99	78	NA	0.144	F	12
		88	161	08/09/99	89	NA	0.182	M	12
	N. Pride	23	709	30/03/99	69	3.5	0.115	M	11
		14	619	20/03/99	100	11.5	0.207	F	11
		9	384	14/03/99	76	3	0.128	F	12
		17	754	23/03/99	89	6.5	0.128	M	12
		10	486	16/03/99	87	7	0.138	F	12
		2	463	07/03/99	86	NA	0.167	F	12
		17	708	23/03/99	83	5.5	0.176	M	12
		2	447	07/03/99	76	NA	0.178	F	12
		8	750	13/03/99	86	7	0.182	M	12
		17	707	23/03/99	94	9	0.200	M	12
		3	471	08/03/99	97	12	0.205	F	12
		17	736	23/03/99	104	12	0.205	M	12

Patagonian toothfish
11-12 yr group (CQFE 3C)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	67	281	01/09/99	67	NA	0.104	F	11
		85	128	07/09/99	72	NA	0.116	M	11
		88	105	08/09/99	80	NA	0.120	F	11
		81	71	06/09/99	82	NA	0.124	M	11
		85	80	07/09/99	75	NA	0.128	F	11
		113	58	18/09/99	79	NA	0.140	F	11
		69	279	31/08/99	75	NA	0.112	F	12
		57	330	28/08/99	76	NA	0.116	M	12
		92	174	09/09/99	75	NA	0.128	M	12
	N. Pride	7	589	12/03/99	65	3.5	0.098	M	11
		12	821	18/03/99	71	5	0.118	M	11
		8	363	13/03/99	74	5	0.121	F	11
		17	604	23/03/99	81	5	0.122	F	11
		23	725	30/03/99	74	4	0.128	F	11
		22	679	29/03/99	84	5	0.132	F	11
		3	562	08/03/99	96	11.5	0.139	F	11
		17	637	23/03/99	86	6	0.148	F	11
		6	485	09/03/99	82	9	0.163	F	11
		20	626	27/03/99	70	3.5	0.123	M	12
		10	610	16/03/99	83	6	0.124	F	12
		9	459	16/03/99	80	6	0.127	F	12
		10	493	16/03/99	72	5	0.128	M	12
		6	346	11/03/99	88	8	0.145	M	12
		18	634	24/03/99	83	5.5	0.152	F	12
		11	437	17/03/99	76	5	0.157	F	12
		4	501	09/03/99	91	9.5	0.163	M	12
		15	390	21/03/99	103	12	0.215	F	12

Patagonian toothfish
15-16 yr group (CQFE 4A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	64	269	31/08/99	92	NA	0.156	F	15
		110	19	17/09/99	94	NA	0.175	M	15
		80	333	06/09/99	68	NA	0.127	M	16
		80	285	06/09/99	89	NA	0.151	M	16
		92	162	09/09/99	77	NA	0.155	F	17
		64	319	31/08/99	89	NA	0.172	F	17
	N. Pride	9	432	16/03/99	80	5.5	0.169	M	15
		8	819	13/03/99	94	9	0.178	F	15
		8	552	13/03/99	94	10	0.179	F	15
		11	809	17/03/99	97	9	0.183	F	15
		23	717	30/03/99	93	9	0.225	F	15
		7	340	12/03/99	106	11.5	0.229	M	15
		10	466	16/03/99	75	5	0.127	F	16
		7	582	12/03/99	79	6.5	0.135	F	16
		18	816	24/03/99	84	5	0.157	F	16
		3	439	08/03/99	88	8	0.176	M	16
		18	818	24/03/99	94	9	0.179	F	16
		18	691	24/03/99	122	20	0.227	F	16
		11	424	17/03/99	81	6	0.150	F	17
		15	430	21/03/99	86	7	0.179	F	17
		22	766	29/03/99	90	7	0.179	F	17
		14	763	20/03/99	90	7.5	0.205	F	17
		12	669	18/03/99	97	10	0.224	F	17
		25	580	01/04/99	100	12	0.228	F	17
		17	812	23/03/99	88	6.5	0.268	F	17

Patagonian toothfish
15-16 yr group (CQFE 4B)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	85	117	07/09/99	72	NA	0.126	F	15
		85	109	07/09/99	81	NA	0.166	F	16
		85	115	07/09/99	84	NA	0.198	M	16
		85	126	07/09/99	81	NA	0.157	M	17
	N. Pride	19	756	25/03/99	84	6	0.127	M	15
		2	529	07/03/99	79	NA	0.142	M	15
		26	344	02/06/99	107	11	0.150	F	15
		4	468	09/03/99	86	9	0.152	F	15
		15	414	21/03/99	83	7	0.157	F	15
		3	567	08/03/99	98	9	0.163	M	15
		19	683	25/03/99	80	5	0.174	F	15
		7	548	12/03/99	86	7.5	0.181	M	15
		7	383	12/03/99	NA	NA	0.194	NA	15
		4	351	09/03/99	105	14	0.231	F	15
		20	641	27/03/99	101	10	0.232	M	15
		6	449	11/03/99	91	7.5	0.158	F	16
		23	599	30/03/99	103	9	0.187	F	16
		11	546	17/03/99	97	8.5	0.201	F	16
		7	417	12/03/99	90	8	0.211	M	16
		15	392	21/03/99	74	7	0.226	M	16
		4	431	09/03/99	82	5	0.147	F	17
		8	465	13/03/99	86	7	0.167	M	17
		4	538	09/03/99	92	7.5	0.176	F	17
		22	759	29/03/99	88	5.5	0.182	M	17

Patagonian toothfish
15-16 yr group (CQFE 4C)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	81	87	06/09/99	85	NA	0.132	F	15
		105	37	15/09/99	82	NA	0.164	F	15
		85	124	07/09/99	86	NA	0.165	F	16
		85	79	07/09/99	78	NA	0.117	F	17
		92	135	09/09/99	80	NA	0.128	M	17
		64	323	31/08/99	88	NA	0.192	M	17
	N. Pride	8	551	13/03/99	78	5	0.127	F	15
		8	605	13/03/99	72	4.5	0.136	F	15
		6	484	11/03/99	80	5.5	0.157	M	15
		6	436	11/03/99	99	10	0.209	F	15
		9	757	14/03/99	95	10	0.211	F	15
		23	620	30/03/99	91	8.5	0.290	F	15
		11	509	17/03/99	82	6	0.150	F	16
		6	386	11/03/99	78	6	0.162	M	16
		15	788	21/03/99	97	10.5	0.168	F	16
		15	650	21/03/99	88	6	0.177	M	16
		22	729	29/03/99	93	7.5	0.180	M	16
		3	534	08/03/99	115	17	0.283	M	16
		3	537	08/03/99	86	7	0.146	M	17
		10	796	16/03/99	90	8	0.195	F	17
		10	539	16/03/99	114	15	0.197	F	17
		7	543	12/03/99	100	10	0.204	M	17
		15	768	21/03/99	84	6.5	0.212	M	17
		12	561	18/03/99	97	10	0.246	F	17

Patagonian toothfish
20-24 yr group (CQFE 5A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21		143	09/09/99	93	NA	0.184	M	20
			173	09/09/99	91	NA	0.187	M	20
			274	08/09/99	79	NA	0.214	M	21
			75	08/09/99	95	NA	0.247	F	21
			136	09/09/99	88	NA	0.184	F	22
Kerguelen 2	Kerguelen		187	10/10/1999	101	NA	0.241	M	20
			313	23/10/99	106	NA	0.266	M	20
			383	25/10/99	93	NA	0.208	F	21
			11	2/10/1999	110	NA	0.216	M	21
			343	24/10/99	96	NA	0.325	M	21
			333	23/10/99	133	NA	0.328	F	21
			17	2/10/1999	130	NA	0.356	F	21
			171	10/10/1999	109	NA	0.232	F	22
			185	10/10/1999	95	NA	0.260	M	22
			324	23/10/99	105	NA	0.277	M	22
			664	21/02/00	120	17.5	0.289	F	22
			707	24/02/00	98	9	0.255	F	23
			717	24/02/00	101	8.5	0.255	M	23
Kerguelen 1	N. Pride		590	01/04/99	89	7.5	0.165	M	20
			495	08/03/99	97	10.5	0.176	M	21
			549	13/03/99	89	9	0.180	M	21
			630	25/03/99	85	6	0.222	M	21
			408	13/03/99	88	8.5	0.162	M	22
			396	13/03/99	93	8	0.189	F	22
			646	20/03/99	95	10.5	0.193	M	22
			490	07/03/99	96	NA	0.230	F	22
			440	12/03/99	105	11	0.210	F	23
			609	29/03/99	93	6.5	0.212	M	23
			622	12/03/99	92	8	0.241	M	23
			353	09/03/99	93	9	0.246	F	23
			600	27/03/99	97	8.5	0.194	M	24
			752	30/03/99	96	8	0.202	M	24
			710	29/03/99	93	7	0.221	M	24
			475	14/03/99	88	7.5	0.225	M	24
			480	09/03/99	101	12.5	0.256	M	24

Patagonian toothfish
20-24 yr group (CQFE 5B)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21		138	09/09/99	89	NA	0.152	M	21
Kerguelen 2	Kerguelen		362	24/10/99	103		0.263	F	20
			340	24/10/99	126		0.327	F	20
			396	25/10/99	75		0.119	M	21
			710	24/02/00	103	10.5	0.210	F	21
			731	24/02/00	85	6	0.183	M	22
			741	25/02/00	87	8.5	0.215	M	22
			339	24/10/99	96		0.245	M	22
			23	2/10/1999	98		0.256	M	22
			189	10/10/1999	91		0.195	M	23
			207	10/10/1999	93		0.203	M	24
			168	10/10/1999	115		0.348	F	24
Kerguelen 1	N. Pride		375	18/03/99	90	6.5	0.178	M	20
			647	24/03/99	101	12.5	0.242	F	20
			564	02/04/99	107	10	0.304	F	20
			697	12/03/99	96	11	0.197	F	21
			550	08/03/99	91	10.5	0.215	F	21
			478	07/03/99	90	NA	0.240	F	21
			399	09/03/99	106	12.5	0.252	F	21
			800	23/03/99	118	17.5	0.305	F	21
			777	20/03/99	99	10.5	0.180	M	22
			651	16/03/99	89	7	0.184	F	22
			672	14/03/99	83	6.5	0.200	M	22
			659	09/03/99	92	11	0.213	F	22
			374	20/03/99	93	9	0.222	M	22
			354	09/03/99	113	19	0.235	F	22
			676	14/03/99	99	9	0.280	F	22
			737	13/03/99	106	10.5	0.328	F	22
			378	09/03/99	89	7	0.150	M	23
			602	29/03/99	87	6.5	0.167	M	23
			655	17/03/99	78	5	0.180	F	23
			795	23/03/99	93	8	0.240	M	23
			633	23/03/99	103	12.5	0.255	F	23
			810	27/03/99	83	6	0.156	M	24
			482	21/03/99	99	10	0.214	M	24

