ARE MARINE MIGRATIONS OF STRIPED BASS GENETICALLY PRE-DETERMINED? AN INVESTIGATION OF ALBEMARLE SOUND-ROANOAKE RIVER STRIPED BASS MIGRATORY PATTERNS

By Wesley S. Patrick

August 2010

Directors: Roger A. Rulifson and Edmund J. Stellwag

Coastal Resources Management Ph.D. Program

Striped bass, *Morone saxatilis*, is one of the most thoroughly studied anadromous fish species in the United States, with records governing the management of the species dating back to the late 1600s. However, management of this species has been difficult because of the species' anadromous behavior that takes it between fresh and marine waters, crossing numerous geopolitical boundaries. In the 20th century, the fishery experienced two dramatic declines in abundance. Studying the fishery after the declines resulted in major advancements in scientific understanding and management for this species, and striped bass is now an example of a successfully rebuilt fishery, key questions about population dynamics and migration patterns still persist. These unanswered questions reduce confidence in managing the species as a whole, and instead encouraging precautionary measures applied to small geographic areas, such as a natal river.

This dissertation begins with a thorough review of the history of striped bass, including the key scientific findings and management measures instrumental in its recent recovery. Chapter 2 explores how scientists have approached the major challenge in striped bass management: defining the management unit so allocations can be made fairly and sustainably. The array of genetic techniques that have been employed, their limitations, and the populations studied with those techniques, is reviewed. Among the studies reviewed is one suggesting North Carolina striped bass migration may be genetically linked; this

suggestion forms the basis for this dissertation's hypothesis. Answering this question can help resource managers better understand population dynamics, genetic interplay, and migration patterns – important for creating effective management and fair allocation between states. Chapter 3 explores the biotic and abiotic factors that can influence the results of an otolith microchemistry analysis, and Chapter 4 contains the discussion of the findings about the 112 striped bass examined.

With biases accounted for, this dissertation concludes that marine migration was not linked to the genes examined. However, an interesting post-hoc observation can be made: though the behavior was not found to be genetically linked, striped bass in the first year of life proved to be residents, stagers, or sprinters, with different growth rates associated with these behaviors.

ARE MARINE MIGRATIONS OF STRIPED BASS GENETICALLY PRE-DETERMINED? AN INVESTIGATION OF ALBEMARLE SOUND-ROANOAKE RIVER STRIPED BASS MIGRATORY PATTERNS

A Dissertation

Presented To

The Faculty of the Coastal Resources Management PhD Program

East Carolina University

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

By

Wesley S. Patrick

August, 2010

ARE MARINE MIGRATIONS OF STRIPED BASS GENETICALLY PRE-DETERMINED? AN INVESTIGATION OF ALBEMARLE SOUND-ROANOAKE RIVER STRIPED BASS MIGRATORY PATTERNS

by

Wesley S. Patrick

APPROVED BY:

DIRECTOR OF DISSERTATION:_____
Roger A. Rulifson, PhD.

DIRECTOR OF DISSERTATION:_____
Edmund J. Stellwag, PhD.

COMMITTEE MEMBER:_____
Lauriston King, PhD.

COMMITTEE MEMBER:_____
Joseph Luczkovich, PhD.

COMMITTEE MEMBER:_____
J. P. Walsh, PhD.

DIRECTOR OF THE PROGRAM IN COASTAL RESOURCES MANAGEMENT:

_____
Hans Vogelsong, PhD.

DEAN OF THE GRADUATE SCHOOL:

_____
Paul J. Gemperline, PhD.

ACKNOWLEDGEMENTS

I owe thanks to North Carolina Wildlife Resources Commission (NCWRC), North Carolina Division of Marine Fisheries, and North Carolina Sea Grant's Fisheries Resource Grant Program (Project 04-EP-08), who all provided support for this research. Thanks are also due to the many people who assisted me in collecting striped bass during this project, including various NCWRC Enforcement Officers and Hatchery Staff; East Carolina University alumni David Gentry and Anthony VanHoy; and Captain George Beckwith, Jr. of Down East Guide Service, Inc. I am also indebted to John Babaluk (Fisheries and Oceans of Canada) who assisted me in every aspect of the otolith preparation for microchemistry analysis and data interpretation. My committee and dissertation advisors provided helpful editorial comments throughout this process, for which I am very grateful. Finally, I am especially indebted to my wife, Christine, for her many hours supporting this project over the last seven years, and for providing edits and suggestions for the content and structure of this dissertation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

The striped bass, *Morone saxatilis*, is one of the most studied anadromous fish species in the United States, with more than 1,000 peer-reviewed publications and likely several thousand more publications in grey literature. The importance of this species as a natural resource dates back the late 1600s, when some of the first regulations governing fisheries were put in place to protect striped bass from overexploitation.

Throughout these four chapters, I refer to different geographic units of striped bass as stocks, management units, spawning populations or more generally as populations. The use of these terms has a unique meaning in this dissertation; thus, it is important to define these terms. The most confusing of these terms is "stock", which has several different meanings. When used as a verb, it means to supplement or add fish to a system that were either raised under aquaculture conditions or transferred from one water system to another to increase the numbers of fish in the system judged to have a population deficit (also referred to as cross-stocking). However, stock is most often used as noun. When used as a noun, it describes a management of unit of fish that has been identified as needing specific management measures. The delineation is usually based on state/federal boundaries for marine species, watershed boundaries, or in some cases based on population genetics. Thus, the terms stock and management unit are used interchangeably in this dissertation. The term "spawning population" refers to a group of interbreeding fish that spawn in a specific geographic area, which for striped bass is usually a river (e.g., Roanoke River spawning population). Multiple spawning populations may make up a stock or management unit; for example, the Chesapeake Bay stock may have six or more spawning populations. Lastly, the term "population" refers to a group of interbreeding

organisms living in a given area, which I use generically to describe fish that inhabit large geographic regions (e.g., northern versus southern populations of striped bass, Atlantic coast population, etc.). This term can be used without specific reference to the location in which these fish were spawned or even in which they have lived previously. In most instances it simply refers to the location at which the fish was collected.

CHAPTER 1: STRIPED BASS POPULATION RECOVERY ALONG THE ATLANTIC COAST: A REVIEW OF EFFECTIVE MANAGEMENT AND POLICY IMPLEMENTATION

Introduction

The striped bass, *Morone saxatilis*, is a temperate sea bass endemic to the Atlantic coast, ranging from the Tchefuncte River, Louisiana to the Saint Lawrence River, Canada (Pearson 1938). Striped bass is valued commercially and recreationally, with a commercial fishery landing of 3,205 mt (valued at $15 million in ex-vessel landings; NMFS 2009a) and a recreational fishery landing of 11,700 mt in 2008 (NMFS 2009b). The overall economic value of these fisheries, which includes both direct and indirect benefits, is unknown for catches landed in 2008. However, since the commercial fishery alone was valued at $200 million in 1998 for the 3,035 mt landed (Richards and Rago 1999), it is likely that the overall economic impact value of commercial and recreational fisheries combined significantly exceeds that number now.

The commercial fishery for striped bass is restricted to northern populations ranging from North Carolina to Maine (NMFS 2009a), while recreational fisheries occur throughout the native and introduced range of striped bass. The difference in localities of commercial and recreational fisheries is somewhat related to the varying life history traits of striped bass and historical user groups. Striped bass populations south of the Albemarle Sound in North Carolina are considered year round residents of their natal watershed, which are either fresh- or brackish water. Northern populations are considered anadromous, which means they spend the majority of their adult life in marine waters, returning to freshwater only to spawn (Myers 1949). Within the U.S., commercial fisheries for striped bass have traditionally been restricted to marine and sometimes

brackish waters; thus, the mostly freshwater striped bass populations south of the Albemarle Sound in North Carolina have been fished only recreationally.

Northern populations of striped bass, as they regularly occupy brackish and marine waters, have been exploited commercially since the 1600s (Chapoton and Sykes 1961, Holland and Yelverton 1973, Alperin 1986). These northern populations consist mainly of four large stocks, or management units. The largest of these stocks is referred to as the Chesapeake Bay stock, which includes multiple spawning populations from Maryland, Virginia and District of Columbia coastal rivers (Setzler *et al*. 1980, Van Winkle *et al.* 1988). The other three large stocks include the Hudson River (NY), Delaware River (DE), and Roanoke River/Albemarle Sound (NC). Fish from these four management units also form an oceanic migratory stock. Ocean-going individuals are usually large adult striped bass, which are assumed to enter the ocean during the summer to escape high water temperatures and to follow schools of prey (Dorazio *et al*. 1994). Tag recapture studies have shown that individual migratory stocks travel as far as Nova Scotia during the summer and fall months, fueling commercial fisheries in New England, where there are no local spawning populations (Little 1995 in Collette and Klein-MacPhee 2002). A portion of the migratory stock returns to the coast of North Carolina to overwinter, and the remainder returns to the various natal watersheds in the spring to spawn (Boreman and Lewis 1987, Rulifson *et al.* 1987).

The life history and various users of the striped bass makes the management of this species dynamic and complicated, which may help explain why the fishery has experienced two major declines over the last 100 years (Alperin 1986). Yet today, the biomass of the Atlantic coast striped bass is at one of the all-time highs (Figure 1), and many managers credit this to the Striped Bass Conservation Act (SBCA) of 1984 (Richards and Rago 1999). This Chapter

reviews the changes in striped bass abundance over the last 100 years; the management and policy procedures implemented to recover the population; the changing makeup of the fishing sectors; and, an assessment of the various aspects of the SBCA that likely had the greatest positive effect on striped bass recovery.

Management history of the striped bass: 1600s to present

Alperin (1987) noted that striped bass, along with Atlantic cod, were probably the first natural resources in Colonial America to be protected from overexploitation by statutory laws. The first of these laws was enacted in 1639, when the General Court of Massachusetts Bay Colony ordered that these species not be used for fertilizer (Rulifson 1982, Alperin 1987). Other early management measures included laws in 1776 in New York and Massachusetts, which prohibited the sale of striped bass during winter months (Alperin 1987) – a period during which striped bass could be easily caught as they congregated in the lower watersheds of their natal habitats before the spawning season (Richards and Deuel 1987). Despite its recognition as a valuable resource that deserved protection from overfishing, in 1934 striped bass landings had reached an all-time low of 497.5 mt (1.1 million lbs) after a gradual but steady decline (Raney 1952, Koo 1970). It is speculated that the decline was a result of overfishing, dam construction, and pollution (Pearson 1938, Koo 1970).

Although striped bass landings began increasing in 1938, the Council of State Governments – a body of legislators and state officials – recognized that the striped bass fishery, as well as others, needed to be better managed; discussions were initiated for creating an inter-state compact for managing the fishery resources of the Atlantic seaboard (Alperin 1987). While the original intention of the compact was to create an inter-state regulatory body, a majority of

state legislators objected to the creation of a regulatory body that would have the power to supersede the rights of states to establish their own regulations (Alperin 1987). Therefore, the Atlantic States Marine Fisheries Compact, passed by Congress in 1942, created an advisory body with no regulatory authority: the Atlantic States Marine Fisheries Commission (ASMFC). At that time, and now, the ASMFC was meant to help manage fisheries in state waters and nearshore ocean out to three miles from the coastline.

At the first full business meeting of the ASMFC in 1942, the U.S. Fish and Wildlife Service (FWS), in an attempt to improve the dollar yield of striped bass for commercial fishers, suggested that a minimum size limit for striped bass be set at a fork length of 41 cm (16 in) (Alperin 1986). This limit would allow the capture of larger three-year-old fish, and would exclude the one- and two-year olds that were previously allowed within the then established 31–35 cm (10–12 in) fork length size limits, which were the length limits accepted by some state fisheries (Koo 1970, Alperin 1987, Richards and Rago 1999). The ASMFC passed the measure, and the 41-cm fork length minimum size limit was adopted by nearly all the states north of Pennsylvania (see Koo 1970). However, North Carolina, Maryland, Virginia, and Delaware fisheries continued to fish for one- and two-year old fish.

The ASMFC remained a relatively minor fisheries management entity until about 1971-1972, when the Anadromous Fisheries Conservation Act (PL 96-118), enacted in 1965, provide a state-federal cost share program to encourage states to conserve, develop, and enhance of anadromous fish populations (e.g., life history research, habitat restoration, etc.) (Alperin 1987). The program's funds were allocated to the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA Fisheries), and then transferred to the ASMFC, which was charged with administering the funds to the state agencies developing management plans

(Alperin 1987). Prior to the 1970s, federal oversight of striped bass management was exclusively performed by the FWS. However, beginning in 1970, the federal management of striped bass was split equally between FWS and the newly created NOAA Fisheries (Saundry 2008).

The cost-sharing program implemented to create effective interstate management plans came a little late; in 1973, one year after the program was initiated, striped bass landings reached an all-time high in the ASMFC's area, reaching 6,686 mt (Figure 1). A population crash soon followed: by 1976, the commercial landings had declined by 56% (2,966 mt). In 1977, a striped bass workshop was held by the FWS and NOAA-Fisheries to discuss the status of striped bass, and to recommend that the ASMFC develop an Interstate Fisheries Management Plan (IFMP) encompassing populations from North Carolina to Maine (Alperin 1986). Because populations south of North Carolina were not considered to be anadromous, and therefore did not support commercial fisheries, states south of North Carolina were not included in the management plan.

While the striped bass IFMP was being developed, landings continued to fall. In 1979, Congress re-authorized the Anadromous Fisheries Conservation Act (PL 96-118), which included a $1 million appropriation each year for three years to be used in federal-state cost-share studies on striped bass. The emergency studies were authorized to investigate the status of the stocks, factors responsible for stocks' decline, and the economic importance of the recreational and commercial fisheries (Chafee 1980, Deuel 1987). The coordination and implementation of the emergency studies was a joint responsibility of the FWS and NOAA Fisheries, and the agencies created a strategy and action plan. Two groups, the Planning and Coordination Committee and the Project Management Team, were formed to carry out the

strategy and action plan (Deuel 1987). Through 1994, the groups received several more appropriations to continue the cost-share studies (Table 1) (Deuel 1987, NMFS and FWS 2005).

