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Recommended Citation

Brooks, Cassandra M., "Radiometric age validation and spatial distribution of the Antarctic Toothfish, (Dissostichus mawsoni) : implications for a deep-sea Antarctic fishery" (2008). *Capstone Projects and Master's Theses*. 74.
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RADIOMETRIC AGE VALIDATION AND SPATIAL DISTRIBUTION OF THE ANTARCTIC TOOTHFISH, (*DISSOSTICHUS MAWSONI*): IMPLICATIONS FOR A DEEP-SEA ANTARCTIC FISHERY

A Thesis
Presented to
The Faculty of Moss Landing Marine Laboratories

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
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June, 2008

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ABSTRACT

RADIOMETRIC AGE VALIDATION AND SPATIAL DISTRIBUTION OF THE ANTARCTIC TOOTHFISH, *DISSOSTICUS MAWSONI*: IMPLICATIONS FOR A DEEP-SEA ANTARCTIC FISHERY

by Cassandra M. Brooks

Antarctic toothfish (*Dissostichus mawsoni*) are subject to an increasingly important commercial fishery in the Southern Ocean, yet their life history characteristics and population structure remain largely unknown. In this study, Antarctic toothfish otoliths were obtained from American long-line fishing vessels in the Ross Sea, Antarctica. Age estimates obtained by counting annual growth increments in otolith sections indicate Antarctic toothfish live to at least 39 years of age. Lead-radium dating was used to validate ages up to 27.3 (range 21.7 -34.1) and provided support for ages up to 39 years of age using the methodology applied in this study. Validation also provided support for VBGF parameters, which indicate toothfish grow relatively slowly ($k = 0.111$; $L_\infty = 158.9$; $t_0 = -0.605$). Fish ages were then superimposed on a habitat map of the Ross Sea, Antarctica and broken into discrete spatial areas. Differences in age data within these areas was tested using ANOVA. There was a relationship between fish age and maturity increasing with depth; younger, less mature fish were more often found on the shallower continental shelf and older fish were more often found in the deeper regions on the continental slope. However, there was far more variability than expected and

other oceanographic and ecological factors likely effect age structure distribution significantly. Older and most mature individuals were found on ridges in the northern Ross Sea, consistent with the hypothesis of an austral summer spawning migration. An effective management strategy might focus on protecting the northern ridge habitat to potentially maintain long-term viability of Antarctic toothfish populations. Additionally, Antarctic toothfish vital rates should be considered before expanding the Ross Sea fishery.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the help, encouragement and continued support of my mentors, colleagues, friends and family.

A deep thanks to Dr. Gregor Cailliet who has been a wonderful teacher, advisor and mentor. Being his student has been a truly enjoyable experience and I thank him for always making time for me amidst the dozens of other students. My sincere appreciation goes out to Dr. Julian Ashford for constantly challenging me to understand the scientific process better. Working under him has given me invaluable insight into the ecology of toothfish and I thank him for his patience and continued support. My deepest gratitude goes out to Allen Andrews for being a simultaneous friend, mentor and colleague. Working with him has been a pleasure and I cannot thank him enough for all his encouragement, time and support, all of which led directly to my success as a student at MLML. Thanks to Dr. Gary Greene for providing insight on habitat and for his continued support. These four individuals, who all served on my thesis committee, have played a huge role in helping me become the scientist I am today.

A warm thanks to Dr. Valerie Loeb and the entire AMLR crew for providing an amazing Antarctic experience, without which I may have never laid my eyes and hands (and chopsticks) on a live Antarctic toothfish. Special thanks to AMLR scientists Dr. Christian Reiss and Chris Jones.

The age and growth portion of this study was made possible with the help of those at the CQFE lab at Old Dominion University. Special thanks to Nakul Ramanna for time put in reading otoliths and Karen Underkoffler for training me in the intricate details of sectioning toothfish otoliths.

Thanks also to Craig Lundstrom for ICPMS processing of all samples.

Deep gratitude to Dr. Brian Wells for providing invaluable insight into the world of statistics and for his continued friendship.

Thanks to Bryan Dieter for his insight into the world of GIS and to Yusuf Sinan Husrevoglu at Old Dominion University for help in formatting my data. Without both of your help, the habitat portion of this study may not have been possible.

Thanks to all the Antarctic toothfish scientists who have me obtain a better understanding of this species and its environment. Special thanks to Dr. Joe Eastman, and the folks at NIWA, including Peter Horn, Stuart Hanchet, Alistair Dunn and Dr. Malcom Francis.

A heartfelt thanks to the folks at MLML who have now become dear life-long friends. Thanks to Elsie Tanadjaja for being my partner in all things beautiful and silly. Thanks to Tonatiuh Trejo for your continued love and support throughout my tenure at MLML. Thanks to Ashley Greenley for sharing in endless ridiculousness. Thanks to Berkeley Kauffman for your relentless friendship. Thanks also to Kristen Green, Phil Hoos and all the other wonderful members of the Moss Landing community that have offered their friendship and support.

Special thanks to the members of the Ichthyology lab, the library staff, the IT staff and Shop guys. Thanks to the administrative staff, especially Kenneth Coale and Donna Kline. Thanks to the wonderful faculty and their contagious enthusiasm for teaching students about the marine science world.

My deepest gratitude goes out to my entire immediate and extended family in New England. My eldest sister, Dr. Lisa Brooks, has always been an inspiration and

role-model for me. I cannot thank her enough for her consistent positive support and celebration of my accomplishments. She is largely the reason I had the confidence to pursue graduate school and continues to be a strong and guiding force in my life. I thank both of my parents for working hard for the duration of their lives to afford me the opportunities of a good education and the freedom to choose my own career. I thank my mother for giving me a hard work ethic and for her continued support of my life choices. I thank my father for giving me incredible organization skills and a sense of adventure in all that I do. I thank the rest of my siblings, my nieces, and all of my extended family for their love and support.

The age and growth portion of this project was funding by the National Science Foundation as part of the larger project “Collaborative Research: Age estimation of toothfish in support of radiometric age validation,” grant # 0232000. The habitat portion of this study was funded in part by NOAA’s Environmental Entrepreneurship Program. Additional funding was provided the Project Aware Foundation.

PREFACE

This thesis presents an application of lead-radium dating to the Antarctic toothfish which was further used to assess spatial age structure of this species in the Ross Sea, Antarctica. Chapter one provides an introduction to the Antarctic toothfish fishery, age and growth, lead-radium dating and the importance of habitat. Chapter two is the results of an age and growth study with radiometric age validation on Antarctic toothfish using lead-radium dating. Chapter three is a comprehensive geological history of the Ross Sea, Antarctica giving background regarding the processes that shape the seafloor habitat. Chapter four provides the habitat characterizations of the Ross Sea, Antarctica and the relationship between Antarctic toothfish life history and habitat. Both chapter two and four are in journal submission format; Canadian Journal of Fisheries and Aquatic Sciences is the intended journal for chapter two and the journal for chapter four has yet to be determined.

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CHAPTER 1 – Introduction

An important international resource

Antarctic toothfish (*Dissostichus mawsoni*) is a large nototheniid endemic to Antarctica (Figure 1). This piscivorous, bentho-pelagic species has a circumpolar distribution and young to mature adults have been collected between 500 and 3,000 m in depth (Hanchet *et al,*. 2003a). Juveniles occupy the shallow end of this depth distribution, but as adults achieve neutral buoyancy and descend into deeper waters (Eastman and DeVries, 2000; Near *et al.,* 2003). Antarctic toothfish reach maturity around an estimated 10 years of age, or about 100 cm in length based on otoliths (Hanchet *et al.*, 2003a). They can grow to more than 2 m in length and weigh in excess of 100 kg; along with their sister species Patagonian toothfish (*Dissostichus eleginoides*), they are the largest fishes in the Southern Ocean (Eastman and DeVries, 2000).

Despite their large size, Antarctic toothfish remained largely unnoticed by commercial fishermen until recently. Historically commercial fisheries have targeted near-shore shallow water species. As nearshore populations became over-exploited and the demand for fishery resources continued to grow, fishermen were forced into deeper and more remote waters (Koslow, 2000; Pauly *et al.,* 2002; Morato *et al.,* 2006). Following these trends, commercial long-line fishermen moved into the northern regions of the Southern Ocean in pursuit of Patagonian toothfish in the mid-1980s.

Patagonian toothfish live primarily north of 60°S on the continental shelf breaks of South America and the Southern Ocean, including sub-Antarctic islands and seamounts from South Georgia to Macquarie Island. Intensive fishing, including illegal, unreported and unregulated (IUU) fishing[1], of Patagonian toothfish has seriously compromised sustainable management and caused substantial population declines leading to stock closures (Agnew *et al.*, 2002; Sabourenkov and Miller, 2004). High profit margins and stock depletions of Patagonian toothfish have caused fishing vessels to push further south, initiating the targeted exploitation of Antarctic toothfish, which are most abundant south of 60°S. Both Antarctic and Patagonian toothfish are known on the commercial market as "Chilean Sea Bass." The local retail price of toothfish is over $20 per pound, or through seafood retailers, as high as $50-$60 per pound[2], evidence of the high value of this fishery.

The primary commercial fishery region for Antarctic toothfish is the Ross Sea, an embayment between the landmasses of East Antarctica and West Antarctica. Much of the Ross Sea is covered by sea ice year-round with the exception of the peak summer months of January and February when the sea ice retreats enough to allow commercial fishing vessels access to the Ross Sea continental slope and shelf. Since 1997, New Zealand has participated in an exploratory fishery for the Antarctic toothfish during January and February when fishing boats can access the continental shelf and slope (Hanchet *et al.*, 2003b). From late February until May, sea ice begins to form closer to the continent and boats must continuously move north to continue fishing. An international fishery (Table 1) has developed as a result of this exploratory fishery, with overall Antarctic toothfish landings steadily increasing from 40 tons in 1998 to over 4600 tons in 2006 (CCAMLR, 2007).

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[1] IUU fishing has been estimated at seventy percent of the total harvest of Patagonian toothfish (SC-CCAMLR XV1/4, 1997).

[2] http://www.gortonsfreshseafood.com/product/9

The Ross Sea falls under the jurisdiction of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), the international managing body responsible for Southern Ocean biota and their habitat. The aim of CCAMLR is to conserve marine life in the Southern Ocean and to ensure the harvesting of marine resources is done in a rational manner without disrupting the Antarctic ecosystem. Where IUU fishing has seriously depleted Patagonian toothfish populations, the heavy ice cover and New Zealands's regulatory enforcement in the Ross Sea, have limited IUU fishing of the Antarctic toothfish. Yet, in a recent press release, the New Zealand government reported that the first illegal fishing vessel was detected (Barker, 2008).

Age and growth estimates

To prevent over fishing and properly manage the Antarctic toothfish fishery, it is imperative to understand population vital rates. Age and growth data are fundamental in providing estimates of growth, age at maturity, recruitment and mortality, all of which are used in fisheries management stock assessment models. Accurate measurements of these population parameters are crucial in understanding the effect of fishing on the population structure, generating accurate stock models and developing a sustainable fishery.

Age and growth estimates for fishes are traditionally obtained by examining and counting growth zones in calcified structures, most commonly otoliths (Beamish and McFarlane, 1987). Both scales and otoliths have been used to age Patagonian toothfish, but comparisons between them revealed that scale counts lead to significantly younger age estimates in older fish (Ashford *et al.*, 2001; Everson, 2001). Due to these discrepancies between scales and otolith age estimates, the WG-FSA (Working Group-

Fish Stock Assessment) at the CCAMLR meeting in 2001 determined that otoliths should be used in any future age estimation studies of toothfish (SC-CAMLR, 2001).

Age and growth estimates of Antarctic toothfish, are limited to only a few published studies, none of which have fully validated age estimates (Burchett *et al.*, 1984; Horn, 2002; Horn *et al.*, 2003). Age estimates were based on growth increments in otolith sections which showed that Antarctic toothfish were moderately fast growing until they reach maturity, after which time, growth slows considerably (Burchett *et al.,* 1984; Horn, 2002). Longevity has been estimated to be at least 35 years based on growth zone counts (Horn, 2002).

Though otoliths were determined to be the best structure for age estimation, they have proved difficult to interpret in both species of toothfish. This was due to the indefinite nuclear region and narrow and irregular growth zones (Cassia, 1998; Ashford, 2001). Additionally, annuli were considerably compressed in older fish, which made growth zones harder to read. These compressions are likely due to the fish's long life and slow growth as an adult (Burchett *et al.*, 1984).

The effectiveness of fisheries management stock models is dependent on the quality of the age and growth data. Yet traditional age and growth methods, like reading otolith growth zones, have two major problems associated with them. First, there is a high degree of subjectivity in the interpretation of age readers, which contributes error to all age determinations (Campana, 2001). Second, growth zones do not always accumulate annually or form a complete growth sequence throughout the life of the animal (Campana, 2001). In numerous fisheries throughout the past (e.g. orange roughy), ageing error, usually underestimation, has led to serious overexploitation (Campana, 2001). Ageing error affects accuracy (the proximity of the age estimate to the true age value), and precision (whether repeated measurements are reproducible and reliably consistent; Kalish *et al.*, 1995). Precision can be measured through calculating average percent error (APE; Beamish and Fournier, 1981), coefficient of variance (CV; Chang, 1982) or assessed through between reader comparisons (Campana *et al.*, 1995). Additionally, having a reference set can be used to detect and correct for drift in age estimates by individual readers over time (Campana, 2001).

Accuracy of age estimates can be tested through age validation studies that confirm or refute the estimated periodicity of growth zone formation. Traditional age validation techniques include tag-recapture studies, laboratory rearing and marginal increment analysis (MIA; Beamish and McFarlane, 1987). Validation using these techniques in toothfish has had limited success. MIA showed weak evidence for annual growth zone periodicity in Patagonian toothfish (Ashford, 2001; Horn, 2002). Using modal analysis, Ashford *et al.* (2002) showed length modes in young Patagonian toothfish reflecting underlying age classes estimated from growth zones. However neither of these technique directly estimated accuracy and modal analysis only addresses juvenile fish during fast growth. Tag-recapture studies in Patagonian and Antarctic toothfish using strontium-chloride and oxytetracycline respectively, have showed support for annual periodicity in growth zone accumulation (Krusic-Golub and Green, 2001; Horn *et al.*, 2003). However, these studies had low-recapture rates, thus low sample sizes, and could not confirm annual periodicity throughout the lifespan of the fish.

These traditional age validation techniques have limited applicability to deep-water or long-live species such as toothfish. MIA is best used in young, fast-growing fish, often giving misleading results in older fish (Campana, 2001). Tag-recapture studies tend to cause barotrauma and mortality in deep-water species, resulting in sampling bias towards younger fish that are not representative of the whole population. Laboratory rearing is impractical for long-lived fishes (Campana, 2001). A more appropriate technique suited for potentially long-lived, deep-dwelling species is radiometric dating using lead-radium dating.

Lead-radium dating/Age validation

Lead-radium dating uses the disequilibria of lead-210 (^{210}Pb) and radium-226 (^{226}Ra) as a natural chronometer in fish otoliths to test the accuracy of growth zone counts. This technique provides an independent measure of age that can be compared against age data estimated from counting growth zones (Campana, 2001). Lead-radium dating has proved successful for many long-lived species, including Patagonian toothfish (Bennett *et al.*, 1982; Campana *et al.*, 1990; Burton *et al.*, 1999; Andrews *et al.*, 1999; Andrews *et al.*, 2001; Andrews *et al.*, 2002; Stevens *et al.*, 2004; Andrews *et al.*, in Preparation).

Radium-226 is a naturally occurring analog to calcium and thus is incorporated into calcified structures, including otoliths. Radium-226 subsequently decays into its daughter isotope, ^{210}Pb. If this decay occurs in a closed system (such as an otolith), the daughter isotope, ^{210}Pb ($t_{1/2}$=22.26 years), builds into secular equilibrium with the parent isotope, ^{226}Ra ($t_{1/2}$ = 1620 years; Figure 2; Campana *et al.*, 1990; Smith *et al.*, 1991; Ivanovich and Harmon, 1992). By measuring the disequilibria of these two radioisotopes inside the otolith core (representing the first few years of life), an independent estimate of age can be determined based on the known ingrowth rate of ^{210}Pb and ^{226}Ra (Smith *et al.,* 1991; Kimura and Kastelle, 1995; Francis, 2003). The estimate can then be compared directly to that obtained from counting growth zones.

Validation using lead-radium dating rests on three assumptions (Bennett *et al.,* 1982; Campana *et al.*, 1990; Fenton *et al.*, 1990). First, the otolith must act as a closed system for ^{226}Ra (and all its daughter products). The second assumption is that significant levels of ^{210}Pb are not incorporated during the formation of the otolith, but comes solely from the decay of ^{226}Ra within the otolith. This factor can be accounted for by measuring the initial amount of ^{210}Pb present in the juvenile otoliths. The third assumption is that the rate of ^{226}Ra incorporation is constant within the otolith as it grows. Using cored, instead of whole otoliths, largely eliminates reliance on the last assumption.

Age validation is a necessary step in testing whether age data and the criteria used to estimate ages are accurate and reliable (Beamish and McFarlane, 1983). Sound management practices can best be achieved with reliable and accurate age data. Recognizing this, scientists from CCAMLR member nations held a workshop in 2001 to compare age estimation techniques for toothfish. While generally good agreement was found with regards to age estimation protocols and criteria, the members recognized greater need for precision and accuracy among ageing facilities. Out of the recommendations of this workshop, the CCAMLR otolith network (CON) was established to facilitate exchange of previously aged otolith reference sets. This would help assess any bias present between laboratories as well as provide reference material for any new labs engaging in toothfish age and growth studies. While CON provides a measure of precision between labs, the accuracy of age estimates was still unknown, thus the workshop regarded age validation tests to be of the highest priority (SC-CAMLR, 2001). This study met that call in completing the first thorough age validation study, which can now provide accurate age and growth information for management. This study also provides a validated reference otolith set for CON that can be used in training for future Antarctic toothfish age and growth studies and should be used as a CCAMLR wide standard to detect biases between labs.

The importance of habitat in life history

Often as fish age they utilize different habitats that may be critical to the persistence of the population (Cushing, 1981). Proper fisheries management rests on understanding habitat requirements for vital processes, such as foraging, refuge from predators, reproduction and recruitment (Stoner, 2003). Many species of eastern North Pacific rockfishes (genera *Sebastes* and *Sebastolobus),* which are deep-dwelling like Antarctic toothfish, depend on the availability of habitat. Habitat characterizations and associations for rockfishes can lead to designating meaningful marine protected areas (MPAs) and management practices (Yoklavich *et al.*, 2000).

Patagonian and Antarctic toothfish appear to occupy similar habitats in their respective regions; however this has been more thoroughly studied for the Patagonian species. Both occupy waters down to 3,000 m and are found in shelf areas as well as submarine banks (SC-CAMLR XX, 2001). In general, juvenile toothfish inhabit waters less than 1,000 m (WG-FSA, 1995; Agnew *et al.*, 1999), whereas, adult fish migrate within island shelf areas and move to deeper waters as they mature (Agnew *et al.*, 1999). Many studies have reported a linear length-depth relationship for Patagonian toothfish, showing that as fish grow larger, and presumably older, they move deeper (Zhivov and Krivoruchko, 1990; Duhamel, 1991; Moreno, 1991; Agnew *et al.*, 1999; Ashford *et al.*, 2007). Similar length-depth relationships have been reported for the Antarctic toothfish (Hanchet *et al.*, 2003a). Highest reported catches of Antarctic toothfish in the Ross Sea occur between 800-1,800 meters (Hanchet *et al.*, 2003a).

Toothfish distribution and movement during spawning events and reproduction is less quantified for both species. Agnew *et al.* (1999) reported movement of Patagonian toothfish up and down the slope at particular times of the year, suggesting the downslope movement was related to spawning events. There is evidence that Antarctic toothfish make a spawning migration from the shelf break to the Antarctic Polar Front (Eastman and DeVries, 2000; Fenhaughty, 2006). Spawning, and the associated migration, likely begin in June and continues into October (Yukhov 1982; Eastman and DeVries, 2000; Fenaughty, 2006).

The distribution of many marine species is often associated with particular bathymetric features, which can be classified into distinct habitat types (e.g. Greene et al. 1999). The Ross Sea, Antarctica, where Antarctic toothfish are abundant, has been strongly affected by tectonic and glacial processes. These dual forces have created complex and diverse habitats, including ice scoured banks and basins as well as seamounts and ridges. When bathymetric habitat is used in conjunction with fish life history, distribution, and abundance data, habitat classification schemes are effective in identifying habitat fish utilize. In doing so, we gain a better understanding of where fish occur in space and time and what their habitat requirements are.