Patagonian toothfish
20-24 yr group (CQFE 5B)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21		165	09/09/99	57	NA	0.241	F	22
			176	09/09/99	99	NA	0.228	M	23
Kerguelen 2	Kerguelen		645	20/02/00	85	6.5	0.184	M	20
			24	2/10/1999	100		0.253	F	20
			385	25/10/99	96		0.200	M	21
			309	23/10/99	106		0.232	M	21
			204	10/10/1999	114		0.285	M	21
			617	20/02/00	95	8.5	0.211	M	22
			321	23/10/99	100		0.213	F	22
			10	2/10/1999	100		0.246	M	22
			223	16/10/99	92		0.252	M	22
			200	10/10/1999	124		0.328	F	22
			387	25/10/99	93		0.209	F	23
			344	24/10/99	123		0.215	F	23
			689	21/02/00	105	11.5	0.237	F	23
			202	10/10/1999	110		0.254	F	23
			323	23/10/99	104		0.255	M	23
			306	23/10/99	98		0.218	M	24
Kerguelen 1	N. Pride		533	11/03/99	90	7	0.172	M	20
			559	12/03/99	84	6	0.173	M	20
			458	18/03/99	93	9	0.179	F	20
			652	12/03/99	88	7	0.235	F	20
			814	24/03/99	89	6.5	0.205	M	21
			394	12/03/99	82	7	0.212	M	21
			702	14/03/99	95	10	0.224	F	21
			352	11/03/99	115	18.5	0.246	M	21
			712	29/03/99	101	9.5	0.315	F	21
			442	09/03/99	97	11	0.179	M	22
			454	13/03/99	93	10	0.235	M	23
			503	09/03/99	91	10	0.348	F	23
			782	20/03/99	85	6.5	0.188	M	24
			775	14/03/99	93	8.5	0.198	M	24
			401	09/03/99	96	11	0.215	M	24
			575	01/04/99	95	10	0.238	M	24
			611	21/03/99	125	25	0.304	F	24

Patagonian toothfish
25-27 yr group (CQFE 6A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	88	261	08/09/99	78	NA	0.235	M	25
		105	28	15/09/99	89	NA	0.221	M	26
		88	76	08/09/99	89	NA	0.237	M	26
		81	81	06/09/99	89	NA	0.203	M	27
		92	84	09/09/99	86	NA	0.221	M	27
		64	260	31/08/99	105	NA	0.254	F	27
	N. Pride	24	746	31/03/99	84	5.5	0.154	M	25
		15	406	21/03/99	89	7	0.183	M	25
		12	398	18/03/99	100	10	0.198	M	25
		9	664	25/03/99	96	9	0.198	M	25
		25	588	01/04/99	91	7.5	0.202	M	25
		15	598	21/03/99	90	8.5	0.234	M	25
		24	668	31/03/99	108	13	0.242	F	25
		8	794	13/03/99	99	10	0.267	F	25
		9	688	14/03/99	94	10	0.270	M	25
		9	747	14/03/99	102	10.5	0.289	M	25
		4	631	09/03/99	114	14.5	0.358	F	25
		3	416	08/03/99	98	10.5	0.168	F	26
		12	670	18/03/99	96	10	0.191	M	26
		11	613	17/03/99	90	6	0.208	M	26
		22	789	29/03/99	89	8	0.223	F	26
		8	741	13/03/99	110	15	0.227	F	26
		9	389	16/03/99	98	9.5	0.228	F	26
		6	423	11/03/99	100	10	0.242	M	26
		20	722	27/03/99	93	5.5	0.243	M	26
		19	685	25/03/99	89	7.5	0.252	F	26
		22	696	29/03/99	117	14.5	0.265	F	26
		22	624	29/03/99	111	14.5	0.272	F	26
		15	784	21/03/99	99	9.5	0.302	M	26
		9	370	16/03/99	106	10.5	0.321	F	26
		20	765	27/03/99	111	14	0.345	F	26
		25	591	01/04/99	94	8	0.211	M	27
		22	644	29/03/99	88	6	0.211	M	27
		20	692	27/03/99	91	7.5	0.225	M	27
		6	341	09/03/99	92	12.5	0.254	M	27
		15	400	21/03/99	99	10	0.269	F	27
		9	824	14/03/99	93	10	0.274	F	27
		17	787	23/03/99	96	10	0.280	F	27
		25	583	01/04/99	97	10	0.286	F	27
		12	438	18/03/99	96	9	0.287	M	27
		11	807	17/03/99	91	8	0.296	F	27
		8	595	13/03/99	108	10	0.313	F	27
		3	542	08/03/99	110	15	0.320	F	27
		6	441	11/03/99	119	18	0.326	F	27

Patagonian toothfish
28-34 yr group (CQFE 7A)

Project #	Call Sign	Palangre #	CQFE #	Collection date	Length (TL cm)	Weight (Kg)	Otolith Wt. (g)	Sex	Estimated age (yr)
Kerguelen 1	KDT21	88	95	08/09/99	90	NA	0.277	M	28
		80	332	06/09/99	98	NA	0.237	M	29
		113	49	18/09/99	97	NA	0.259	F	29
	N. Pride	3	473	11/03/99	100	11	0.224	F	28
		20	663	27/03/99	89	7	0.228	M	28
		20	811	27/03/99	100	10	0.302	F	28
		16	496	20/03/99	101	10.5	0.217	F	29
		19	665	25/03/99	95	8	0.236	M	29
		3	460	08/03/99	91	12	0.239	M	29
		17	715	23/03/99	103	11	0.252	M	29
		6	421	11/03/99	116	18.5	0.257	F	29
		25	435	01/04/99	96	8.5	0.263	F	29
		3	461	08/03/99	99	12	0.273	F	29
		22	607	29/03/99	96	8.5	0.173	M	30
		22	666	29/03/99	95	9	0.208	M	30
		15	678	21/03/99	99	10	0.312	M	30
		22	648	29/03/99	90	6.5	0.251	M	31
		15	596	21/03/99	98	10.5	0.372	F	31
		26	336	02/04/99	107	12	0.181	F	32
		11	355	17/03/99	95	8	0.243	M	32
		20	689	27/03/99	99	9.5	0.262	F	32
		17	751	23/03/99	108	14	0.322	F	32
		12	684	18/03/99	103	10	0.341	M	32
		7	615	12/03/99	99	7.5	0.196	F	33
		6	704	11/03/99	122	20	0.202	F	33
		11	429	17/03/99	97	10	NA	M	33
		3	535	08/03/99	101	14	0.206	F	34
		19	653	25/03/99	107	12	0.246	M	34

Appendix 1b. List of CAF Patagonian toothfish samples used in the radiometric analyses with the details of each fish listed for consideration. Some reference numbers are meant for those using the system. Collection date was provided in the mm/dd/yy format. Fish weight was unavailable, as was sex for many samples.

Patagonian toothfish
5-7 yr group (CAF 2A)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	282	sc131870	1/19/01	521	0.070	NA	5
	330	sc131904	1/19/01	603	0.065	NA	5
	359	sc132043	1/20/01	433	0.046	NA	5
	360	sc132042	1/20/01	402	0.043	NA	5
	372	sc132032	1/20/01	542	0.088	NA	5
	418	sc132058	1/21/01	524	0.099	NA	5
	467	sc132158	1/22/01	514	0.056	NA	5
	486	sc132702	1/23/01	469	0.060	NA	5
	494	sc132707	1/23/01	459	0.048	NA	5
	498	sc132718	1/23/01	499	0.067	NA	5
	541	sc133051	1/26/01	440	0.055	NA	5
	131	sc131371	1/11/01	546	0.060	NA	6
	193	sc131655	1/13/01	557	0.055	NA	6
	207	sc131634	1/13/01	504	0.071	NA	6
	215	sc131669	1/13/01	565	0.075	NA	6
	234	sc131614	1/13/01	489	0.064	NA	6
	348	sc131978	1/19/01	654	0.083	NA	6
	421	sc132052	1/21/01	526	0.072	NA	6
	422	sc132066	1/21/01	564	0.091	NA	6
	425	sc132302	1/22/01	515	0.057	NA	6
	428	sc132311	1/22/01	504	0.062	NA	6
	431	sc132139	1/22/01	538	0.072	NA	6
	441	sc132291	1/22/01	545	0.061	NA	6
	447	sc132233	1/22/01	538	0.075	NA	6
	448	sc132127	1/22/01	551	0.084	NA	6
	516	sc132700	1/23/01	533	0.070	NA	6
	194	sc131640	1/13/01	594	0.087	NA	7
	198	sc131666	1/13/01	605	0.091	NA	7
	206	sc131668	1/13/01	614	0.087	NA	7
	211	sc131629	1/13/01	643	0.097	NA	7
	328	sc131902	1/19/01	477	0.063	NA	7
	346	sc131818	1/19/01	627	0.089	NA	7