In 1981, as the studies were ongoing, the ASMFC completed the Striped Bass IFMP. The management plan called for: (1) minimum size limits of 36 cm (14 in) in bays and tributaries of the Albemarle Sound, Chesapeake and Delaware bays, and the Hudson River; (2) a minimum size limit of 61 cm (24 in) in the ocean fishery, except for hook and line fishers, who could retain four fish per day of any size, and for net fishers, who could retain 5% of their daily catches between the size of 41 and 61-cm; and (3) recommended spawning ground closures during the spawning season in spring (ASMFC 1981).

In 1982, four of the 12 affected states (New Hampshire, Massachusetts, Connecticut, and Pennsylvania) complied with ASMFC recommendations (Ballou 1987), and by 1984, ten of the twelve states had adopted the size limit recommendations. However, the implementation of spawning ground closures was ignored by many states (Reviewed in USDOI and USDOC 1986, Ballou 1987).

Despite the new management measures, striped bass landings continued to decline, and in 1983 reached yet another all-time low of 775 mt. This trajectory caused many non-governmental organizations to petition the federal government to list the species as endangered under the Endangered Species Act (USDOI and USDOC 1985). NOAA Fisheries determined the findings were not warranted under the guidelines of the ESA, and the petition was denied (see §4 of the ESA for guidelines on petitions). However, the continued decline of striped bass landings led managers to amend the management plan substantially in 1984 (USDOI and USDOC 1984; Ballou 1987).

The amendments of the striped bass IFMP (i.e., 1 and 2) focused on reducing fishing mortality in each state by 55% (in addition to original plan), but allowed states some flexibility in how these reductions would be implemented (Ballou 1987). Amendment 1 stated that alternate management measures had to be quantifiable and reasonably certain of sufficiently reducing fishing mortality, and that the management measures should be reviewed and approved by the ASMFC (although this language would come to be contested in 1985). Amendment 2 introduced a performance measure for the short-term recovery of Chesapeake Bay striped bass, based on Maryland's juvenile index (i.e., 3-year average above 8.0 juveniles per tow was considered recovered).

Concurrent with the approval of these amendments, Congress passed the Atlantic Striped Bass Conservation Act (SBCA) of 1984 (P. L. 98-613). The main purpose of the Act was to temporarily strengthen the ASMFC by giving it indirect power to impose moratoria on those states that did not comply with the IFMP (Ballou 1987), thereby enforcing economic equity between the states during a time of recovery. The Act required the ASMFC to review, on a biannual basis, whether all participating states had adopted and implemented the regulatory measures of the IFMP and its amendments. If the ASMFC found a state to be out of compliance, it was required to notify the Secretaries of Commerce and Interior, who in turn would be required to conduct an independent review within 30 days of notification. If the state was found to be out of compliance, the Secretaries were required to declare a moratorium on the state's striped bass fishery, until that state had taken corrective action (Reviewed in Ballou 1987). The Act also continued appropriations for additional striped bass studies (Table 1).

In its first compliance evaluation in June of 1985, the ASMFC concluded that all twelve states had adopted or would be adopting the regulatory and statutory measures shortly (Ballou

1987). Yet not all efforts were equal: while all states were in compliance with the 55% reduction in fishing mortality (Reviewed in Ballou 1987), the majority of this fishing pressure was reduced by Maryland and Delaware regulations. Ballou (1987) noted that some observers alleged that the ASMFC evaluation "was marred by impropriety and possible illegality" because the effects of many states' regulations could not be proven to reduce fishing mortality by 55%.

Following these findings and discrepancies, the Secretaries of Commerce and Interior in 1985 reviewed the effectiveness of the IFMP, and concluded that the ASMFC needed to strengthen its plan to protect the especially strong 1982 year-class of Chesapeake Bay striped bass, until they had an opportunity to reproduce at least once (Ballou 1987). The ASMFC approved Amendment 3 in October of 1985, which required states to reduce their fishing mortality such that they could protect 95% of the females from that 1982-year class until the young-of-the-year index reached the specified threshold of recovery (i.e., 8.0 YOY per tow) (USDOI and USDOC 1986). Because ~90% of the ocean fishery consisted of Chesapeake Bay striped bass (Berggren and Lieberman 1978, Wirgin *et al.* 1997), this Amendment applied to all twelve states. Age-length data indicated that for 95% of that 1982-year class to spawn at least once, in most cases, fishers would have to exclude all fish below 97 cm (38 in) from the catch (USDOI and USDOC 1990). Therefore, each state had essentially two options: (1) close its fishery or (2) substantially increase minimum size limits to approximately 97 cm (38 in) for inland and marine waters – an increase of 22 inches. Maryland and Delaware chose to close their fisheries, while the other states chose to implement the minimum size limit.

These regulations focused on the Chesapeake Bay stock because it made up 90% of the entire ocean striped bass population, but the Albemarle Sound-Roanoke River (AR) striped bass stock was also in trouble, and showing no signs of recovery. A 1988 amendment 2 to the SBCA

(P.L. 100-589) sought to address the AR stock by requiring the USFWS and NOAA Fisheries to explore the impacts of fishing pressure, water flows, and any other factor responsible for the decline of the AR population. This Amendment also gave the ASMFC the right to declare a state's management scheme out of compliance at any time, rather than after end-of-year reports. The Amendment also required the Secretary of Commerce to regulate the fishery in the economic exclusive zone (EEZ).

The ASMFC plan (Amendment 3) stipulated that fishing rates could not be increased in the Chesapeake Bay until the young-of-the-year index reached the threshold of 8.0 YOY per tow. Recruitment had been poor in 1987 and 1988, and the threshold was not met. However, a large year class in 1989 – 25.4 fish/tow – brought the three-year average above 8.0 for that year, and met the threshold (Richards and Rago 1999). So, despite known low young-of-the-year classes in 1987 and 1988, and recommendations from the ASMFC Scientific and Statistical Committee to delay the reopening of the fishery, the fishery was reopened in 1990 (Richards and Rago 1999).

This reopening was accompanied by new amendments to the management plan to better ensure conservative fishing rates on the Chesapeake Bay stock, and the ASMFC took an adaptive management approach. Target fishing mortality rates (F) were set at $F = 0.25$, which means 33% of the striped bass population can be exploited on an annual basis, and the amendments allowed individual states to decide how to achieve this target rate. The states used a variety of management tools to accomplish this, including: (1) minimum size limits of 71 cm (28 in) along the coast and 46 cm (18 in) in estuarine and freshwater systems; (2) bag limits for recreational fishers, limiting their catch to 1 or 2 fish/day (depending on the state); (3) seasonal closures; and (4) harvest caps or quota systems (Richards and Rago 1999). The amendment also required all

states to monitor their spawning populations and required states with high recreational fishing pressure to estimate recreational catch.

To manage the fishery in accordance with the new size restrictions and exploitation rates, many states made striped bass a recreational-only fishery (USDOI and USDOC 1994, Richards and Rago 1999). States that retained their commercial fisheries found themselves landing only about 20% of what had been landed annually during the period from 1972–1979, regardless of the management strategy they used to meet the 1990 amendment on fishing mortality.

Because of the new amendments, recreational fishing became ever more important in the striped bass fishery. Between 1990 and 1993, 76% of the annual striped bass harvest was allocated to the recreational fisheries (USDOI and USDOC 1994, Richards and Rago 1999). The decline in commercial fishing was marked by a reciprocal increase in striped bass populations: by 1993, recruitment of striped bass was high, and spawning populations in New York, Virginia, Maryland and North Carolina waters seemed to be recovering. In 1995, the Chesapeake Bay stock was declared recovered, and a new amendment to the ASMFC plan was created to manage the fishery. Amendment 5 to the ASMFC plan set fishing mortality rates at F = 0.33 (40%), and allowed states to choose how to meet the target. Two years later, in 1997, the AR stock was declared recovered by the ASMFC. From 1995 to 2003, striped bass populations of the Chesapeake Bay and AR system continued to increase. In 2000, commercial (but not recreational, which continued to increase until 2007) landings began showing signs of leveling off (Figure 1). To respond to the changing fishery, between 1995 and 2003, the ASMFC adopted five addenda under Amendment 5 of the IFMP.

In 2003, the ASFMC approved Amendment 6 to address the management complexity of the fishery, prevent overfishing by setting the F target = 0.30 (0.27 for the Chesapeake Bay and

AR stocks), and allow both the commercial and recreational fisheries to grow (*Federal Register* Volume 68, Number 139, Pages 43074-43075). Amendment 6 also included recommendations for managing the EEZ, suggesting that NOAA-Fisheries should reopen the EEZ by implementing a 71 cm (28 inch) minimum size limit and should allow states to adopt more restrictive rules for fishermen and vessels licensed in their jurisdictions.

Despite that recommendation in 2003 from the ASFMC, NOAA Fisheries decided against opening the EEZ, and federal waters continued to be closed to both recreational and commercial catch. However, in October 2007, President Bush opened recreational-only striped bass and red drum fisheries in the EEZ (Executive Order 13449). The Executive Order also encouraged states to declare striped bass a game fish where appropriate. This attempt to make striped bass a game fish within state waters failed, because none of the states historically supporting commercial fisheries changed the status of striped bass to game fish only. The topic had been debated within states in the past, with no change toward recreational fishing, so the reaction this time was not unexpected (Griffiths 1999).

Today, striped bass landings along the East Coast are the highest that have been recorded, mainly due to recreational landings. However, there are concerns that populations are at unsustainable levels. In the Chesapeake Bay, striped bass have shown signs of decreased health (*i.e.,* reduced growth and condition factors), outbreaks of skin lesions (*i.e., Mycobacterium*), and a change in diet (*i.e.,* declines from preferred prey) (Reviewed in Hartman and Margraf 2003). Within the AR population, similar concerns have been expressed, including the observation of mycobacterium in striped bass there (Stine et al. 2009). In addition, Gentry (2006) documented signs of decreased growth and conditions factors, but changes in diet have so far not been observed (Patrick and Rulifson 2003, Gentry 2006).

Reasons for the recovery

While the SBCA was intended to be a temporary Act to allow the recovery of striped bass, the amendments and reauthorizations of the SBCA have caused it to play a principal role in striped bass management for the last 25 years. The SBCA is regarded by the public, fishery managers, and politicians as a prime example of effective policy implementation and fishery management (Ballou 1987, Richards and Rago 1999). The SBCA's framework was the foundation for the Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA) of 1993 (P. L. 103-206), which gave the ASMFC management authority for 21 other important coastal migratory fishes. However, 16 years later, 14 of those 21 fisheries are considered overfished, are undergoing overfishing, or have unknown status (ASMFC 2007), suggesting that the management authority conferred in the SBCA and the ACFCMA might not be the key factor, or the only key factor, in fishery recovery.

Certainly, the authority conferred on the ASMFC through the SBCA was very important in the recovery of a species that crosses many state boundaries. As described earlier, regulations on the harvest striped bass existed before the SBCA was passed in 1984, but they were inadequate to effectively protect against overfishing. In fact, the first minimum size limit for striped bass was created to increase the dollar value of striped bass for commercial fishermen. When striped bass landings began to decline, the time came to increase the minimum size limits to reverse overfishing. However, the migratory behavior of striped bass caused problems between the states: because the species traverses state boundaries, no one state had an incentive to increase its minimum size limits if there was no guarantee of other states doing the same.

In 1981, the ASMFC created an interstate striped bass fishery management plan to help states cooperatively recover the fishery. Many states did adopt the management plan the ASMFC created; however, the specific restrictions were minimal and therefore required minimal sacrifice. It is reasonable to assume that the ASMFC states would not have adopted Amendments 2 and 3 to the IFMP, which essentially closed the Chesapeake Bay fishery, if the SBCA had not been passed, giving authority to the ASMFC to enforce state compliance with the IFMP.

One example of the effectiveness of the ASFMC's new enforcement authority was the 1986 non-compliance findings for the District of Columbia and New Jersey. In October 1986, in the ASMFC's second compliance evaluation, both D.C. and New Jersey were found to be out of compliance with the IFMP. As required under the SBCA, the ASFMC forwarded its findings to the Secretaries of Commerce and Interior (Ballou 1987). In February 1987, the Secretaries determined that New Jersey and D.C. were out of compliance with the IFMP and agreed a moratorium on the fishery could be enforced. However, the Secretaries agreed that since the states were making an effort to meet the requirements of the management plan, the moratorium could be delayed several months, until April (Ballou 1987). By the end of March, both jurisdictions had modified their regulations and were found to be in compliance by the ASMFC, and narrowly avoided the moratorium. The ASFMC and the Secretaries of Commerce and Interior had shown that their new authority could and would be applied when appropriate, and it compelled action on the part of the ASFMC member states.

Increased state or federal agency regulatory authority alone does not necessarily lead to the recovery of a population; good management measures are also vitally important. The Emergency Striped Bass Study (ESBS) appropriated under the 1979 amendment to the

Anadromous Fishery Conservation Act allowed for the collection of much of the data needed for making sound management measures. The ESBS was given $1.0 million to sponsor research to determine the status of the fishery and the possible causes in the decline of the stock – which were not limited to over-exploitation of the stock by fishermen. These funds were distributed through a cost-share arrangement with states. Research conducted under the direction of the Emergency Striped Bass Study included projects such as status surveys (e.g., juvenile and spawning stock surveys), reduced or unfavorable water quality from anthropogenic sources (e.g., agricultural runoff, toxins, stream flow, etc.), predator-prey studies, and determining if unfavorable natural occurrences was a factor in the decline of striped bass.

Several studied funded by the ESBS were useful in identifying sources for striped bass population declines. For example, Rulifson and Manooch (1990) found the decline in Roanoke River striped bass (North Carolina) was the result of improper flow regimes created by an upstream hydropower plant. Coutant and Benson (1990) found the habitat suitability in the upper basin of the Chesapeake Bay declined significantly from 1962 to 1987, as did juvenile abundance indexes, with the decline in habitat suitability linked to temperature-oxygen depletion zones within the Chesapeake Bay.

One of the most important studies made possible by the ESBS was tag-recapture studies to determine mortality rates, growth-age data, and maturation schedules (Berlinskey *et al.* 1995). Without an accurate assessment of mortality rates, growth-age data, and maturation schedules, Amendment 3 of the management plan (which required 95% of the striped bass in the 1982-year class to spawn at least once) could not have been developed and defended. The SBCA reduced the financial burden of conducting research on states significantly: initially, the federal

government offered a 50% cost-share on research projects, and soon enlarged this to a 90% federal cost-share in 1985.