The objectives of the age and growth part of this study were to: 1) estimate age from otolith growth zone counts; 2) establish criteria for ageing Antarctic toothfish; and 3) test the accuracy of age counts using lead-radium dating. For the habitat study, the objectives were to: 1) give a thorough geological history of the Ross Sea, Antarctica (the forces responsible for bathymetric habitat); 2) characterize the benthic habitats of the Ross Sea, building on the habitat scheme created by Greene *et al.* (1999); 3) create a habitat map using ArcGIS; 4) superimpose validated age data on the habitat map; and 5) test if available habitat effects the age distribution of Antarctic toothfish.

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Table 1. Countries participating in the Ross Sea, Antarctic toothfish fishery in the years from 1997-2006. Values are reported in tons of whole fish (CCAMLR, 2007).

Country	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03	2003/04	2004/05	2005/06
Argentina							162	253	213
Australia						117	26		
Chile	1							211	73
Japan									63
New Zealand	41	296	751	582	1354	1060	1157	1828	1403
Norway							98	210	385
Korea							105	237	280
Russia						703	261	666	907
South Africa				21		149	110		
Spain							114	405	543
Ukraine							154		
UK							16	260	407
USA							194		
Uruguay				23			187	367	373
Subtotal	42	296	751	626	1354	2029	2584	4438	4647

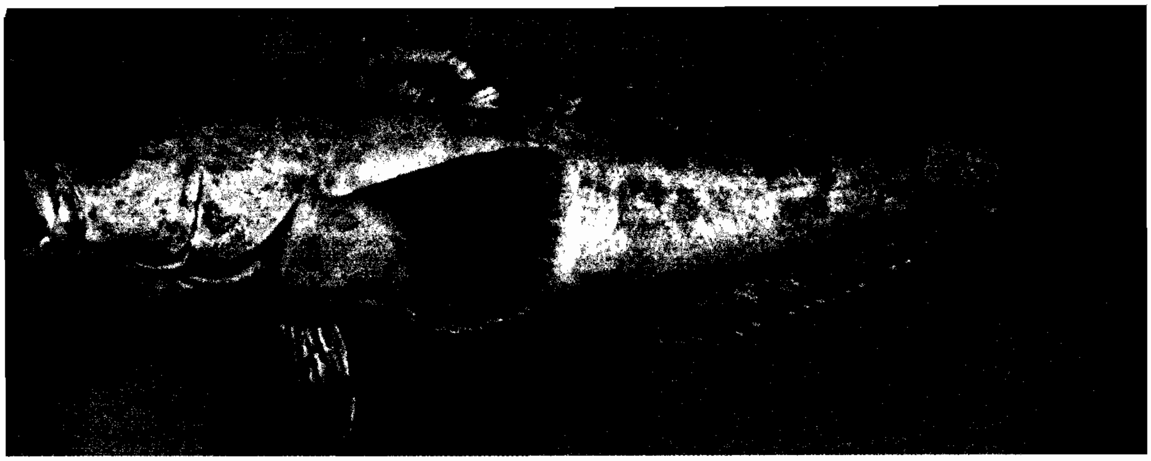

Figure 1. Antarctic toothfish (*Dissostichus mawsoni*) caught off the Antarctic Peninsula (100 cm TL).

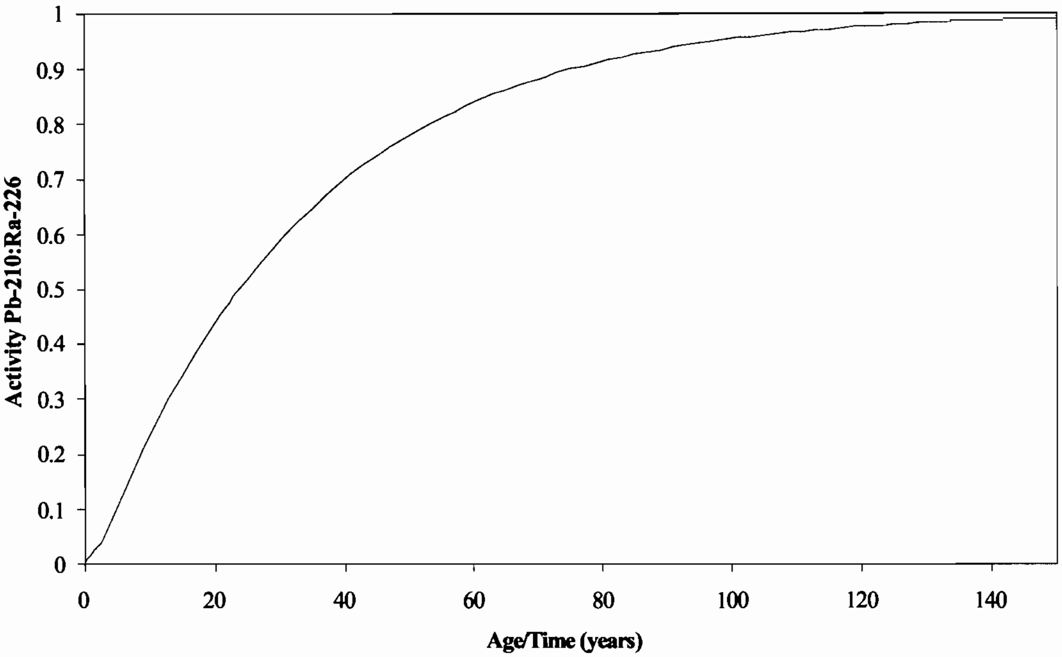

Figure 2. Ingrowth curve of the ^{210}Pb:^{226}Ra ratio. As the isotopes decay, ^{210}Pb builds into secular equilibrium with parent isotope ^{226}Ra over time. The inflexion point at 3 years is compensation for the 3 year gradient in the extracted otolith core.

CHAPTER 2

Age estimation and lead-radium dating of Antarctic toothfish

To be submitted for publication: Canadian Journal of Fisheries and Aquatic Sciences

Abstract

Antarctic toothfish (*Dissostichus mawsoni*) are subject to an increasingly important commercial fishery in the Southern Ocean, yet many of their life history characteristics, including vital rates, remain unknown. In this study, Antarctic toothfish were aged using otolith age estimation criteria established for Patagonian toothfish, *D. eleginoides*, a closely related species. To validate estimated ages, the radioactive disequilibrium of lead-210 and radium-226 in otolith cores was measured and used as an independent chronometer to determine age. Age estimates indicated Antarctic toothfish live to at least 39 years of age. Estimated and radiometric ages were in close agreement, confirming age estimation criteria and an annual periodicity of otolith growth zones. Von Bertalanffy growth function parameters indicate Antarctic toothfish are relatively slow-growing ($k = 0.111$; $t_0 = -0.605$), especially in relation to their maximum size ($L_\infty = 158.9$ cm). These vital rates are discussed in the context of the growing Antarctic toothfish fishery.

Introduction

The Antarctic toothfish (*Dissostichus mawsoni*) is a large nototheniid endemic to Antarctica. This piscivorous, bentho-pelagic species has a circumpolar distribution and young to mature adults have been collected between 500 and 3,000 m in depth (Hanchet et al. 2003). Juveniles occupy the shallow end of this depth distribution (less than 1,000 m), but as adults achieve neutral buoyancy and descend into deeper waters (Eastman and DeVries 2000; Near et al. 2003). Antarctic toothfish reach maturity around an estimated 10 years of age when fish reach about 100 cm in total length (Hanchet et al. 2003). They can grow to more than 2 m in length and in excess of 100 kg in weight; along with their sister species Patagonian toothfish (*Dissostichus eleginoides*), they are the largest fish in the Southern Ocean (Eastman and DeVries 2000).

Currently, Patagonian and Antarctic toothfish are the largest and most valuable commercial fin-fisheries in the Southern Ocean (CCAMLR 2007). Both of these notothenioids are more commonly known by their market name "Chilean Sea Bass." Patagonian toothfish, which usually occur north of 60°S latitude (Figure 1), have been fished only since the mid-1980s. Despite international efforts to regulate this fishery, extensive illegal, unreported and unregulated (IUU) fishing compromised management and caused substantial population declines, leading to stock closures by the mid-1990s (Agnew et al. 2002). High profit margins and depletions of Patagonian toothfish have caused have fishing vessels to push further south, initiating the targeting exploitation of Antarctic toothfish, which are most abundant south of 60°S latitude (Figure 1).

New Zealand initiated an exploratory fishery for Antarctic toothfish in 1997 in the Ross Sea, Antarctica. Since then, it has grown into an international fishery, with annual landings increasing from 42 tons in 1997 to over 4,600 tons in 2006 (CCAMLR 2007). The Ross Sea is the primary commercial fishing region for the Antarctic toothfish and falls under the jurisdiction of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), the international management body responsible for Southern Ocean biota and their habitat. The aim of the Convention is to conserve marine life in the Southern Ocean and to ensure that harvesting of marine resources is done in a rational manner without disrupting the Antarctic ecosystem.

To prevent over fishing and to properly manage the Antarctic toothfish fishery, it is imperative to understand population vital rates. Accurate age and growth information are fundamental in providing estimates of age at maturity, recruitment, and mortality, all of which are critical components of developing a sustainable fishery (Jones 1992). Age and growth estimates for fishes are traditionally obtained by counting growth zones in calcified structures, most commonly otoliths. This method has been employed with Antarctic toothfish otoliths, but is limited to only a few published studies, none of which have fully validated age estimates (Burchett et al. 1984; Horn 2002; Horn et al. 2003). In traditional ageing studies, the annual periodicity of growth increments is often subjectively assumed and this bias can contribute error to all age determinations (Campana 2001). Ageing error, usually leading to underestimation of age, has resulted in the overexploitation of other deep-sea fishes such as the Pacific ocean perch (*Sebastes alutus*; Archibald et al. 1983, Beamish 1979) and the orange roughy (*Hoplostethus atlanticus*; Mace et al. 1990, Beamish and McFarlane 1983).

To avoid overexploitation, age estimations need to be validated for the Antarctic toothfish. Lead-radium dating is a validation technique which has been successfully used in other deep-dwelling, potentially long-lived fishes (e.g., Andrews et al. 1999a; Campana et al. 1990; Stevens et al. 2004). Radium-226 (^{226}Ra) is a natural occurring analog to calcium and is incorporated into calcified structures, including otoliths. Radium subsequently decays into lead-210 (^{210}Pb), building into secular equilibrium over time. By measuring the disequilibria of these two radioisotopes inside the otolith core (representing the first few years of life), an independent estimate of age can be determined base on the known ingrowth rate of ^{210}Pb and ^{226}Ra (Smith et al 1991; Kimura and Kastelle 1995; Francis 2003). The estimate can then be compared directly to that obtained from counting growth zones.

The objectives of this study were to: 1) estimate age from otolith growth zone counts using criteria agreed upon by CCAMLR for the Patagonian toothfish; 2) establish criteria for ageing Antarctic toothfish; and 3) test the validity of age estimates, growth parameters and age estimation procedures with lead-radium dating. The ultimate goal of these objectives was to provide CCAMLR with accurate age and growth information that could be utilized in management and to provide a validated reference set and ageing criteria to CON.

Methods

Estimation of age and precision using otolith growth zones

Otoliths were collected by fishery observers aboard the American commercial fishing vessels *American Warrior* and *America 1* in the Ross Sea, Antarctica during the 2004 fishing season (January to March). Otolith pairs were obtained for this study from a total of 1,596 fish; however only 1,508 of these were used because 88 were either broken or only one otolith was recovered. One otolith (left or right) was randomly selected from each fish and prepared for reading according to a protocol developed at the Center for Quantitative Fisheries Ecology (CQFE) at Old Dominion University specifically for Patagonian toothfish otoliths (Underkoffler 2006) and the remaining otolith was used for lead-radium dating.

To estimate age, otoliths were processed to reveal growth zones (opaque and translucent rings) that could be counted (Figure 2a). The randomly selected otoliths were baked at 365°F for about 5 minutes to obtain a caramel color which facilitated growth zone reading. Once otoliths cooled, a Hillquist® Thin Section Machine was used to grind away the anterior end of the otolith. The anterior end was ground down to about 2 mm away from the nucleus. To polish the exposed edge of the otolith, a Diamond® polisher with 30M polishing film was used. Otoliths were then mounted on labeled slides using Loctite® adhesive and placed under a UV light approximately an hour until the adhesive was hardened. Once the otolith had adhered, the posterior end of the otolith was ground down to a thickness of 0.5 mm from the nucleus using the Hillquist® Thin Section Machine. The exposed edge was then polished on the Diamond® polisher until the transverse plane became visible revealing the primordium surrounded by the nucleus with the translucent and opaque zones clearly exposed. Once otoliths were dried, they were covered in a layer of Flo-Texx® which helped preserve the reading surface of the otolith for long-term use. Once the Flo-Texx® hardened, the otoliths were stored in micro-slide boxes for later age estimation.

Sectioned otoliths were randomized and aged independently by two readers, the author (Reader 1) and a reader at CQFE (Reader 2). Otoliths were read according to the criteria agreed to at the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) workshop on Estimating Age in Patagonian toothfish (SC-CAMLR 2001; Underkoffler 2006). Because Patagonian toothfish and Antarctic toothfish have similar otoliths, it was assumed these criteria were appropriate. An annulus consisted of one opaque and one translucent zone, read at magnifications ranging from 10-40x. The count path began at the nucleus and followed the annuli along the dorsal-distal axis, until this axis became compressed, upon which the reader followed the annulus around to the proximal side (Figure 2a and b). A subset of 200 otoliths was designated as a reference set and was used in the initial training of the two independent readers. Once consistency was established between readers, the reference set was then randomly mixed back into the full set to monitor any bias in age reading over time. Each reader read the full sample set once (n = 1,508).

Precision was assessed by calculating average percent error (APE; Beamish and Fournier 1981) and coefficient of variation (CV; Chang 1982). Age bias plots were also used to determine if systematic differences were present between readers (Campana et al. 1995). A von Bertalanffy growth function (VBGF) was fitted to the age data and used to generate growth parameters and growth curves using Sigmaplot. This function was chosen due to its suitable fit and to compare the parameters to the results of other toothfish studies (Burchett 1984; Ashford 2001; Horn 2002). The ages from Reader 1, which achieved higher precision, were used to estimate VBGF parameters and for the validation study.

Validation: Age-group determination and core extraction

Otoliths were selected for radiometric analysis based on their age estimated from otolith growth zones and pooled into the following age classes: 3-5, 6-7, 10-11, 14-15, 18-19 and 23-34 years. All age classes had three replicates, except for 3-5 (two replicates), and 23-24 (one replicate). Age classes were chosen to be representative of the range of ages estimated, but were limited to 23-24 years as the oldest group because of the lack of older individuals.

For radiometric age determination, the otolith core (representing the first few years of growth) was the region of interest. Core size was based on an average size of whole juvenile Antarctic toothfish otoliths aged at 5 years (n= 46). Core sizes were approximately 5.5 mm wide x 7 mm long and 1 mm thick. Thirty-five otoliths were pooled to obtain a sample of approximately 1.5 g. Sample size was based on results from a parallel study on lead-radium dating in Patagonian toothfish (Andrews et al. in Preparation).

To extract the core, otoliths were ground down on the proximal surface using a Buehler Ecomet III® lapping wheel with 600 grit silicon-carbide paper. Otoliths were then mounted with cytoseal (ground side down) onto a slide and left to dry. Once dry, otoliths were ground on the distal surface to juvenile core thickness (1 mm), revealing sagittal growth zones. A New Wave® micromill machine was then used to drill out the center core according to the dimensions of a 5 year old core and modified as necessary to agree with sagittal growth zones (Figure 3). Otoliths were drilled with 500 μm carbide Brasseler® drill bit tip, at 35% speed, 400 μm spacing, and 150 μm/s plunge speed resulting in a mounted core (Figure 3c). Otoliths were removed from slides with toluene and pooled into age groups (Figure 3d).

Validation: Radiometric analysis

Radiometric procedures and analysis for ^{210}Pb and ^{226}Ra followed methods previously described in Andrews et al. (1999a, 1999b). Trace metal precautions were used throughout sample processing because of the low ^{210}Pb and ^{226}Ra levels that tend to occur in otoliths (Watters et al. 2006). All acids used were double distilled (GFS Chemicals®) and dilutions were made using Millipore®-filtered Milli-Q (MQ) water. Otolith cores were thoroughly cleaned, dried and weighed to the nearest 0.0001g.

To assess if any exogenous ^{210}Pb was present in the otoliths, whole juvenile otoliths from the 3-5 year age group were analyzed first. This step successfully tested the assumption that the otolith is a closed system, that ^{210}Pb in the otolith occurs only from the ingrowth of ^{226}Ra. To determine ^{210}Pb activity in otoliths, the activity of its daughter isotope Polonium-210 (^{210}Po; $t_{1/2}$ = 138 days) was used as a proxy. This proxy can be determined with higher precision and accuracy than can the parent, ^{210}Pb, which has a weak beta particle emission and high background counts associated with its detection (Flynn 1968). Polonium-210 enters into secular equilibrium with ^{210}Pb after about 2 years, (when the activity ratio of a daughter and parent isotope equal one). After this time, it can be safely assumed that the activity of ^{210}Pb is equal to the activity of ^{210}Po. All samples were collected in 2004 and thus this assumption was met at the very least by time since collection.

Pooled samples were dissolved in acid-cleaned 100 ml Teflon® PFA griffin beakers on hot plates by adding 6N HCl in 1-2 ml aliquots. The sample was then dissolved and re-dried repeatedly in an aqua regia of 6N HCl and 7.7N HNO_3 until the sample was very white, indicating most organics were removed. To put the residue into the chloride form necessary for ^{210}Po determination, aliquots of 6N HCl were added and dried down.

In preparation for ^{210}Po analysis, samples were gravimetrically spiked with a ^{208}Po yield tracer. The amount added was estimated at five times the expected activity of ^{210}Po in the sample to reduce error in the ^{210}Pb determination. Spiked samples were then redissolved in approximately 50 ml 0.5N HCl on a hot plate covered with a watch glass. The polonium isotopes were autodeposited onto a purified silver planchet held in a rotating Teflon holder over a four-hour period while stirring on a hot plate. Activity was measured with ion implant surface barrier detectors in an Ortec® α-spectrometer using Maestro Version 6.01 software. Due to low ^{210}Pb levels in samples, they were counted for 60 days, at which point ^{210}Po counts from the α-spectrometer were used to determine ^{210}Pb levels (Appendix). Leftover samples from plating were dried over heat and conserved for ^{226}Ra analysis.

To prepare samples for ^{226}Ra determination, each sample was gravimetrically spiked with a ^{228}Ra yield tracer. The amount of ^{228}Ra added to each sample was estimated to attain a ^{226}Ra:^{228}Ra atom ratio close to one. The samples were then dissolved in 6N HCl and 7.7N HNO_3 and brought to dryness repeatedly until the sample residue was white as possible, indicating most of the organic material had been removed.

To ensure good ionizing efficiency from inductively coupled plasma mass spectroscopy (ICPMS), calcium and barium had to be removed from the sample. This was accomplished in a three-step elemental separation procedure using ion-exchange chromatography columns. The first two column runs removed calcium by passing the sample through a cation exchange column containing a slurry of Bio-Rad AG® 50W-X8 cation exchange resin. The third column run removed barium by passing the sample through a second column type with a custom 150 µl microcolumn containing a slurry of Sr® resin. Isolated radium samples were collected in 3 ml Teflon® PFA sample vials and dried over heat. If the sample spot in the vial was not clear, an aqua regia solution of 6N HCL and 7.7N HNO_3 was repeatedly added to the sample and dried down until the sample was as clear as possible. Samples were then sent to University of Illinois at Urbana-Champaign for ICPMS processing. The measured ratios of ^{226}Ra:^{228}Ra were used to calculate ^{226}Ra activity (Appendix). Blanks were processed throughout all sample preparation and analysis to account for any ^{210}Pb or ^{226}Ra contamination.

Statistical analysis

A radiometric age, including analytical uncertainty for each sample, was calculated using the measured ^{210}Pb and ^{226}Ra values (Appendix) and compared to age estimates counted using growth zones. Lead-210:Radium-226 activities for each age group were plotted against the total sample age (estimated age plus the time since capture) with respect to the expected ^{210}Pb:^{226}Ra ingrowth curve. Estimated ages and radiometric ages were also regressed against each other and compared to a 1:1 hypothetical line of agreement. A t-test was performed to test for differences in slope between the line generated by the regression and the 1:1 line. Error associated with the analytical uncertainty was expressed as two standard deviations and were included as a reference in both the ingrowth plot and regression. This measurement of error rests on the assumption of normally distributed residuals. This assumption was met based on the large quantities of otoliths that went into each sample (n = 35). According to the Central Limit Theorem, with large sample sizes, randomly sampled means should follow a normal distribution.