Patagonian toothfish 5-7 yr group (CAF 2B)							
Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	197	sc131617	1/13/01	490	0.058	NA	5
	397	sc132067	1/21/01	418	0.055	NA	5
	403	sc132055	1/21/01	487	0.076	NA	5
	427	sc132288	1/22/01	507	0.048	NA	5
	475	sc132659	1/23/01	513	0.069	NA	5
	483	sc132695	1/23/01	495	0.072	NA	5
	496	sc132717	1/23/01	496	0.056	NA	5
	497	sc132515	1/23/01	448	0.049	NA	5
	506	sc132690	1/23/01	475	0.060	NA	5
	153	sc131344	1/11/01	516	0.081	NA	6
	195	sc131665	1/13/01	596	0.104	NA	6
	243	sc131683	1/16/01	481	0.059	NA	6
	363	sc132041	1/20/01	522	0.073	NA	6
	515	sc132655	1/23/01	535	0.070	NA	6
	33	sc130555	1/5/01	605	0.072	NA	7
	86	sc131209	1/10/01	733	0.129	NA	7
	94	sc131175	1/10/01	689	0.111	NA	7
	115	sc131186	1/10/01	653	0.084	NA	7
	119	sc131350	1/11/01	656	0.110	NA	7
	171	sc131566	1/12/01	642	0.094	NA	7
	201	sc131653	1/13/01	603	0.087	NA	7
	233	sc131664	1/13/01	585	0.072	NA	7
	242	sc131686	1/16/01	523	0.061	NA	7
	344	sc131981	1/19/01	633	0.105	NA	7
	350	sc131863	1/19/01	654	0.114	NA	7
	352	sc131846	1/19/01	618	0.090	NA	7
	353	sc131825	1/19/01	656	0.091	NA	7
	377	sc132030	1/20/01	578	0.082	NA	7
	383	sc132090	1/21/01	782	0.101	NA	7
	404	sc132072	1/21/01	557	0.080	NA	7
	449	sc132238	1/22/01	557	0.080	NA	7
	465	sc132220	1/22/01	524	0.079	NA	7

Patagonian toothfish
5-7 yr group (CAF 2C)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	2	Sc130541	1/5/01	464	0.047	NA	5
	25	sc130543	1/5/01	412	0.031	NA	5
	213	sc131623	1/13/01	502	0.052	NA	5
	235	sc131627	1/13/01	471	0.059	NA	5
	366	sc132037	1/20/01	441	NA	NA	5
	388	sc132054	1/21/01	477	0.079	NA	5
	395	sc132059	1/21/01	504	0.059	NA	5
	402	sc132062	1/21/01	449	0.047	NA	5
	411	sc132082	1/21/01	420	0.048	NA	5
	464	sc132252	1/22/01	520	0.048	NA	5
	476	sc132554	1/23/01	508	0.064	NA	5
	479	sc132670	1/23/01	486	0.060	NA	5
	502	sc132649	1/23/01	558	0.071	NA	5
	39	sc130554	1/5/01	541	0.065	NA	6
	40	sc130544	1/5/01	545	0.077	NA	6
	200	sc131659	1/13/01	506	0.070	NA	6
	286	sc131856	1/19/01	560	0.067	NA	6
	335	sc131819	1/19/01	606	0.071	NA	6
	343	sc131871	1/19/01	617	0.084	NA	6
	349	sc131949	1/19/01	657	0.091	NA	6
	419	sc132064	1/21/01	528	0.073	NA	6
	458	sc132253	1/22/01	550	0.061	NA	6
	474	sc132653	1/23/01	512	0.070	NA	6
	492	sc132711	1/23/01	494	0.069	NA	6
	513	sc132714	1/23/01	539	0.069	NA	6
	80	sc131204	1/10/01	702	0.141	NA	7
	105	sc131172	1/10/01	596	0.090	NA	7
	161	sc131571	1/12/01	615	0.092	NA	7
	226	sc131654	1/13/01	576	0.072	NA	7
	230	sc131628	1/13/01	586	0.085	NA	7
	333	sc131830	1/19/01	608	0.076	NA	7
	452	sc132153	1/22/01	638	0.099	NA	7

Patagonian toothfish
11-12 yr group (CAF 3A)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	1	Sc133848	1/2/01	987	0.182	NA	11
	20	sc130552	1/5/01	693	0.113	NA	11
	37	sc130565	1/5/01	777	0.12	NA	11
	113	sc131194	1/10/01	766	0.15	NA	11
	145	sc131341	1/11/01	735	0.101	NA	11
	203	sc131636	1/13/01	834	0.139	NA	11
	257	sc131884	1/19/01	780	0.138	NA	11
	270	sc132009	1/19/01	793	0.133	NA	11
	272	sc131847	1/19/01	807	0.154	NA	11
	316	sc131961	1/19/01	877	0.116	NA	11
	387	sc132091	1/21/01	808	0.144	NA	11
	424	sc132113	1/21/01	811	0.134	NA	11
	97	sc131191	1/10/01	744	0.111	NA	12
	285	sc131948	1/19/01	727	0.116	NA	12
	312	sc131998	1/19/01	776	0.132	NA	12
	393	sc132115	1/21/01	857	0.14	NA	12
	399	sc132096	1/21/01	836	0.149	NA	12
	405	sc132124	1/21/01	846	0.145	NA	12
	410	sc132099	1/21/01	882	0.153	NA	12
	466	sc132335	1/22/01	930	0.172	NA	12
	477	sc132400	1/23/01	903	0.136	NA	12
	484	sc132406	1/23/01	907	0.139	NA	12
	505	sc132440	1/23/01	1002	0.202	NA	12
32	150	sc135751	2/9/01	1032	0.203	NA	11
	88	sc134889	2/5/01	1009	0.221	NA	12
	89	sc134845	2/5/01	987	0.168	NA	12

Patagonian toothfish
11-12 yr group (CAF 3B)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	67	sc130950	1/7/01	731	0.109	NA	11
	87	sc131183	1/10/01	750	0.103	NA	11
	98	sc131201	1/10/01	684	0.14	NA	11
	114	sc131203	1/10/01	765	0.128	NA	11
	184	sc131579	1/12/01	727	0.102	NA	11
	218	sc131621	1/13/01	663	0.099	NA	11
	260	sc131988	1/19/01	924	0.144	NA	11
	313	sc131987	1/19/01	779	0.11	NA	11
	374	sc132044	1/20/01	786	0.151	NA	11
	412	sc132104	1/21/01	852	0.154	NA	11
	442	sc132179	1/22/01	823	0.147	NA	11
	459	sc132324	1/22/01	891	0.148	NA	11
	489	sc132429	1/23/01	931	0.159	NA	11
	284	sc132005	1/19/01	795	0.128	NA	12
	288	sc132019	1/19/01	849	0.123	NA	12
	315	sc132017	1/19/01	869	0.143	NA	12
	329	sc131965	1/19/01	913	0.168	NA	12
	379	sc132107	1/21/01	898	0.166	NA	12
	440	sc132332	1/22/01	864	0.169	NA	12
	443	sc132190	1/22/01	827	0.126	NA	12
	460	sc132329	1/22/01	896	0.179	NA	12
32	39	sc133856	2/2/01	924	0.158	NA	11
	46	sc133866	2/2/01	916	0.164	NA	11
	33	sc133948	2/2/01	952	0.166	NA	12
	41	sc133625	2/2/01	872	0.125	NA	12
	198	sc136281	2/13/01	1074	0.214	NA	12

Patagonian toothfish
15-17 yr group (CAF 4A)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	297	sc131983	1/19/01	788	0.148	NA	15
	303	sc131959	1/19/01	827	0.138	NA	15
	319	sc131955	1/19/01	881	0.159	NA	15
	406	sc132109	1/21/01	841	0.129	NA	15
	414	sc132093	1/21/01	863	0.171	NA	15
	262	sc131968	1/19/01	941	0.158	NA	16
32	10	sc133901	2/2/01	999	0.201	NA	15
	22	sc133840	2/2/01	881	0.174	NA	15
	54	sc134124	2/3/01	931	0.163	NA	15
	106	sc135294	2/7/01	1067	0.214	NA	15
	92	sc134842	2/5/01	986	0.211	NA	16
	136	sc135401	2/8/01	1173	0.165	NA	16
	158	sc135866	2/10/01	1125	0.209	NA	16
	193	sc136285	2/13/01	1019	0.178	NA	16
	14	sc134000	2/2/01	1076	0.209	NA	17
	29	sc133975	2/2/01	1196	0.189	NA	17
	32	sc133870	2/2/01	1138	0.269	NA	17
	62	sc134099	2/3/01	994	0.174	NA	17
	83	sc134791	2/5/01	964	0.195	NA	17
	87	sc134624	2/5/01	1127	0.217	NA	17
	175	sc136199	2/13/01	1166	0.198	NA	17
	192	sc136293	2/13/01	1016	0.251	NA	17
33	6	al281680	4/10/01	1033	0.199	F	15
35	12	al296598	6/8/01	1045	0.177	F	17
	13	al296610	6/8/01	1082	0.243	F	17
36	16	sc172871	9/18/01	1271	0.336	F	17
	41	sc175504	9/29/01	1205	0.264	F	17
	49	sc175503	9/29/01	1163	0.195	F	17
	52	sc175509	9/29/01	1180	0.232	NA	17

Patagonian toothfish
15-17 yr group (CAF 4B)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	163	sc131583	1/12/01	973	0.181	NA	15
	469	sc132216	1/22/01	1065	0.201	NA	15
	485	sc132434	1/23/01	905	0.178	NA	15
	300	sc131832	1/19/01	817	0.129	NA	17
32	35	sc133993	2/2/01	954	0.169	NA	15
	74	sc134622	2/5/01	1157	0.197	NA	15
	100	sc134935	2/6/01	986	0.175	NA	15
	113	sc135307	2/7/01	1205	0.288	NA	15
	132	sc135306	2/7/01	1048	0.201	NA	15
	151	sc135578	2/9/01	1219	0.275	NA	15
	21	sc133835	2/2/01	940	0.161	NA	16
	28	sc133949	2/2/01	1124	0.254	NA	16
	64	sc134283	2/4/01	1022	0.206	NA	16
	94	sc134837	2/5/01	1103	0.177	NA	16
	95	sc134840	2/5/01	981	0.21	NA	16
	105	sc135205	2/7/01	1060	0.183	NA	16
	27	sc133750	2/2/01	956	0.167	NA	17
	65	sc134282	2/4/01	1104	0.17	NA	17
	70	sc134529	2/4/01	999	0.181	NA	17
	98	sc135095	2/6/01	1150	0.26	NA	17
	110	sc135292	2/7/01	1038	0.229	NA	17
	116	sc135288	2/7/01	1023	0.19	NA	17
	120	sc135171	2/7/01	1268	0.287	NA	17
35	16	sd155645	6/4/01	1252	0.213	F	16
36	14	sc172880	9/18/01	1269	0.315	F	15
	27	sc173867	9/23/01	1026	0.219	F	15
	22	sc173106	9/19/01	1094	0.243	F	16
	25	sc173639	9/21/01	1184	0.203	F	16
	28	sc174794	9/25/01	1148	0.247	F	16
	37	sc175358	9/28/01	1226	0.248	F	17