As noted above, the ACFCMA was modeled on the SBCA, and granted the ASMFC regulatory power over an additional 21 species. However, compared to the SBCA, the ACFCMA suffered from inadequate funding of scientific research on those 21 species. The SBCA funded only about $1 million a year for striped bass research, and most of the time the state only needed to provide 10% of the research budget. The ACFCMA, on the other hand, had $5 million a year for 21 species (an average of less than $250,000 per species), and required that states cover 50% of the research bill. Without essential information about mortality rates, growth-age data, and maturation schedules for each species, formulating an effective rebuilding and recovery plan can be difficult (see Rosenberg *et al.* 2006). The Chesapeake Bay and Albemarle Sound-Roanoke River striped bass stocks were officially recovered within 15 years of the SBCA, while after 15 years of the ACFCMA most of the 21 species have an unknown status due to a lack of life history data and/or funding.

In conclusion, the Emergency Striped Bass Study and the Striped Bass Conservation Act provided funding and authority to create and enforce effective fisheries management for the recovery of depleted striped bass populations. Without either of these factors in adequate supply, recovery of the striped bass population was questionable. The Atlantic Coast Fisheries Cooperative Management Act enlarged the Atlantic States Marine Fisheries Commission's authority to the additional 21 species in its jurisdiction, but the Act was not accompanied by the same level of funding. The appropriate level of funding to study a species is not necessarily obvious, but the most significant difference between the successful striped bass recovery and the

failed recovery of other ASMFC species appears to be the large discrepancy in funding for life history research.

Literature Cited

Alperin, I. M. 1986. Management of migratory Atlantic coast striped bass: an historical perspective, 1938-1986. Fisheries 12: 2-3.

ASMFC (Atlantic States Marine Fisheries Commission). 1981. Interstate fisheries management plan for the striped bass. ASMFC, Fisheries Management Report 1, Washington, D. C.

ASMFC. 2007. Atlantic States Marine Fisheries Commission Stock Status Overview. ASMFC, Washington, D.C.

Ballou, R. 1987. The Atlantic striped bass conservation act: reauthorized and put to the test. Territorial Sea: Legal Defense in the Management of Interjurisdictional Resources 7: 1-12.

Berggren, T. J., and J. T. Lieberman. 1978. Relative contribution of Hudson, Chesapeake and Roanoke striped bass, *Morone saxatilis*, stocks to the Atlantic coast fishery. Fishery Bulletin 76: 335-345.

Berlinsky, D. L., M. C. Fabrizio, J. F. O'Brien, and J. L. Specker. 1995. Age at maturity estimates for Atlantic coast female striped bass. Transactions of the American Fisheries Society 124: 207-215.

Boreman, J. and R. Rhett Lewis. 1987. Atlantic coastal migration of striped bass. American Fisheries Society Symposium 1: 331-339.

Boreman, J. and H. M. Austin. 1985. Production and harvest of anadromous striped bass stocks along the Atlantic coast. Transactions of the American Fisheries Society 114: 3-7.

Chafee, J. H. 1980. The outlook for striped bass recovery. Pages 5 – 7 in H. Clepper (editor). Proceedings of the Fifth Annual Marine Recreational Fisheries Symposium. Sport Fishing Institute, Washington, D. C.

Chapoton, R. B. and J. E. Sykes. 1961. Atlantic Coast migration of large striped bass as evidenced by fisheries and tagging. Transactions of the American Fisheries Society 90: 13-20.

Collette, B. B. and G. Klein-MacPhee (eds). 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C. Pages 377 – 389.

Coutant, C. C. and D. L. Benson. 1990. Summer habitat suitability for striped bass in Chesapeake Bay – reflections on a population decline. Transactions of the American Fisheries Society 119: 757-778.

Deuel, D. 1987. The role of the National Marine Fisheries Service in the Emergency Striped Bass Research Study. Fisheries 12: 7-8

Dorazio, R. M., K. A. Hattala, C. B. McCollough and J. E. Skjeveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Transactions of the American Fisheries Society 123: 950-963.

Gentry, D. E. 2006. Evaluation of striped bass, *Morone saxatilis*, condition in coastal North Carolina using physiological and condition indices. Master's Thesis, Department of Biology, East Carolina University, Greenville, NC. 105 p.

Griffiths, D. C. 1999. The estuary's gift: an Atlantic Coast cultural biography. The Pennsylvania State University Press, University Park, PA.

Hartman, K. J., and F. J. Margraf. 2003. US Atlantic coast striped bass: issues with a recovered population. Fisheries Management and Ecology 10: 309-312.

Holland, B. F. and G. F. Yelveton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sport Fisheries. Morehead City, North Carolina. 156 p.

Koo, T. S. Y. 1970. The striped bass fishery in the Atlantic states. Chesapeake Science 11: 73-93.

Myers, G.S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia: 89-97.

National Marine Fisheries Service (NMFS). 2009a. Annual commercial landing statistics. National Marine Fisheries Service, Office of Science and Technology, Silver Spring, MD. Web link: http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html.

NMFS. 2009b. Recreational fisheries statistics query. National Marine Fisheries Service, Office of Science and Technology, Silver Spring, MD. Web link: http://www.st.nmfs.noaa.gov/st1/recreational/queries/index.html.

NMFS and U.S. Fish and Wildlife Service (FWS). 2005. Atlantic striped bass studies 2005 biennial report to Congress, submitted to the: Committee on Resources of the United States House of Representatives and Committee on Congress, Science and Transportation of the United States Senate. Prepared by the National Marine Fisheries Service and U.S. Fish and Wildlife Service, Washington, D.C. 31 pp.

Patrick, W. S., and R. A. Rulifson. 2003. The seasonal food habits of striped bass in the Albemarle Sound, North Carolina. Final Report to North Carolina Sea Grant, Project Number 00-EP14.

Pearson, J. C. 1938. The life history of the striped bass, or rockfish, *Roccus saxatilis* (Walbaum). U. S. Bureau of Fisheries Bulletin 49: 825-860.

Raney, E. C. 1952. The life history of the striped bass, *Roccus saxatilis* (Walbaum). Bulletin of the Bingham Oceanographic Collection, Yale University 14: 5-97.

Richards, R. A. and D. G. Deuel. 1987. Atlantic striped bass: stock status and the recreational fishery. U. S. National Marine Fisheries Service Marine Fisheries Review 49: 58-66.

Richards, R. A. and P. J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. North American Journal of Fisheries Management 19: 356-375.

Rosenberg, A. A., J. H. Swasey, and M. Bowman. 2006. Rebuilding US fisheries: progress and problems. Frontiers in Ecology and the Environment 4: 303-308.

Rulifson, R. A. and C. S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10: 397-307.

Rulifson, R. A., S. A. McKenna, and M. L. Gallagher. 1987. Tagging studies of striped bass and river herring in upper Bay of Fundy, Nova Scotia. Completion Report for Project AFC-28-1 for North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, NC. 175 pp.

Peter Saundry (Lead Author); J. Emmett Duffy (Topic Editor);. 2008. "National Marine Fisheries Service, United States." In: Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment). [First published in the Encyclopedia of Earth January 2, 2007; Last revised April 17, 2008; Retrieved July 17, 2010]

Setzler, E. M., et al. 1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). NOAA Technical Report NMFS Circular 433, Washington, D.C. 69 p.

Stine, C. B., J. M. Jacobs, M. R. Rhodes, A. Overton, M. Fast, and A. M. Baya. 2009. Expanded range and new host species of *Mycobaterium shottsii* and *M. pseuodshottsii*. Journal of Aquatic Animal Health 21: 179-183.

USDOI (U. S. Department of Interior) and USDOC (U. S. Department of Commerce). Emergency striped bass research study. Report for 1982 and 1983. USDOC, National Marine Fisheries Service, Silver Spring, MD.

USDOI and USDOC. 1985. Emergency striped bass research study. Report for 1984. USDOC, National Marine Fisheries Service, Silver Spring, MD.

USDOI and USDOC. 1986. Emergency striped bass research study. Report for 1985. USDOC, National Marine Fisheries Service, Silver Spring, MD.

USDOI and USDOC. 1990. Emergency striped bass research study. Report for 1989. USDOC, National Marine Fisheries Service, Silver Spring, MD.

USDOI and USDOC. 1994. Emergency striped bass research study. Report for 1994. USDOC, National Marine Fisheries Service, Silver Spring, MD.

Van Winkle, W., K. D. Kumar, and D. S. Vaughan. 1988. Relative contributions of the Hudson River and Chesapeake Bay striped bass stocks to the Atlantic coastal population. Pages 255-266 in L. W. Barnthouse, R. J. Klauda, D. S. Vaughan, and R. L. Kendall, editors. Science, law, and Hudson River power plants: a case study in environmental impact assessment. American Fisheries Society, Monograph 4, Bethesda, Maryland.

Wirgin, I. I., J. R. Waldman, L. Maceda, J. Stabile, and V. J. Vecchio. 1997. Mixed stock-analysis of Atlantic coast striped bass (*Morone saxatilis*) using nuclear DNA and mitochondrial DNA markers. Canadian Journal of Fisheries and Aquatic Sciences 54: 2814-2826.

Table 1. A summary of the appropriations provided in the AFCA, AFCA Emergency Striped Bass Study, SBCA, and ACFCMA, and their adjusted values in 2008 dollars. Data for all years was not available, thus totals summarized here are for comparison purposes only to demonstrate the disparity between funding sources for striped bass compared to other species managed by the Atlantic States Marine Fisheries Commission.

	Appropriations in millions of dollar, inflation adjusted to 2008 dollars					
Year	Anadromous Fish Conservation Act (AFCA)	AFCA - Emergency Striped Bass Study	Striped Bass Conservation Act (SBCA)	Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA)	Total Available for Striped Bass	Total available for 21 species managed under ACFCMA
1984	$15.35	$2.05			$17.40	
1985	$12.84	$1.98			$14.82	
1986			$0.39		$0.39	
1987	$14.41		$0.37		$14.78	
1988	$14.20		$0.36		$14.56	
1989	$13.89		$0.34		$15.95	
1990	$13.18	$1.72	$0.33		$15.13	
1991	$12.49	$1.63	$0.31		$14.37	
1992	$12.13	$1.56	$0.30		$13.95	
1993	$11.78	$1.52	$0.29		$13.54	
1994	$11.48	$1.47	$0.29	$4.30	$13.20	$4.30
1995	$11.20	$1.43		$7.00	$11.20	$7.00
1996				$9.51		$9.51
1997	$5.35			$9.35	$5.35	$9.35
1998	$5.59		$1.38	$9.21	$6.97	$9.21
1999	$5.44		$1.34	$8.96	$6.79	$8.96
2000	$5.26		$1.30	$8.67	$6.56	$8.67
2001			$1.52	$12.19	$1.52	$12.19
2002			$1.49	$11.90	$1.49	$11.90
2003	$5.55		$1.46	$11.68	$7.01	$11.68
2004	$5.37			$11.31	$5.37	$11.31
2005	$5.47			$10.94	$5.47	$10.94
2006	$5.34				$5.34	
Totals	$186.32	$13.36	$11.47	$115.02	$211.16	$115.02

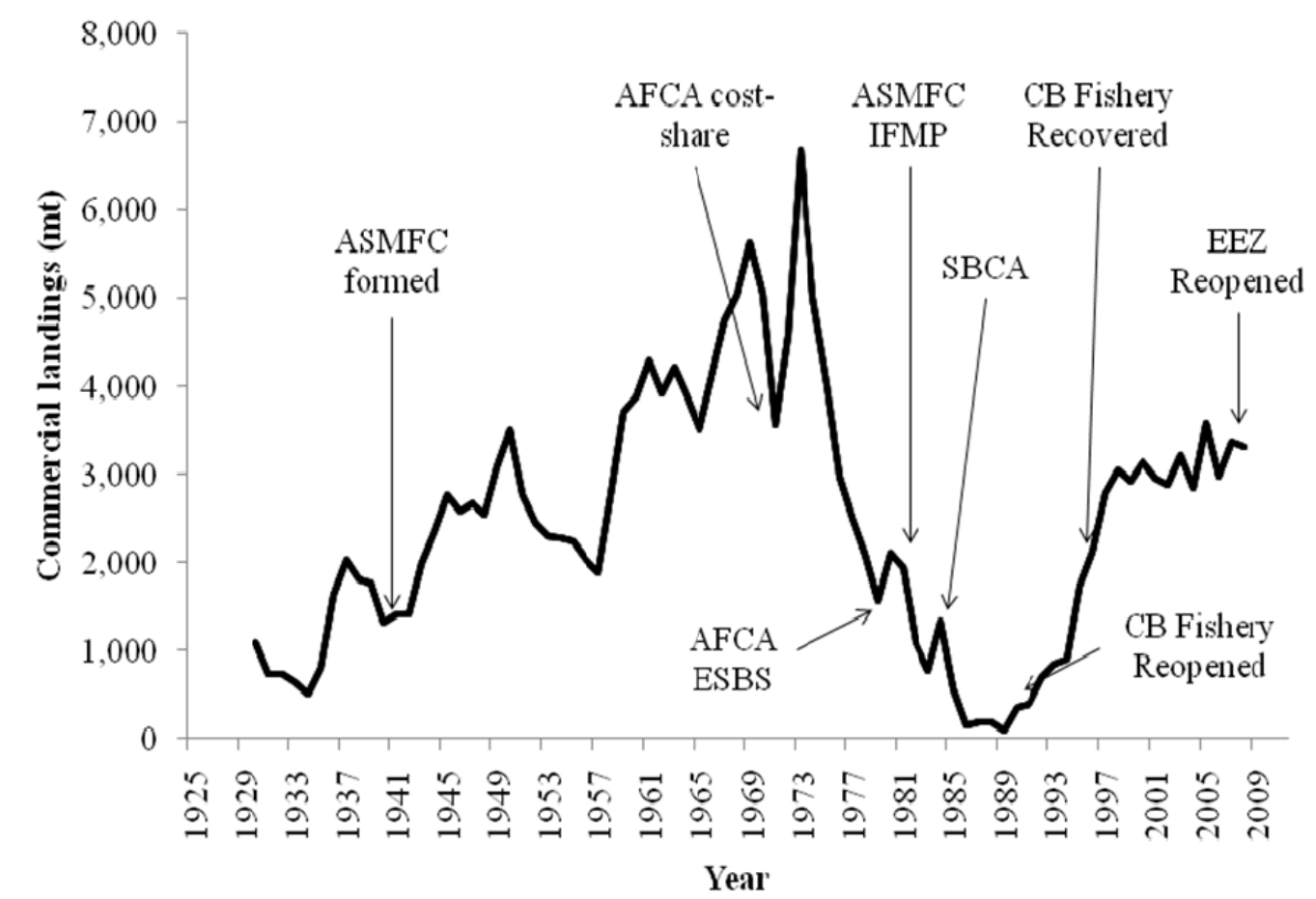


Figure 1. Commercial landings of striped bass from 1930 to 2008, with significant management actions highlighted.