Results

Estimation of Age and Precision

Estimated ages were determined for 1,508 Antarctic toothfish by Reader 1 and Reader 2. Precision estimates showed agreement among and between readers, with a slight positive bias; the distribution of the number of paired observations is offset by about +1 year. Overall age estimates between readers were within +/-1 year 43% of the time, and within +/-5 years 95% of the time (Figure 4). Between repeat readings by Reader 1, age estimates were within +/-1 year 73% of the time and +/-3 years 96% of the time. Disagreement between readers was measured as APE at 9.9% and CV at 14.0%. Within reader error values for Reader 1 were 4.5% APE and 6.4% CV; and for Reader 2, 5.8% APE and 8.2 % CV.

An age bias plot between indicated a slight positive bias between Reader 1 and Reader 2 (Figure 5). A two-tailed t-test showed that the age estimated by Reader 1 were significantly different from those estimated by Reader 2 (two-tailed t-test, df = 27, t = 3.127, P = 0.0001) and a visual assessment shows that Reader 1 systematically over-aged by about two years with relation to Reader 2. Variability between readers increased with fish age and may have been caused by fewer old age replicates or because growth zones were more difficult to interpret due to compression at older ages.

Estimated ages using growth zones counts of Antarctic toothfish were between 3 and 39 years for fish ranging in size from 54 to 194 cm total length (TL). Fitting the VBGF to age-length data resulted in slightly different growth curves and parameters for males and females (Figure 6). The growth coefficient, k, was 0.124 (+/- 0.03) for males and 0.111 (+/- 0.03) for females. The asymptotic length was 150 (+/- 8.8) cm TL for males and 162 (+/- 10.4) cm TL for females (Table 1) t_0.

Radiometric analysis

Radiometric analysis of all age groups (n=14) resulted in successful determination of ^{210}Pb and ^{226}Ra activities. Age groups ranged between 3-5 years of and 22-24 years of age with replicates for all age groups except for the 22-24 year group. Sample weights for the age groups ranged from 1.519 to 1.913 grams and 35 otoliths were used in each sample, except for age groups 3-5 A & B, which had 22 otoliths per sample (Table 2).

Activities of ^{210}Pb were slightly variable and usually increased with estimated age, ranging from 0.0036 +/- 21% dpm/g to 0.0135 +/- 12% dpm/g. Radium values were fairly consistent for most age groups ranging between 0.0192 +/- 14% dpm/g to 0.0271 +/- 3.7 % dpm/g. A few samples (14-15G, 18-19A & B, 22-24) had poor radium recovery and therefore an average radium value was used for these groups. This was acceptable because of the consistency among all other sample radium values (0.0031 +/- 7.1%; Table 3). The ratio of the ^{210}Pb and ^{226}Ra activities increased with growth-zone derived age as expected and ranged from 0.1513 +/- 0.03 to 0.5844 +/- 0.08 (Table 3). The oldest growth-zone age-group was 22.6 +/- 0.79 yr; radiometric age was determined to be 27.3 yr (range of 21.7 to 34.1 yr). Greater radiometric uncertainty for the oldest samples was due to the asymptotic nature of the ingrowth curve. Replicate age groups had similar ^{210}Pb values and lead-radium ratios (Table 3).

Accuracy of age estimates

Radiometric ages were in agreement with predicted ages, as evidenced by concordance of ^{210}Pb:^{226}Ra activity in otolith cores with the expected ingrowth curve through time (Figure 7). Of the 14 pooled otolith groups, 10 had radiometric age ranges that fully encompassed the predicted age range, and four resulted in overlapping age ranges.

The regression of the radiometric ages against the estimated ages and their respective 2 SE showed agreement when compared with the 1:1 hypothetical line of agreement (Figure 8). The regression and the t-test of difference between slope generated by the regression and the slope of the 1:1 line indicated there was no significant difference in elevation (regression, $df = 4$, $t = -1.123$, $P=0.283$) or slope (two-tailed t-test, $df = 4$, $t = 2.3583$, $P = 0.0781$) between the two lines. Thus, the estimated age and radiometric age exhibited a 1:1 ratio, supporting the accuracy of the estimated ages.

Discussion

Estimation of Age and Precision

Antarctic toothfish otoliths were difficult to interpret at all ages due to various complications. Interpretation of the first three to eight growth zones was complicated because of the presence of "checks," or false annual growth rings, which have also been described in Patagonian toothfish otoliths (Ashford et al. 2005). Furthermore, readability of the older growth zones was difficult because of growth zone compression with increasing age. This compression was especially apparent in growth zones greater than age twenty and was reflected in the relatively high APE and CV values between readers. These precision values were similar to other toothfish ageing studies (Horn 2002) and other deep-dwelling species with difficult to read otoliths (Burton 1999). APE and CV values within both readers were considerably smaller than between readers, with Reader 1 having the highest precision.

It is important to note that all measures of precision, including APE and CV, are inflated by any bias that exists between readers (Campana 2001). The age bias plots showed a bias between Reader 1 and Reader 2, with Reader 1 consistently ageing fish a few years older than Reader 2. Furthermore, age estimates for Reader 1 were better supported by lead-radium dating because the distribution of age estimates was closer to agreement between techniques. If the age estimates for Reader 2 were plotted relative to the lead-radium ingrowth curve at a bias of about 2 years younger than Reader 1 (based on the between reader comparison), the data points would be shifted to the left and away from agreement with the ingrowth curve. This bias would inflate the APE and CV between readers to values greater than within readers. The age frequency histogram is another measure of precision that indicated there was 95% agreement between readers at a level of +/- 5 years. This margin of uncertainty resides within the margin of error (2 SE) for lead-radium dating.

Age estimates from transverse otolith sections indicated Antarctic toothfish are relatively slow growing and long-lived. The results of this study indicate they may live to 39 years of age, which is similar to a reported maximum age of 35 years (Horn 2002). The growth coefficient generated in this study (k = 0.111 +/- 0.02) indicated Antarctic toothfish are a moderately slow-growing species in relation to their maximum size (L_∞=158.9 +/- 7.4) and is similar to the findings of Horn (2002). While Antarctic toothfish are not as slow growing as other deep dwelling species, such as yelloweye rockfish (k= 0.046; Andrews et al. 2002), they are among the slowest growing Antarctic notothenoid fishes (La Mesa and Vacchi 2001). It is important to note that the k value (0.111) is for the entire lifespan of the Antarctic toothfish and that Antarctic toothfish reach a length of about one meter in the first ten years. It is at this point they reach maturity and growth slows considerably. In addition, the growth rate for Antarctic toothfish is similar to Patagonian toothfish (k = 0.085-0.23; Horn 2002; Ashford et al. 2005).

Antarctic toothfish VBGF parameters k and t_0 generated in this study were similar to those derived by Horn (2002), but L_∞ values were significantly smaller for both males and females, as was indicated by the non-overlapping 95% CI intervals for L_∞. The mean L_∞ value in this study was 15-22 cm smaller for males and females, respectively. A comparison of the growth curves between the two studies indicated there were fewer larger and older individuals sampled in this study, especially with female fish. Because both studies sampled populations in the Ross Sea using commercial long-line operations, the observed reduction in L_∞ may reflect a declining trend in the size distribution of Antarctic toothfish. Fishing typically targets the larger individuals of a species and as a result the average size, and presumably age, of the population can decrease (Hutchings and Reynolds 2004; Anderson et al. 2008). A decline in the abundance of large individuals in the Ross Sea toothfish population in such a short period of time is plausible based on observed of changes in Patagonian toothfish populations at South Georgia and Kerguelen Islands in just 15 years (Lord et al. 2006; Shust and Kozlov 2006).

While the differences in L_∞ between this study and Horn (2002) may be early evidence for size truncation in Antarctic toothfish, these differences may instead be driven by temporal and spatial differences in commercial fishing operations. The timing and location of fishing has varied considerably from year to year in the Ross Sea. Spatial variation of fishing effort is largely driven by the distribution of sea-ice, which in some years can restrict vessels to less optimal fishing grounds. The samples in this study were collected in 2004, which was a fishing season reported as limited by extensive sea-ice conditions (Hanchet et al. 2007). When comparing the growth curves generated in this study with that of Horn (2002), it is also apparent that the fish aged in this study show more variability in length at a given age. This may be due to differences in ageing criteria or differences in fish sampled according to region or due to sampling bias. To address this issue, it is recommended that ageing criteria between facilities be compared to test for differences in age estimation procedures.

All samples in this study were collected using commercial long-line fishing vessels and are subject to a potential bias from gear selectivity. Different gear types can select for or against different sized fish and sub-samples may not represent the whole population (Ashford et al. 2005). For example, long-line gear tends to fish deeper waters when compared to trawling and may select larger (and presumably older) fish while avoiding juvenile fish. This selectivity can cause differences in the generated growth parameters (Ashford et al. 2005). All samples in this study were obtained by long-line gear, which explains the lack of juveniles in the data set, and likely contributed to the negative t_0 VBGF parameter. Despite selective pressures on larger individuals by long-line gear, the data in this study included very few large individuals, which caused the fairly low L_∞ and may be further evidence for size truncation in the targeted Antarctic toothfish population.

Otoliths were collected by fisheries observers on the commercial long-line vessels and are subject to sampling error. Sampling by observers may not be random and hence may not be an unbiased representation of the population or catch size and age distribution. Instead it may be more haphazard and opportunistic with no real sampling design. Observers may select towards one size class (e.g., smaller fish are easier to handle), which would affect the determination of growth parameters from aged fish. While there is no way to know what the observer bias is in this study, the large sample size may alleviate an observer bias effect.

Radiometric analysis

This application of lead-radium dating contained an unprecedented number of samples and included age group replicates, comparable only to the recent parallel study on Patagonian toothfish (Andrews, In Preparation). Usually an application of lead-radium dating is limited by the number of aged otoliths available and replicate age groups are not possible. In addition, the application of this approach is costly because it is time consuming and requires specialized equipment and supplies. Most testing of age estimate accuracy for Antarctic fishes has been limited to techniques that are limited to younger periods of growth, like marginal increment analysis (Morales-Nin et al. 2003), but this application of lead-radium dating was successful in validating age up to 24 years.

Age determination using lead-radium dating was successful because of some adjustments that were necessary to increase the accuracy and confidence of the core sampling design. The otolith samples in this study had particularly low radium-226 levels, which may be a typical factor for the Southern Ocean environment based on similar findings for Patagonian toothfish otoliths (Andrews In Preparation). Increasing sample size (number of otoliths) in each age group allowed for successful measurement of both lead-210 and radium-226 despite the low levels. In some studies, just a few otoliths were necessary because radium-226 levels were relatively high (i.e., Andrews et al. 2001), but most require pooling numerous otoliths to acquire enough material. Because of the low levels encountered for this species, more than 30 otoliths were used to reach more than 1 g of cored otolith material. In addition, because otoliths were cored using a micromill machine, the coring process was a repeatable in size, shape and mass, increasing the overall precision and confidence in the age determinations. This advancement in technology leading to a successful lead-radium dating provides a strong basis for future successful applications of lead-radium dating to other Antarctic fishes.

Accuracy of age estimates

Age estimates from lead-radium dating indicated there was close agreement with ages estimated from growth zone counts in otoliths, thus providing support for the age estimation criteria. The radiometric age for each pooled sample of 35 otoliths was not significantly different from their mean estimated age, indicating that on average the estimated ages and criteria are accurate. This agreement validated the estimated age of all age groups up to 24 years and provided support for ages up to 39 years, as long as the same criteria are employed.

This study provides invaluable data for management in the form of accurate age and growth information that can be used in stock assessment models, as well as a validated otolith reference set for the CCAMLR otolith network (CON). Determining life history characteristics, such as recruitment, survivorship, maturation, longevity, and mortality, can now be based on validated age and growth information. Moreover, using this data, CCAMLR can now make more confident management decisions and begin to address sustainable harvest practices for this species. Furthermore, the age validated set of 1,508 sectioned otoliths generated by this study will be made available to CON as a reference set for training and as a tool to measure inter-facility age reader bias.

Implications for Management

Historically, fishermen targeted nearshore, shallow water species that were easy to access, but over the last 50 years, many nearshore fisheries have collapsed forcing fishermen to look elsewhere (Koslow 2000; Haedrich et al. 2001; Morato et al. 2006). To keep up with world demands despite stock depletions, fishermen have had to constantly expand their fishing territories and look for new grounds. Food and Agricultural Organization of the United Nations (FAO) statistics published for 2006 show that 29% of the world's fisheries have collapsed, 28% are overfished and 38% are fully exploited, leaving only 3% of the world's fisheries undeveloped (FAO 2007). It is this trend that has driven fishermen into the deep and remote regions of Antarctica looking for new fisheries.

The fisheries trends in Antarctica have been the same as those worldwide. Targeting commercial fin-fisheries began in the mid-1960s off the shallower and less remote sub-Antarctic islands. International fisheries built up so fast that most targeted stocks were almost completely depleted within 20 years (Haedrich et al. 2001). The marbled rockcod (*Notothenia rossii*), one of the first species targeted for the region, was depleted as a fishery by the early 1970s and is estimated to remain at less than 5% of its pre-exploitation abundance (Agnew and Nichol 1996; Kock 1992). Even relatively new fisheries, such as the Patagonian toothfish, have shown rapid declines and localized depletions with less than 10 years of commercial fishing (Agnew et al. 2002; Constable 2000). IUU fishing has been a major contributing factor in causing populations of Patagonian toothfish to decline so swiftly, but it was not considered a threat to Ross Sea commercial Antarctic toothfish fisheries due to its remoteness. However, the recent finding of an IUU fishing vessel in January of 2008 targeting the Antarctic toothfish in the Ross Sea is an indication there is cause for concern (Barker 2008).

The sustainability of deep-sea fisheries has been disputed based on the life history characteristics that most deep-sea fishes have in common. These characteristics include slow growth, moderate to high longevity, late maturity and in some cases low fecundity

(Koslow 2000; Cailliet et al. 2001). These factors make them highly vulnerable to overfishing with little resilience to over-exploitation (Koslow 2000; Clark 2001; Haedrich et al. 2001; Morato et al. 2006). A classic example is orange roughy (*Hoplostethus atlanticus*) fisheries. Orange roughy can live over 100 years and do not reach maturity until their mid-20s or 30s (Horn et al. 1998; Branch 2001). The fishery developed rapidly, and within ten years had collapsed to within 20% of pre-exploitation level. The current sustainable annual take of this species is estimated at 1.5% of their biomass, evidence of the extremely low productivity of this deep-sea fish (Clark 2001).

The Antarctic toothfish fishery is still in its early stages and while this study confirms slow growth and a relatively long lifespan, much about its life history and its role in the Antarctic ecosystem remains uncertain. We still know very little regarding toothfish reproduction and fecundity, especially relative to the age structure of the population. Studies of other fishes have demonstrated that female fecundity increases with body mass. Large females, often targeted by commercial fisheries, can be the most successful spawners because they produce higher quantities of viable larvae and more viable young (Berkeley et al. 2004a and 2004b; Bobko and Berkeley 2004; Birkeland and Dayton 2005). For species where fecundity is particularly low, reducing fishing pressure on large females may be an important consideration for the effective conservation of the species population structure and this approach should be considered for Antarctic toothfish. Furthermore, Antarctic toothfish is the dominant piscine predator in Antarctic waters, occupying a high trophic level in the Antarctic ecosystem. Fishing pressures on high trophic level species, especially those that are slow-growing and long-lived, has historically had disruptive effects on the entire food web (Pauly et al. 1998). Caution should be exercised before expanding the Antarctic toothfish fishery, for the conservation of this species and the Antarctic ecosystem.

Collectively, the data from this study demonstrate Antarctic toothfish are a moderately long-lived species that may be vulnerable to overfishing. The now validated age estimates and criteria make a contribution towards sustainable management and provide a validated reference set for all other Antarctic toothfish ageing facilities. Because the Antarctic toothfish fishery is still in its early stages, there is time to implement these confirmed life history characteristics into protective management before Antarctic toothfish follow the trend of other deep-water fisheries.

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Table 1. Von Bertalanffy growth function parameters (with 95% confidence intervals) for this study compared with Horn (2002) for combined sexes, females and males. All lengths are in centimeters total length (TL).

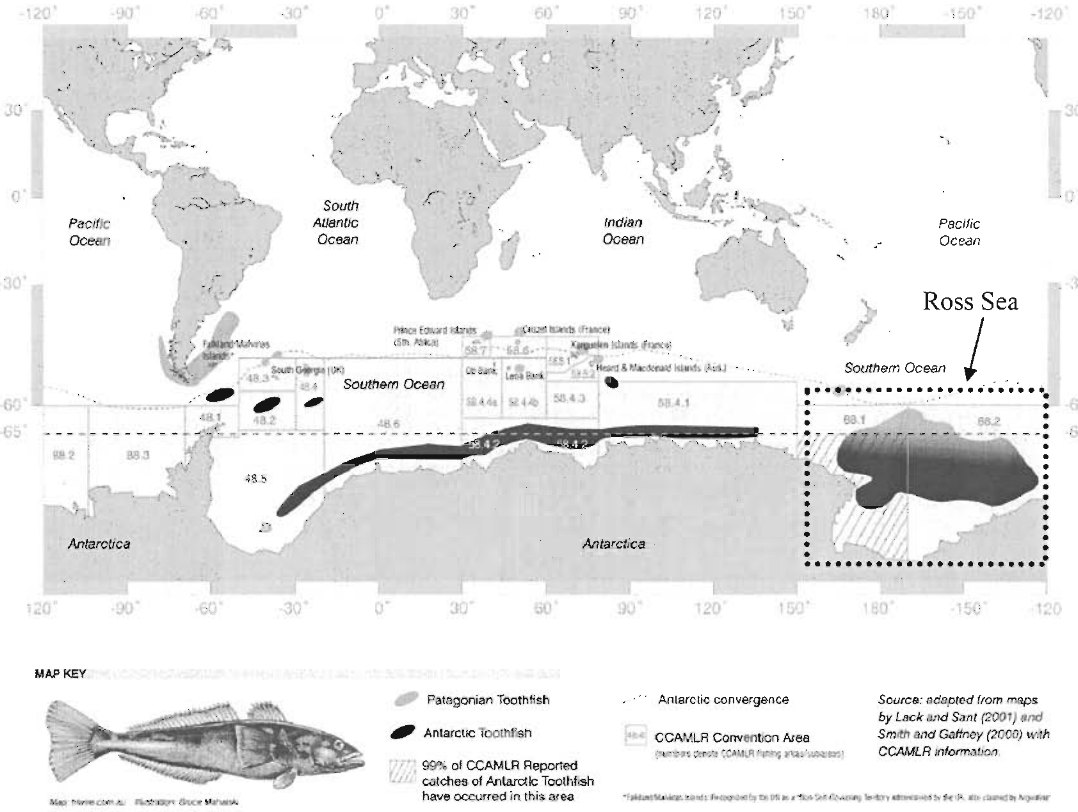
		n	L_∞	k	t_0
Brooks 2008	All	1508	**158.9** (151.5 - 166.3)	**0.111** (0.091 - 0.130)	**-0.605** (-1.511 to 0.301)
	Female	841	**162.3** (151.9 - 172.7)	**0.111** (0.085 - 0.134)	**-0.278** (-1.491 to 0.935)
	Male	670	**149.7** (141.0 - 158.5)	**0.124** (0.094 - 0.154)	**-0.605** (-1.830 to 0.620)
Horn 2002	Female	864	**184.5** (178.3 - 190.8)	**0.103** (0.092 - 0.114)	**1.02** (0.52 to 1.51)
	Male	661	**165.0** (159.3 - 170.6)	**0.119** (0.104 - 0.134)	**1.19** (0.64 to 1.74)

Table 2. Age groups utilized in this study, indicating the number of replicates in each age group and the number of otoliths in each replicate. * indicates juvenile samples that were not cored.

Age group (yr)	Average age	# of otoliths	Sample weight (g)	Average core weight
3 – 5A*	4.7	22	1.644	0.0747
3 – 5B*	4.7	22	1.608	0.0731
6 – 7B	6.4	35	1.576	0.0450
6 – 7C	6.5	35	1.632	0.0466
6 – 7D	6.4	35	1.623	0.0464
10 – 11A	10.4	35	1.662	0.0475
10 – 11B	10.6	35	1.810	0.0517
10 – 11C	10.6	35	1.708	0.0488
14 – 15B	14.5	35	1.803	0.0515
14 – 15D	14.4	35	1.913	0.0546
14 – 15G	14.5	35	1.728	0.0494
18 – 19A	18.5	35	1.534	0.0438
18 – 19B	18.5	35	1.576	0.0450
22 – 24	22.6	35	1.519	0.0434

Table 3. Measured ^{210}Pb and ^{226}Ra activities and ratios for each sample. Error is expressed as two standard errors (SE). Activities are expressed as disintegrations per minute per gram (dpm/g). The measured activity radio of ^{210}Pb:^{226}Ra was used to determine the overall age of the sample, which was corrected for elapsed time between collection and sample processing (3 years).