Patagonian toothfish
15-17 yr group (CAF 4C)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	212	sc131673	1/13/01	971	0.222	NA	15
	214	sc131675	1/13/01	1009	0.209	NA	15
	221	sc131677	1/13/01	1028	0.195	NA	15
	269	sc131976	1/19/01	953	0.173	NA	15
	416	sc132094	1/21/01	842	0.117	NA	15
	470	sc132323	1/22/01	897	0.192	NA	15
	341	sc131969	1/19/01	855	0.138	NA	16
	378	sc132101	1/21/01	892	0.182	NA	16
	456	sc132349	1/22/01	904	0.18	NA	16
32	7	sc133952	2/2/01	1047	0.282	NA	15
	66	sc134461	2/4/01	938	0.215	NA	15
	80	sc134623	2/5/01	982	0.186	NA	15
	8	sc133894	2/2/01	925	0.186	NA	16
	23	sc133868	2/2/01	1008	0.191	NA	16
	24	sc133846	2/2/01	945	0.19	NA	16
	34	sc133633	2/2/01	927	0.202	NA	16
	49	sc134156	2/3/01	953	0.174	NA	16
	58	sc134116	2/3/01	924	0.138	NA	16
	96	sc134953	2/6/01	1085	NA	NA	16
	107	sc135302	2/7/01	1095	0.233	NA	16
	173	sc136284	2/13/01	1159	0.234	NA	16
	90	sc134839	2/5/01	975	0.188	NA	17
	177	sc136318	2/13/01	1067	0.19	NA	17
	186	sc136290	2/13/01	1184	0.262	NA	17
	199	sc136309	2/13/01	1019	0.165	NA	17
33	14	al283210	4/17/01	1021	0.214	F	17
	18	al283225	4/22/01	1145	0.258	F	17
35	19	sd156120	6/19/01	1130	0.228	F	17
36	32	sc175050	9/26/01	1144	0.218	F	16
	30	sc175048	9/26/01	1257	0.234	F	17

Patagonian toothfish 20-24 yr group (CAF 5A)							
Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	227	sc131678	1/13/01	1486	0.285	NA	22
32	188	sc136308	2/13/01	1164	0.318	NA	20
	167	sc136225	2/13/01	1306	0.268	NA	21
	183	sc136280	2/13/01	1063	0.221	NA	21
	108	sc135295	2/7/01	1092	0.224	NA	22
	133	sc135405	2/8/01	1244	0.238	NA	22
	179	sc136291	2/13/01	1377	0.301	NA	22
	12	sc133873	2/2/01	1313	0.242	NA	23
	129	sc135311	2/7/01	1455	0.270	NA	23
	149	sc135785	2/9/01	1038	0.258	NA	23
	189	sc136282	2/13/01	1136	0.297	NA	23
	194	sc136227	2/13/01	1425	0.365	NA	23
	144	sc135408	2/8/01	1246	0.220	NA	24
33	7	al281603	4/10/01	1405	0.219	F	20
	9	al281678	4/11/01	1086	0.180	F	20
	17	al283226	4/22/01	1061	0.221	F	20
	5	al281606	4/10/01	1305	0.273	F	22
35	15	sc131584	1/12/01	1066	0.263	NA	20
	1	al295217	6/1/01	1311	0.288	NA	23
36	53	sc175596	9/30/01	1234	0.208	F	20
	12	sc172875	9/18/01	1450	0.295	F	24
	51	sc175502	9/29/01	1366	0.334	F	24

Patagonian toothfish 20-24 yr group (CAF 5B)							
Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	380	sc132126	1/21/01	1358	0.259	NA	21
	332	sc131975	1/19/01	1234	0.367	NA	22
32	52	sc134098	2/3/01	968	0.183	NA	20
	63	sc134281	2/4/01	1017	0.160	NA	20
	141	sc135507	2/8/01	1151	0.219	NA	20
	157	sc136174	2/12/01	1336	0.215	NA	20
	181	sc136292	2/13/01	1372	0.328	NA	20
	112	sc135308	2/7/01	1295	0.352	NA	21
	47	sc133847	2/2/01	885	0.140	NA	22
	187	sc136223	2/13/01	1318	0.272	NA	22
	123	sc135290	2/7/01	1002	0.191	NA	23
	128	sc135299	2/7/01	1167	0.255	NA	24
	178	sc136289	2/13/01	1388	0.308	NA	24
	191	sc136319	2/13/01	1223	0.283	NA	24
36	24	sc173408	9/20/01	1260	0.285	F	20
	43	sc175501	9/29/01	1315	0.277	F	21
	11	sc172876	9/18/01	1031	0.337	F	22
	42	sc175500	9/29/01	1267	0.240	F	22
	31	sc175051	9/26/01	1378	0.314	F	23
	36	sc175361	9/28/01	1480	0.249	F	24
	38	sc175360	9/28/01	1590	0.320	F	24
37	3	sc181126	11/16/01	1410	0.241	F	23

Patagonian toothfish
20-24 yr group (CAF 5C)

Batch	Number	Serial number	Collection date	Length (TL mm)	Otolith Wt. (g)	Sex	Estimated age (yr)
31	188	sc131588	1/12/01	992	0.174	NA	20
	445	sc132217	1/22/01	1449	0.330	NA	23
32	104	sc135096	2/6/01	1146	0.239	NA	20
	148	sc135579	2/9/01	1466	0.342	NA	20
	176	sc136226	2/13/01	1386	0.273	NA	20
	53	sc134087	2/3/01	946	0.187	NA	21
	81	sc134836	2/5/01	1085	0.205	NA	21
	102	sc135097	2/6/01	1156	0.358	NA	21
	117	sc135309	2/7/01	1333	0.250	NA	21
	162	sc136224	2/13/01	1276	0.318	NA	21
	166	sc136317	2/13/01	1235	0.254	NA	21
	195	sc136249	2/13/01	1281	0.233	NA	21
	37	sc133872	2/2/01	1312	0.313	NA	22
	71	sc134284	2/4/01	1340	0.262	NA	22
	145	sc135407	2/8/01	1218	0.235	NA	22
	182	sc136288	2/13/01	1378	0.411	NA	22
	140	sc135432	2/8/01	1297	0.309	NA	24
35	5	al296077	6/6/01	1153	0.257	M	23
36	6	sc172424	9/15/01	1480	0.336	F	20
	8	sc172733	9/17/01	1298	0.312	F	20
	19	sc173289	9/19/01	1203	0.262	F	20
	46	sc175507	9/29/01	1272	0.265	F	23

Appendix 2. List of orange roughy (ORH) samples used in the radiometric analyses with the details of each fish listed for consideration. Otolith weight was provided for only some of the samples used; therefore, all otoliths were weighed independently at MLML. Each age group was separated to define sample specificity. No data was represented as "n.d." in the table.

ORH Samples

25-30 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA) (g)	Otolith wt. (MLML) (g)	Sex	Estimated age (yr)
155	39	8-Jul-2003	25	0.58	0.067	0.069	1	25
155	45	8-Jul-2003	31	1.00	0.116	0.116	1	25
155	94	8-Jul-2003	32	0.82	0.097	0.099	1	25
155	97	8-Jul-2003	31	0.76	0.099	0.100	1	25
155	155	9-Jul-2003	29	0.66	0.076	0.079	1	25
155	138	9-Jul-2003	29	0.66	0.094	0.095	2	26
155	202	10-Jul-2003	29	0.80	0.107	0.107	1	26
155	220	10-Jul-2003	32	1.08	0.13	0.132	1	26
155	226	10-Jul-2003	34	1.18	0.158	0.156	2	26
155	54	8-Jul-2003	34	1.10	0.128	0.131	1	27
155	58	8-Jul-2003	29	0.88	0.097	0.097	1	27
155	154	9-Jul-2003	29	0.84	0.092	0.097	2	27
155	175	9-Jul-2003	35	1.26	0.12	0.125	2	27
155	13	8-Jul-2003	33	1.08	0.124	0.123	2	28
155	14	8-Jul-2003	31	1.04	0.122	0.103	2	28
155	32	8-Jul-2003	31	0.86	0.101	0.106	1	28
155	44	8-Jul-2003	33	1.16	0.108	0.105	1	28
155	87	8-Jul-2003	31	0.94	0.119	0.118	1	28
155	140	9-Jul-2003	34	1.36	0.12	0.119	2	28
155	145	9-Jul-2003	27	0.52	0.085	0.083	1	28
155	152	9-Jul-2003	30	0.84	0.118	0.120	2	28
155	189	10-Jul-2003	36	1.38	0.123	0.124	1	28
155	209	10-Jul-2003	33	1.22	0.133	0.131	1	28
155	56	8-Jul-2003	35	n.d.	0.173	0.171	2	29
155	91	8-Jul-2003	30	0.80	0.102	0.098	1	29
155	96	8-Jul-2003	32	0.92	0.139	0.134	1	29
155	98	8-Jul-2003	33	1.12	0.148	0.157	1	29
155	130	9-Jul-2003	36	1.50	0.141	0.141	2	29
155	143	9-Jul-2003	36	1.50	0.163	0.153	1	29
155	57	8-Jul-2003	34	1.16	0.11	0.105	1	30
155	182	10-Jul-2003	36	1.46	0.156	0.15	1	30

ORH SAMPLES
40-45 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA)	Otolith wt. (MLML)	Sex	Estimated age (yr)
155	46	8-Jul-2003	35	1.36	0.141	0.141	2	40
155	157	9-Jul-2003	35	1.34	0.196	0.200	2	40
155	166	9-Jul-2003	37	1.38	0.197	0.207	2	40
155	212	10-Jul-2003	36	1.50	0.155	0.160	2	40
155	263	10-Jul-2003	33	1.28	0.144	0.150	1	40
155	271	10-Jul-2003	34	1.18	0.158	0.153	1	40
155	361	11-Jul-2003	36	1.50	0.195	0.197	2	40
155	390	11-Jul-2003	38	1.64	0.22	0.211	2	40
155	113	9-Jul-2003	38	1.90	0.256	0.249	2	41
155	324	10-Jul-2003	33	1.11	0.133	0.129	1	41
155	347	11-Jul-2003	37	1.75	0.243	0.234	2	41
155	354	11-Jul-2003	37	1.70	0.167	0.164	2	41
155	252	10-Jul-2003	34	1.32	0.155	0.147	1	42
155	255	10-Jul-2003	32	1.12	0.132	0.138	2	42
155	408	11-Jul-2003	38	1.42	0.24	0.229	2	42
155	74	8-Jul-2003	33	1.08	0.15	0.155	1	43
155	149	9-Jul-2003	30	0.86	0.129	0.130	2	43
155	274	10-Jul-2003	33	1.18	0.165	0.161	1	43
155	336	10-Jul-2003	36	1.40	0.205	0.185	1	43
155	362	11-Jul-2003	37	1.55	0.191	0.190	2	43
155	193	10-Jul-2003	33	1.48	0.187	0.157	1	44
155	195	10-Jul-2003	36	1.44	0.245	0.231	2	44
155	208	10-Jul-2003	34	1.20	0.146	0.155	2	44
155	246	10-Jul-2003	34	1.46	0.166	0.163	2	44
155	253	10-Jul-2003	39	1.58	0.223	0.215	2	44
155	299	10-Jul-2003	35	1.32	0.11	0.118	2	44
155	337	10-Jul-2003	36	1.30	0.191	0.189	1	44
155	12	8-Jul-2003	39	1.84	0.201	0.193	2	45
155	112	9-Jul-2003	36	1.54	0.174	0.180	2	45
155	120	9-Jul-2003	37	1.72	0.225	0.212	2	45
155	153	9-Jul-2003	36	1.34	0.19	0.182	2	45
155	381	11-Jul-2003	41	1.82	0.237	0.228	2	45