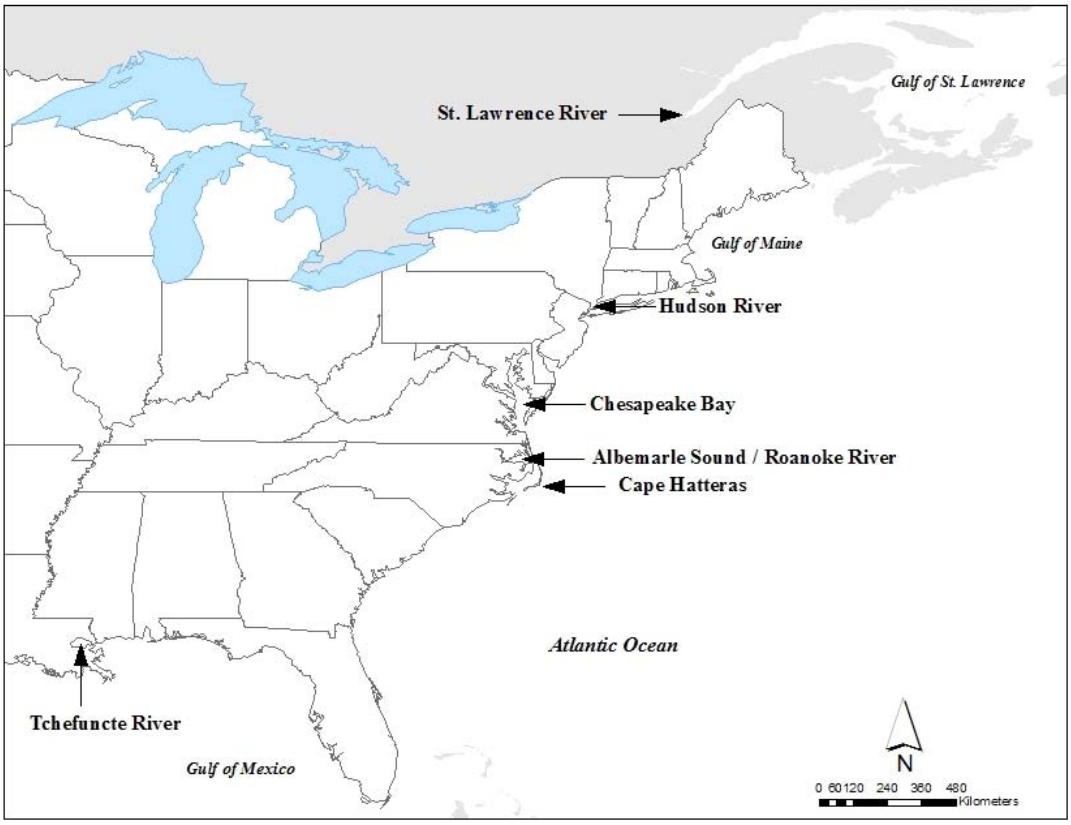


Figure 2. The geographic range of striped bass, spanning from the Tchefuncte River, Louisiana to the St. Lawrence River, Canada. Major spawning populations of the Albemarle Sound, Chesapeake Bay, and Hudson River are also noted. Cape Hatteras is referenced, to note the dividing line between southern and northern populations of striped bass.

CHAPTER 2: IDENTIFYING CONSERVATION UNITS OF STRIPED BASS USING THE ADAPTIVE APPROACH

Introduction

A fundamental problem that has challenged fishery managers for many years is how to appropriately assess the status of a fishery that consists of multiple stocks (i.e., management or conservation units) of a species, and also how to protect the less abundant of these stocks from becoming overfished (Ruzzante *et al*. 1999, Waples *et al*. 2008). This is especially true for fishery managers of striped bass (*Morone saxatilis*), who have been studying this problem since the 1930s (Waldman *et al*. 1988). In general, assessing the status of a stock involves four steps: 1) identifying the range of the stock being assessed; 2) fitting a model to the data; 3) using results of the model to make inferences about the stock (e.g., responses to fishing pressures); and 4) evaluating alternative management actions to determine if they satisfy the management goal (Waples *et al*. 2008). This paper focuses on step one: identifying the appropriate range of stock being assessed.

To identify the range of the stock or conservation unit, fishery scientists traditionally have relied on physical tag-recapture methods (e.g., anchor tags, coded wire tags, ultrasonic transmitters, etc.). However, these traditional methods are susceptible to biases resulting from tagging location, size of fish tagged, and sampling of tagged fish (Pollock *et al*. 2001, 2002; Hearn *et al*. 2003). The use of innate tags (e.g., genetic and phenotypic tags), which rely on character traits specific for a defined population, are not subject to tag-recapture biases and have been used effectively by fishery scientists to identify conservation units of a species (see Begg *et al*. 1999 and Booke 1999). The ability to identify innate characteristics relies on the "stock

concept." The stock concept predicts that species can be subdivided into local geographical populations called stocks (or conservation units), and that these stocks are genetically distinct due to genetic drift (changes within the gene pool that occurs by chance), mutation, and natural selection (MacLean and Evans 1981). This concept is contingent on the definition of a stock as a population that has been sufficiently isolated from other populations for genetic differentiation to occur. Total isolation from other populations is not a prequiste for genetic differentiation to occur, rather only during periods of reproduction (Palumbi 1994, Bilton *et al*. 2002, Cowen *et al*. 2006). Typically for striped bass and other anadromous species that exhibit signs of homing behavior, conservation unit studies sample spawning populations, because it is assumed that this stage in the life history represents a period when the population is geographically isolated from other populations with which it may mix during other portions of its life history (e.g., nursery grounds, estuaries, and marine environments) (Brown *et al*. 1996, Tessier *et al*. 1997, Grunwald *et al*. 2008).

Waldman *et al*. (1988) reviewed approaches for discriminating among conservation units of striped bass, including using phenotypic and genetic markers. Though their analysis lacked an overall description of the striped bass stock structure across its range, the majority of studies they reviewed concluded that striped bass exhibited some of the lowest levels of genetic diversity observed among anadromous fish populations. Waldman *et al*. (1988) suggested that the use of new methods such as nuclear deoxyribonucleic acid (nDNA) microsatellites may shed new light on the diversity of striped bass and provide a method for further discriminating among stocks. Since then, researchers have investigated additional genetic markers (nDNA restriction fragment length polymorphisms (nDNA RFLPs), random amplified polymorphic DNA (RAPD), and sequencing of mitochondrial DNA (mtDNA)), and have further defined the genetic diversity of

striped bass (Table 1). Garber and Sullivan (2006) addressed a portion of these studies in their review of *Morone* biology and potential avenues for genetically improving the selective breeding of hybrid striped bass. They concluded that enough significant genetic variation occurs within and among sub-populations to make selective breeding feasible.

A missing link in the review of striped bass population genetics is clear guidance on whether managers should conserve the genetic diversity of spawning populations on a river-by-river, drainage, or regional basis. Waldman *et al*. (1997) proposed that the population genetic structure could be deduced from a comprehensive analysis of all available stock information previously known.

This chapter will review the best available scientific information – current population genetics literature, including behavior and physiological studies – to suggest how best to define conservation units for striped bass. By doing so, I hope to improve the prospects of striped bass stock assessments and to address issues related to the management of the species for commercial and recreational fisheries.

Identifying conservation units to promote genetic diversity

An ongoing challenge for fishery managers has been the identification of conservation units as a means to assist in the development of management strategies designed to promote the preservation of genetic diversity (Booke 1999). A first step in addressing this challenge is to identify the appropriate methods for characterizing the level of genetic diversity and establishing whether populations can be distinguished from one another genetically. Waples *et al*. (2008) divided this issue into three categories: (1) biological realities, or how to define populations (i.e., ecological vs. evolutionary measures of migration); (2) uncertainty inherent in available

methodologies; and (3) institutional issues, because limited jurisdictional authority can result in a mismatch between management units and biological units.

The most highly contentious of these three issues is uncertainty inherent in available methodologies (see Mortiz 1994, Pennock and Dimmick 1997, Bowen 1998, Waples 1998, Bowen 1999, Dimmick *et al*. 1999, Karl and Bowen 1999, Paetkau 1999, de Guia and Saitoh 2007). Fraser and Bernatchez (2001) note that much of the contention involves the role neutral genetic markers play in determining conservation units, versus the role of other characteristics, like adaptive traits. Fraser and Bernatchez *et al*. (2001) offered an alternative adaptive method incorporating the major themes of the debated techniques. Their adaptive approach has three steps for delineating conservation units: 1) genetic data are not required because other information like behavior, physiological, and phenotypic data can be used; 2) when genetic data are available, there must be significant mutations in genetic data (not to be confused with statistical significance (Waples 1998); and 3) subtle differences (such as differences in frequency distributions of genotypes) can be used to define conservation sub-units or management units within the conservation unit.

My methodology follows the path laid by Fraser and Bernatchez *et al*. (2001), with one modification. While they suggested that phenotypic data are useful in delineating conservation units, the approach here will not include morphological or meristic traits. Phenotypic differences can be linked to genetic traits; however, several studies have shown that meristic (Lindsey and Harrington 1972, Ali and Lindsey 1974, Blaxter 1984, Swain and Lindsey 1986) and morphometric (Meyer 1987, Currens *et al*. 1989) traits are plastic and capable of changing within one generation. Therefore, my methodology will incorporate the advice of Booke (1999) who suggested that researchers consider only stock discrimination markers that are inherited in a

reliable fashion. Similarly, my analysis will not evaluate phospholipid profiles, because variations among populations are generally correlated with diet, temperature, salinity, and growth factors, and are therefore not inherited in a reliable fashion (Morris and Culkin 1989, Bergey *et al*. 2003).

Striped bass genetic studies: 1987 to present

This review of striped bass population genetics only includes studies conducted after 1987, which is when mtDNA restriction fragment length variants (RFLVs) first demonstrated relatively high levels of genetic diversity in striped bass stocks (Chapman 1987). Prior to this, cytogenetics, protein electrophoresis, isoelectric focusing, and immunogenetics studies concluded that striped bass were either monomorphic or exhibited very low levels of diversity (Waldman *et al*. 1988).

Mitochondrial DNA restriction fragment length variants (MtDNA RFLVs)

MtDNA RFLVs identify differences in the size of the mtDNA genome due to a duplication of 16 to 100 base pair regions (Wirgin *et al*. 1989). The methodology found five common length variants in striped bass, and the frequency of these length variants differ among sub-populations. However, the use of mtDNA RFLVs to identify inheritable markers has been questioned and debated in the literature. Chapman (1990) noted the results of his study using mtDNA RFLVs should be "viewed as conservative and provisional" due in part to how size polymorphisms are inherited. Chapman found evidence that some length variants in striped bass were not passed from parent to offspring, and therefore were not inherited in a reliable fashion. Stellwag *et al*. (1994) also questioned the utility of RFLVs, as his study on Roanoke River striped bass showed there was no correlation between haplotypes identified using mtDNA RFLV

and mtDNA restriction fragment length polymorphisms (RFLPs) markers (described in next section). The conclusions of Stellwag *et al*. (1994) were later debated in the scientific literature by Waldman and Wirgin (1995) and Stellwag and Rulifson (1995). Waldman and Wirgin (1995) posited that mtDNA RFLVs are stable enough to provide useful genetic markers for stock discrimination, while Stellwag and Rulifson (1995) provided several references showing that mtDNA RFLV's are not stably inherited. This debate was never resolved. Use of mtDNA RFLVs continues today, but often without reference to Chapman's caveat or the unresolved debate.

MtDNA, nDNA and Polymerase Chain Reaction (PCR) restriction fragment length polymorphisms (RFLPs)

As opposed to mtDNA RFLVs, which identify mtDNA-related genome length variation that results from a process of replication slippage, mtDNA RFLPs identify changes in the DNA sequence usually as a result of nucleotide substitutions, the most common form of mutation. MtDNA RFLP methodologies were widely considered useless for discriminating among sub-populations of striped bass, as a number of studies using different restriction enzymes found a paucity of RFLPs in comparison of striped bass sampled from the major historical spawning populations (Waldman *et al*. 1998). However, as noted above, Stellwag *et al*. (1994) used twelve restriction enzymes, two of which had never been used before, to identify six unique haplotypes within the spawning population of Roanoke River striped bass. Other mtDNA studies have also shown marginal success with mtDNA RFLPs when comparing Gulf of Mexico to Atlantic striped bass (Wirgin and Maceda 1991). However, with the rise of alternate genetic techniques, including nDNA microsatellites, mtDNA RFLPs have not been used in subsequent studies.

Wirgin *et al*. (1991) was the first to use nDNA RFLPs (also referred to DNA fingerprinting by the authors) to differentiate between striped bass stocks. Wirgin *et al*. (1991) included a heritability test that demonstrated markers were inherited in a Mendelian fashion in four of the five crosses performed. The fifth cross was not tested, as the researchers were unable to obtain suitable DNA for testing. The marker identified a unique genotype in Gulf of Mexico striped bass that was not observed in Atlantic coast populations. However, nDNA RFLPs have not been shown to be useful at small geographic scales, such as within the Chesapeake Bay.