Age group (yr)	^{210}Pb activity (dpm/g) ± error	^{226}Ra activity (dpm/g) ± error	^{210}Pb:^{226}Ra activity ratio	Ave. growth zone age (yr)	Radiometric age (yr)	Radiometric age range (yr)
3 – 5A	0.0042 ± 18	0.0265 ± 5.8	0.1605	4.7	5	3.9 – 6.2
3 – 5B	0.004 ± 20	0.0246 ± 5.2	0.1642	4.7	5.2	3.9 – 6.5
6 – 7B	0.0048 ± 18	0.0194 ± 7.2	0.2483	6.4	8.5	6.5 – 10.6
6 – 7C	0.0036 ± 21	0.0241 ± 5.1	0.1513	6.5	4.6	3.4 – 5.8
6 – 7D	0.0046 ± 17	0.0271 ± 3.7	0.1685	6.4	5.2	4.1 – 6.3
10 – 11A	0.0074 ± 15	0.0216 ± 5.0	0.3433	10.4	12.8	10.3 – 15.5
10 – 11B	0.0062 ± 15	0.023 ± 5.8	0.2717	10.6	9.4	7.6 – 11.4
10 – 11C	0.0072 ± 14	0.0222 ± 9.2	0.3246	10.6	11.9	9.4 – 14.5
14 – 15B	0.0089 ± 13	0.0192 ± 14.5	0.4608	14.5	19.1	14.1 – 24.9
14 – 15D	0.0096 ± 12	0.0229 ± 8.5	0.4204	14.4	16.8	13.5 – 20.4
14 – 15G	0.0081 ± 13	0.0231 ± 7.1	0.3533	14.5	13.2	10.7 – 16.0
18 – 19A	0.0113 ± 12	0.0231 ± 7.1	0.4898	18.5	20.7	16.8 – 25.2
18 – 19B	0.0109 ± 12	0.0231 ± 7.1	0.4748	18.5	19.8	15.9 – 24.2
22 – 24	0.0135 ± 12	0.0231 ± 7.1	0.5844	22.6	27.3	21.7 – 34.1



Source: adapted from maps by Lack and Sant (2001) and Smith and Gaffney (2000) with CCAMLR information.

Figure 1. Distribution map of Patagonian and Antarctic toothfishes. The region of interest in this study is the Ross Sea, Antarctica, outlined by the dotted line. From Lack (2001) with permission.

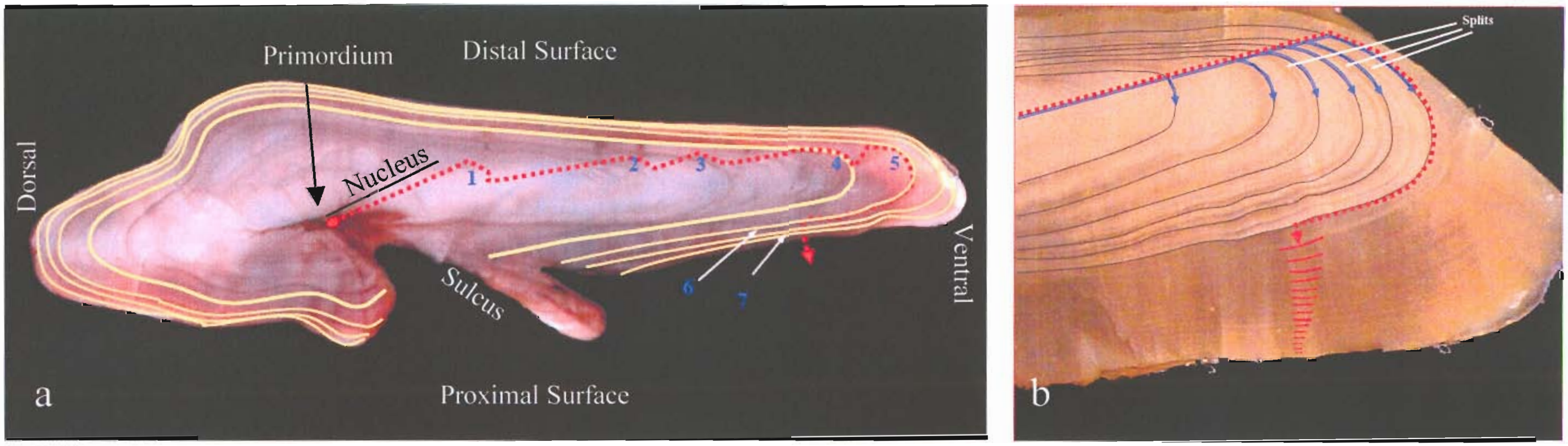


Figure 2. (a)Transversely sectioned Patagonian toothfish otolith (similar to Antarctic toothfish otoliths) prepared according to CQFE methodology and viewed under reflected light. Diagram illustrates growth zone count path utilized in this study. (b) Zoomed in image of an older Patagonian toothfish otolith featuring the difficulties of counting growth zones in toothfish, including false "checks" and compression of growth zones with age (Underkoffler 2006).

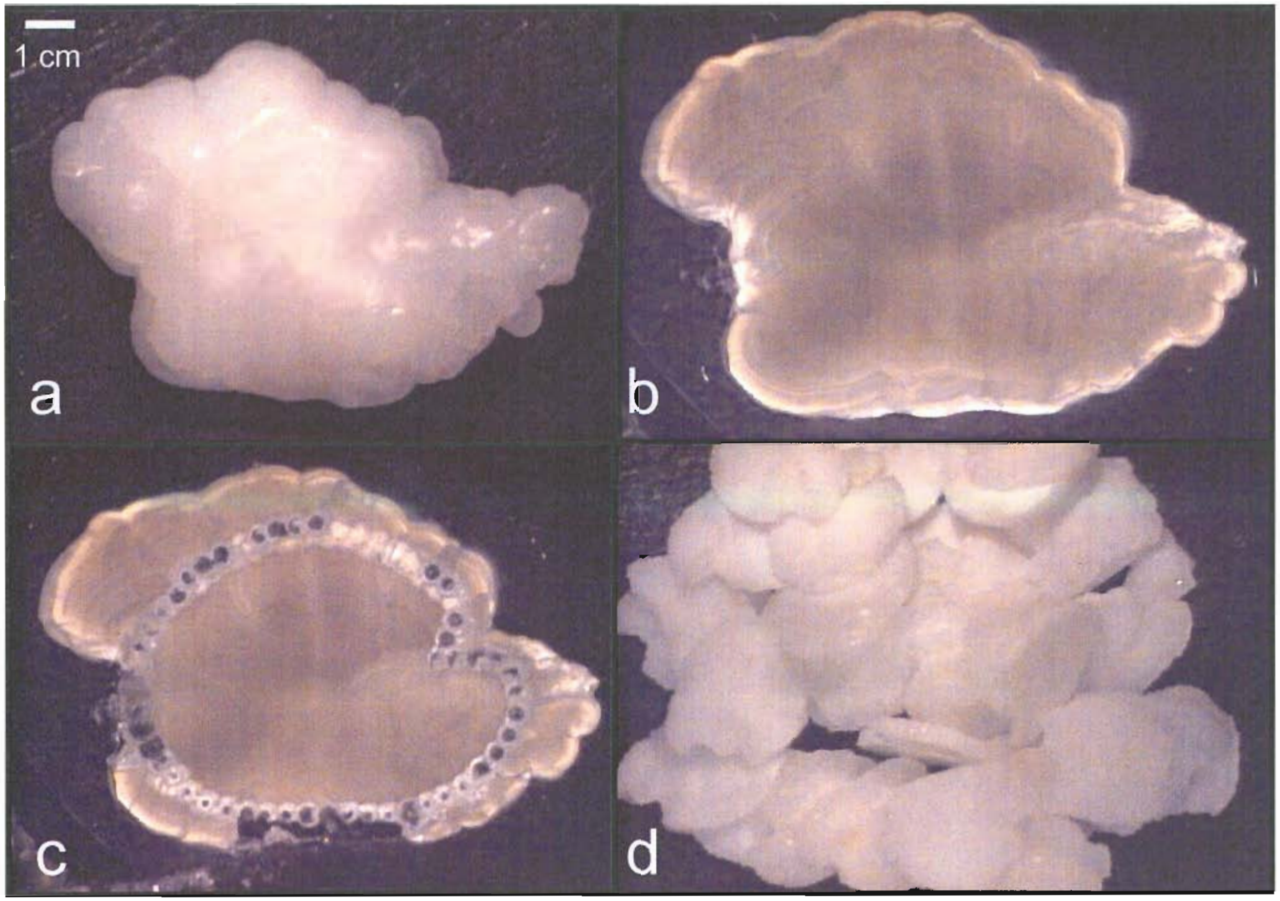


Figure 3. (a) *Dissostichus mawsoni* otoliths flattened in the sectional plane (b) before and (c) after coring with the micromill. (d) Group of cored otoliths ready for dissolution and radiometric analyses.

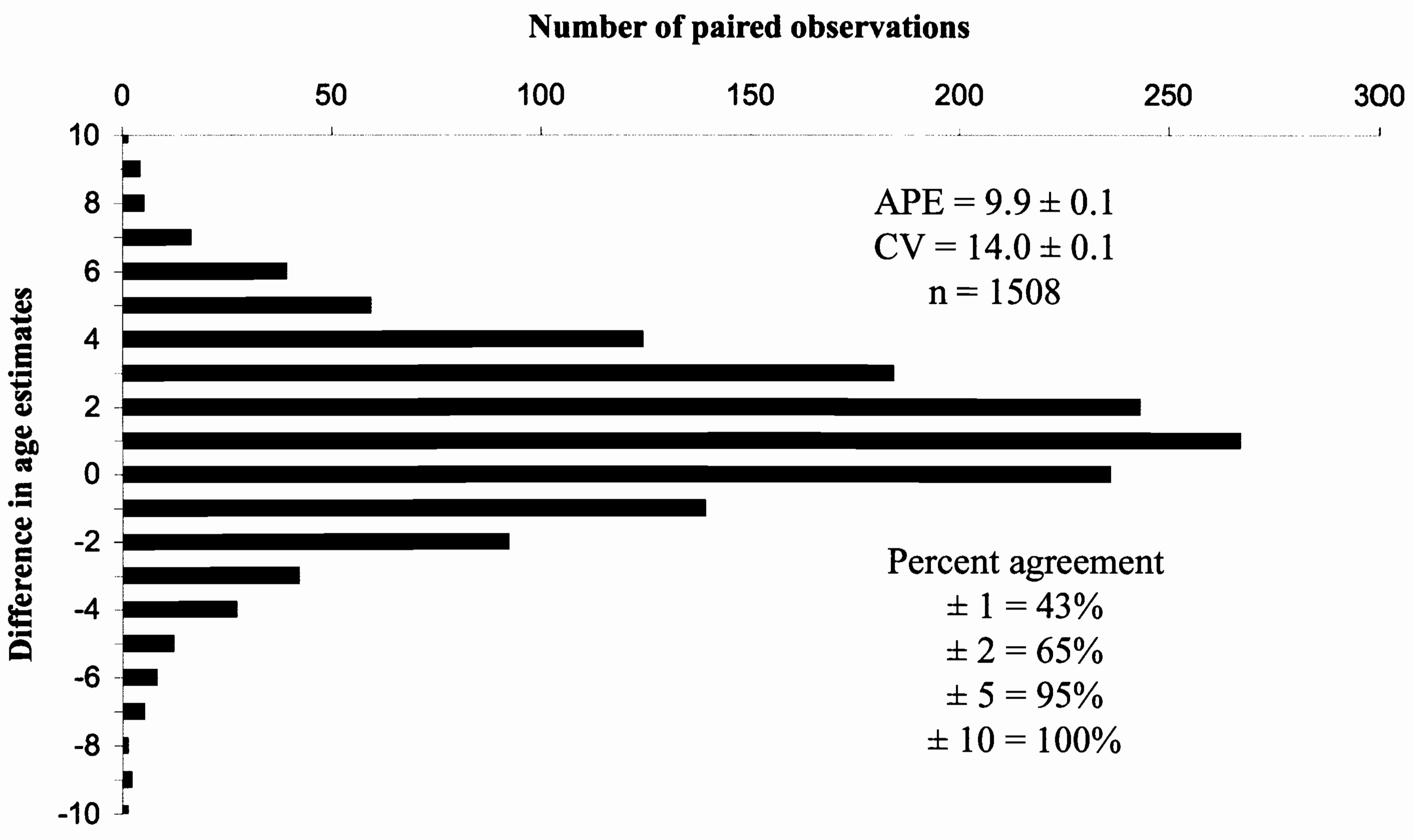


Figure 4. Age frequency histogram showing differences in age estimates between reader 1 and reader 2. Precision values and percent agreement are given to allow comparison with other species.

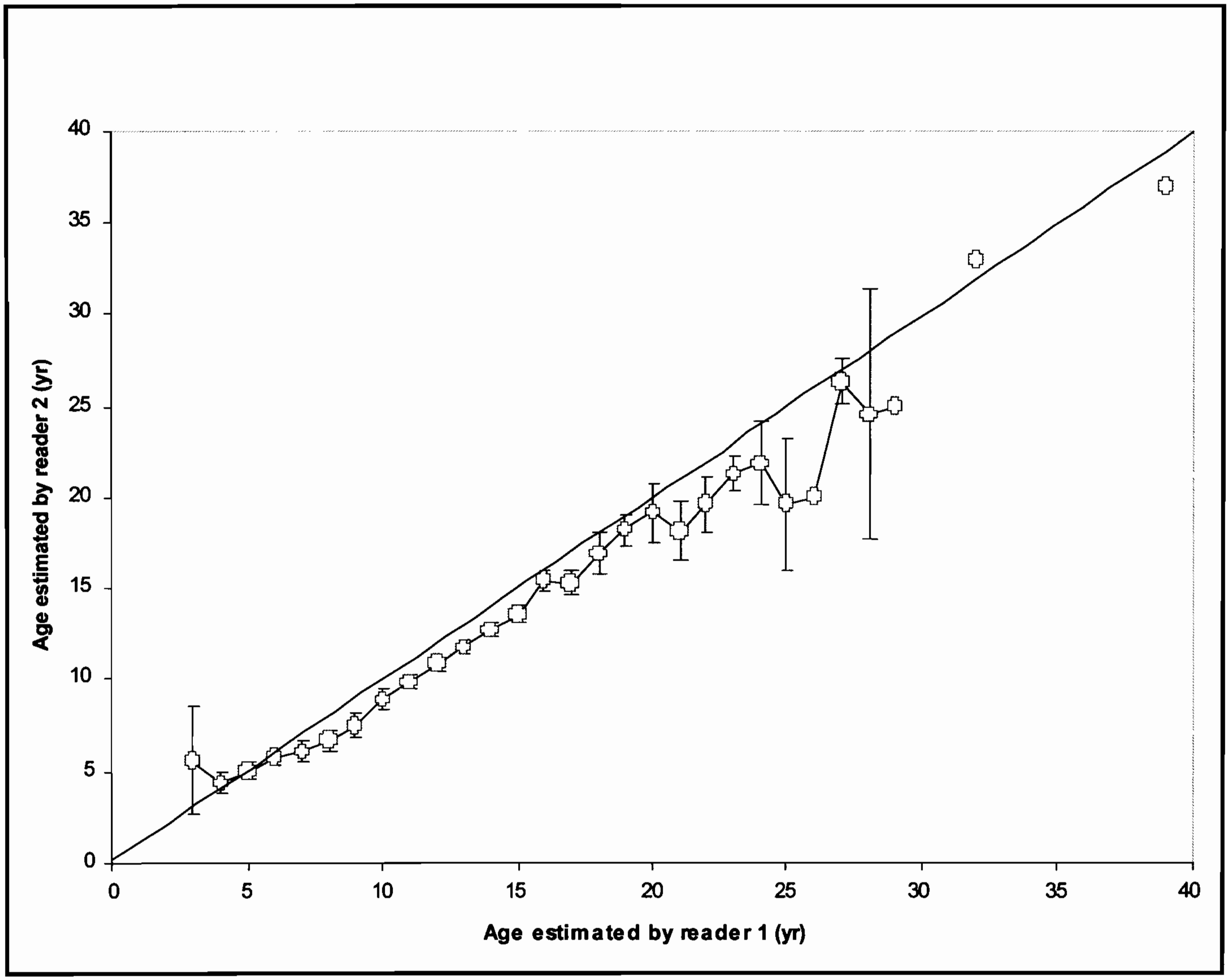


Figure 5. Age bias plots between Reader 1 (first author) and Reader 2. Each data point corresponds to average age of reader one against reader two. Error bars represent the 95% confidence intervals.

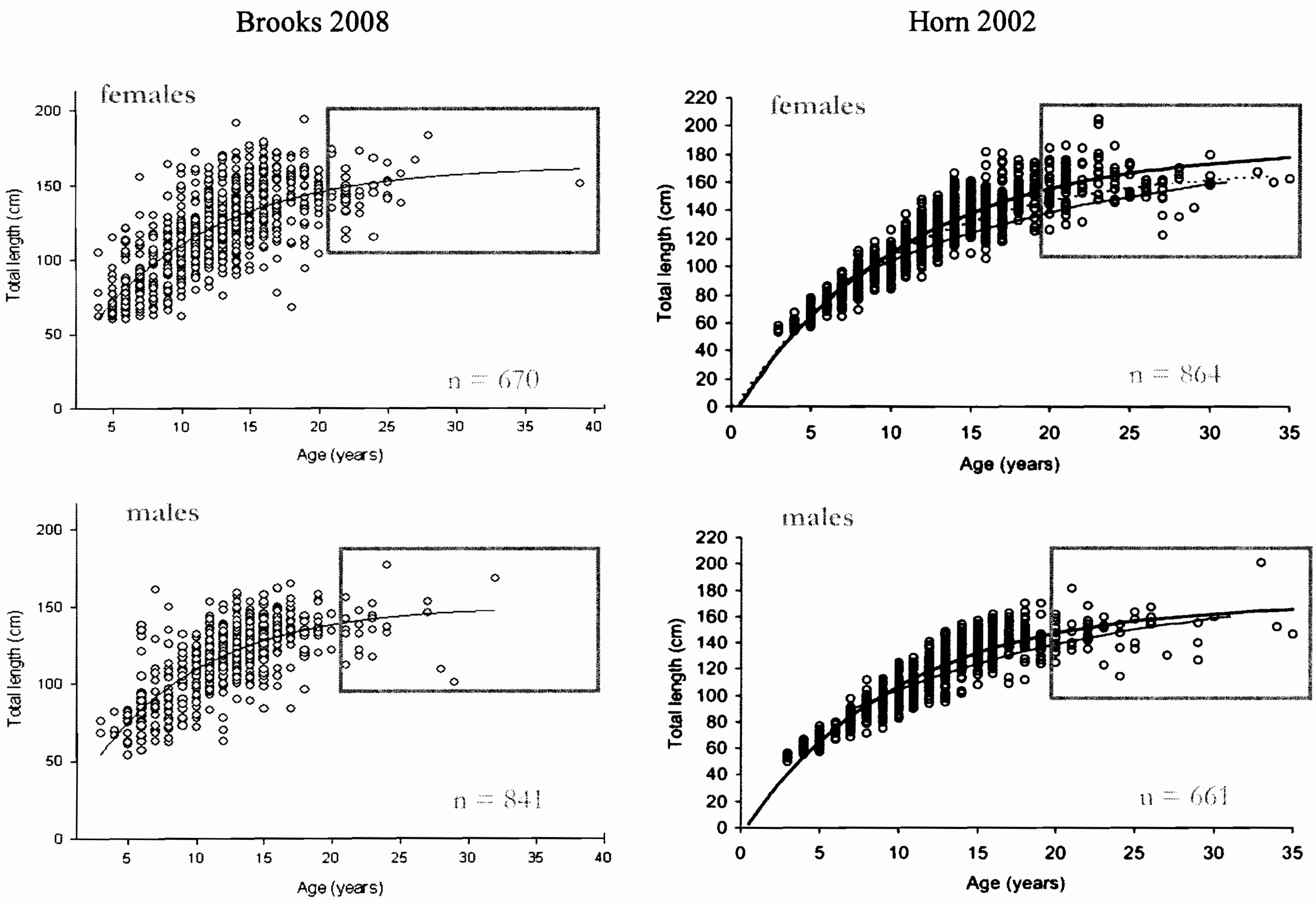


Figure 6. Von Bertalanffy growth curves fitted to the age estimates derived from growth zones counts for each sex for this study and Horn (2002). Curve parameters k and t_0 were similar but L_∞ was larger for Horn (2002). The regions within the box highlight length data for ages 20-40, demonstrating that Horn's (2002) data included more individuals in this age range, especially for females.