ORH SAMPLES
60-69 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA)	Otolith wt. (MLML)	Sex	Estimated age (yr)
155	510	18-Jul-2003	35	1.38	0.162	0.165	1	60
155	409	11-Jul-2003	37	1.50	0.254	0.258	1	61
155	6	8-Jul-2003	39	1.90	0.239	0.247	2	62
155	356	11-Jul-2003	34	1.15	0.167	0.175	1	63
155	764	20-Jul-2003	33	1.04	0.16	0.162	1	63
155	201	10-Jul-2003	38	1.84	0.19	0.198	2	64
155	293	10-Jul-2003	37	1.76	0.207	0.191	2	64
155	587	18-Jul-2003	38	1.80	0.238	0.260	2	65
155	205	10-Jul-2003	37	1.58	0.28	0.292	1	66
155	210	10-Jul-2003	39	1.76	0.33	0.335	2	66
155	281	10-Jul-2003	40	1.96	0.31	0.297	2	66
155	652	19-Jul-2003	38	1.52	0.294	0.328	2	67
155	248	10-Jul-2003	38	1.92	0.236	0.236	2	68
155	655	19-Jul-2003	37	1.50	0.229	0.240	2	69
155	770	20-Jul-2003	39	1.68	0.324	0.344	2	69
137	69	12-Jul-2002	39.8	0.90	n.d.	0.259	2	60
137	42	11-Jul-2002	37	1.64	n.d.	0.338	2	63
137	160	17-Jul-2002	35.2	1.42	n.d.	0.185	2	65
137	247	18-Jul-2002	39	2.10	n.d.	0.254	2	65
137	408	22-Jul-2002	37.5	1.68	n.d.	0.293	2	65
137	98	13-Jul-2002	36.2	1.88	n.d.	0.239	2	66
137	220	18-Jul-2002	36.2	1.38	n.d.	0.337	1	66
137	25	n.d.	37	1.50	n.d.	0.273	1	67
137	219	18-Jul-2002	38.5	1.84	n.d.	0.315	1	67

ORH SAMPLES

70-80 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA)	Otolith wt. (MLML)	Sex	Estimated age (yr)
155	186	10-Jul-2003	37	1.62	0.248	0.250	1	71
155	321	10-Jul-2003	37	1.56	0.252	0.245	1	71
155	633	19-Jul-2003	37	1.66	n.d.	0.292	2	74
155	270	10-Jul-2003	34	1.28	0.204	0.204	1	75
155	618	19-Jul-2003	38	1.74	0.238	0.243	2	75
155	663	19-Jul-2003	39	1.60	0.217	0.222	2	76
137	192	17-Jul-2002	36	1.42	n.d.	0.276	1	70
137	251	18-Jul-2002	39.5	1.94	n.d.	0.428	1	70
137	152	17-Jul-2002	36.5	1.76	n.d.	0.230	2	72
137	184	17-Jul-2002	33	1.00	n.d.	0.240	1	73
137	218	18-Jul-2002	38.5	1.74	n.d.	0.306	1	73
137	296	19-Jul-2002	33.2	1.24	n.d.	0.227	2	73
137	37	n.d.	31.1	0.98	n.d.	0.158	1	74
137	393	22-Jul-2002	32	1.67	n.d.	0.336	2	75
137	156	17-Jul-2002	40	1.94	n.d.	0.237	2	77
137	167	17-Jul-2002	37.5	2.08	n.d.	0.307	2	79
154	213	13-Jul-2003	40.5	2.39	0.22	0.242	2	70
154	484	19-Jul-2003	36	1.44	0.268	0.266	1	70
154	421	16-Jul-2003	36.5	1.46	0.285	0.273	2	72
154	357	16-Jul-2003	38.5	1.74	0.278	0.274	2	73
154	517	19-Jul-2003	36.5	1.52	0.308	0.316	2	77
154	485	19-Jul-2003	37.5	1.94	0.399	0.366	1	78
144	344	n.d.	34.8	1.30	0.31	0.300	1	71
144	541	n.d.	35	1.37	0.304	0.315	1	73
144	342	n.d.	36.8	1.57	0.423	0.413	1	78
144	461	n.d.	38	1.71	0.279	0.287	1	78

ORH SAMPLES
81-88 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA)	Otolith wt. (MLML)	Sex	Estimated age (yr)
155	291	10-Jul-2003	39	2.08	0.335	0.340	2	81
155	236	10-Jul-2003	41	2.28	0.347	0.342	2	83
155	700	19-Jul-2003	38	1.66	0.219	0.232	2	83
155	330	10-Jul-2003	40	1.80	0.318	0.333	1	87
155	499	12-Jul-2003	38	1.80	0.216	0.219	2	87
155	176	9-Jul-2003	40	1.96	0.311	0.323	2	88
137	353	21-Jul-2002	40	1.86	n.d.	0.322	2	83
137	164	17-Jul-2002	37.3	1.98	n.d.	0.190	2	88
154	260	13-Jul-2003	36.5	1.38	0.318	0.301	1	82
154	311	15-Jul-2003	33	1.27	0.249	0.242	1	87
144	492	n.d.	36.8	1.65	0.379	0.378	1	85
144	537	n.d.	37.7	1.58	0.401	0.378	1	85
144	221	n.d.	39.7	2.37	0.35	0.354	2	88
144	532	n.d.	33.6	1.39	0.295	0.285	1	88

90-108 yr group

Batch	Specimen	Collection date	Fish Length (SL cm)	Fish wt. (kg)	Otolith wt. (NIWA)	Otolith wt. (MLML)	Sex	Estimated age (yr)
155	351	11-Jul-2003	36	1.60	0.22	0.232	2	90
155	288	10-Jul-2003	37	1.52	0.373	0.377	1	91
155	481	12-Jul-2003	40	1.70	0.287	0.299	2	92
154	286	14-Jul-2003	37.5	1.51	0.288	0.293	1	93
154	491	19-Jul-2003	36.5	1.45	0.368	0.378	1	96
155	258	10-Jul-2003	38	1.78	0.269	0.268	2	98
154	511	19-Jul-2003	40	2.10	0.28	0.289	2	98
154	74	10-Jul-2003	37.5	1.72	0.344	0.351	2	101
144	463	n.d.	37.4	1.83	0.497	0.482	2	101
144	504	n.d.	34.5	1.28	0.294	0.294	1	101
144	524	n.d.	33.7	1.16	0.3	0.302	1	102
137	178	17-Jul-2002	39.5	1.58	n.d.	0.280	2	104
155	702	19-Jul-2003	43	2.16	0.357	0.359	2	108

Appendix 3. Synopsis of radium-226 values ($\text{dpm}\cdot\text{g}^{-1}$) from otoliths for the northeastern Pacific Ocean region.

Region: Northeastern Pacific Ocean										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Albatrossia pectoralis Subregions: Alaska, Oregon Burton (1999)	Adult	Cored	0.0463	0.0006	1.3	1SE	0.0524	0.0116	0.0292	0.0694
	Adult	Cored	0.0514	0.0006	1.1	1SE				
	Adult	Cored	0.0550	0.0006	1.1	1SE				
	Adult	Cored	0.0561	0.0007	1.2	1SE				
	Adult	Cored	0.0566	0.0010	1.8	1SE				
	Adult	Whole	0.0292	0.0003	1.1	1SE				
	Adult	Whole	0.0413	0.0005	1.1	1SE				
	Adult	Whole	0.0422	0.0007	1.6	1SE				
	Adult	Cored	0.0522	0.0006	1.1	1SE				
	Adult	Cored	0.0585	0.0008	1.4	1SE				
	Adult	Cored	0.0593	0.0007	1.1	1SE				
	Adult	Cored	0.0621	0.0007	1.1	1SE				
	Adult	Cored	0.0630	0.0007	1.1	1SE				
	Adult	Cored	0.0638	0.0012	1.9	1SE				
	Adult	Cored	0.0694	0.0008	1.1	1SE				
	Adult	Whole	0.0312	0.0003	1.0	1SE				
Anoplopoma fimbria Subregion: California Kastelle et al. (1994)	Juvenile	Whole	0.2880	0.0121	4.2	1SD	0.4140	0.0998	0.2880	0.5170
	Adult	Cored	0.3860	0.0170	4.4	1SD				
	Adult	Cored	0.4650	0.0191	4.1	1SD				
	Adult	Cored	0.5170	0.0212	4.1	1SD				
Coryphaenoides acrolepis Subregions: Washington, Oregon, California Andrews et al. (1999)	Juvenile	Whole	0.1245	0.0024	1.9	1SE	0.0634	0.0267	0.0419	0.1245
	Adult	Cored	0.0419	0.0006	1.4	1SE				
	Adult	Cored	0.0510	0.0007	1.4	1SE				
	Adult	Cored	0.0546	0.0007	1.3	1SE				
	Adult	Cored	0.0583	0.0006	1.1	1SE				
	Adult	Cored	0.0639	0.0028	4.4	1SE				
	Adult	Cored	0.0711	0.0017	2.5	1SE				
	Adult	Whole	0.0419	0.0012	2.9	1SE				
Gadus macrocephalus Subregions: Alaska Andrews (2005)	Adult	Cored	0.0570	0.0063	11.0	1SE	0.0769	0.0221	0.0570	0.1007
	Adult	Cored	0.0730	0.0039	5.4	1SE				
	Adult	Cored	0.1007	0.0051	5.1	1SE				
Hippoglossus stenolepis Subregions: Alaska Kastelle and Forsberg (2002)	Adults	Whole	0.0060	0.0028	47.0	1SD	0.0097	0.0033	0.0060	0.0124
	Adults	Whole	0.0063	0.0031	49.0	1SD				
	Adults	Whole	0.0118	0.0027	23.0	1SD				
	Adults	Whole	0.0122	0.0037	30.0	1SD				
	Adults	Whole	0.0124	0.0033	27.0	1SD				
Sebastes aleutianus Subregions: Gulf of Alaska, Washington, Oregon Kastelle et al. (2000)	Juvenile	Whole	0.0450	0.0050	11.1	1SD	0.0645	0.0168	0.0450	0.0860
	Adult	Cored	0.0630	0.0050	7.9	1SD				
	Adult	Cored	0.0860	0.0070	8.1	1SD				
	Adult	Whole	0.0640	0.0060	9.4	1SD				
Sebastes alutus Subregions: Gulf of Alaska, Washington, Oregon Kastelle et al. (2000)	Juvenile	Whole	0.0450	0.0050	11.1	1SD	0.0742	0.0151	0.0450	0.0900
	Juvenile	Whole	0.0590	0.0050	8.5	1SD				
	Juvenile	Whole	0.0800	0.0040	5.0	1SD				
	Adult	Cored	0.0630	0.0050	7.9	1SD				
	Adult	Cored	0.0820	0.0060	7.3	1SD				
	Adult	Cored	0.0860	0.0060	7.0	1SD				
	Adult	Cored	0.0900	0.0040	4.4	1SD				
	Adult	Whole	0.0780	0.0040	5.1	1SD				
	Adult	Whole	0.0850	0.0099	11.7	1SD				