As an alternative to nDNA RFLPs, Leclerc *et al*. (1996) suggested using a similar approach called polymerase chain reaction (PCR)-RFLP where genomic DNA regions are randomly chosen and amplified, and then analyzed with a battery of 20 to 30 restriction enzymes to identify restriction sites that are polymorphic. This approach was capable of identifying genotypes that varied significantly ($P < 0.05$) between the Congree River in South Carolina and the Choptank River in Maryland. Leclerc *et al*. (1996) noted that the use of these single-locus nDNA markers demonstrates that gentoypes are inherited in a Mendelian fashion, given that these markers identify mutations within nDNA genome.

nDNA microsatellites and minisatellites

While nDNA microsatellite methodologies have been a useful stock discrimination tool for anadromous fish populations, their use in striped bass studies has provided mixed results. Wirgin *et al*. (1991) and Wirgin *et al*. (2005) were only capable of detecting minute differences between Atlantic and Gulf striped bass populations using nDNA minisatellites (repeat regions of 14 to 100 base pairs in length) and nDNA microsatellites (repeat regions of 2 to 5 base pairs in length), respectively. Microsatellite methodologies have shown similar results (i.e., no significant differences) when applied to sub-populations of striped bass in the Chesapeake Bay

(Laughlin and Turner 1996, Brown *et al*. 2005). However, a study by Rexroad *et al*. (2006) showed that there was a significant difference between broodstock collected from Maryland and North Carolina, which suggests that microsatellite markers may be useful in some instances at large geographic scales.

nDNA Randomly Amplified Polymorphic DNA (RAPD)

The use of RAPD originally first described by Williams *et al*. (1990) has been used extensively to detect genetic variations in fish populations. As opposed to RFLP methodologies that use restriction enzymes, RAPD methodologies use a battery of primers (i.e., single-stranded DNA, usually 20 to 50 base pairs in length, that is complementary to a region of DNA) to create DNA fragments. This approach has been used only once for striped bass population genetics (Bielawski and Pumo 1997). Bielawski and Pumo (1997) evaluated 40 different primers, eight of which exhibited polymorphisms among five populations sampled along the Atlantic coast. Bielawski and Pumo (1997) concluded that Atlantic coast striped bass are genetically subdivided, but that gene flow (the introduction of new genetic material from one population of a species to the next) prevents fixation of genetic markers while allowing for significant differences in frequencies of the expressed markers.

MtDNA sequencing

The method of sequencing sections of the mtDNA has shown some success for differentiating between striped bass stocks in North Carolina (May 2001, Patrick 2002, Morris *et al*. 2005). Sequencing 370 base pairs in the mtDNA d-loop region identified six distinct haplotypes. Some sub-populations showed significantly different ($P < 0.05$) frequencies of the six haplotypes in some instances, for instance the Neuse River spawning population compared to the Tar and Roanoke River spawning populations. Roanoke River spawning populations

displayed haplotype frequency distributions previously observed in Stellwag et al. (1994), who had used mtDNA RFLP markers. Preliminary results from Patrick (2002) suggested that these haplotypes were dramatically different (i.e., 19 base pair substitutions) from sequence data available on striped bass collected from the Hudson River.

Behavior and physiological studies

Physiological studies on striped bass are somewhat limited and normally focused selective breeding needs; thus, many of the studies examine first- or second-generation offspring, rather than wild-caught striped bass. The methodologies used in physiological studies (e.g. growth rates, thermal tolerances, and differences in egg buoyancies) are generally straightforward, so an in-depth review of techniques is not needed here. A review of the results of physiological studies is provided in the next section.

I was unable to identify any striped bass behavioral studies that were useful for identifying conservation units. While striped bass from different regions and even within spawning populations have been observed to display different migration behaviors, these do not appear to be genetically linked or unique to a specific spawning population. Regionally, striped bass exhibit one of two main migratory profiles: they are either lifetime residents of their natal watershed (Texas to South Carolina) or anadromous populations that at some point usually participate in marine migrations (North Carolina to Canada). This regional difference in migratory behavior is thought to be environmentally induced, where the cooler waters of the estuaries and riverine habitat are preferred over the warmer marine waters in the south. Within spawning populations, some authors have observed that some contingents of the population remain freshwater residents, others inhabit estuarine portions of their watersheds, and still others

participate in marine migrations (Secor *et al*. 2001, Gemperline *et al*. 2002, Morris *et al*. 2005). Of these studies, only Morris *et al*. (2005) hypothesized that these intra-population migration patterns may be genetically linked, although that study included only 6 samples that were analyzed genetically. In chapter 4 of this dissertation, this hypothesis is tested on a larger sample, and is rejected.

Results and discussion

Genetics overview

Since 1987, 33 studies have evaluated the genetic structure of striped bass ranging from the Gulf of Mexico to the St. Lawrence River, Canada (Table 1). In almost every case, these studies have found striped bass exhibit significant differences ($P < 0.05$) in frequency distributions among the various genetic markers used. Only in areas in which spawning populations share an estuary with relatively few or small drainage basins were frequency distributions similar (i.e., Apalachicola-Chattahoochee-Flint (ACF), (FL), Santee-Cooper (SC), Ashepoo-Combahee-Edisto (SC)). This is probably because the likelihood of increasing gene flow increasing is tied to the proximity of spawning locations.

In larger estuaries where multiple drainage basins converge, the findings vary. Within the Albemarle-Pamlico Sound, the Roanoke, Tar, and Neuse Rivers support the largest spawning populations, and share the same major haplotypes that account for 96% of the observed genetic diversity (Patrick 2002). However, Neuse River mtDNA haplotype frequencies were significantly different from those of other two spawning populations. The reason is not immediately clear, since the Neuse and Tar both drain into the Pamlico Sound, while the Roanoke River is the outlier, draining into the Albemarle Sound.

Within the Chesapeake Bay, the striped bass populations have been studied extensively using multiple genetic markers, but conclusions conflict. Earlier studies using mtDNA RFLVs "provisionally" grouped the spawning populations into three aggregations that were based on genetic distance cluster analysis (Chapman 1989, Chapman 1990). Wirgin *et al*. (1990, 1997) also examined a subset of the Chesapeake Bay spawning populations (i.e., Rappahannock, Potomac, Choptank, and Upper Chesapeake Bay) and found that combining the results of mtDNA RFLV, mtDNA RFLP, and nDNA RFLP, yielded significantly different (P = 0.001 - 0.0120) geno/haplotype data frequencies among these spawning populations. However, on an individual basis, none of the three methodologies yielded significant differences (P = 0.001 – 0.0120) in geno/haplotype frequencies among the spawning populations.

Laughlin and Turner (1996) and Brown *et al*. (2005) demonstrated similar findings using nDNA microsatellites. Laughlin and Turner (1996) concluded different Chesapeake Bay spawning populations exhibited different frequencies of genotypes, but there was sufficient gene flow among the spawning populations to prevent fixation (i.e., when an allele becomes unique to a population due to a lack of gene flow) of these genotypes. Brown *et al*. (2005) tested the genetic diversity of the Chesapeake Bay spawning populations using fixation indices and concluded they should be considered one population.

Brown *et al*. (2005) also re-analyzed the mtDNA data of Chapman (1989) and Wirgin *et al*. (1990, 1997) and calculated fixation indices to determine if mtDNA exhibited similar genetic diversity to nDNA. Brown's analysis of Chapman's data suggested that mtDNA fixation indices were significantly different among spawning populations, but that the data collected by Wirgin et al.(1990, 1997) did not show significantly different mtDNA fixation indices. Brown et al. (2005) concluded that "asymmetric homing" (males having higher straying rates than females) of

striped bass in the Chesapeake Bay could have biased the nDNA analysis. Thus, the maternally inherited mtDNA markers provided a different conclusion than those in nDNA, although that did not explain the difference between results in Chapman (1989) and Wirgin *et al*. (1990, 1997), who both used mtDNA. Brown et al. (2005) concluded, based on these findings and the analysis of nDNA microsatellites, that the Chesapeake Bay population should be considered panmictic and managed as a single conservation unit.

Striped bass spawning populations found at the outer edges of the species range (i.e., maritime Canada and Gulf of Mexico) have been shown to display varying degrees of genetic diversity. In maritime Canada, spawning populations from the Bay of Fundy and Gulf of St. Lawrence have been evaluated using mtDNA RFLV and nDNA microsatellite markers (Wirgin *et al*. 1993, 1995; Robinson *et al*. 2004). Both mtDNA length variant frequencies and nDNA genotypes were found to be significantly different between these populations, and when compared to the Hudson River spawning population in the U.S. (Table 1). While frequency distributions varied, only three of the five common mtDNA length variants observed in more southern populations were found in Canadian spawning populations, suggesting Canadian populations are genetically less diverse. Fixation indices also found little evidence of genetic differentiation, further supporting the idea that the Canadian spawning populations are not genetically unique from their southern counterparts. Robinson *et al*. (2004) noted that the lack of genetic diversity in these northern spawning populations is likely due to the founder effect (restricted gene pool resulting from the establishment of a population with relatively few individuals that are isolated from parental populations). Canadian spawning populations probably have been reproductively isolated from one another only since the Wisconsin Glaciation period, approximately 10,000 years ago.

At the other outer edge of its range, the Gulf of Mexico historically supported multiple spawning populations ranging from Louisiana to Florida (Pearson 1938, Wooley and Crateau 1983, Nicholson 1986). However, these spawning populations declined during the 1950s and 1960s, most likely due to anthropogenic impacts (reviewed in Wirgin et al. 1997). By the 1970s, only the ACF spawning populations (Florida) were believed to be viable. To supplement these Gulf spawning populations, the ACF and other spawning populations were stocked with striped bass from the Santee-Cooper River, South Carolina. Wirgin *et al*. (1989) confirmed using mtDNA RFLP analyses that despite the stocking, genetic structure of the ACF spawning populations had not been replaced with Santee-Cooper haplotypes. The XbaI enzyme identified a unique haplotype in the ACF spawning populations that was not observed in Atlantic coast spawning populations. That haplotype was observed in 60% of the samples collected from ACF spawning populations (Wirgin *et al*. 1989, 1997). Similarly, Wirgin *et al*. (2005) showed that the ACF spawning population expressed a high percentage (64-84%) of alleles (microsatellite loci SB 20, 111, and 1021) that were absent or rarely expressed in Atlantic coast spawning populations. An introgression model (i.e., ADMIX 2.0) also estimated that 51.5% of the alleles expressed in ACF spawning populations were of Atlantic coast origin. Therefore, it appears that ACF spawning populations contain a unique genetic marker that is absent in Atlantic coast spawning populations, but that there has been significant admixture from Atlantic coast fish. Other Gulf spawning populations from rivers that were supported by Santee-Cooper River, such as Trinity (TX), Sabine-Toledo (TX), and Mississippi (LA, MS), only exhibit the haplotypes carried by the stocked fish from South Carolina.

Physiological overview

Overall, I reviewed four physiological studies of striped bass that were useful in my analysis. These physiological studies examined varying growth rates, thermal tolerances to changing water temperatures, and varying egg characteristics.

The growth rates of striped bass have been studied to determine if there is a "strain" best suited for use in hatcheries. Jacobs *et al*. (1999) compared the growth rates of five wild populations of striped bass ranging from Florida to New York. A total of 19 families were created from wild-caught striped bass, and offspring were reared in two grow-out facilities for 150 days under controlled environmental conditions. Results showed that randomly selected full-sibling families of differing geographic locations displayed significant differences in growth rates. Overall, offspring from the Apalachicola River (FL), and Maryland (river not specified) families had significantly higher growth rates ($P = 0.0001$) compared to families from South Carolina and New York (rivers not specified). Offspring from the St. John's River in Florida exhibited moderate growth rates and were not significantly different from any of the other spawning populations (Table 1).

Woods (2001) also evaluated the growth rates of captive first-generation (F1) striped bass that originated from the Chesapeake and Delaware Canal area and the Choptank and Nanticoke Rivers in Maryland in 1983. By age 3, F1 striped bass from each of the locations were significantly different from one another ($P < 0.05$). Second-generation (F2) striped bass created in 1992 were compared to F1 generation families from Nova Scotia, New York, North Carolina, South Carolina, and Florida (rivers not specified). Jacobs *et al*. (1999) found that Maryland striped bass exhibited higher growth rates compared to all other families, and that there was significant variance ($P < 0.05$) in growth rates observed among geographic locations (Table 1).

While it is debatable which spawning populations have fastest growth rates, these data suggest that spawning populations can exhibit varying growth rates on intra- and inter-population scales.

Cook *et al*. (2006) recently examined the thermal tolerance of Shubenacadie (Canada) striped bass. In that study, wild striped bass eggs were collected and reared under various ambient water temperatures to a juvenile stage. Examining both static and dynamic thermal tolerance, Cook *et al*. (2006) concluded that Shudenacadie striped bass displayed higher tolerances for rapid temperature changes, compared to studies of striped bass that were collected from more southern reaches of the range. It was speculated that this thermal tolerance was an adaption to the Shubenacadie's tidal bore river system, in which temperatures change rapidly (see Rulifson and Tull 1999). Unfortunately, the authors were unable to compare thermal tolerances among wild-caught striped bass, as the southern populations examined were either striped bass hybrids, unidentified striped bass raised in an Illinois hatchery, or striped bass collected from an Oklahoma reservoir.

Bergey *et al*. (2003) observed differences in striped bass egg buoyancy among various watersheds of the Atlantic coast. Compared to eggs of striped bass from slower-moving watersheds, eggs from striped bass from watersheds with high physical energy were heavier and larger, had smaller oil globule sizes (i.e., less buoyant), smaller surface-to-volume ratios, and larger amounts of fatty acids. Since unsuspended eggs or eggs that too quickly enter brackish waters have a poor chance of surviving (Talbot 1966), Bergey hypothesized that the difference in egg buoyancy may be an indicator that striped bass are adapted to their native watershed. This hypothesis also aligns with Rulifson and Manooch's (1990) findings that restoring the stream flow of a watershed to historical conditions could enhance the spawning success of striped bass.

These physiological studies suggest that in many cases striped bass spawning populations exhibit unique growth rates, varying degrees of thermal tolerance, and possess unique egg characteristics, dependent on the physical energy of the watershed.

Conclusions

As noted in Waldman *et al*. (1988), common problems in population genetics are that scientists studying the population genetics of striped bass use different types of genetic markers, limit their analysis to relatively small geographic areas, and use multiple statistical approaches. Because of these differences, examining striped bass across regions can be difficult unless individual studies themselves encompass the range of the species. There is also significant debate about which statistical analyses are most reliable for genetic studies when trying to identify conservation units of species (i.e., communication issue described earlier).