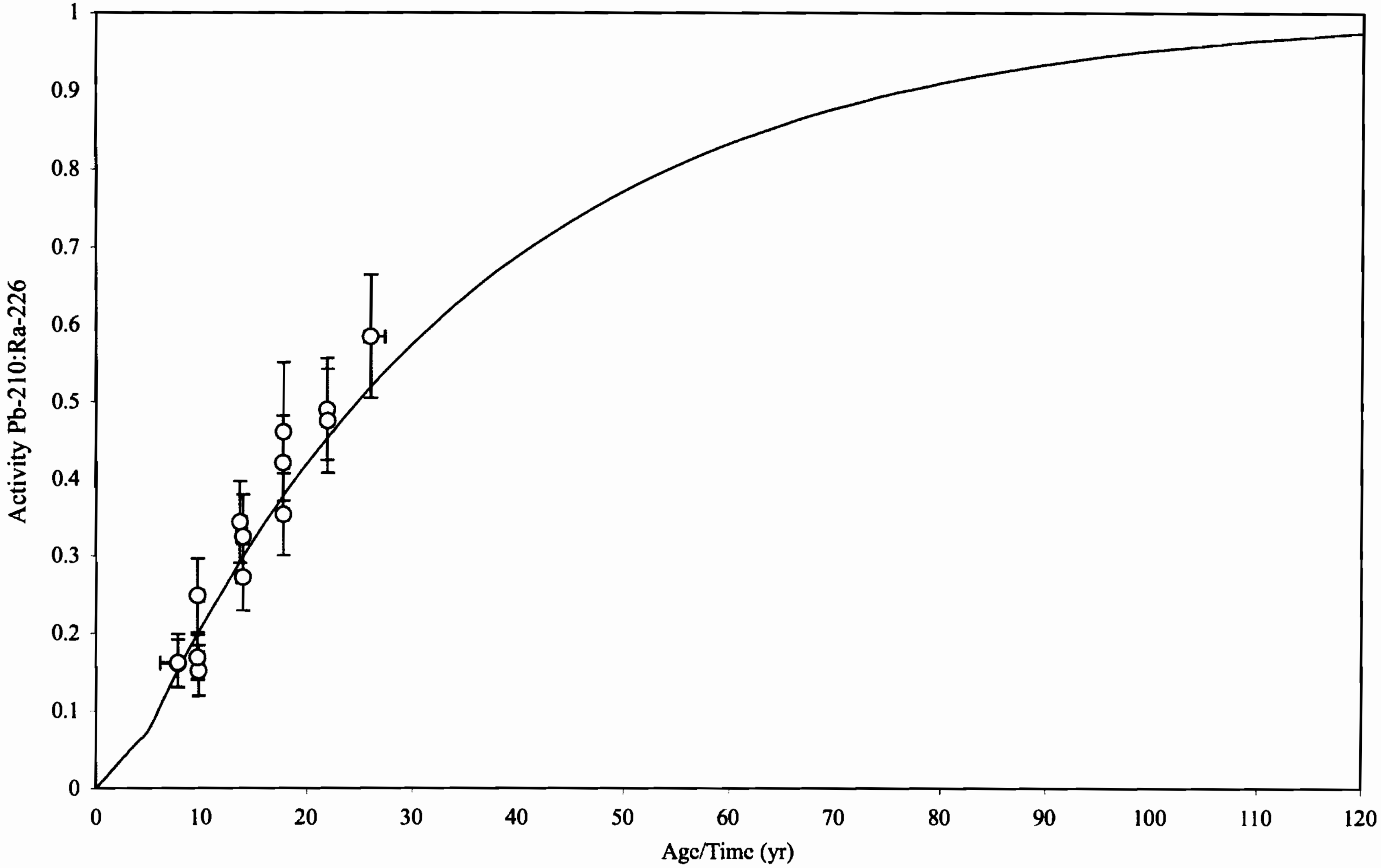


Figure 7. Measured ^{210}Pb:^{226}Ra ratios with respect to total sample age (growth-zone counts and the time since capture), with the expected ^{210}Pb:^{226}Ra ratio (ingrowth curve) for the Antarctic toothfish. Horizontal error bars represent the age range for each group. Vertical error bars represent analytical uncertainty associated with measuring ^{210}Pb and ^{226}Ra measured in 2 SE.

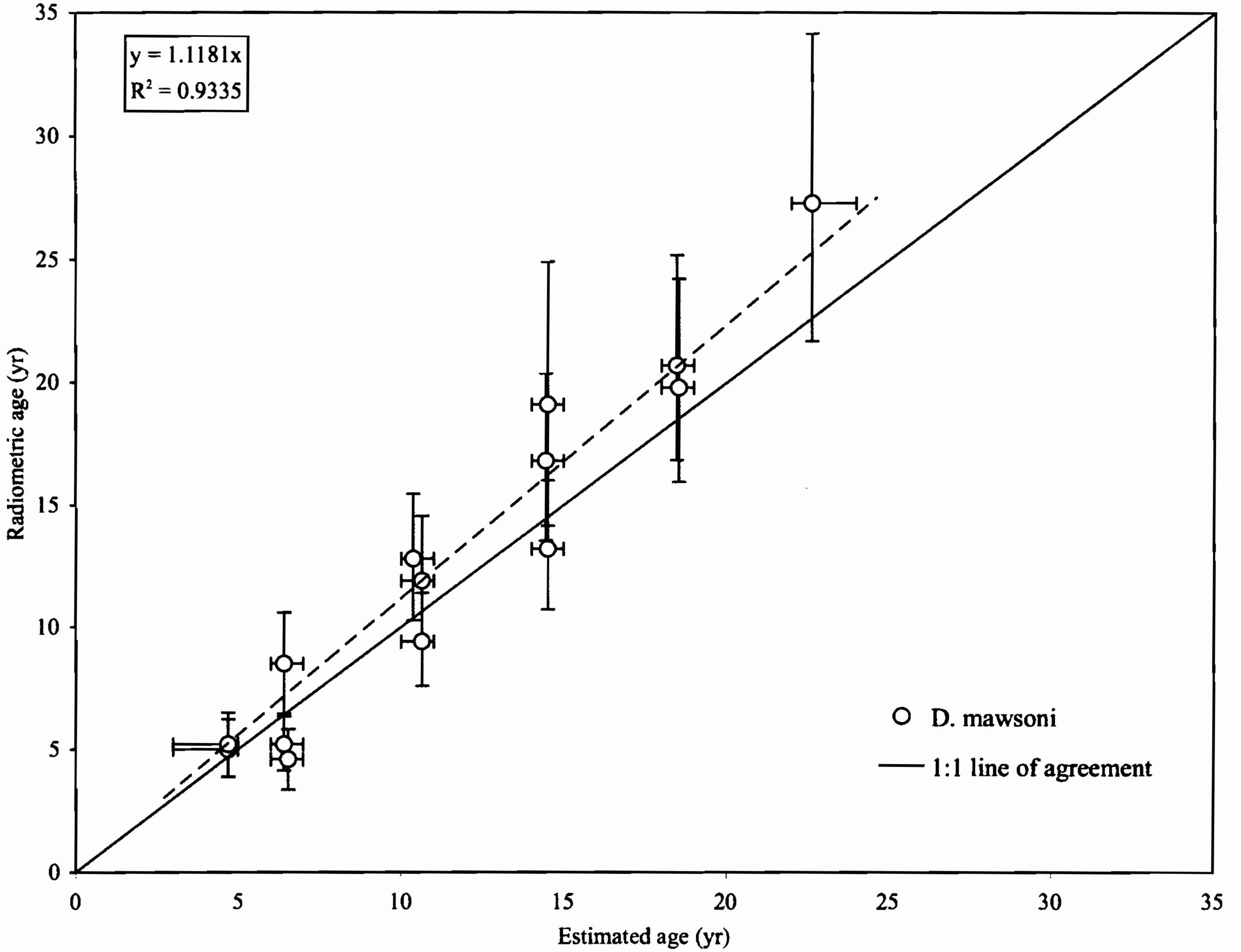


Figure 8. Antarctic toothfish age agreement plot of growth zone derived age estimates versus radiometric age estimates (corrected for date of capture). Horizontal error bars represent the age range associated with each age group, while vertical error bars represent 2 SE for the analytical uncertainty associated with measuring ^{210}Pb and ^{226}Ra. The solid line represents a hypothetical 1:1 line of agreement and the dashed line is the line generated by the data.

CHAPTER 3

Geological history of the Ross Sea, Antarctica

The Ross Sea, Antarctica is the primary commercial fishery region where Antarctic toothfish are targeted. This region has complex bathymetry dominated by tectonic and glacial processes. For many fish species, the availability of habitat for biological functions is critical to the long-term persistence of the species. Despite a steady increase in landings, Antarctic toothfish habitat associations remain unknown. To understand the geological habitat, the geological history must be examined. The historical tectonic and ice processes which characterized the Ross Sea geological habitat are reviewed in the following paragraphs.

Antarctic geological history

In the Precambrian (Table 1), Antarctica was made mostly of a typical craton (stable continental area of mostly igneous and metamorphic rocks). In the late Precambrian to early Palaeozoic, there is geological evidence of an active plate margin, which formed the Transantarctic Mountains. Geological evidence embedded in the geological structure referred to as the Victoria Group, forms the Gondwanaland sequence of Antarctica. This sequence is characterized by fluvial sedimentary rocks with interbedded volcanic ash and breccia in the upper part and has great similarities with Gondwanaland sequences elsewhere, especially in South Africa (Elliot, 1985).

A geological formation referred to as the Ferrar Supergroup, which consists of a related set of lavas, sills and massive plutonic rocks, marks the first geological event 180 mya related to the break up of Gondwanaland. The outcrop is found only along the Antarctic Peninsula, the coast of West Antarctica and on the continental shelves. The sedimentary basins of the Ross Sea are several kilometers thick with post Gondwanaland break-up strata, which are early Cretaceous aged sediments (Domack *et al.*, 1980). Connections with the Gondwanaland mainland diminished during the Late Mesozoic to the Early Cenozoic until sometime between 30-25 mya when the South Tasman rise cleared the coast of Antarctic resulting in the final break up of Gondwanaland (Eliot, 1985). During this same time period (28 mya) the Drake Passage opened and deep water circulation was initiated.

Diminishing land connections with the other Gondwanaland continents played a large role in changing Antarctica's climate since during this time there was a major cooling of Antarctica's surface waters. This cooling is believed to be caused by the South Tasman rise clearing and the Drake Passage opening, both of which contributed to deep water circulation around Antarctica. By 30 mya, ice started accumulating, and by 25 mya, substantial ice bergs were being calved into the Ross Sea region. By 15 mya the East Antarctic ice sheet reached its present dimensions. However, the climate did not become cold enough for ice shelves to form until about 7 mya (Eliot, 1985).

Ross Sea geological history

The Ross Sea is an embayment between the landmasses of East Antarctica and West Antarctica. It is bounded to the east by Marie Byrd Land and the west by the

Transantarctic Mountains and Victoria Land. To the south is the Ross Ice Shelf, which is an extension of the West Antarctic Ice Sheet and covers a large area of the southern Ross Sea (Figure 1).

There are two major tectonic provinces, one being the relatively stable East Antarctic Craton, and the other being the West Antarctic Rift System (WRS). The Transantarctic Mountains represent the southern boundary of the WRS and Marie Byrd Land represents the less well defined northern boundary (Winberry and Anandakrishnan, 2004). Although the WRS is largely aseismic, it is considered one of the largest active continental rift systems on Earth because of late Cenozoic volcanism and tectonism in the region (Behrendt *et al.*, 1991a). The geological habitat of the Ross Sea continental shelf has been extensively shaped by the WRS, which has been evolving since the 120 mya break-up between Australia, New Zealand and Antarctica (LeMasurier and Rex, 1989; LeMasurier, 1990; Behrendt *et al.* 1991b; Lawver *et al.*, 1991).

The WRS has had a complex history during the past 100 mya complicating efforts of plate-circuit reconstructions (Cande *et al.*, 2000). However, many studies have shown evidence of middle Cretaceous to Cenozoic rifting in West Antarctica produced several hundred kilometers of displacement between Marie Byrd Land and East Antarctica (Di Venere *et al.,* 1994; Luyendyk *et al.*, 1996; Cande *et al.*, 2000; Winberry and Anandakrishnan, 2004). Prior to 105 mya, the New Zealand microcontinent was still attached to the Antarctic continent and the Phoenix plate was subducting beneath the region. Between 105 and 95 mya there was a switch in the magmatic character of the region and indicated a change from subduction to extension (Weaver *et al.*, 1994).

Studies by Bradshaw (1989) and Luyendyk (1995) also show that major extension in the region commenced at about 105 mya.

Other studies also show evidence for significant extension in the Ross Sea as a result of motion of the WRS. Cande *et al.* (2000) used seafloor spreading rotations to show that there was roughly 180 km of separation in the western Ross Sea embayment during the Eocene and Oligocene. Winberry and Anandakrishnan (2004) observed thin (average thickness of 25 meters) isostatically compensated crust throughout much of the WRS, which is further evidence that West Antarctica underwent a significant phase of extension from the Cretaceous to middle Cenozoic. Evidence for this extension continuing into the Cenozoic are the episodic continual uplift of the Transantarctic Mountains (starting 50-55 mya) (Fitzgerald *et al.,* 1986; Fitzgerald, 1992) and the development of sedimentary basins with more than 7 km of Cenozoic sediments in the western part of the Ross Sea embayment (Cooper *et al.*, 1987; Davey and Brancolini, 1995).

The estimated amounts of Cenozoic extension are debated and estimates vary widely (Lawver and Gahagan, 1994; Trey *et al.* 1999). Though the major extension in the WRS is generally agreed to have ceased by the middle Cenozoic (Cande *et al.* 2000; Hamilton *et al.*, 2001). Cande *et al.* (2000) proposed that an important change in southwest Pacific tectonic motion occurred at this time when extension ceased between 28 and 26 mya when the Adare trough spreading terminated. During this time in the West Antarctica region, widespread volcanism erupted across Marie Byrd Land. Also at 30 mya, there was a fundamental change in axis of tectonic extension in the Ross Sea region from ENE-WSW to WNW-ESE (Cande *et al.,* 2000).

Clearly the WRS was a major force shaping the Ross Sea seafloor directly through extension and through associated volcanism and uplift. However, historical and present glacial and ice sheet processes have also played a huge role in creating the diverse morphology of the sea floor.

Ross Sea glaciology

Glacial processes historically shaped the Ross Sea seafloor through the direct influence of the East and West Antarctic Ice Sheet and the Ross Ice Shelf. Glacial processes started influencing the Ross Sea in the mid-Oligocene, when glaciers first advanced and grounded along the Ross Sea continental shelf (Barrett *et al.,* 1989; Harwood *et al.*, 1989; Rieck, 1989). Since then, the Ross Sea has had a dynamic ice sheet history (Naish *et al.,* 2001a) with significant cooling, glacial intensification and Antarctic ice sheet expansion (Miller *et al.*, 1991). Naish *et al.* (2001b) studied cores off the Victoria Land coast and found cycles of advance, retreat and re-advance of the ice sheet margin by tens of meters across the western Ross Sea continental shelf which had durations of similar lengths to Milankovitch frequencies (41ky-100ky).

The last glacial maximum (LGM) is defined as the most recent time period of ice sheet extension. During the LGM (21.5 ka), the East Antarctic ice sheet and West Antarctic ice sheet coalesced in the western Ross Sea. Outlet glaciers from the East Antarctic ice sheet expanded becoming part of a large ice sheet that extended into the Ross Sea. Reconstructions of the LGM have suggested that grounded ice advanced seaward near the western Ross Sea continental shelf break (Thomas and Bentley, 1978;

Denton *et al.*, 1989; Anderson *et al.*, 1992). Though more recently Licht *et al.* (1996; 1999) has suggested the ice sheet of the LGM did not cover the outer continental shelf.

The Ross Sea's continental shelf has a distinct and irregular bathymetry which can be explained by ice processes. Shelf depths range from 250 meters to greater than 1,200 meters with an average of more than 500 meters due to ice loading (Barnes and Lien 1988; Davey 1994; Licht *et al.* 1999). The most distinct feature of the Ross Sea continental shelf is the deepening towards the continent and becoming shallower in the offshore direction. Many advances and retreats in the ice shelf grounding line across the continental shelf produced erosion on the inner shelf and deposition on the outer continental shelf (Figure 2; Johnson *et al.*, 1982; Ten Brink *et al.*, 1995; Brambati *et al.*, 2000). These processes are responsible for the typical landward-deepeening bathymetric profile observed in the Ross Sea (Cooper *et al.*, 1991).

Geologists have observed a series of NE-SW trending banks and troughs, or basins, on the Ross Sea continental shelf (Davey, 1987; De Santis *et al.*, 1999). These major troughs on the continental shelf are specifically thought to have been glacially eroded by two processes. The first being the grounding of ice causing glacial scour, or erosion, and the other being from the subsequent retreat of the ice resulting in ice streams that erode the continental shelf causing further erosion (Shipp *et al.,* 2002). These ice shelves advanced and retreated across the continental shelf several times since the onset of glaciation (Hughes, 1973; Licht *et al.*, 1999). The deepest of these troughs, caused by ice streams, is the Drygalski trough adjacent to Victoria Land (Licht *et al.* 1999). Each trough on the continental shelf is believed to represent an independent retreat history (Domack *et al.*, 1999).

Historical glacial processes have shaped the morphology of the Ross Sea continental shelf and continue to have a dominant influence in the present. Currently the Ross Ice Shelf extends over 560,000 km^2 and its massive thickness ranges from 300 to 600 meters thick (Williams and Robinson, 1979). Outlet and valley glaciers from the East Antarctic ice sheet flow through the Transantarctic Mountains and contribute ice to the western Ross Sea. The largest outlet glacier is David Glacier which terminates as the floating Drygalski Ice Tongue (De Santis *et al.* 1999). Glacial processes have been influential on other oceanographic processes including sedimentation.

Sedimentation in the Ross Sea

Glacial processes dominated the sedimentary history of the Antarctic margin and drive present day sedimentation from processes associated with the actions of ice sheets, glaciers, icebergs and sea ice (Nishimura *et al.,* 1996). Sedimentary sequences record long-term environmental changes and, therefore, the historical tectonic and glacial processes have been determined by the study of sediment cores.

Sedimentation as recorded in cores

Continental shelf sediments of the Ross Sea provide valuable insight into past oceanic and climatic conditions. The continental shelf of the Ross Sea is covered by diatomaceous ooze, mud and diamicton (defined as poorly sorted deposits consisting of mud, sand and gravel; evidence of glacial deposits) at various consolidation states of Late Quaternary age (Nishimura *et al.*, 1996; Licht *et al.*, 1999; Roberts *et al.*, 2003). Sediment cores collected from various depths on the continental shelf of the Ross Sea show two lithologic units: soft diatomaceous mud in the upper unit of Holocene age (Kellogg *et al.*, 1979) and compound glacio-marine sediments in the lower unit of Late Quaternary age (Nishimura *et al.*, 1996)

These two units exemplify typical characteristics of an interglacial and glacial period. Higher rates of biogenic sedimentation are shown to occur during deglacial and interglacial periods, caused by strongly enhanced productivity (Ceccaroni *et al.*, 1998). This upper unit demonstrates it was deposited under high ocean productivity as demonstrated by the abundance of diatoms and ice-rafted debris (Agyingi et al, 1995). This is the same sedimentary environment that occurs today (Nishimura *et al.*, 1996). In contrast, glacial periods generally display lower accumulation rates of biogenic sediments (Ceccaroni *et al.,* 1998). The lower unit lithology is variable and complex, but generally shows high gravel content, including basal till and glacio-marine sediments and is thus believed to be glacio-marine sediments from the last glacial advance (Kellogg *et al.*, 1979). This lower unit also shows consolidation under the ice sheet which covered most of the Ross Sea continental shelf in the last glacial time (Nishimura *et al.,* 1996). Many cores from the Ross Sea continental shelf show overconsolidation of layers in the lower units, which may indicate oscillations of the ice sheet (Corradi *et al.*, 1997). Overconsolidation is a result of sea level rising, followed by a glacial sheet forming and loading the sediment. When the sheet recedes, it leaves behind overconsolidated sediments (Edwards *et al,* 1987).