Appendix 3 (cont.). Synopsis of radium-226 (dpm·g^{-1}) values from otoliths for the northern Pacific Ocean region.

Region: Northeastern Pacific Ocean

Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Sebastes borealis	Juvenile	Whole	0.0640	0.0050	7.8	1SD	0.0691	0.0192	0.0350	0.0900
Subregions: Gulf of	Adult	Cored	0.0620	0.0060	9.7	1SD				
Alaska,	Adult	Cored	0.0640	0.0050	7.8	1SD				
Washington, Oregon	Adult	Cored	0.0810	0.0060	7.4	1SD				
Kastelle et al. (2000)	Adult	Cored	0.0880	0.0060	6.8	1SD				
	Adult	Cored	0.0900	0.0070	7.8	1SD				
	Adult	Whole	0.0350	0.0040	11.4	1SD				
Sebastes diploproa	Juvenile	Whole	0.0430	0.0082	19.0	1SD	0.0430	0.0086	0.0330	0.0540
Subregions: West Coast	Adult	Whole	0.0330	0.0069	21.0	1SD				
USA, Canada	Adult	Whole	0.0420	0.0059	14.0	1SD				
Bennett et al. (1982)	Adult	Whole	0.0540	0.0092	17.0	1SD				
Sebastes melanostomus	Juvenile	Whole	0.0680	0.0009	1.3	1SE	0.0643	0.0035	0.0587	0.0681
Subregion: California	Adult	Cored	0.0587	0.0040	6.8	1SE				
Stevens et al. (2004)	Adult	Cored	0.0613	0.0019	3.1	1SE				
	Adult	Cored	0.0628	0.0021	3.4	1SE				
	Adult	Cored	0.0647	0.0021	3.3	1SE				
	Adult	Cored	0.0663	0.0014	2.1	1SE				
	Adult	Cored	0.0681	0.0016	2.3	1SE				
Sebastes paucispinis	Juvenile	Whole	0.0111	0.0002	1.5	1SE	0.0116	0.0018	0.0087	0.0148
Subregion: California	Juvenile	Whole	0.0137	0.0002	1.4	1SE				
Andrews et al. (2005)	Adult	Cored	0.0087	0.0001	1.5	1SE				
	Adult	Cored	0.0095	0.0001	1.4	1SE				
	Adult	Cored	0.0101	0.0002	1.7	1SE				
	Adult	Cored	0.0102	0.0003	3.3	1SE				
	Adult	Cored	0.0105	0.0002	1.8	1SE				
	Adult	Cored	0.0120	0.0002	1.7	1SE				
	Adult	Cored	0.0123	0.0002	2.0	1SE				
	Adult	Cored	0.0128	0.0003	2.0	1SE				
	Adult	Cored	0.0129	0.0001	1.1	1SE				
	Adult	Cored	0.0148	0.0002	1.5	1SE				
Sebastes pinniger	Juvenile	Whole	0.1220	0.0074	6.1	2SE	0.0988	0.0135	0.0803	0.1220
Subregion: Canada	Adult	Cored	0.0803	0.0010	1.3	2SE				
Andrews et al. (2007)	Adult	Cored	0.0888	0.0030	3.4	2SE				
	Adult	Cored	0.0899	0.0058	6.4	2SE				
	Adult	Cored	0.0924	0.0079	8.6	2SE				
	Adult	Cored	0.1020	0.0044	4.3	2SE				
	Adult	Cored	0.1060	0.0147	13.9	2SE				
	Adult	Cored	0.1090	0.0087	8.0	2SE				
Sebastes polyspinis	Juvenile	Whole	0.1200	0.0060	5.0	1SD	0.1212	0.0211	0.0980	0.1430
Subregions: Gulf of	Adult	Cored	0.0980	0.0060	6.1	1SD				
Alaska, Washington,	Adult	Cored	0.1030	0.0060	5.8	1SD				
Oregon	Adult	Cored	0.1420	0.0070	4.9	1SD				
Kastelle et al. (2000)	Adult	Cored	0.1430	0.0100	7.0	1SD				

Appendix 3 (cont.). Synopsis of radium-226 (dpm·g^{-1}) values from otoliths for the northern Pacific Ocean region.

Region: Northeastern Pacific Ocean										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Sebastes ruberrimus Subregion: Alaska Andrews et al. (1999b) Andrews et al. (2002)	Adult	Cored	0.0255	0.0004	1.8	1SE	0.0312	0.0027	0.0255	0.0347
	Adult	Cored	0.0272	0.0004	1.4	1SE				
	Adult	Cored	0.0281	0.0005	1.9	1SE				
	Adult	Cored	0.0283	0.0014	4.9	1SE				
	Adult	Cored	0.0296	0.0007	2.3	1SE				
	Adult	Cored	0.0298	0.0006	1.9	1SE				
	Adult	Cored	0.0301	0.0004	1.2	1SE				
	Adult	Cored	0.0305	0.0008	2.5	1SE				
	Adult	Cored	0.0313	0.0004	1.3	1SE				
	Adult	Cored	0.0321	0.0006	1.8	1SE				
	Adult	Cored	0.0324	0.0006	1.8	1SE				
	Adult	Cored	0.0331	0.0004	1.2	1SE				
	Adult	Cored	0.0331	0.0012	3.7	1SE				
	Adult	Cored	0.0331	0.0005	1.5	1SE				
	Adult	Cored	0.0335	0.0004	1.3	1SE				
	Adult	Cored	0.0342	0.0004	1.1	1SE				
	Adult	Cored	0.0343	0.0012	3.5	1SE				
	Adult	Cored	0.0347	0.0004	1.2	1SE				
	Adult	Whole	0.0263	0.0018	6.7	1SE				
Sebastes rufus Subregion: California Watters et al. (2006)	Adult	Whole	0.0706	0.0019	2.7	1SD	0.0728	0.0031	0.0706	0.0750
	Adult	Whole	0.0750	0.0018	2.4	1SD				
Sebastolobus alascanus Subregions: California, Oregon Kline (1996)	Adult	Whole	0.0387	0.0035	9.0	1SD	0.0430	0.0064	0.0387	0.0504
	Adult	Whole	0.0399	0.0032	8.0	1SD				
	Adult	Whole	0.0504	0.0035	7.0	1SD				
Sebastolobus alascanus Subregions: Gulf of Alaska, Washington, Oregon Kastelle et al. (2000)	Juvenile	Whole	0.0450	0.0030	6.7	1SD	0.0590	0.0122	0.0450	0.0670
	Adult	Cored	0.0650	0.0040	6.1	1SD				
	Adult	Whole	0.0670	0.0040	6.0	1SD				
Sebastolobus altivelis Subregions: California, Oregon Kline (1996)	Adult	Whole	0.0425	0.0017	4.0	1SD	0.0454	0.0019	0.0425	0.0476
	Adult	Whole	0.0441	0.0066	15.0	1SD				
	Adult	Whole	0.0442	0.0049	11.0	1SD				
	Adult	Whole	0.0456	0.0050	11.0	1SD				
	Adult	Whole	0.0466	0.0051	11.0	1SD				
	Adult	Whole	0.0475	0.0024	5.0	1SD				
	Adult	Whole	0.0476	0.0043	9.0	1SD				
Theragra chalcogramma Subregion: Alaska Kastelle and Kimura (2006)	Juvenile	Whole	0.1210	0.0075	6.2	1SD	0.1775	0.0304	0.1210	0.2310
	Juvenile	Whole	0.1290	0.0080	6.2	1SD				
	Adult	Cored	0.1570	0.0110	7.0	1SD				
	Adult	Cored	0.1720	0.0081	4.7	1SD				
	Adult	Cored	0.1730	0.0111	6.4	1SD				
	Adult	Cored	0.1730	0.0111	6.4	1SD				
	Adult	Cored	0.1760	0.0141	8.0	1SD				
	Adult	Cored	0.1790	0.0100	5.6	1SD				
	Adult	Cored	0.1910	0.0099	5.2	1SD				
	Adult	Cored	0.1920	0.0109	5.7	1SD				
	Adult	Cored	0.1980	0.0101	5.1	1SD				
	Adult	Cored	0.2150	0.0099	4.6	1SD				
	Adult	Cored	0.2310	0.0099	4.3	1SD				
					Grand Regional Ave		0.0756	0.0762	SD	

Appendix 4. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for the north central Pacific Ocean region.

Region: North Central Pacific Ocean										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Pristipomoides	Juvenile	Whole	0.0259	0.0034	13.0	2SE	0.0311	0.0072	0.0259	0.0393
filamentosus	Juvenile	Whole	0.0393	0.0087	22.0	2SE				
Subregion: Hawaii	Adult	Core	0.0282	0.0020	7.1	2SE				
Andrews (2008b)										

Appendix 5. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for oceanic regions of Australia.