To resolve these issues, I used a modified version of Fraser and Bernatchez's (2001) adaptive approach for how to determine conservation units. The two most important points in this approach are: (1) genetic data are not required, because other information like physiological data can be used to infer differences among spawning populations; and (2) differences in genetic data must be significant mutations (not to be confused with statistical significance).

From a genetic standpoint, the majority of striped bass populations reviewed here displayed frequency differences in geno- or haplotypes. However, in only a few cases have striped bass spawning populations exhibited unique mutations that would be considered significant under the adaptive method of delineating conservation units (e.g., unique geno- or haplotype, significantly different fixation rates). As noted by Hedrick (1999) and Waples (1998) statistical significance may not always reflect biologically meaningful differences because the

patterns of adaptive loci may not be correlated with the neutral genetic marker, which may have a high mutation rate.

To explain the low genetic diversity observed in striped bass, several authors have suggested that population bottlenecks (the sudden loss of genetic diversity in small populations due to genetic drift) may have occurred from a combination of overfishing (Koo 1970, Boreman and Austin 1985) and cross-stocking of spawning populations (Wirgin *et al*. 1991, Garber and Sullivan 2006). Fishing pressure during the 1970s and 1980s severely reduced the spawning biomass, with some regions recording their lowest levels in the last 100 years (reviewed in Chapter 1). During the same timeframe, cross-stocking (hatchery programs in which brood stock from one spawning population is used to supplement other populations) could have severely reduced genetic diversity (Rulifson and Laney 1999, Wirgin *et al*. 2005). This appears to be the case in some of the Gulf of Mexico spawning populations, which are now indistinguishable from their South Carolina striped bass broodstock (Wirgin *et al*. 2005). Waldman *et al*. (1998) also observed a similar bottleneck event from the stocking of Atlantic coast striped bass into Pacific waters during the late 1800s. Among spawning populations that experienced stocking from elsewhere, even the healthiest spawning populations in the ACF exhibit only ~50% of their native genotypes. It is reasonable to assume that genetic diversity in smaller populations that endured a severe reduction of biomass as a result of fishing effort in the 1970s and 80s may have been heavily impacted by cross-stocking practices.

The colonization patterns of striped bass may also explain the low genetic diversity observed among populations, which is assumed to have originated in the south Atlantic and moved northward into maritime Canada, as striped bass moved to inhabit these waters (Wirgin *et al*. 1993, 1995). Watersheds along the Atlantic coast experienced many dramatic changes in

climate and resultant sea level changes over the last 125,000 years (MacKenzie and Mackenzie 1995, Sager *et al*. 1998, Rudolph 1999). 10,000 to 30,000 years ago, southern coastal rivers periodically extended to the continental shelf, and the climate on the Atlantic coast was similar to that of central Canada and supported boreal forest. Under these climatic conditions, the striped bass, a member of the temperate family Moronidae, would have retreated to more southerly waters. Not until approximately the mid-Holocene (5,000 years ago) did the sea level rise to present day levels; permanent colonization of Mid-Atlantic, New England, and Maritime Canada watersheds probably would not have not taken place until then. From colonization to present-day, DNA substantially mutated to levels of interspecific differentiation, with the greatest differentiation likely appearing in the oldest population (i.e., those in southern regions). This theory of colonization and genetic mutation is supported by the findings of Wirgin *et al*. (1993, 1995) and Robinson *et al*. (2004), who concluded that maritime Canada populations displayed the lowest level of genetic diversity along the Atlantic coast.

Whether genetic bottlenecks or colonization explain the observed genetic diversity, it appears that gene flow prevented the fixation of alleles. At the same time, there appears to be low enough gene flow to enable frequency differences to occur in most cases. Based on genetic data, only the ACF spawning population appears to exhibit unique genotypes that could possibly warrant designation as conservation units.

The physiological evidence suggests spawning populations express unique features such as varying growth rates, unique egg characteristics, and possible differences in thermal tolerances in response to their physical environments. However, it is difficult to link differences to geography. Growth rate differences were scattered among the populations, egg characteristics were related to flow rates of river system rather than geography, and thermal tolerance was

studied only in a very limited way. Therefore, it is difficult to determine if individual spawning populations should be defined as conservation units.

To err on the side of preserving genetic diversity, some fishery managers may decide to take a precautionary approach and define conservation units at the level of spawning populations. As it appears that genetic diversity has been lost due to not preserving the likely low gene flow that has occurred historically between native spawning populations (i.e., cross-stocking). For stocking programs, the implication of this option is that each spawning population should have a dedicated broodstock if that spawning population needs support through a stocking program to preserve genetic diversity. For stock assessments, this means that each spawning population should be measured separately for an accurate picture of its status. While this option is likely to cost more than the status quo, it could be an interim management strategy until more conclusive evidence suggests other options.

Ideally, a comprehensive genetic study should be conducted that focuses on single nucleotide sequence polymorphisms, the most stable form of genetic variation. With the advent of deep sequencing technologies and advances in long-range PCR, it would be feasible to amplify the entire mtDNA genome for a number of spawning striped bass from the major spawning populations and conduct complete mtDNA genome sequencing. A comprehensive comparison of these sequences would reveal a collection of informative population/sequence markers: screening more than 16,000 maternally-inherited base pairs would show lineage-dependent change. This level of analysis could rectify the problems with previous studies (e.g., limited number of: spawning populations analyzed; relatively small regions of the genome evaluated; small sample sizes, etc.) and put striped bass population genetics on firmer footing.

Literature cited

Ali, M. Y. and C. C. Lindsey. 1974. Heritable and temperature-induced meristic variation in the medaka *Oryzia latipes*. Canadian Journal of Zoology 52: 959-976.

Begg, G. A., K. D. Friedland, and J. B. Pearce. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research 43: 1-8.

Bergey, L. L., R. A. Rulifson, M. L. Gallagher, and A. S. Overton. 2003. Variability of Atlantic coast striped bass egg characteristics. North American Journal of Fisheries Management 23: 558-572.

Bielawski, J. P. and D. E. Pumo. 1997. Randomly amplified polymorphic DNA (RAPD) of Atlantic Coast striped bass. Heredity 78: 32-40.

Bilton, D. T., J. Paula, and J. D. D. Bishop. 2002. Dispersal, genetic differentiation and speciation in estuarine organisms. Estuarine Coastal and Shelf Science 55: 937-952.

Blaxter, J. H. S. 1984. Ontogeny, systematic, and fisheries. American Society of Ichthyologists and Herpetologists Special Publication 1: 1-6.

Booke, H. E. 1999. The stock concept revisited: perspectives on its history in fisheries. Fisheries Research 43: 9-11.

Boreman, J. and H. M. Austin. 1985. Production and harvest of anadromous striped bass stocks along the Atlantic Coast. Transactions of the American Fisheries Society 114: 3-7.

Bowen, B. W. 1999. What is wrong with ESUs? The gap between evolutionary theory and conservation principles. Journal of Shellfish Research 17: 1355-1358.

Brown, B. L., J. M. Epifanio, P. E. Smouse, and C. J. Kobak. 1996. Temporal stability of mtDNA haplotype frequencies in American shad stocks: to pool or not to pool across years? Canadian Journal of Fisheries and Aquatic Sciences 53: 2274-2283.

Brown, K. M., G. A. Baltazar, and M. B. Hamilton. 2005. Reconciling nuclear microsatellite and mitochondrial markers estimates of population structure: breeding population structure of Chesapeake Bay striped bass (*Morone saxatilis*). Heredity 94: 606-615.

Chapman, R. W. 1987. Changes in the population structure of male striped bass, *Morone saxatilis*, spawning in three areas of Chesapeake Bay from 1984 to 1986. Fishery Bulletin 85: 167-171.

Chapman, R. W. 1989. Spatial and temporal variations of mitochondrial DNA haplotype frequencies in the striped bass 1982 year class. Copeia 1989: 344-348.

Chapman, R. W. 1990. Mitochondrial DNA analysis of striped bass populations in Chesapeake Bay. Copeia 1990: 355-366.

Cook, A. M., J. Duston, and R. G. Bradford. 2006. Thermal tolerance of a northern population of striped bass *Morone saxatilis*. Journal of Fish Biology 69: 1482-1490.

Cowen, R. K. C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 311: 522-527.

Currens, K. P., C. S. Sharpe, R. Hjort, C. B. Schreck, and H. W. Li. 1989. Effects of different feeding regimes on the morphometrics of Chinook salmon (*Oncorhynchus tshawystscha*) and rainbow trout (*O. mykiss*). Copeia 1989: 689-695.

De Guia, A. P. O. and T. Saitoh. 2007. The gap between the concept and definitions in the Evolutionary Significant Unit: the need to integrate neutral genetic variation and adaptive variation. Ecological Research 22: 604-612.

Dimmick, W. W., M. J. Ghedotti, M. J. Grose, A. M. Maglia, D. J. Meinhardt, and D. S. Pennock. 1999. The importance of systematic biology in defining units of conservation. Conservation Biology 13: 653-660.

Fraser, D. J. and L. Bernatchez. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology 10: 2741-2752.

Garber, A. F. and C. V. Sullivan. 2006. Selective breeding for the hybrid striped bass (*Morone chrysops*, Rafinesque x *M. saxatilis*, Walbaum) industry: status and perspectives. Aquaculture Research 37: 319-338.

Gemperline, P. J., R. A. Rulifson, and L. Paramore. 2002. Multi-way analysis of trace elements in fish otoliths to track migratory patterns. Chemometrics and Intelligent Laboratory Systems 60: 135-146.

Grunwald, C., L. Maceda, J. Waldman, J. Stabile, and I. Wirgin. 2008. Conservation of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*: delineation of stock structure and distinct population segments. Conservation Genetics 9: 1111-1124.

Hearn, W. S., J. M. Hoenig, K. H. Pollock, and D. A. Hepworth. 2003. Tag reporting rate estimation, 3. Use of planted tags in one component of a multicomponent fishery. North American Journal of Fisheries Management 23: 66–77.

Hedrick, P. W. 1999. Perspective: highly variable genetic loci and their interpretation in evolution and conservation. Evolution 53: 313-318.

Jacobs, J. M., S. Lindell, W. V. Heukelem, E. M. Hallerman, and R. M. Harrell. 1999. Strain evaluation of striped bass (*Morone saxatilis*) under controlled conditions. Aquaculture 173: 171-177.

Karl, S. A. and B. W. Bowen. 1999. Evolutionary significant units versus geopolitical taxonomy: molecular systematic of an endangered species. Conservation Biology 13: 990-999.

Koo, T. S. Y. 1970. The striped bass fishery in the Atlantic states. Chesapeake Science 11: 73-93.

Laughlin, T. F. and B. J. Turner. 1996. Hypervariable DNA markers reveal high genetic variability within striped bass populations of the lower Chesapeake Bay. Transactions of the American Fisheries Society 125: 49-55.

Leclerc, G. M., M. Diaz, and B. Ely. 1996. Use of PCR-RFLP assays to detect genetic variation at single-copy nuclear loci in striped bass (*Morone saxatilis*). Molecular Marine Biology and Biotechnology 5: 138-144.

Lindsey, C. C., and R. W. Harrington, Jr. 1972. Extreme vertebral variation induced by temperature in a homozygous clone of the self-fertilizing cyrprinodontid fish *Rivulus marmoratus*. Canadian Journal of Zoology 50: 733-744.

Mackenzie, F. T. and J. A. Mackenzie. 1995. Our changing planet: an introduction to earth system science and global environmental change. Prentice Hall, Englewood Cliffs.

MacLean, J.A. and D. O. Evans. 1981. The stock concept, discreteness of fish stocks, and fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 38: 1889-1898.

May, P. G. 2001. Genetic and morphological characterization of striped bass *Morone saxatilis* collected from the Roanoke River, North Carolina during the 1999 spawning season. Master's Thesis. East Carolina University, Department of Biology, Greenville, North Carolina.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, *Chichlidae*) and their implications for speciation in chichild fishes. Evolution 41: 1357-1369.

Moritz, C. Defining "Evolutionary Significant Units" for conservation. Trends in Ecology and Evolution 9: 373-375.

Morris, R. J., and F. Culkin. 1989. Fish. In: Ackman, R. G. (Ed.), Marine Biogenic Lipids, Fats, and Oils, vol. 2. CRC Press, FL, pp. 145-178.

Morris, J. A., R. A. Rulifson, J. A. Babaluk, P. G. May, and J. L. Campbell. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry 34: 301-305.

Mortiz, C. 1994b. Defining "Evolutionary Significant Units" for conservation. Trends in Ecology and Evolution 9: 373-375.

Nicholson, L. (ed.). 1986. Striped Bass Fishery Management Plan (Gulf of Mexico). Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Paetkau, D. 1999. Using genetics to identify intraspecific conservation units: a critique of current methods. Conservation Biology 13: 1507-1509.

Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. Annual Review of Ecology and Systematics 25: 547-572.

Patrick, W. S. 2002. Genetic structure of striped bass, *Morone saxatilis*, populations from the Roanoke, Tar, and Neuse Rivers of North Carolina. Master's Thesis. East Carolina University, Department of Biology, Greenville, North Carolina.

Pearson, J. C. 1938. The life history of the striped bass, or rockfish, *Roccus saxatilis* (Walbaum). United States Bureau of Fisheries Bulletin 49: 825-851.

Pennock, D. S. and W. W. Dimmick. 1997. Critique of the Evolutionary Significant Unit as a definition for "distinct population segments" under the U.S. Endangered Species Act. Conservation Biology 11: 611-619.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation, 1. An evaluation of the high-reward tagging method. North American Journal of Fisheries Management 21:521–532.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2002. Tag reporting rate estimation, 2. Use of high reward tagging and observers in multicomponent fisheries. North American Journal of Fisheries Management 22:727–736.

Rexroad, C., R. Vallejo, I. Coulibaly, C. Couch, A. Garber, M. Westerman, and C. Sullivan. 2006. Identification and characterization of microsatellites for striped bass from repeat-enriched libraries. Conservation Genetics 7: 971-982.