Cores of the Late Quaternary age from the continental slope show the dominant sediment type is silty clay alternating with clayey silt (Ceccaroni *et al.*, 1998), similar to present day sedimentation (Anderson *et al.*, 1992). Present day sedimentation is mainly represented by terrigenous input of glaciers through ice shelves, sheets and tongues and the accumulation of biogenic, mainly siliceous and/or calcareous, remains (Anderson *et al*, 1992). Sediments of the Ross Sea in particular have been shown to accumulate high amounts of biogenic silica (Ledford-Hoffman *et al.*, 1986). Sediments close to the ice sheet contain more gravels due to proximity of the ice sheet, whereas sediments subject to areas of strong ocean currents are not subject to accumulation (Ravaioli *et al.,* 1999). Sedimentation rates are estimated at 1.2 -3.8 cm/kyr (Ceccaroni *et al.*, 1998) including terrigenous and biogenic material. The deep-sea basins of the Ross Sea are made of foraminiferal ooze, siliceous mud, and terrigenous mud (Nishimura *et al.*, 1996). The physical properties of all recovered cores from the Ross Sea are typical for high-latitude sediments worldwide (Edwards *et al.*, 1987).

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Table 1. Geological time scale. Assigned ages simplified from Harland *et al.*, 1982.

Geological Time Scale

Era	Period	Epoch		Age in Ma
			Holocene	
	Quaternary			
			Pleistocene	
				2
			Pliocene	
		Late		5
CENOZOIC			Miocene	
				25
	Tertiary		Oligocene	
				38
		Early	Eocene	
				55
			Palaeocene	
				65
	Cretaceous			144
MESOZOIC	Jurassic			
				213
	Triassic			
				248
	Permian			
				286
	Pennsylvanian			
				320
	Mississippian			
				360
PALAEOZOIC	Devonian			
				408
	Silurian			
				438
	Ordovician			
				505
	Cambrian			
				590
PRECAMBRIAN				4500

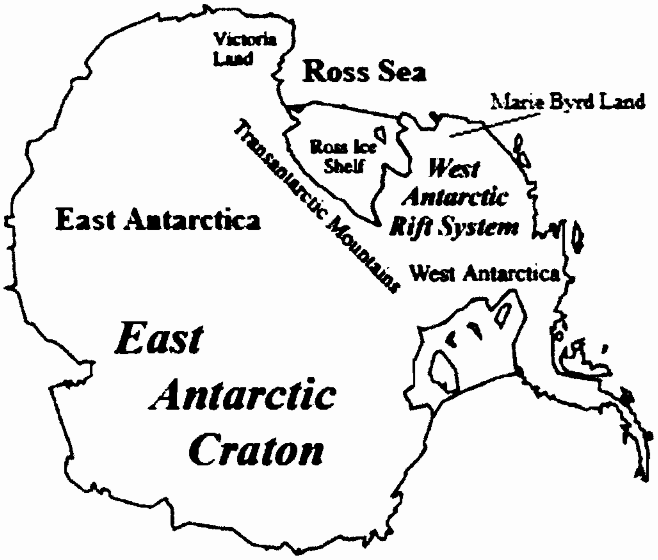

Figure 1. Map of Antarctica showing major geographic features, including those which border the Ross Sea. The Transantarctic Mountains serve as a boundary between the East Antarctic Craton and the West Antarctic Rift System. Modified after Licht *et al.*, (1999).

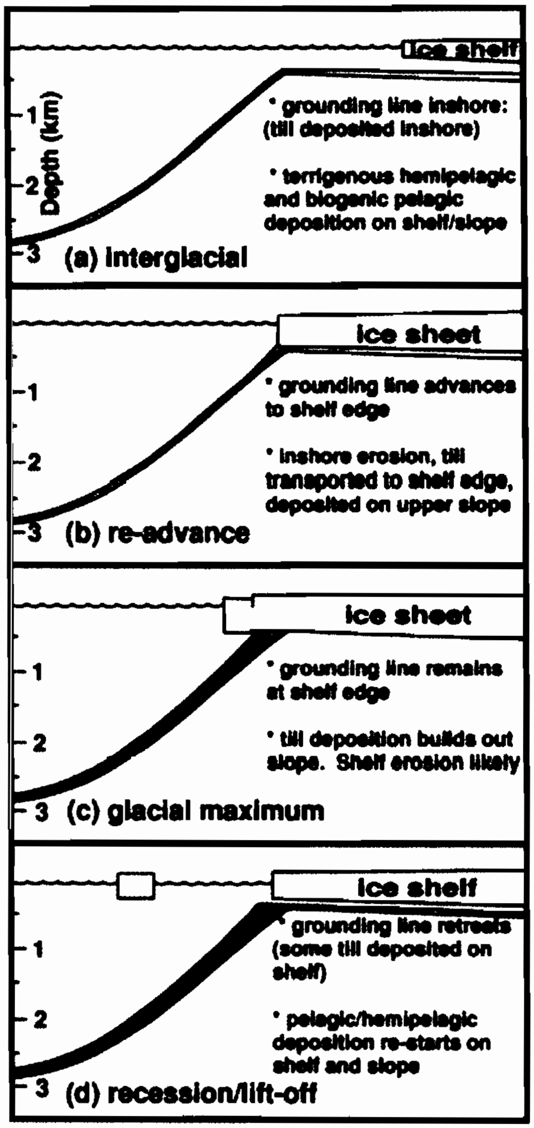

Figure 2. Sequence model of deposition and erosion on continental shelf through a glacial cycle (from Barker *et al.,* 1999).

CHAPTER 4

Spatial distribution and age structure of the Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica

To be submitted for publication: Journal to be determined

Abstract

The Ross Sea has been geologically characterized by tectonic and glacial processes. These processes have created diverse habitat, including distinct banks and basins. For many fish species the availability of habitat is critical to the long-term viability of the population. Antarctic toothfish (*Dissostichus mawsoni*) are subject to an increasingly important commercial fishery in the Ross Sea and yet little is known about habitat associations for different life history stages. To define and assess the availability of habitat for Antarctic toothfish a benthic habitat map of the Ross Sea was created based on the habitat mapping scheme developed by Greene *et al.* (1999). Fish age data from the long-line fishery in the Ross Sea were superimposed on the habitat map and broken into discrete spatial areas. Differences in age distributions between these areas were found using ANOVA. These distributions were consistent with an ontogenetic movement of fish from shallow continental shelf habitats to deep-water continental slope was documented. Younger, less mature fish were located on the continental shelf and older fish were located on the continental slope. In addition, the older and most mature individuals were found on ridges in the northern Ross Sea, consistent with the hypothesis

of an austral summer spawning migration from continental slope to the ridge habitat of the North Ross Sea. An effective management strategy might focus on protecting the northern ridge habitat to maintain long-term viability of Antarctic toothfish populations.

Introduction

Antarctic toothfish (*Dissostichus mawsoni*) is a large nototheniid fish endemic to the deep-water areas of the Southern Ocean surrounding the Antarctic continent. Its closest living relative, Patagonian toothfish (*D. eleginoides*), also occurs in the Southern Ocean and together are marketed to consumers as “Chilean sea bass.” Both species have been caught by a long-line fishery operating in the Southern Ocean since the mid-1980s; however, landings of Patagonian toothfish have historically dominated the fishery because this species typically occurs north of 60 degrees South latitude, while Antarctic toothfish are generally found in more remote regions to the south (Figure 1). The Patagonian toothfish fishery expanded rapidly and overexploitation of some populations resulted in stock closures (Agnew *et al.,* 2002). These management actions also had the effect of increasing fishing pressure on the Antarctic toothfish as fishing vessels moved further south. The Antarctic toothfish fishery operates primarily in the Ross Sea, Antarctica, where melting of sea-ice during summer months allows for long-line operations. The Ross Sea fishery is still considered to be in an exploratory phase, yet Antarctic toothfish landings have increased steadily, from 42 tons in 1997 to more than 4,600 tons in 2006 (CCAMLR, 2007).

Antarctic toothfish are piscivorous and bentho-pelagic, located at depths between 500 and 3,000 m (Hanchet *et al.,* 2003). Adults are typically located in deeper water than juveniles (Near *et al.,* 2003) and can grow to more than 2 m in length and in excess of 100 kg in weight. Together with Patagonian toothfish, they are the largest fishes in the Southern Ocean (Eastman and DeVries, 2000). Recent age and growth studies have confirmed that toothfish grow slowly, and longevity is estimated at 35-39 years of age (Horn, 2002; Brooks, 2008).

Often as fish age, they utilize different habitats, which may be critical to the persistence of the species (Cushing, 1981). Understanding habitat requirements for vital processes, such as foraging, refuge from predators, reproduction or recruitment, are crucial in implementing proper fisheries management (Stoner, 2003). Essential habitat has been defined as habitat that is physically discrete and indispensable for the survival of at least one life stage of a particular species and can include space required for foraging, refuge from predators in early life stages, and reproduction or recruitment of juveniles (Valentine and Lough, 1991; Langton *et al.,* 1996; Stoner, 2003). Studies have shown that for many species of eastern North Pacific rockfishes (genera *Sebastes* and *Sebastolobus*), which are deep-dwelling like Antarctic toothfish, the availability of habitat is critical (Yoklavich *et al.,* 2000). Deep-sea fishes are generally considered more vulnerable to commercial harvesting because of their life history characteristics, including slow growth, low fecundity, and late maturity (Koslow *et al.,* 2000; Clark, 2001; Morato *et al.,* 2006); therefore, understanding habitat associations and requirements should be a high priority for management.

The Ross Sea, Antarctica, where Antarctic toothfish are abundant, has been strongly influenced by tectonic and glacial processes. These dual forces have created a geological setting for fish habitat that is complex and very diverse, included distinct banks and basins as well as seamounts and ridges (Figure 2). The Ross Ice Shelf, which is an extension of the continental West Antarctic Ice Sheet, extends over 560,000 km^2 and is between 300-600 meters thick (Williams and Robinson, 1979). Millennia of scouring and erosion by this massive ice shelf have created a particularly deep continental shelf that deepens landward (Johnson *et al.,* 1982; Cooper *et al.,* 1991; Ten Brink *et al.* 1995; Brambati *et al.*, 2000). Shelf depths range from 250 m to greater than 1200 m deep, with an average depth of over 500 meters. The shelf break occurs at about 800 m, with the slope dropping 3,000 m into the abyss (Barnes and Lien, 1988; Davey, 1994; Licht *et al.,* 1999).

Fish habitat utilization is strongly influenced by ecological and oceanographic conditions that change through space and time; however, the distribution of most marine species is typically associated with particular bathymetric features which can be classified into distinct habitat types (e.g. Greene *et al.*, 1999). When used in conjunction with fish life history, distribution, and abundance data, habitat classification schemes can be effective in identifying essential habitat. With this approach, we can gain a better understanding of where fish occur in space and time and provide information on habitat associations and requirements.

How Antarctic toothfish utilize benthic habitats in the Ross Sea is not well understood at this time. In the congeneric Patagonian toothfish, many studies have reported a linear length-depth and age-depth relationship, showing that as fish grow larger, they move deeper (Zhivov and Krivoruchko, 1990; Duhamel, 1991; Moreno, 1991; Agnew *et al.*, 1999; Ashford *et al.*, 2007). Reports published by NIWA (National Institute for Water and Atmospheric Research) and based on the Antarctic toothfish fishery in the Ross Sea, indicate there were differences in length distribution and abundance from region to region based on the spatial variability where vessels fish. In general larger, older fish tend to be caught in deeper waters (Hanchet *et al.,* 2003; 2007).

If the ontogenetic nature of ATF relative to habitat utilization can be identified, managers can begin to consider protective measures. The objectives of this study were to: 1) characterize the benthic habitats of the Ross Sea, Antarctica according to Greene *et al.* (1999), an established deep-sea habitat mapping scheme; 2) create a potential habitat map using ArcGIS®; 3) superimpose fish age data on the habitat map to examine how the distribution of the species is associated with the habitat; and 4) test if available habitat effects the age distribution of Antarctic toothfish. The role of essential habitat in this rapidly developing deep-sea fishery is discussed and recommendations are made.

Methods

Data Collection

Data regarding Antarctic toothfish were obtained from federal fisheries observers on American commercial long-line fishing vessels in the Ross Sea, Antarctica. Fisheries observers collected biological data, such as otoliths, maturity stage, weights and lengths of fish. From collected otoliths, 1,508 Antarctic toothfish were aged in a concurrent study (Brooks, 2008). Fisheries observers also collected haul data, such as geographic location of each haul (latitude and longitude) and depth, as well as the total number and weight of all fish caught per haul. Location data and abundance of Antarctic toothfish caught for each haul were compiled into a spreadsheet by the Center for Quantitative Fisheries Ecology (CQFE).

Digital data corresponding to the bathymetry of the Ross Sea were downloaded through the New Zealand Institute of Geological and Nuclear Sciences (GNS) ftp site accessed through the internet (ftp://ftp.gns.cri.nz/pub/vaughan/antall_16_july.grd). These data provided a grid corresponding to a 1:5,000,000 map and were made using GMT (generic mapping tools). The data spanned from 140°E to 240°W and 60°S to 85°S with a cell size of 0.033/0.01667 °(2′ x 1′) and included only the Ross Sea with no corresponding land mass. The grid was made with the WGS84 (World Geodetic System 1984) datum, which defines a reference frame for the earth with the latest revision dating from 1984.

The data used to compile the grid corresponded to about 50 million bathymetry points from a variety of technologies ranging from old single beam sonar to recent multibeam data. The data were collected from the National Geophysical Data Centre (NGDC) (http://www.ngdc.noaa.gov/ngdc.html) as well as additional U.S., Italian, German and New Zealand data sources. Swath bathymetry data were obtained through RV Nathanial B Palmer, RV Maurice Ewing and RV Tangaroa. Bathymetry data between the Ross Ice Shelf were from Davey *et al.* (1987), Greischer *et al.* (1992) and GNS data files. Coastline and ice edge data were from the Antarctic Digital Database (http://www.add.scar.org/add_main.html). The gravity data used to determine water depth were derived from satellite altimetry observations (Smith and Sandwell, 1997).

Gravity data north of 72°S were from NGDC, data south of 72°S were from McAdoo and Laxon (1997).

Data processing was performed by GNS as follows. Bathymetric data were cleaned and aggregated to a resolution of no less than 50 meters. Cleaning the data involved discerning differences in depth of each data point to the mean depth of the nearest 29 neighboring points. Data points whose values were more than 70% of the largest differences were deleted. This cleaning procedure was repeated until the difference between each bathymetry value and its neighbors was less than 30 meters. Final cleaning was followed by a visual quality check. Satellite derived data were used to determine water depth in areas of sparse bathymetric data coverage using the method of Woodward and Wood (2000). Water depth was calculated for all points on triangular networks of bathymetry (sides up to 6.5 km long) by minimizing the difference between the observed and predicted gravity anomalies. Vaughan Stagpoole of GNS compiled the final resulting bathymetric map.

Habitat Map

The grid data corresponding to the bathymetric map from GNS was formatted from GMT and imported into ArcGIS®. The grid was then georeferenced and projected using Universal Polar Projection (UPS). The UPS projection was chosen for the base of this map because it is generally used for areas north of 84° N and south of 80° S and provides the least amount of distortion for the Polar Regions. Habitats were then interpreted according to the habitat classification scheme of Greene *et al.* (1999). Seabed features and bathymetry at the mesohabitat level (with a resolution of kilometers to tens of meters) were used to classify regional habitat types. Habitats were defined and traced in ArcGIS® by forming polygons according to habitat type. Polygons were then edited and color-coded to create the final habitat map.

Fish age data analysis

Latitude and longitude data for each long-line haul, 195 total lines, were overlain on the habitat map in ArcGIS®. Each haul line had between 1 – 51 age data points. Because I was interested in testing how fish were utilizing habitat at different life stages, haul lines were grouped, based on specific habitat types where haul lines were aggregated, and broken up into 11 spatial areas. Most spatial areas were dominated by one habitat type and corresponded to distinct physical features. Region 1 was on the Pacific-Antarctic Ridge system, region 2 and 4 were on the Iselin Bank, regions 5, 6, 7 and 8 corresponded to the shelf and slope off Mawson Bank, region 11 was on the shelf and slope off Cape Adare and regions 3 and 10 were mostly contained within the Adare Basin. Testing between individual haul lines would have been statistically impossible based on some of the very small sample sizes (i.e. 1 – 5 fish), and would not necessarily define difference in age structure between habitats. When haul lines were grouped together, sample sizes were larger, allowing for better statistical analysis.

Fish age data (n = 1,508), corresponding to the haul lines in each of the 11 spatial areas were then compiled. In addition to age data, stage of maturity was also analyzed according to each spatial area. For toothfish, maturity was broken down into five stages (CCAMLR, 2006). Stage 1 was immature. Stage 2 was maturing and developing where ovaries and testes were quite small. Stage 3 was when the fish were about to spawn.

During this stage, the ovaries and testes were large and developed with visible eggs. Stage 4 was gravid, ripe and actively spawning. During this stage, eggs filled most of the body cavity and the testes were large and full of milt. Stage 5 was classified as "spent," after the fish has spawned and their ovaries and testes were small, shrunken and flaccid. Four of the spatial areas (area 2, 3, 5 and 9) were omitted from the statistical analysis due to small sample sizes ($n < 34$). Areas 1, 4, 6, 7, 8, 10, and 11 were used in the analysis. Areas 6 and 7 were combined for a more robust sample size because their habitat types were similar and were not significantly different. Area 6 and 7 will henceforth be referred to as area 6_7.

A one-way analysis of variance (ANOVA) was used to determine if there were significant ($\alpha = 0.05$) differences in mean size and age across areas. Data fulfilled the assumption of homoscedasticity (Levene's test, $F = 0.68$, $df = 5, 1435$, $P = 0.6424$). Levene's test was chosen over other tests of variance, such as Fmax tests, because it was less sensitive to departures from normality. Data were not normally distributed in any area (Kolmogorov- Smirnov, $p<0.01$; Table 1). Box Cox, Archer, natural log, reciprocal and square root transformations were applied, but no single transformation fulfilled normality across all regions. Examination of the data indicated that the distributions were dissimilar between regions. All areas had some degree of skewness and kurtosis (Table 1) that caused departures from normality, yet these were not dramatic. Since ANOVA is robust to mild departure from normality, these were unlikely to greatly affect significance tests (Dowdy and Wearden, 1991; Underwood, 1995). Duncan's Multiple Range test was used to evaluate the differences in spatial areas and was chosen because it protects against type II error.

Results

Habitat Map

The habitat of the Ross Sea, Antarctica was described based on bathymetric and geological observations using the classification scheme devised by Greene *et al.* (1999) with modifications (Table 2; Figure 3). Mega-habitats were described at the tens of meters to hundreds of meters scale and meso-habitats were described at the meters to tens of meters scale. Mega-habitats included the continental shelf, slope and rise, as well as basin floors, abyssal plains and ridges. A fracture zone mega-habitat, which was not part of the Greene *et al.* (1999) scheme, was also described. Further ridges, mounds, depressions, basins, banks, and plateaus within the mega-habitats were described at the meso-habitat scale. Dominant habitat types in the Ross Sea were the fracture zone (~25%), continental shelf (~20%), ridge system (~20%) and the continental rise (~20%). The least dominant habitats were the abyssal plains (~10%), continental slopes (>5%) and basins (<5%). Banks were the most common mesohabitat features associated with the continental shelf, occupying ~40% of the continental shelf not covered by the Ross Ice Shelf.

Fish age data analysis

Fishing activity was focused on the western Ross Sea (Figure 4). Most fishing took place on the continental slope (~68%), including over flanks (54%), depressions (2%), mounds (3%) and plateaus (9%) on the slope. Fishing also occurred on the shallower continental shelf (~22%) in the western Ross Sea as well as on deep-sea ridges further north (~10%). All fishing occurred between 493-2200 meters in depth.