Region: Southern Australia										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Allocyttus niger	n.r.	Whole	0.0809	0.0186	23.0	1SD	0.1308	0.0401	0.0809	0.1782
Subregion: Tasmania	n.r.	Whole	0.0811	0.0072	8.9	1SD				
Fenton 1996	n.r.	Whole	0.0913	0.0058	6.3	1SD				
	n.r.	Whole	0.1120	0.0081	7.2	1SD				
	n.r.	Whole	0.1391	0.0081	5.8	1SD				
	n.r.	Whole	0.1567	0.0088	5.6	1SD				
	n.r.	Whole	0.1623	0.0130	8.0	1SD				
	n.r.	Whole	0.1753	0.0098	5.6	1SD				
	n.r.	Whole	0.1782	0.0249	14.0	1SD				
Allocyttus verrucosus	Juvenile	Whole	0.0491	0.0035	7.1	1SD	0.0533	0.0086	0.0391	0.0694
Subregion: Tasmania	Juvenile	Whole	0.0506	0.0041	8.1	1SD				
Stewart et al. (1995)	Juvenile	Whole	0.0513	0.0030	5.8	1SD				
	Adult	Whole	0.0391	0.0031	8.0	1SD				
	Adult	Whole	0.0488	0.0051	10.5	1SD				
	Adult	Whole	0.0496	0.0064	13.0	1SD				
	Adult	Whole	0.0518	0.0031	6.0	1SD				
	Adult	Whole	0.0534	0.0038	7.1	1SD				
	Adult	Whole	0.0552	0.0036	6.5	1SD				
	Adult	Whole	0.0679	0.0041	6.0	1SD				
	Adult	Whole	0.0694	0.0076	11.0	1SD				
Hoplostethus atlanticus	Adult	Whole	0.0522	0.0036	6.9	1SD	0.0574	0.0073	0.0522	0.0625
Subregion: Tasmania	Adult	Whole	0.0625	0.0030	4.8	1SD				
Fenton et al. (1991)										
Macruronus	Juvenile	Whole	0.0750	0.0083	11.0	1SD	0.0268	0.0291	0.0040	0.0840
novaezelandiae	Juvenile	Whole	0.0840	0.0092	11.0	1SD				
Subregion: Tasmania	Adult	Whole	0.0040	0.0060	150.0	1SD				
Fenton and Short	Adult	Whole	0.0050	0.0040	80.0	1SD				
(1990)	Adult	Whole	0.0050	0.0050	100.0	1SD				
	Adult	Whole	0.0060	0.0060	100.0	1SD				
	Adult	Whole	0.0140	0.0099	71.0	1SD				
	Adult	Whole	0.0160	0.0099	62.0	1SD				
	Adult	Whole	0.0180	0.0090	50.0	1SD				
	Adult	Whole	0.0180	0.0050	28.0	1SD				
	Adult	Whole	0.0500	0.0050	10.0	1SD				
Macruronus	Adult	Core	0.0179	0.0026	14.5	1SD	0.0223	0.0041	0.0179	0.0290
novaezelandiae	Adult	Core	0.0203	0.0043	21.0	1SD				
Subregion: Tasmania	Adult	Core	0.0222	0.0040	18.0	1SD				
Fenton et al. (1995)	Adult	Core	0.0223	0.0038	17.0	1SD				
	Adult	Core	0.0290	0.0035	12.0	1SD				
Neocyttus rhomboidalis	n.r.	Whole	0.2590	0.0070	2.7	1SD	0.4887	0.2054	0.2590	0.8966
Subregion: Tasmania	n.r.	Whole	0.2948	0.0147	5.0	1SD				
Fenton 1996	n.r.	Whole	0.3780	0.0060	1.6	1SD				
	n.r.	Whole	0.3912	0.0160	4.1	1SD				
	n.r.	Whole	0.4379	0.0057	1.3	1SD				
	n.r.	Whole	0.4440	0.0302	6.8	1SD				
	n.r.	Whole	0.6072	0.0291	4.8	1SD				
	n.r.	Whole	0.6895	0.0648	9.4	1SD				
	n.r.	Whole	0.8966	0.0395	4.4	1SD				
Pseudocyttus maculatus	n.r.	Whole	0.2236	0.0130	5.8	1SD	0.9663	0.3980	0.2236	1.3409
Subregion: Tasmania	n.r.	Whole	0.4785	0.0172	3.6	1SD				
Fenton 1996	n.r.	Whole	0.7333	0.0345	4.7	1SD				
	n.r.	Whole	0.9959	0.0508	5.1	1SD				
	n.r.	Whole	1.2102	0.0157	1.3	1SD				
	n.r.	Whole	1.2102	0.1162	9.6	1SD				
	n.r.	Whole	1.2504	0.0575	4.6	1SD				
	n.r.	Whole	1.2535	0.0577	4.6	1SD				
	n.r.	Whole	1.3409	0.0603	4.5	1SD				
					Grand Regional Ave		0.2746	0.3851	SD	

Appendix 6. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for Bay of Carpentaria, Australia.

Region: Northern Australia										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Lutjanus erythopterus Subregion: Bay of Carpentaria Milton et al. (1995)	Juvenile	Whole	0.2277	0.0132	5.8	1SD	0.1744	0.0484	0.1331	0.2277
	Adult	Cored	0.1331	0.0087	6.5	1SD				
	Adult	Whole	0.1623	0.0088	5.4	1SD				
Lutjanus malabaricus Subregion: Bay of Carpentaria Milton et al. (1995)	Juvenile	Whole	0.1014	0.0064	6.3	1SD	0.1467	0.0785	0.0582	0.2942
	Juvenile	Whole	0.2390	0.0110	4.6	1SD				
	Adult	Cored	0.0582	0.0049	8.4	1SD				
	Adult	Cored	0.0728	0.0066	9.1	1SD				
	Adult	Whole	0.0916	0.0053	5.8	1SD				
	Adult	Whole	0.1080	0.0068	6.3	1SD				
	Adult	Whole	0.1219	0.0078	6.4	1SD				
	Adult	Whole	0.1678	0.0087	5.2	1SD				
	Adult	Whole	0.2118	0.0163	7.7	1SD				
	Adult	Whole	0.2942	0.0141	4.8	1SD				
Lutjanus sebae Subregion: Bay of Carpentaria Milton et al. (1995)	Juvenile	Whole	0.1036	0.0064	6.2	1SD	0.1288	0.0663	0.0460	0.2143
	Adult	Cored	0.1756	0.0098	5.6	1SD				
	Adult	Cored	0.2143	0.0114	5.3	1SD				
	Adult	Whole	0.0460	0.0042	9.1	1SD				
	Adult	Whole	0.1046	0.0058	5.5	1SD				
					Grand Regional Ave		0.1463	0.0693	SD	

Appendix 7. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for oceanic regions of New Zealand.

Region: New Zealand										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Cyttus traversi Subregion: North Island Tracey et al. (2007)	Juvenile	Whole	0.0334	0.0011	3.3	2SE	0.0397	0.0089	0.0334	0.0460
	Adult	Cored	0.0460	0.0022	4.7	2SE				
Epigonus telescopus Subregion: Chatham Rise, Mid-East Coast Andrews and Tracey (2007)	Juvenile	Whole	0.2225	0.0091	4.1	2SE	0.1225	0.0490	0.0659	0.2225
	Adult	Cored	0.0659	0.0014	2.1	2SE				
	Adult	Cored	0.0738	0.0015	2.1	2SE				
	Adult	Cored	0.0825	0.0017	2.1	2SE				
	Adult	Cored	0.0848	0.0018	2.1	2SE				
	Adult	Cored	0.0889	0.0018	2.1	2SE				
	Adult	Cored	0.1084	0.0022	2.1	2SE				
	Adult	Cored	0.1103	0.0023	2.1	2SE				
	Adult	Cored	0.1380	0.0028	2.1	2SE				
	Adult	Cored	0.1430	0.0030	2.1	2SE				
	Adult	Cored	0.1727	0.0036	2.1	2SE				
	Adult	Cored	0.1790	0.0037	2.1	2SE				
Hoplostethus atlanticus Subregion: not reported Whitehead and Ditchburn (1996)	Adult	Portion	0.0562	0.0031	5.5	1SD	0.1003	0.0324	0.0562	0.1370
	Adult	Portion	0.0810	0.0045	5.5	1SD				
	Adult	Portion	0.1044	0.0084	8.0	1SD				
	Adult	Portion	0.1230	0.0066	5.4	1SD				
	Adult	Portion	0.1370	0.0096	7.0	1SD				
Hoplostethus atlanticus Subregion: Chatham Rise, Mid-East Coast, Bay of Plenty Andrews (Chapter 4)	Juvenile	Whole	0.2090	0.0113	5.4	2SE	0.0878	0.0460	0.0599	0.2090
	Adult	Cored	0.0692	0.0021	3.0	2SE				
	Adult	Cored	0.0755	0.0016	2.2	2SE				
	Adult	Cored	0.0784	0.0017	2.2	2SE				
	Adult	Cored	0.0672	0.0021	3.2	2SE				
	Adult	Cored	0.0688	0.0018	2.6	2SE				
	Adult	Cored	0.0795	0.0017	2.2	2SE				
	Adult	Cored	0.0826	0.0019	2.2	2SE				
	Adult	Cored	0.0599	0.0031	5.1	2SE				
Polyprion oxygeneios Subregion: not reported Whitehead and Ditchburn (1996)	n.r.	Whole	0.0072	0.0078	108.0	1SD	0.0110	0.0068	0.0012	0.0246
	n.r.	Whole	0.0083	0.0034	41.0	1SD				
	n.r.	Whole	0.0096	0.0031	32.0	1SD				
	n.r.	Whole	0.0097	0.0039	40.0	1SD				
	n.r.	Whole	0.0116	0.0028	24.0	1SD				
	n.r.	Whole	0.0156	0.0059	38.0	1SD				
	n.r.	Whole	0.0246	0.0066	27.0	1SD				
	n.r.	Portion	0.0012	0.0003	22.0	1SD				
Scomber australasicus Subregion: North Island Andrews (2008a)	Juvenile	Whole	0.2100	0.0111	5.3	2SE	0.1309	0.0696	0.0742	0.2300
	Juvenile	Whole	0.2300	0.0085	3.7	2SE				
	Adult	Whole	0.0742	0.0076	10.2	2SE				
	Adult	Whole	0.0869	0.0037	4.3	2SE				
	Adult	Whole	0.0906	0.0063	6.9	2SE				
	Adult	Whole	0.0935	0.0033	3.5	2SE				
	n.r. = not reported	portion = ~15% whole otolith			Grand Regional Ave		0.0884	0.0606	SD	

Appendix 8. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for the northern Atlantic Ocean.