Robinson, M., S. Courtenay, T. Benfey, L. Maceda, and I. Wirgin. 2004. Origin and movements of young-of-the-year striped bass in the southern Gulf of St. Lawrence, New Brunswick. Transactions of the American Fisheries Society 133: 412-426.

Rudolph, G. L. 1999. Holocene evolution of a drowned tributary estuary, Croatan Sound, North Carolina. Master's Thesis. East Carolina University, Department of Geology, Greenville, North Carolina.

Rulifson, R. A. and R. W. Laney. 1999. Striped bass stocking programs in the United States: ecological and resource management issues. Canadian Stock Assessment Secretariat Research Document 99/007. Ottawa, Canada.

Rulifson, R. A. and C. S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10: 397-307.

Rulifson, R. A. and K. A. Tull. 1999. Striped bass spawning in a tidal bore river: The Shubenacadie Estuary, Atlantic Canada. Transactions of the American Fisheries Society 128: 613-624.

Ruzzante, D. E., C. T. Taggart, and D. Cook. 1999. A review of the evidence for genetic structure of cod (*Gadus morhua*) populations in the NW Atlantic and population affinities of larval cod off Newfoundland and the Gulf of St. Lawrence. Fisheries Research 43: 79-97.

Sager, E. D., S. R. Riggs, and S. W. Snyder. 1998. Models for Holocene valley-fill history of Albemarle Sound, North Carolina. In C. Alexander, V. J. Henry, and R. Davis (editors), Tidalities: Processes and Products. Journal of Sedimentary Research, Special Publication 61: 119-127.

Secor, D. H., J. R. Rooker, E. Zlokovitz, and V. S. Zdanowicz. 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. Marine Ecology Progress Series 211: 245-253.

Stellwag, E. J., E. S. Payne, and R. A. Rulifson. 1994. Mitochondrial DNA diversity of Roanoke River striped bass. Transactions of the American Fisheries Society 123: 321-334.

Stellwag, E. J. and R. A. Rulifson. 1995. Mitochondrial DNA stability and striped bass stock identification: response to comment. Transactions of the American Fisheries Society 124: 956-959.

Swain, D. P. and C. C. Lindsey. 1986. Meristic variation in a clone of the cyprinodont fish *Rivulus marmoratus* related to temperature history of the parents and of the embryos. Canadian Journal of Zoology 64: 1444-1455.

Talbot, G. B. 1966. Estuarine environmental requirements and limiting factors for striped bass. Transactions of the American Fisheries Society 95: 37.

Tessier, N., L. Bernatchez, and J. M. Wright. 1997. Population structure and impact of supportive breeding inferred from mitochondrial and microsatellite DNA analyses in land-locked Atlantic salmon *Salmo salar* L. Molecular Ecology 6: 735-750.

Waldman, J. R., J. Grossfield, and I. Wirgin. 1988. Review of stock discrimination techniques for striped bass. North American Journal of Fisheries Management 8: 410-425.

Waldman, J. R. and I. I. Wirgin. 1995. Comment: mitochondrial DNA stability and striped bass stock identification. Transactions of the American Fisheries Society 124: 954-956.

Waldman, J. R., R. E. Bender, and I. I. Wirgin. 1998. Multiple population bottlenecks and DNA diversity in populations of wild striped bass, *Morone saxatilis*. Fishery Bulletin 96: 614-620.

Waples, R. S. 1998. Evolutionary Significant Unites, distinct population segments, and the Endangered Species Act: reply to Pennock and Dimmick. Conservation Biology 12: 718-721.

Waples, R. S., A. E. Punt, and J. M. Cope. 2008. Integrating genetic data into management of marine resources: how can we do it better? Fish and Fisheries 9: 423-449.

Williams, J. G. K., A. R. Kubelik, K. J. Livak, J. A. Rafalski, and S. V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic-markers. Nucleic Acids Research 18: 6531-6535.

Wirgin, I., D. Currie, N. Roy, and L. Maceda. 2005. Introgression of nuclear DNA (nDNA) alleles of stocked Atlantic Coast striped bass with the last remaining native Gulf of Mexico population. North American Journal of Fisheries Management 25: 464-474.

Wirgin, I. I., C. Grunwald, S. J. Garte, and C. Mesing. 1991. Use of DNA fingerprinting in the identification and management of a striped bass population in the southeastern United States. Transactions of the American Fisheries Society 120: 273-282.

Wirgin, I., B. Jessop, S. Courtenay, M. Pedersen, S. Maceda, and J. R. Waldman. 1995. Mixed-stock analysis of striped bass in two rivers of the Bay of Fundy as revealed by mitochondrial DNA. Canadian Journal of Fisheries and Aquatic Sciences 52: 961-970.

Wirgin, I. I. and L. Maceda. 1991. Development and use of striped bass-specific RFLP probes. Journal of Fish Biology 39 (Supplement A): 159-167.

Wirgin, I, I., L. Maceda, J. Stabile, and C. Mesing. 1997. An evaluation of introgression of Atlantic coast striped bass mitochondrial DNA in a Gulf of Mexico population using formalin-preserved museum collections. Molecular Ecology 6: 907-916.

Wirgin, I. I., T-L. Ong, L. Maceda, J. R. Waldman, D. Moore, and S. Courtenay. 1993. Mitchondrial DNA variation in striped bass (*Morone saxatilis*) from Canadian rivers. Canadian Journal of Fisheries and Aquatic Sciences 50: 80-87.

Wirgin, I. I., R. Proenca, and J. Grossfield. 1989. Mitochondrial DNA diversity among populations of striped bass in the southeastern United States. Canadian Journal of Zoology 67: 891-907.

Wirgin, I. I., P. Silverstein, and J. Grossfield. 1990. Restriction endonuclease analysis of striped bass mitochondrial DNA: the Atlantic coastal migratory stock. Pages 475-491 in N.C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, (eds). Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Woods III, L. C. 2001. Domestication and strain evaluation of striped bass (*Morone saxatilis*). Aquaculture 202: 343-350.

Wooley, C. M., and E. J. Crateau. 1983. Biology, population estimates, and movements of native and introduced striped bass, Apalachicola River, Florida. North American Journal of Fisheries Management 3: 383-394.

Table 1. Summary of striped bass population genetic and physiology studies, 1987 to present.

Source	Populations Sampled	Technique
Genetics		
Bielawski and Pumo (1997)	Atlantic coastal migratory stocks; Hudson River, NY; Delaware River, DE; Chesapeake Bay; Roanoke River, NC	RAPD
Brown et al. (2003)	New markers	nDNA microsatellites
Brown et al. (2005)	Chesapeake Bay	mtDNA RFLV and nDNA microsatellites
Bulak et al. (2004)	Pee Dee, Congaree, Wateree, Combahee, and Edisto Rivers, SC	nDNA RFLP
Chapman (1987)	Chesapeake Bay	mtDNA RFLV
Chapman (1989)	Chesapeake Bay	mtDNA RFLV
Chapman (1990)	Chesapeake Bay	mtDNA RFLV
Cook et al. (2006)	Subenacadie River, Canada	Thermal tolerance
Couch et al. (2006)	New markers	nDNA microsatellites
Diaz et al. (1998)	Santee-Cooper and Congaree Rivers, SC	PCR-RFLP
Dunham et al. (1988)	Apalachicola River, FL; Chattahoochee-Flint, Ogeechee, and Savannah Rivers, GA; Santee-Cooper River, SC; Tallapoose River, AL; and Chesapeake Bay	mtDNA RFLP and mtDNA RFLV
Han and Ely (2002)	New markers	nDNA RFLP
Han et al. (2000)	New markers	nDNA microsatellites
Laughlin and Turner (1996)	Chesapeake Bay	nDNA microsatellites

Table 1. continued.

Source	Populations Sampled	Technique
Leclerc et al. (1996)	Congaree River, SC and Choptank River, MD	PCR-RFLP
May (2001)	Roanoke River, NC	mtDNA sequencing
Morris et al. (2003)	Roanoke River, NC	mtDNA sequencing
Patrick (2002)	Neuse, Tar, and Roanoke Rivers, NC	mtDNA sequencing
Rexroad et al. (2006)	New markers	nDNA
Robinson and Courtenay (1999)	Maritime Canada	mtDNA; RFLV; PCR-RFLP; nDNA RFLP; nDNA microsatellites
Robinson et al. (2004)	Gulf of St. Lawrence, Canada	mtDNA RFLV and nDNA microsatellites
Roy et al. (2000)	New markers	nDNA microsatellites
Stellwag et al. (1994)	Roanoke River, NC	mtDNA RFLP
Toombs (2000)	New markers	nDNA microsatellites
Wirgin and Maceda (1991)	Apalachicola-Chattahoochee-Flint Rivers, FL; Santee-Cooper Rivers, SC; York and Rappahannock Rivers, VA; Hudson River, NY	nDNA RFLP
Wirgin et al. (1989)	Apalachicola River, FL; Atlantic stocks	mtDNA RFLV
Wirgin et al. (1991)	Apalachicola-Chattahoochee-Flint Rivers, FL; Atlantic stocks	nDNA minisatellites
Wirgin et al. (1993a)	Hudson River, NY; Chesapeake Bay; New York Bight	mtDNA RFLV
Wirgin et al. (1993b)	Miramichi, Shubenacadie, and Tabusintac Rivers, Canada; Hudson River, NY; Chesapeake Bay; Long Island, NY	mtDNA RFLV

Table 1. continued.

Source	Populations Sampled	Technique
Wirgin et al. (1995)	Bay of Fundy, Canada	mtDNA RFLV
Wirgin et al. (1997a)	Hudson River, NY; Chesapeake Bay; Long Island, NY	mtDNA RFLVs and nDNA RFLPs
Wirgin et al. (1997b)	Apalachicola-Chattahoochee-Flint Rivers, FL; Atlantic stocks	PCR-RFLP and mtDNA sequencing
Wirgin et al. (2005)	Apalachicola-Chattahoochee-Flint Rivers, FL; Atlantic stocks	nDNA microsatellites
Physiology		
Bergey et al. (2003)	Miramichi and Shubenacadie Rivers, Canada; Lake Lanier and Savannah River, GA; Dan River, NC; Stauton and Pamunkey Rivers, VA; Choptank and Nanitoke Rivers, MD	Egg characteristics
Cook et al. (2006)	Shubenacadie River, Canada; Illinois hatchery; Oklahoma resvoir	Thermal tolerance
Jacobs et al. (1999)	St. John's and Appalachicola Rivers, FL; South Carolina; Maryland; New York	Growth rates
Woods (2001)	Florida; South Carolina; North Carolina; Choptank and Nanticoke Rivers, and C&D Canal, MD; Nova Scotia, Canada	Growth rates

CHAPTER 3: A REVIEW OF ABIOTIC AND BIOTIC FACTORS INFLUENCING THE STRONTIUM UPTAKE IN ROANOKE RIVER STRIPED BASS OTOLITHS

A brief overview of striped bass migratory patterns

The striped bass (*Morone saxatilis*) is an anadromous fish that supports a large commercial and recreational fishery on both the Atlantic and Pacific coasts. Anadromy refers to fish that spend most of their lives in the sea and migrate to freshwater to breed (Meyers 1949, McDowall 1992). The native range of this species extends along the Atlantic Ocean from the Saint Lawrence River, Canada to St. John River, Florida, and throughout the northern Gulf of Mexico to Texas (Pearson 1938).

Along the Atlantic coast, striped bass display varying degrees of anadromy. Populations located south of Cape Hatteras, North Carolina, usually complete the entire life cycle in fresh and brackish waters of their natal watersheds, rarely emigrating to the marine environment (Merriman 1941, Coutant 1985). Juvenile striped bass populations north of Cape Hatteras generally inhabit fresh/brackish water habitat until they mature, at which time they emigrate to the ocean and become part of a migratory population (Merriman 1941, Dorazio *et al*. 1994). The migratory population uses habitat in coastal and estuarine waters from North Carolina to Atlantic Canada (Pearson 1938, Chapoton and Sykes 1961, Holland and Yelverton 1973, Boreman and Lewis 1987). Mature adults usually return to natal rivers to spawn in the spring. Striped bass are iteroparous, spawning multiple times throughout life. After spawning, adults south of Cape Hatteras enter the estuary, while migratory striped bass in the north generally return to the ocean.

The Albemarle Sound/Roanoke River striped bass population

The Albemarle Sound/Roanoke River (AR) striped bass stock is located just north of Cape Hatteras and traditionally has been viewed as an estuarine population that rarely leaves fresh and brackish waters (Boreman and Lewis 1987, Haeseker *et al*. 1996, Greene *et al*. 2009) (Figure 1). In the past, fishery managers believed they did not leave the estuary for the ocean because they were too small; they found that AR size classes were markedly smaller than other striped bass populations that migrate to the ocean, such as Chesapeake Bay striped bass (Dorazio *et al.* 1994). These small sizes were due in part to the truncated age structure of the AR stock: overfishing from the 1970s to the early 1980s limited AR adults to live no more than 5 and 6 years (Hassler *et al.* 1981). However, since the passage of the Striped Bass Conservation Act in 1984 and the resulting recovery measures implemented by the state and the Atlantic States Marine Fisheries Commission, the Roanoke River population rebounded and was declared recovered in 1997 (reviewed in Chapter 1). The age structure of the Roanoke River population has been increasing since 1997 and now supports a large percentage of age 6+ fish (NCDMF 2003). It has been speculated by fishery managers that as the age structure of the Roanoke River population continues to increase, more striped bass will begin emigrating to the ocean.

Results from the North Carolina Division of Marine Fisheries (NCDMF) and North Carolina Wildlife Resources Commission (NCWRC) tagging studies note that emigration to the ocean appears to be increasing, finding a 0% rate in 1980 and a 3% rate in 2001 (Table 1). More recently, Morris *et al.* (2005) suggested that potentially as much as 10 – 15% of Roanoke River striped bass may emigrate to the ocean. The Morris *et al.* (2005) pilot study examined the strontium (Sr) levels in the otoliths of six striped bass, which were selected based on their age (e.g., 5+), sex (3 males and 3 females), and haplotype (e.g., represented the three major haplotypes observed in the Roanoke River – see May 2001 and Patrick 2002). In Chapter 4, my

research expands upon this exploratory research by examining the otoliths of 115 striped bass, ranging in length from 18 inches to 35 inches (TL). This analysis relies on the Sr uptake into the otolith matrix of striped bass, a proxy to determine if striped bass were inhabiting freshwater, estuarine, or marine waters. Several studies have shown that the incorporation of Sr into the otolith matrix can be influenced not only by the salinity of the water, but also water temperature (Reviewed in Campana 1999, Reviewed in Secor and Rooker 2000, Elsdon and Gillanders 2002), ambient concentration of Sr in the water (Reviewed in Secor and Rooker 2000, Walther and Thorrold 2006), the fish's diet (Reviewed in Campana 1999, Kennedy et al. 2000, Buckel et al. 2004, Walther and Thorrold 2006), and maternal contributions to developing yolk-sac larvae (Volk *et al.* 2000).