ANOVA results showed there were significant differences between ages across regions (F = 82.05; df = 5, 1435; P < 0.0001; Table 3). Duncan's tests indicated that all spatial areas were significantly different from each other, with the exception of region 10 and 6_7, which were not significantly different (Table 3). Differences in mean age may be habitat and depth driven (Table 4). Region 11 and 8 had the lowest mean ages (9.9 and 10.9 years respectively) and also were the only regions to have hauls on the shallower continental shelf (~500 m in depth), in addition to the deeper continental slope (greater than 1,000 m). In region eight, 92% of the fish sampled were caught on the continental shelf (which corresponds to 68% of the haul lines in this region). In region eleven, 21% of the fish sampled were on the continental shelf (which corresponds to 8% of the haul lines in this region). Regions 6_7 and 10, had mean ages of 12.6 and 13.3 respectively, and encompassed deeper continental slope habitats, including plateaus and depressions (some greater than 1,800 meters in depth, though the average was roughly 1,200 to 1,400 meters respectively). Area 4 had a slightly older mean age of 14.2 with fish lines primarily occurring in similar areas to areas 6_7 and 10 and higher age range (3-39 years). Areas 6_7, 8, 10 and 11 all had age ranges only reaching into the mid-twenties (Table 4). Individuals older than mid-twenties are uncommon in the entire data set. Region 1 had the highest mean age of 17.3 years and all haul lines occurred on mid-water ridges that were on average greater than 1,700 m in depth. Unlike all the other spatial areas, Area 1 lacked juveniles (Table 4).

Differences in maturity at each spatial area were correlated with age differences and depth differences (Table 5). Regions 11 and 8, which had the youngest mean age and shallower depths, also had the most stage 1 individuals (86% and 76% respectively). Whereas regions 6_7, 10 and 4 all had about 50% stage 1 individuals and about 50% stage 2, with the exception of area 10, which had 13% stage 3. These stage 3 individuals from region 10 were in the northern haul lines of the spatial area located on the deeper continental slope plateau (between 1,000 -1,800 m). Note also that area 10 had a deeper mean depth than the other areas (with the exception of region 1). Region 1, which had the highest mean age and the greatest mean depth, had 77% stage 3 individuals and even one stage 4 individual. Sixty-six percent of all stage 3 individuals from the entire data set were in Region 1.

Discussion

Habitat Map

The habitat map of the Ross Sea, Antarctica revealed complex bathymetry at the meso-habitat level, evidence of the unique environment carved and shaped by glacial and tectonic processes. The habitat map also showed that the Ross Sea continental slope does not gradually descend into the abyss; instead, the slope is very steep in places, and has its own distinct bathymetry including banks, depressions and plateaus. This map encompassed an area much larger than that utilized by the Antarctic toothfish fishery. It can be used for future habitat association studies for other Antarctic species and is also a valuable tool for geologists as baseline work for creating potential habitat maps for future Southern Ocean areas or other glacially influenced areas. This work represents the first habitat map of the Ross Sea and one of the first in the Southern Ocean. Scientists with CCAMLR are also developing bioregionalization maps of the Southern Ocean, which could be used as potential habitat maps (SC-CAMLR-XXVI/11, 2007).

Fish age data analysis

The Ross Sea is a large region with distinct geological features, only some of which appear to important habitat for Antarctic toothfish. The majority of the fish sampled were caught on the continental slope, including the slopes off Mawson and Iselin Banks. Yet, slope habitat only comprises a very small portion of the Ross Sea (estimated at less than 5%). Thus, the availability of this habitat may be a limited factor in the growth of the local Ross Sea population. The continental shelf habitat, including the region between Cape Adare and Mawson Bank, and the ridge habitat (corresponding to the Pacific-Antarctic ridge system) were also important, though less so, and together comprised about 40% of the available habitat.

Of the fish sampled on the continental slope, there was a pattern of older fish being found in deeper regions of the slope, a trend which has also been observed in Patagonian toothfish (Agnew *et al.,* 1999; Moreno, 1991; Duhamel, 1991; Yau *et al.,* 2001). Also, Antarctic toothfish that were found on the shallower continental shelf of the Ross Sea were, on average, younger than those found on the continental slope, further supporting the hypothesis of an ontogenetic movement with depth. This analysis demonstrated that the oldest and most mature individuals were aggregated in the northern regions of the Ross Sea along the Pacific-Antarctic Ridge, which was also the deepest habitat fish were found in. Fish younger than 11 years of age were absent from the northern ridge habitat, meaning only mature fish were present, since maturity is estimated at ten years. Yet when examined in finer spatial detail, there were serious departures from a gradual ontogenetic migration between habitats or to depth, which may be explained by other factors, including sampling bias.

All Antarctic toothfish data used in this study were fishery-dependent, and thus, certain caveats must be considered when interpreting the results. Fishermen were limited by both their gear and the Ross Sea environment. They could only fish as deep as their gear allowed, even though Antarctic toothfish are known to occur in deeper waters, and fishing vessels could not travel further south than the edge of the Ross Ice Shelf. The distance over which long-lines were deployed varied widely, often spanning many kilometers, and fishing occurred over multiple habitats, resulting in little consistency in the number of fish caught and sampled. Gear selectivity can also bias the sample catch by selecting for specific age groups and may have contributed to the data's departures from normality (Figure 5). Long-line gear tends to select larger individuals (Ashford *et al.*, 2005), thus few juveniles were available in the data set and no fish younger than 3 years of age.

Fisheries observers performed all biological sampling, thus subjecting the data to sampling error. The lack of a clear and rigorous sampling design is a major flaw of the CCAMLR observer program. Observers are often not adequately trained or instructed in random sampling. Thus they may sample opportunistically or simply out of convenience or may be selected based on fish size versus taking a random sample. Hauls were not always adequately and equally sampled. There were often wide discrepancies between the number of fish caught and the percentage sampled. Maturity data were often not recorded. Because of these data gaps, results may have become skewed toward haul lines and spatial areas that were more thoroughly sampled. These biases may have also contributed to the data departures from normality. Nonetheless, in remote areas like the Ross Sea, fishery-dependent data are the only data available, and they can still be utilized to draw important conclusions regarding Antarctic toothfish and their habitat. In the future, a rigorous sampling design should be implemented for the fisheries observer program to ensure data are random and representative of the entire fished population.

Other factors that might influence age spatial distributions include prey foraging or predator evasion. Antarctic toothfish adults generally feed on a variety of fish, including *Pleuragramma antarcticum*, icefish, Macrourids and cephalopods and krill (Eastman, 1985; Fenaughty *et al.*, 2003). Little is known about the diet of juvenile Antarctic toothfish, but can be inferred from the diet of Patagonian toothfish juveniles, which were generally piscivorous. Their diet changed with size, with an increase in myctophid fish and krill as the toothfish grew and dispersed. The prey size increased with fish size and a greater range of prey sizes were consumed by larger fish (Collins *et al.*, 2007). Thus Antarctic toothfish spatial distribution may be influenced by their foraging behavior at different ages. Distribution may also be driven by the deep-diving behavior and foraging by seals and killer whales – toothfish may be diving deeper or move to different areas to avoid these predators (Testa *et al.*, 1985; Fuiman *et al.,* 2002; Pitman and Ensor, 2003; Smith *et al.,* 2007).

Very little is known about Antarctic toothfish reproduction; but there is evidence indicating that Antarctic toothfish make a spawning migration from the southern continental shelf break out to the Antarctic Polar Front in the northern Ross Sea. This evidence includes geographical differences in the condition, reproductive development, sex ratio and length distribution of Antarctic toothfish between the northern and southern Ross Sea (Patchell, 2002; Fenaughty, 2006). Spawning, and the associated migration, likely begin in June after the summer freeze and continues into October (Eastman and DeVries, 2000; Patchell, 2002; Fenaughty, 2006). The results from this study, including the lack of any immature individuals in the north, coupled with finding the most older and mature individuals there, further support the spawning migration hypothesis.

Physical oceanography

The region between the southern continental shelf and slope and the north ridges of the Ross Sea is vast and deep. However Antarctic toothfish purportedly make a 600 to 900 km migration across abyssal plains, continental rises, and fracture zones that are over 5,000 m in depth and arrive at the northern ridges of the Ross Sea to spawn. For many continental slope species, deep channels and oceanographic currents can act as barriers to population movement and dispersal (Bailey *et al.,* 1997; Stepien, 1999; Rogers, 2003; Shaw *et al.,* 2004). For example, deep water and oceanographic fronts are presumed to be largely responsible for the genetic isolation of Patagonian toothfish populations in the Southern Ocean (Rogers, 2006; 2007; Ashford *et al.,* 2006; Ashford and Jones, 2007). Antarctic toothfish in the Ross Sea are not genetically differentiated. Thus the individuals from the north and south regions are likely the same population, though they are genetically distinct from fish caught in the South Shetland Islands and the Indian Ocean sector of the Southern Ocean (Kuhn and Gaffney, In Press).

It is possible that oceanographic features may instead be connecting geographically distant areas, and life history stages, of Antarctic toothfish in the Ross Sea. The Ross Sea is characterized by a clockwise, cyclonically circulating gyre (Orsi *et al.*, 1995; Van Woert *et al.,* 2003). This gyre is bounded by the Antarctic continent to the south and by the Antarctic Circumpolar Current (ACC) to the north (Van Woert *et al.,* 2003). After toothfish feed and grow larger in the southern waters of the Ross Sea, they may travel in water flowing westward over and near the continental shelf and north to the Pacific-Antarctic Ridge, where they spawn (and food is lacking; Fenaughty 2006). Antarctic toothfish may utilize the Ross Gyre in larval dispersal, releasing them in the current, which will transport them to the shallower continental slope for settling out. Once spawning has ceased, toothfish could potentially use the Ross Gyre to return south to their feeding grounds. Recent tagging data also supports movement of fish from the southern Ross Sea to the northern ridges (Dunn *et al.*, 2005). Furthermore, a recent study by Ashford *et al.* (2008) indicates that oceanographic currents and fronts maybe responsible for advecting certain life stages of Patagonian toothfish in the Southern Ocean; thus driving their age structure distribution in ways not expected.

In the northern Atlantic Ocean, Atlantic cod (*Gadus morhua*) partake in a similar spawning migration. Mature cod migrate from inshore feeding grounds to offshore breeding areas, covering distances of 500 km or more by utilizing currents and temperature gradients (Rose *et al.*, 1995). Why cod, or toothfish, make long migrations to reproduce is not well understood. Perhaps there are fewer predators in these offshore regions, or offshore currents may help facilitate larval dispersal. The physical oceanographic regime of the Southern Ocean likely influences the distribution and abundance of Antarctic toothfish, and its role in supporting toothfish populations should be further investigated.

Implications for management

The Pacific-Antarctic ridge system likely provides critical habitat for spawning Antarctic toothfish, yet not for juveniles. Fishermen in the Ross Sea begin their fishing season as far south as the ice allows them and as the season progresses, and ice develops, they move north. The last region they fish is the Pacific-Antarctic Ridge; a region not restricted by ice conditions. In the last few years, fishermen have returned to port after fishing the ridge and then returned a second time to fish it again, thus placing a disproportionate amount of fishing effort on this region (Hanchet *et al.,* 2008). Studies of other groundfish species have demonstrated that older, more mature fish are most important to the long-term viability of the population. Fecundity increases with body mass, and thus, larger and older fish are the most successful spawners because they produce more, and more viable offspring; they are crucial for the maintenance of resource stocks (Berkeley *et al.,* 2004a and 2004b; Bobko and Berkeley, 2004). In a recent age and growth study, Brooks (2008) indicated that fishing pressure on Antarctic toothfish in the Ross Sea may already be reducing the numbers of these old, large females. Therefore, protecting spawning fish and their habitat during this critical time may be an appropriate management strategy.

The precautionary approach in fisheries management is based on the premise that decisions should be made in favor of maintaining the integrity of exploited populations and their habitat, especially in cases of high uncertainty or when management error could cause irreversible damage (Garcia, 1996; Auster, 2001). Often, scientific uncertainty regarding life history characteristics or ecological needs, including essential habitat, results in a lack of management action. In the deep sea, where the risk of irreversible damage is high, and particularly in the Antarctic, where levels of uncertainty are high, the precautionary approach should guide most management decisions. For Antarctic toothfish, uncertainty regarding their life history characteristics is a significant impediment to proper management. Reproductive behavior is only now beginning to be understood. Their spawning period, larval dispersal, development and recruitment remain unknown. The establishment of deep-sea protected areas as a precautionary measure prior to large-scale fishing is often suggested to ensure the conservation of exploited deep-sea stocks (Morato *et al.,* 2006).

The ecosystem-wide effects of the Antarctic toothfish commercial fishery also remain unknown. Currently, the trophic linkages in the Ross Sea are considered closer to their natural state than anywhere else in the Antarctic (Smith *et al.*, 2007). Furthermore, the resilience of polar and deep-sea biota to commercial fishing is typically lower than in temperate and shallow water fauna (Smith *et al.,* 2007; Koslow, 2000). Moreover, other than leopard seals (*Hydrurga leptonyx*), Antarctic toothfish are the largest and highest trophic level predators in the Ross Sea. The ecological impacts of fishing, including the possibility of trophic cascades should be considered (Pauly *et al.,* 1998). A precautionary strategy for the management of Antarctic toothfish populations is necessary, especially while basic life history data is still being gathered (Auster, 2001). This study provides preliminary data regarding Antarctic toothfish habitat associations and requirements, however many questions remain unanswered. The Antarctic toothfish fishery is still considered "exploratory" and should remain so until more is known regarding the life history and habitat requirements of this unique deep-sea Antarctic fish.

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Table 1. Values associated with tests of normality, Kolmogorov-Smirnov (KS), degrees of freedom (df) and the associated P-values as well as kurtosis and skewness values.

Area	KS value	df	P-value	kurtosis	skewness
1	0.174	76	<0.01	-0.937	0.319
4	0.128	559	<0.01	4.427	1.112
6_7	0.106	180	<0.01	0.805	0.239
8	0.079	270	<0.01	1.363	0.511
10	0.097	108	<0.01	1.130	0.388
11	0.107	242	<0.01	0.471	0.648

Table 2. Abbreviated codes referring to habitat types utilized. The capital letter in the code refers to the mega-habitat type and the lowercase letter refers to the meso-habitat type (i.e. Am refers to a mound or ridge that is on the continental rise).

Abb. Code	Mega-habitat	Meso-habitat	Depth (m)
Aa	Continental Rise	continental rise	3000-5000
Am	Continental Rise	mound/ridge	3000-5000
Bb	Basin floors	basin floors	1000-2500
Cc	Continent (including islands)	continent	0+
Ci	Continent (including islands)	island	0+
Fd	Continental Slope, Flanks	depression/basin	200-3000
Ff	Continental Slope, Flanks	continental slope, flanks	200-3000
Fm	Continental Slope, Flanks	mound/ridge	200-3000
Fp	Continental Slope, Flanks	plateau/terrace	200-3000
Pp	Abyssal Plains	abyssal plains	>5000
Rm	Ridges, Banks, Seamounts	mound/ridge	200-2500
Rr	Ridges, Banks, Seamounts	ridges, banks, seamounts	200-2500
Sb	Continental and Island Shelves	bank	0-200
Sd	Continental and Island Shelves	depression/basin	0-200
Sf	Continental and Island Shelves	flank	0-200
Sm	Continental and Island Shelves	mound/ridge	0-200
Ss	Continental and Island Shelves	continental and island shelves	0-200
Zz	Zone of Fractures	zones of fractures	200-2500

Table 3. Results from ANOVA and Duncan's testing for differences between ages in spatial areas.

Source	**df**	**SS**	**MS**	**F**	**P**
Model	5	5741.27	1148.25	88.09	<0.0001
Error	1435	18705.72	13.04		
Total	1440	24446.99	1161.29		

———	———	——————	——————	———	———
1	4	10	6_7	8	11

Area	1	4	6_7	8	10
4	+				
6_7	+	+			
8	+	+	+		
10	+	+	NS	+	
11	+	+	+	+	+

Note: Overlapping lines denote no significant difference, segregated lines denote significant difference. In bottom half of table, NS represents no significant difference, while + denotes significant difference between areas ($\alpha = 0.05$).

Table 4. Basic statistics and habitat areas associated with spatial areas used in analysis. See Table 1 for habitat code abbreviations. Areas 2, 3, 5 and 9 were omitted due to small sample sizes (<35) and 6 and 7 were combined due to similarity in habitat type and area to create a larger sample size. * signifies the primary habitat type in the spatial area.

Area	Habitat(s)	# hauls	# fish	age range	mean age	SD age
1	Rm	19	77	11-25	17.3	3.58
4	Ff*, Fd	55	560	3-39	14.2	3.76
6_7	Ff*, Fd, Ss	31	181	4-25	12.6	3.47
8	Ff, Ss	50	271	3-27	10.9	3.54
10	Fp*, Ff	5	109	6-24	13.3	3.07
11	Ff, Fp, Fm, Ss	23	243	4-25	9.9	3.67

Table 5. Depth ranges and mean depth for each spatial area. Mean age and the percentage of fish at different stages of maturity are listed for each spatial region. Stage 1 is immature, stage 2 is maturing, stage 3 is developed and stage 4 is gravid and ripe. For spatial area 6_7, 17% of the fish were not sampled for maturity stage.

Area	depth range (m)	mean depth	mean age	% stage 1	% stage 2	% stage 3	other
1	1432-2200	1742	17.3	1	21	77	1% stage 4
4	805-1452	994	14.2	48	51	1	
6_7	698-1899	1240	12.6	45	37	1	17% N/A
8	502-1440	853	10.9	76	22	2	
10	1028-1814	1428	13.3	47	39	13	
11	493-1910	1065	9.9	86	13	1	

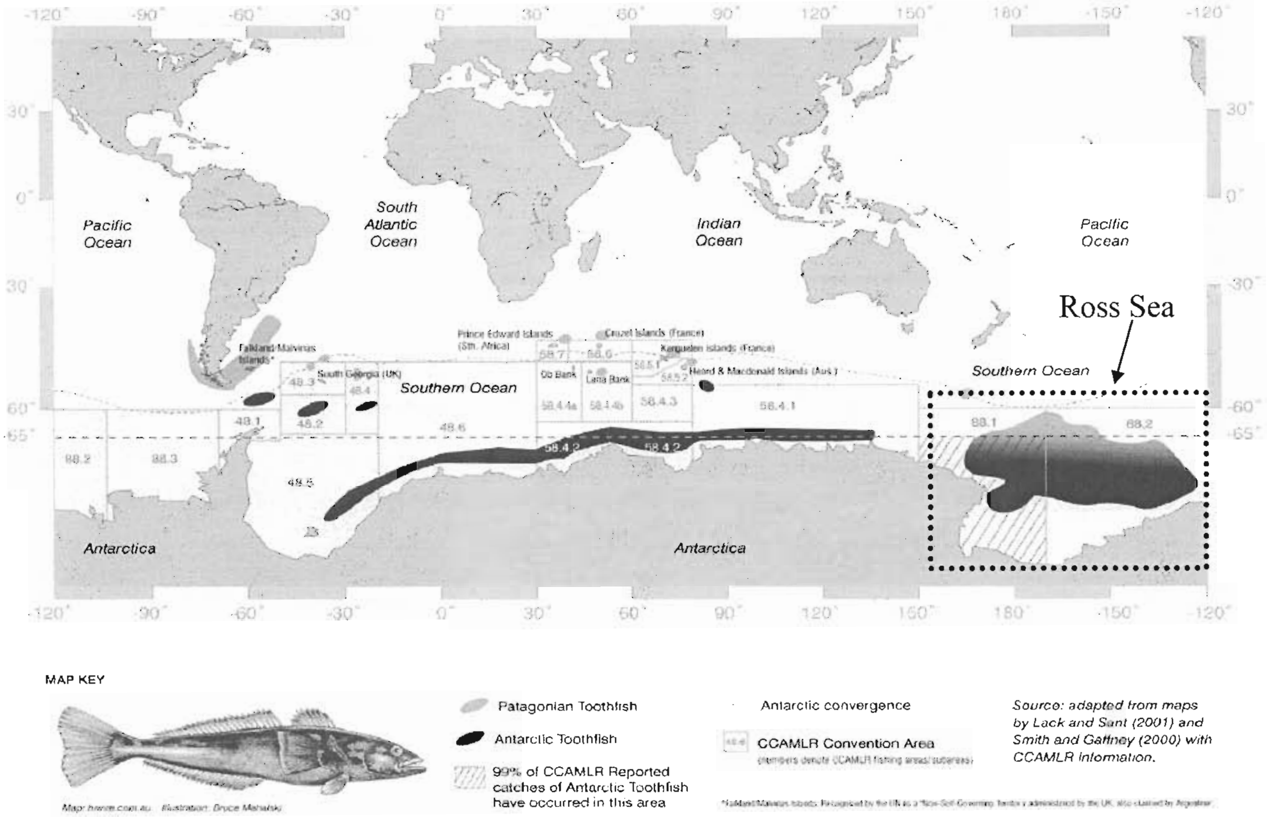

Figure 1. Distribution map of Patagonian and Antarctic toothfishes. The region of interest in this study is the Ross Sea, Antarctica, outlined by the dotted line. From Lack (2001) with permission.