Region: Northern Atlantic Ocean										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Hoplostethus atlanticus Subregion: British Isles West, Allain and Lowrance (2000)	Juvenile	Whole	0.0550	0.0070	12.7	2SE	0.0613	0.0068	0.0550	0.0710
	Adult	Whole	0.0600	0.0040	6.7	2SE				
	Adult	Whole	0.0710	0.0060	8.5	2SE				
	Adult	Whole	0.0590	0.0060	10.2	2SE				
Sebastes marinus Subregion: Iceland Stransky et al. (2005)	Juvenile	Whole	0.0379	0.0028	7.3	1SD	0.0329	0.0070	0.0239	0.0420
	Adult	Cored	0.0364	0.0024	6.6	1SD				
	Adult	Cored	0.0420	0.0026	6.1	1SD				
	Adult	Cored	0.0239	0.0029	12.1	1SD				
	Adult	Cored	0.0280	0.0033	11.9	1SD				
	Adult	Cored	0.0334	0.0022	6.7	1SD				
	Adult	Cored	0.0251	0.0027	10.9	1SD				
	Adult	Cored	0.0418	0.0025	6.0	1SD				
	Adult	Cored	0.0278	0.0026	9.3	1SD				
Sebastes mentella Subregion: Canada Campana et al. (1990)	Adult	Whole	0.0330	0.0020	6.0	1SD	0.0330			
Sebastes mentella Subregion: East Greenland and Irminger Sea Stransky et al. (2005)	Adult	Cored	0.0209	0.0024	11.5	1SD	0.0355	0.0117	0.0209	0.0529
	Adult	Cored	0.0305	0.0020	6.6	1SD				
	Adult	Cored	0.0274	0.0022	8.2	1SD				
	Adult	Cored	0.0224	0.0032	14.4	1SD				
	Adult	Cored	0.0262	0.0028	10.7	1SD				
	Adult	Cored	0.0487	0.0025	5.1	1SD				
	Adult	Cored	0.0435	0.0024	5.6	1SD				
	Adult	Cored	0.0529	0.0025	4.8	1SD				
	Adult	Cored	0.0464	0.0024	5.1	1SD				
	Adult	Cored	0.0364	0.0028	7.7	1SD				
Sebastes sp. Subregion: West Greenland Stransky et al. (2005)	Juvenile	Whole	0.0991	0.0244	24.6	1SD	0.0991			
					Grand Regional Ave		0.0415	0.0182	SD	

Appendix 9. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for the Gulf of Mexico.

Region: Gulf of Mexico										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Lutjanus campechanus	n.r.	Whole	0.0776	0.0093	12.0	1SD	0.2010	0.1086	0.0776	0.3778
Subregion: Alabama,	n.r.	Whole	0.1075	0.0108	10.0	1SD				
Louisiana	n.r.	Whole	0.1135	0.0136	12.0	1SD				
Baker et al. (2001a)	n.r.	Whole	0.1374	0.0192	14.0	1SD				
	n.r.	Whole	0.2366	0.0331	14.0	1SD				
	n.r.	Whole	0.2449	0.0343	14.0	1SD				
	n.r.	Whole	0.3125	0.0719	23.0	1SD				
	n.r.	Whole	0.3778	0.0529	14.0	1SD				
Lutjanus campechanus	Juvenile	Whole	0.9754	0.4292	44.0	1SD	0.4944	0.2858	0.1670	0.9754
Subregion: Alabama,	Adult	Cored	0.2082	0.0521	25.0	1SD				
Louisiana	Adult	Cored	0.3745	0.2172	58.0	1SD				
Baker et al. (2001b)	Adult	Cored	0.4472	0.1968	44.0	1SD				
	Adult	Cored	0.5805	0.2496	43.0	1SD				
	Adult	Whole	0.1670	0.0384	23.0	1SD				
	Adult	Whole	0.7079	0.2265	32.0	1SD				
Megalops atlanticus	Juvenile	Whole	0.2170	0.0023	1.1	1SE	0.1915	0.0982	0.0440	0.4010
Subregion: Florida	Juvenile	Whole	0.2580	0.0027	1.0	1SE				
Andrews et al. (2001)	Adult	Cored	0.0440	0.0007	1.5	1SE				
	Adult	Cored	0.0610	0.0010	1.6	1SE				
	Adult	Cored	0.0850	0.0013	1.5	1SE				
	Adult	Cored	0.0940	0.0013	1.4	1SE				
	Adult	Cored	0.1440	0.0032	2.2	1SE				
	Adult	Cored	0.1630	0.0017	1.1	1SE				
	Adult	Cored	0.1700	0.0023	1.3	1SE				
	Adult	Cored	0.1810	0.0023	1.3	1SE				
	Adult	Cored	0.2430	0.0029	1.2	1SE				
	Adult	Cored	0.2460	0.0025	1.0	1SE				
	Adult	Cored	0.2660	0.0032	1.2	1SE				
	Adult	Cored	0.2990	0.0040	1.4	1SE				
	Adult	Cored	0.4010	0.0041	1.0	1SE				
Sciaenops ocellatus	n.r.	Whole	0.1851	0.0185	10.0	1SD	0.5614	0.3388	0.1851	1.1400
Subregion: Alabama,	n.r.	Whole	0.2239	0.0202	9.0	1SD				
Louisiana	n.r.	Whole	0.4377	0.0350	8.0	1SD				
Baker et al. (2001a)	n.r.	Whole	0.4718	0.0330	7.0	1SD				
	n.r.	Whole	0.6510	0.0391	6.0	1SD				
	n.r.	Whole	0.8202	0.0656	8.0	1SD				
	n.r.	Whole	1.1400	0.0912	8.0	1SD				
Sciaenops ocellatus	Adult	Cored	0.6510	0.0397	6.1	1SD	0.7040	0.0750	0.6510	0.7570
Subregion: Louisiana	Adult	Cored	0.7570	0.2672	35.3	1SD				
Baker et al. (2001b)										
					Grand Regional Average		0.3208	0.2570	SD	

Appendix 10. Synopsis of radium-226 values (dpm·g^{-1}) from otoliths for the Southern Ocean.

Region: Southern Ocean										
Species/Location/Study	Life stage	Cored/ Whole	^{226}Ra	Error	Error (%)	Reported error	Ave ^{226}Ra	SD	Min	Max
Dissostichus eleginoides	Juvenile	Whole	0.0164	0.0004	2.4	2SE	0.0167	0.0025	0.0124	0.0221
Subregion: Kerguelen	Juvenile	Whole	0.0185	0.0003	1.6	2SE				
Andrews (Chapter 4)	Juvenile	Whole	0.0221	0.0003	1.3	2SE				
	Adult	Cored	0.0124	0.0003	2.1	2SE				
	Adult	Cored	0.0126	0.0005	4.2	2SE				
	Adult	Cored	0.0137	0.0003	2.0	2SE				
	Adult	Cored	0.0139	0.0003	2.4	2SE				
	Adult	Cored	0.0142	0.0002	1.6	2SE				
	Adult	Cored	0.0149	0.0004	2.5	2SE				
	Adult	Cored	0.0149	0.0003	2.0	2SE				
	Adult	Cored	0.0154	0.0004	2.4	2SE				
	Adult	Cored	0.0172	0.0005	2.7	2SE				
	Adult	Cored	0.0172	0.0004	2.2	2SE				
	Adult	Cored	0.0172	0.0005	3.1	2SE				
	Adult	Cored	0.0179	0.0004	2.1	2SE				
	Adult	Cored	0.0179	0.0004	2.0	2SE				
	Adult	Cored	0.0181	0.0007	3.7	2SE				
	Adult	Cored	0.0184	0.0004	2.1	2SE				
	Adult	Cored	0.0186	0.0005	2.4	2SE				
	Adult	Cored	0.0190	0.0004	2.1	2SE				
	Adult	Cored	0.0195	0.0003	1.7	2SE				
Dissostichus eleginoides	Adult	Cored	0.0149	0.0003	2.0	2SE	0.0165	0.0014	0.0149	0.0187
Subregion: Heard Island	Adult	Cored	0.0149	0.0008	5.4	2SE				
Andrews (Chapter 4)	Adult	Cored	0.0156	0.0010	6.4	2SE				
	Adult	Cored	0.0158	0.0005	3.1	2SE				
	Adult	Cored	0.0159	0.0011	6.8	2SE				
	Adult	Cored	0.0161	0.0003	2.1	2SE				
	Adult	Cored	0.0169	0.0004	2.2	2SE				
	Adult	Cored	0.0179	0.0008	4.5	2SE				
	Adult	Cored	0.0186	0.0007	3.7	2SE				
	Adult	Cored	0.0187	0.0011	5.7	2SE				
Dissostichus eleginoides	Adult	Whole	0.0258	0.0030	11.5	2SE	0.0258			
Subregion:										
South Georgia										
Andrews (Chapter 4)										
Dissostichus mawsoni	Juvenile	Whole	0.0246	0.0013	5.2	2SE	0.0233	0.0029	0.0192	0.0290
Subregion: Ross Sea	Juvenile	Whole	0.0265	0.0015	5.8	2SE				
Brooks (2008)	Adult	Cored	0.0192	0.0029	14.9	2SE				
	Adult	Cored	0.0194	0.0014	7.2	2SE				
	Adult	Cored	0.0215	0.0010	4.4	2SE				
	Adult	Cored	0.0216	0.0011	5.0	2SE				
	Adult	Cored	0.0222	0.0020	9.2	2SE				
	Adult	Cored	0.0224	0.0012	5.5	2SE				
	Adult	Cored	0.0229	0.0020	8.7	2SE				
	Adult	Cored	0.0230	0.0013	5.8	2SE				
	Adult	Cored	0.0241	0.0012	5.1	2SE				
	Adult	Cored	0.0271	0.0010	3.7	2SE				
	Adult	Cored	0.0290	0.0012	4.0	2SE				
					Grand Regional Ave		0.0188	0.0040	SD	