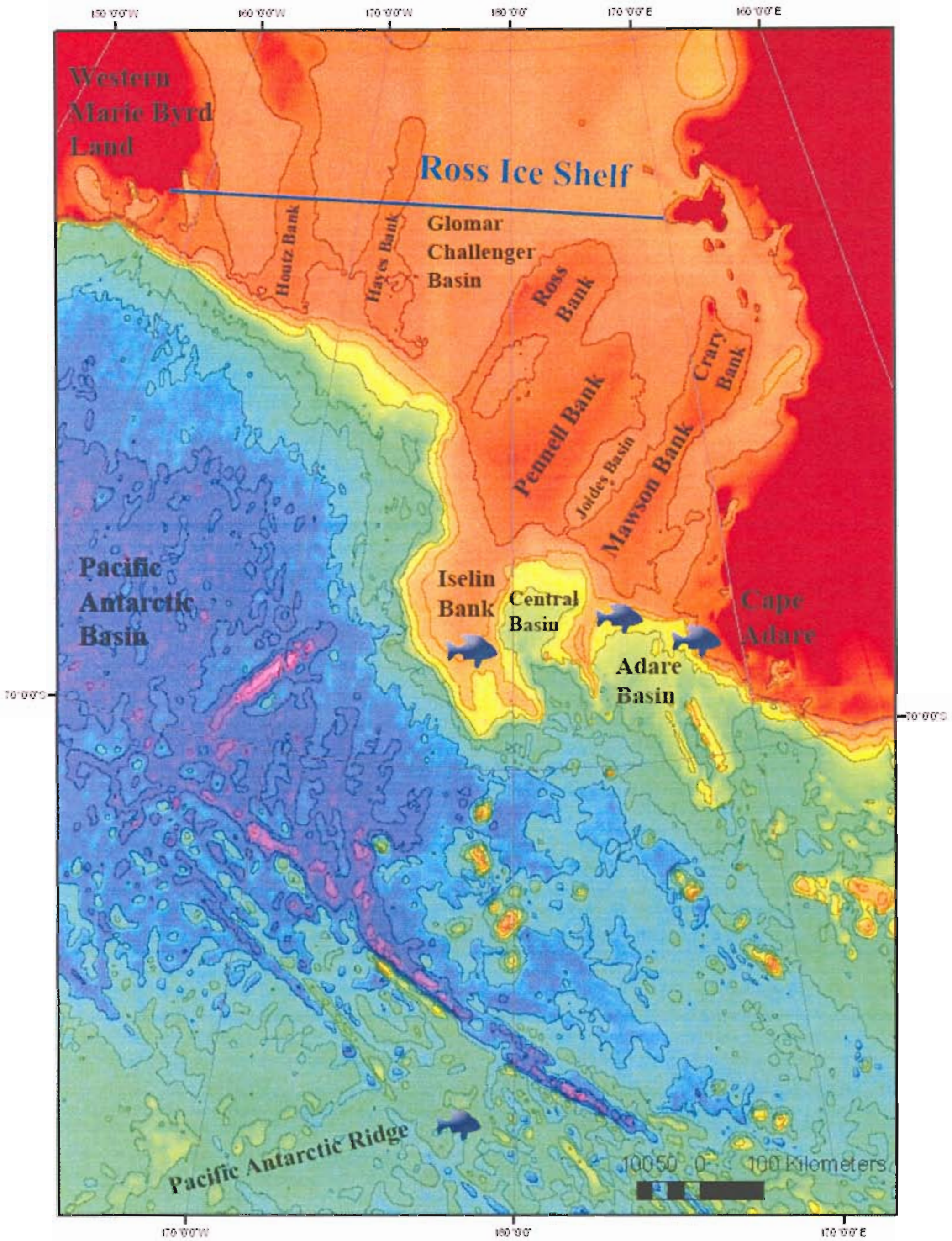

Figure 2. Map demonstrating the major bathymetric and geological features in the Ross Sea. Color scale from brown to blue represents depth; brown corresponds to the continent and shallow continental shelf. With increasing depth, the color contour is yellow, green and blue; dark blue represents the deepest basins. Contour lines (in gray) are in 500 m contours. Fish symbols represent where the majority of samples used in this study were from.

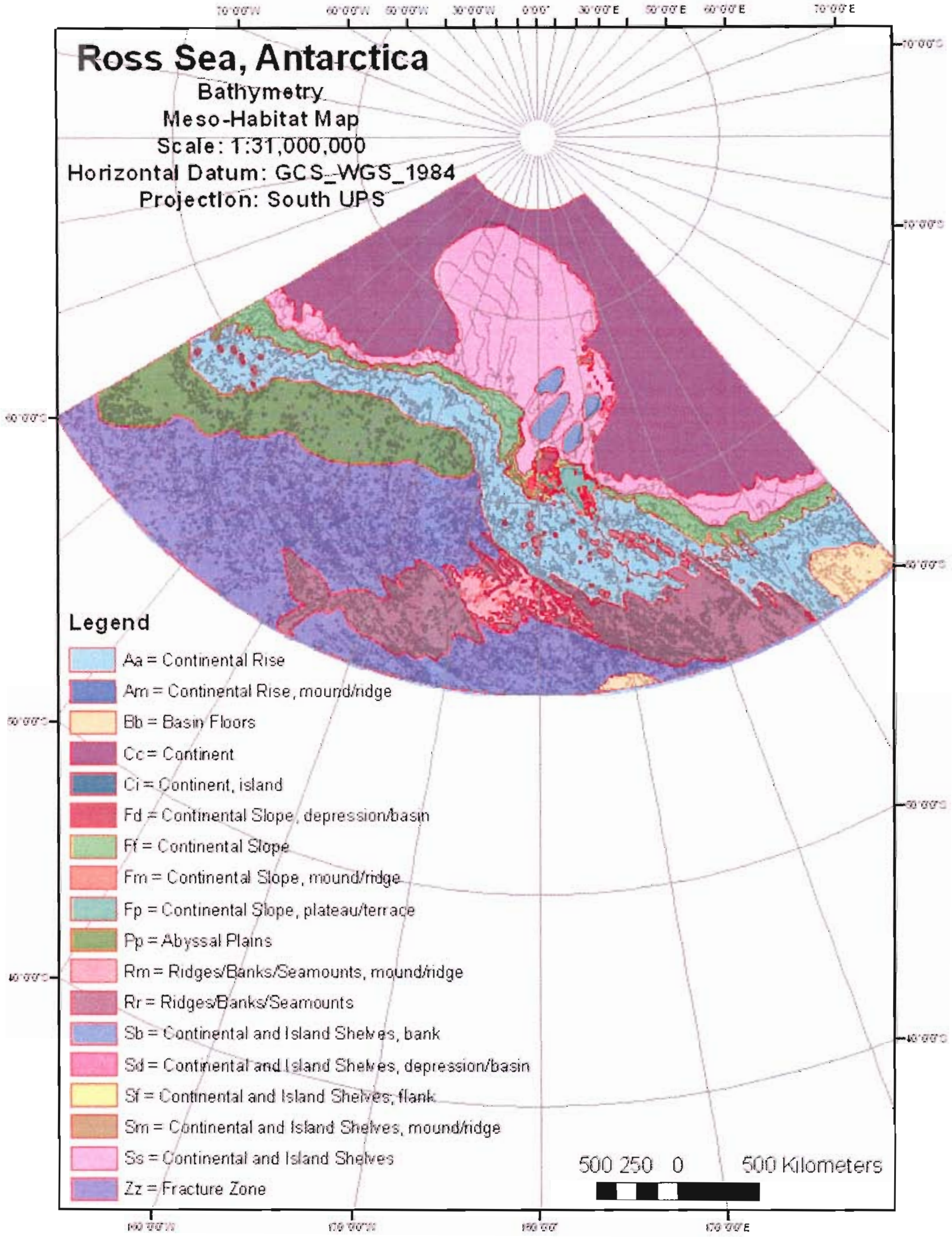

Figure 3. Map showing potential habitat types of the Ross Sea, Antarctica. Habitats were defined at the mega-habitat (tens of meters to hundreds of meters) and meso-habitat scale (meters to tens of meters). Contour lines, in 500-meter intervals, are in gray. The legend shows the colors and code corresponding to each habitat type.

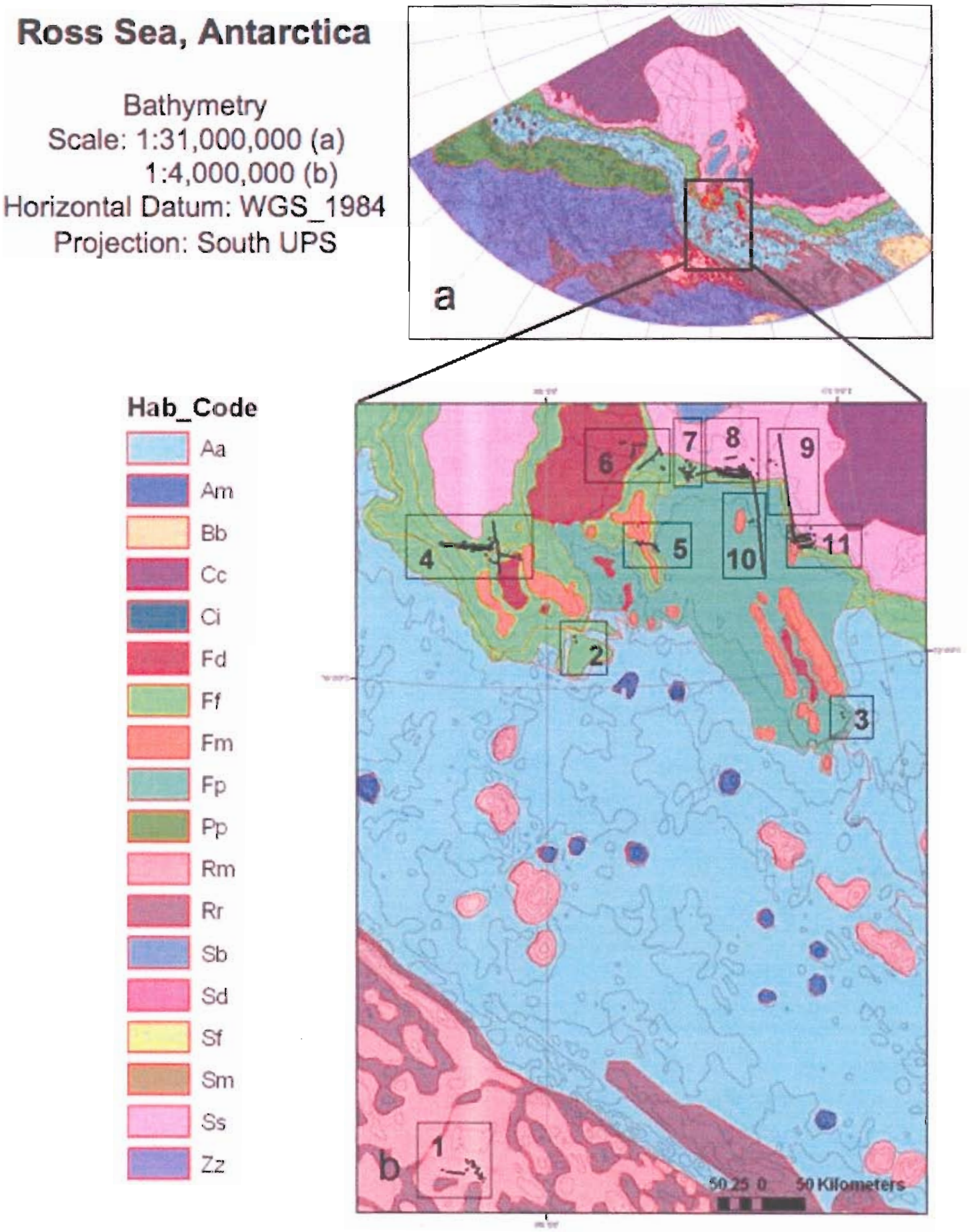

Figure 4. Map showing potential habitat types of the Ross Sea, Antarctica (a) zoomed in on the region where fishing occurred (b). Fishing haul lines are in black. The black boxes around each set of haul lines show designated spatial areas with their corresponding numbers (b).

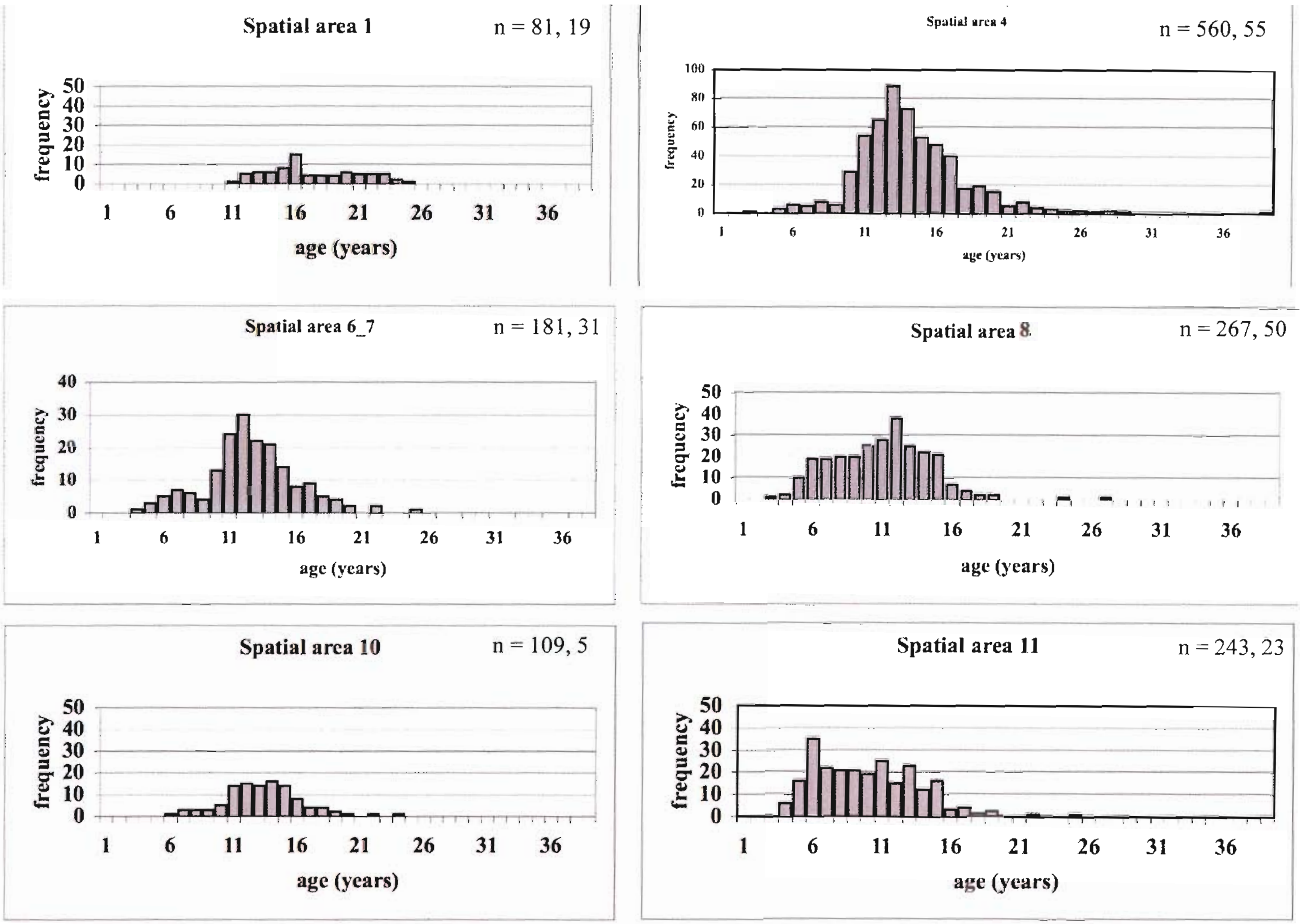

Figure 5. Age frequency histograms of spatial areas. The frequency scale for the spatial area 4 histogram is larger (100 vs. 50) due to the large sample size in this area (5-fold larger than some of the other areas). n refers to the number of fish sampled in each area, followed by the number of haul lines.

APPENDIX: Lead-210 and radium-226 calculations

Isotope dilution analysis

Polonium-210 activity was measured as a proxy for ^{210}Pb because it can be determined with higher precision and accuracy. Polonium-210 is not fully recovered during processing of plating, therefore an isotope dilution analysis was used to solve for this problem by adding a known quantity of a yield tracer ^{208}Po. The ^{210}Po activity was determined using the following equation:

$$A^{210}Po_{unknown} = A^{208}Po_{known} * \left(\frac{Cts^{210}Po}{Cts^{208}Po}\right)$$

where:

$A^{210}Po_{unknown}$ = the unknown ^{210}Po activity from the sample,

$A^{208}Po_{known}$ = the known activity of the ^{208}Po tracer, and

$Cts^{210}Po/Cts^{208}Po$ = is the ratio of the background/blank corrected counts for ^{210}Po and ^{208}Po.

For ^{226}Ra determination the same principle was applied. A known quantity of ^{228}Ra tracer was added to the samples prior to processing and analysis of the refined radium sample using ICPMS provided an atomic count ratio of ^{226}Ra:^{228}Ra, therefore:

$$N^{226}Ra_{unknown} = N^{228}Ra_{known} * R\left(\frac{^{226}Ra}{^{228}Ra}\right)$$

where:

$N^{226}Ra_{unknown}$ = the unknown number of ^{226}Ra atoms,

$N^{228}Ra_{known}$ = the number of 228Ra atoms added from the spike, and

(^{226}Ra/^{228}Ra) = the ratio measured using the ICPMS analysis.

Radium-226 activity was then determined by the following equation:

$$A^{226}Ra = \left(N^{226}Ra\lambda\right)$$

where:

$\lambda = (\ln 2/ t_{1/2})$

$t_{1/2}$ for ^{226}Ra = 1620 years.

Radiometric analysis

^{210}Pb activity determination

Lead-210 activity was calculated by measuring ^{210}Po activity. Sample counts of ^{210}Po and ^{208}Po were corrected for decay during the counting time period in two steps. First, the count-weighted midpoint of the counting interval was determined for each isotope, with the counts before and after this midpoint being equal. This midpoint was calculated using the following equation:

$$t_{mid} = \frac{\ln\left(\left(1 + e^{\left(-\lambda^{2xx}Po * t_{fin}\right)}\right)\right)}{2} * \left(-\lambda^{2xx}Po\right)$$

where:

$\lambda^{2xx}Po$ = the decay constant for ^{208}Po (ln(2)/2.898yr) or ^{210}Po (ln(2)/0.3789yr)

t_{fin} = the time from autodeposition to the end of the counting interval.

t_{mid} was then used to calculate the ^{210}Po and ^{208}Po counts corrected for decay since autodeposition with the following equation:

$$Cts^{208}Po_{ta} = \frac{Cts^{208}Po_m}{\left(e^{\left(\left(-\lambda^{2xx}Po\right)*t_{mid}\right)}\right)}$$

where:

$Cts^{208}Po_{ta}$ = the decay corrected counts to the time of autodeposition

$Cts^{208}Po_m$ = the measured counts

$\lambda^{208}Po$ = the decay constant

$^{208}Po\ t_{mid}$ = the calculated midpoint.

For the calculation of $Cts^{210}Po_{ta}$, values for ^{210}Po were substituted for ^{208}Po values.

Radiometric age determination

Age determination was calculated using the measured ^{210}Pb and ^{226}Ra activities in the following equations. For adult samples where estimated age was greater than the 5 year-old core, radiometric age was calculated using the following equation derived from Smith *et al.* (1991) to compensate for the ingrowth gradient of ^{210}Pb:^{226}Ra in the otolith core.

Age determination was calculated using the corrected measured ^{210}Pb and ^{226}Ra activities in the following equation:

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

where:

t_{age} = total sample age (age of fish plus time since capture)

A^{210}Pb = activity of ^{210}Pb measured from α-spectrometry (dpm/g)

A^{226}Ra = activity of ^{226}Ra measured using ICPMS (dpm/g)

R_0 = the activity ratio of ^{210}Pb:^{226}Ra initially incorporated (0 based on youngest samples)

λ = the decay constant for ^{210}Pb (ln(2)/22.26 years)

T = estimated age of otolith core (5 years)

A radiometric age and age range (from the analytical uncertainty) was calculated for each sample. The analytical uncertainly included error associated with background counts, reagents, spike, calibration, pipetting, α-counting statistics for ^{210}Pb (Wang et al. 1975) and error associated with ICPMS processing for ^{226}Ra. All previous equations and calculations were modeled after Andrews *et al.* (1999a, 1999b; Smith *et al.* 1991) and were executed in an Excel spreadsheet.