As a result, it is important to examine the various life stages of striped bass to determine if any of the abiotic and biotic factors found within the Albemarle Sound/Roanoke River and the Atlantic Ocean could bias the results of the Sr analysis. Abiotic factors are non-living chemical and physical factors of the environment, including water temperature, salinity, and water flow. Biotic factors refer to living organisms of the environment, such as predators and prey of striped bass, including humans. Together, these abiotic and biotic factors make up the environment occupied by striped bass.

Biotic factors - life history of Roanoke River striped bass

Development and habitat use

The life history of striped bass has been extensively studied over the last hundred years (reviewed in Bigelow and Schroeder 1953, Koo 1970, Wirgin *et al.* 1989, Greene *et al.* 2009). Greene *et al.* (2009) provided an in-depth overview of Albemarle Sound/Roanoke River striped

bass histories. Striped bass spawning runs on the Roanoke River usually begin in March when water temperatures reach 7°C to 8°C (Merriman 1941, Trent and Hassler 1968, Greene *et al.* 2009) and peak in May (Hill *et al.* 1989). Early spawning runs are normally dominated by males who enter the spawning grounds early in the season, while females remain in the Albemarle Sound, or offshore if they participated in an oceanic migration (Vladykov and Wallace 1952, Trent and Hassler 1968, Holland and Yelverton 1973). As noted earlier, only a relatively small portion of the AR stock (~0 – 3%) is thought to migrate to the ocean at all, with the remainder staying within the Albemarle (92-100%) and Pamlico Sounds (0-5%) (Winslow 2002). Spawning occurs in the vicinity of Weldon, NC (~river mile 130) when water temperature rise above 15°C (Rulifson and Manooch 1993, Greene *et al.* 2009), with optimum spawning temperature occurring at 17 to 19°C (Shannon and Smith 1968 in Greene *et al.* 2009, Rulifson and Manooch 1993). Spawning does not occur above water temperature of 22°C (McCoy 1959 in Greene *et al.* 2009).

Striped bass are broadcast spawners, depositing their semi-buoyant eggs in surface waters (Merriman 1937; Raney 1952, Bergey *et al.* 2003). Eggs are transported downstream and usually hatch in one to three days from fertilization. The larval yolk-sac phase lasts three to nine days, depending on the water temperature (Reviewed in Greene *et al*. 2009). Larval development continues for up to 65 days (Reviewed in Greene *et al*. 2009). Within the Roanoke River, post-larval to juveniles stages occur in or near the head of the river or the adjacent estuary of the western portion of the Albemarle Sound (Rulifson 1984; Greene *et al*. 2009). At this stage of development, larvae and juveniles form schools and move into the shore-zone to forage throughout the first summer (Reviewed in Greene *et al.* 2009).

Juvenile striped bass (i.e., sub-adults) do not require specific microhabitat conditions, as they use various nearshore microhabitats (Greene *et al*. 2009). In the late summer or early fall, young-of-year generally move further from shore (Reviewed in Greene *et al.* 2009) and into higher salinity areas (Raney 1952; Kernehan *et al.* 1981; Reviewed in Greene *et al*. 2009). Greene et al. (2009) notes that optimal water quality conditions for juvenile striped bass are water temperatures between 18 to 25°C (Coutant 1985, 1986), salinities between 10 to 20 ppt (Bogdanov *et al*. 1967 in Green *et al.* 2009) and dissolved oxygen levels between 6 and 12 mg/L.

As adults, resident AR striped bass do not display any specific habitat preferences (i.e., open water, structure, riverine, etc.), from a study of sonically tagged adults tracked throughout the Sound and tributaries (Haeseker *et al*. 1996). Despite high water temperatures in 1994, they sought no thermal refuges other than the Roanoke River for a brief period of time. The majority of striped bass were found in the deeper waters of the Sound (~ 5.4 to 7.2 m deep) located between the Alligator River and mouths of the Roanoke and Chowan Rivers. Of the 41 sonically tagged fish tracked by Haeseker *et al*. (1996), 26 participated in the 1994 spawning run into the Roanoke River and returned to the Sound in the summer. Forty percent of the fish that participated in the spawning run relocated to the Croatan Sound during the months of December and January, suggesting resident striped bass likely overwinter in the eastern portion of the Albemarle Sound.

AR striped bass and other stocks that participate in oceanic migrations are generally found in surf and nearshore waters no more than 6 to 8 kilometers offshore (Bigelow and Schroeder 1953, Holland and Yelverton 1973, Boreman and Lewis 1987, Greene *et al*. 2009) and may migrate as far north as Gulf of St. Lawrence to overwinter (reviewed in Greene *et al*. 2009). Other overwintering locations include Bay of Fundy, Gulf of Maine, inshore areas near Cape

Henry, Virginia, and Topsail Island, North Carolina (reviewed in Greene *et al*. 2009). Tag recaptures of AR stock were caught primarily in inshore waters of the Chesapeake Bay near Norfolk (Winslow 2002), although AR stock also have been recaptured as far north as Maine. Able and Grothues (2007) and Grothues *et al*. (2009) showed that striped bass used inshore habitat of Great Bay, Delaware, which does not support a spawning population. Using ultra-sonic tagging methods, the researchers observed that migratory striped bass frequented the bay at different intervals usually during the spring and fall, and sometimes traveled far upstream into its tributaries. Oceanic migrations normally include age-2 and older fish (Dorazio *et al*. 1994) and are dominated (~85 to 90%) by females (Bigelow and Schroeder 1953, Holland and Yelverton 1973, Greene *et al*. 2009). While participating in the oceanic migration, striped bass have been captured in water temperatures ranging from 0.1 to 27°C (Raney 1952, Bigelow and Schroeder 1953, Talbot 1966, Clark 1968), but generally prefer temperatures less than 21°C (reviewed in Greene *et al*. 2009).

Predator-prey interactions

The diet of striped bass has been studied extensively since the 1940s (reviewed in Walter *et al*. 2003); however, this report will focus on the diets of AR stocks because the diet of striped bass has been shown to vary among regions (reviewed in Walter *et al*. 2003). Four peer-reviewed diet studies have been published in the literature about the AR stock: 1) adults (Trent and Hassler 1966); 2) juveniles and adults (Manooch 1973); 3) juveniles (Cooper *et al*. 1998); and 4) juveniles and adults (Rudershausen *et al*. 2005).

Trent and Hassler (1966) note that adult AR striped bass fed heavily on blueback herring during their upstream migration of the Roanoke River. During prespawning and post spawning stages, AR striped bass also fed on golden shiner, unidentified minnows, blueback herring, and

gizzard shad (in order of importance). However, during spawning, AR striped bass do not feed (Raney 1952, Trent and Hassler 1966).

As juveniles (30 to 115 mm TL; 30 to 105 days old), AR striped bass feed predominately on mysid shrimp. Cooper *et al*. (1998) repored that striped bass consume mysid shrimp twice as often as copepods and 10 times as often as cladocerans. Until AR striped bass reach an approximate size of 85 mm TL, they consume only small quantities of fish. At this size, copepods vanish from their diet. Cooper *et al*. (1998) noted that western Sound striped bass tended to feed more so on fishes (10%) than did central Sound striped bass (<1%). The opposite trend was observed for the consumption of mysid shrimp, which made up 76% of the diet in the central Sound versus 44% in the western Sound. It was speculated that these differences in diet were related to differences in salinity, as there was no significant difference in the size of striped bass in these regions.

The diet for older juveniles (>125 mm TL) and adults within the Albemarle Sound and Roanoke River is made up predominantly of fish (Trent and Hassler 1966, Manooch 1973, Patrick and Rulifson 2003). Both Manooch (1973) and Patrick and Rulifson (2003) noted that fish was the dominant prey group consumed by AR striped bass (125 to 714 mm TL) in the Albemarle Sound, representing a 90 to 93% frequency of occurrence (FOC). Overall, Atlantic menhaden (*Brevoortia tyrannus*) was consumed 34 to 54% (FOC) of the time, followed by unidentified fish remains (13 to 22%), Alosines (8 to 13%), bay anchovies (*Anchoa mitchilli*) (2 to 13%), and American eels (*Anguilla rostrata*) (0 to 13%). In general, yearling striped bass (age-0; > 125 mm TL) feed primarily (96%) on juvenile soft-rayed finfish, predominantly bay anchovies (29%) (Manooch 1973). Larger striped bass (> age-0) fed primarily on Clupeids,

although invertebrates and spiny-rayed fish were sometimes consumed (each 19%) (Manooch 1973).

Manooch (1973) and Patrick and Rulifson (2003) also reported a significant difference ($P < 0.05$) between food habits of striped bass among seasons and regions. One trend was observed when measured by either percent weight (%W) or FOC: clupeid species are the predominant prey items consumed during all months of the year. Each season, clupeid species represented at least 50% of the prey items, though the dominant clupeid species changed with the season. The number of prey items also changed by season, where clupeids are targeted during the winter, spring, and summer months, with fall finding striped bass consuming more spiny-rayed fishes than other seasons.

During the winter months (Dec – Feb), the majority of striped bass fed on clupeid species, with menhaden making up 73% of the diet, followed by Alosines, unidentified fish, and unidentified clupeid species. Spiny-rayed fish (e.g., Sciaenidae, Moronidae) were found less frequently (11%) (Manooch 1973). During the spring months (Mar – May), striped bass fed primarily on Alosines (76% FOC) or Atlantic menhaden (67% FOC) (Patrick and Rulifson 2003). This observation correlates with the April and May migration of herring (*Alosa aestivalis* and *A. pseudoharengus*) and shad (*A. sapidissima* and *A. mediocris*). During the summer months (Jun – Aug), the majority of striped bass fed on menhaden (62 to 75% FOC). The second most prevalent prey item differed among diet analysis: % weight showed blue crabs (12.3% or 16.2% including crab parts) as dominant, while FOC indicated unidentified clupeids (15.1%). Blue crabs ranked third in the FOC analysis (4.3%); the discrepancy between the weight and FOC of blue crab suggest that blue crabs may provide more caloric benefit per individual consumed. Other prey items included Atlantic croaker (*Micropoganis undulates*) and unidentified clams.

During the fall months (Sep – Nov), striped bass continued to consume menhaden (51 to 64% FOC). The remaining prey items were distributed among a variety of species, including anchovies, blue crabs, clams, sciaenids, gobies (Gobiidae), and moronids.

Food habits of striped bass between eastern and western regions of the Albemarle Sound were significantly different among the top six prey items (i.e., menhaden, clupeid sp., unidentified fish, *Anchoa* sp., spot, and Alosine sp.) (Patrick and Rulifson 2003). While menhaden, unidentified clupeids, and unidentified fish remains were relatively similar among regions, Alosines were never found in the diet of striped bass captured in the eastern Sound (0%, compared to 5.5% in the western Sound). As noted earlier, river herring migrations occur during the spring and usually congregate in the western region of the Sound; therefore it is a reasonable observation that river herring consumption would be greater in this area. Spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogon undulatus*), silver perch (*Bairdiella chrysura*), weakfish (*Cynoscion regalis*) and *Anchoa* species are often found in more saline waters of the Sound, so it is again reasonable that these species were consumed more often by striped bass in the eastern region of the Sound, where salinities are higher (Manooch 1973, Patrick and Rulifson 2003).

AR striped bass that participate in oceanic migrations display varying diets depending on their location and season (Walter *et al*. 2003). Striped bass foraging in inshore areas from North Carolina to Delaware feed on similar taxa as those described above in the Albemarle Sound. Walter *et al*. (2003) noted that Atlantic menhaden generally dominate the diets of large striped bass, followed by scieanids and Alosines. Within the New York Bight, the diet of striped bass is somewhat mixed. Schaefer (1970) reported that bay anchovies were dominant prey items of striped bass collected in the surf on Long Island, New York. Greene *et al*. (2009) reported,

however, that inshore striped bass fed on Atlantic menhaden, while offshore striped bass fed on sand lances (*Ammodytes spp*.). In the Gulf of Maine, Nelson et al. (2003) reported that striped bass diet is dominated mostly by clupeids, silversides (*Menidia sp*.), sand lance, sand shrimp (*Crangon septemspinosa*), rock crab (*Cancer irroratus*) and American lobster (*Homarus americanus*). Walter *et al*. (2003) speculates that the increased predation on invertebrates in the Gulf of Maine may be related to the sporadic availability of some clupeid species and the absence of sciaenids fishes. Lastly, food habits of striped bass in the upper Bay of Fundy, Canada provide similar findings of that observed in the Gulf of Maine. Rulifson and McKenna (1987) observed that young-of-year and age-1 striped bass diet consisted almost solely on sand shrimp while larger striped bass (271 – 360 mm fork length) diets were split between by hake (*Urophycis* sp.) and sand shrimp.

Abiotic factors – a description of striped bass habitat

The Albemarle Sound/Roanoke River watershed includes 18,300 square miles of drainage basin along the North Carolina-Virginia border and can be characterized into three distinct geological features: 1) the upper Roanoke River, 2) the lower Roanoke River, and 3) the Albemarle Sound estuarine system and its tributaries (NCSBSMG 1991). The upper Roanoke River begins in the Blue Ridge Mountains of North Carolina and Virginia and flows southeast into the Piedmont (a plateau region of low rolling hills between the mountains and the coastal plain). However, the flow of water into the lower river basin and Albemarle Sound is controlled by three dams located near the North Carolina-Virginia border. The upper two dams are for flood control (John H. Kerr and Lake Gaston), while the lower dam (Roanoke Rapids) is for hydropower. The lower Roanoke River basin, defined as the drainage area below the Roanoke

Rapids Dam to ~5 miles northeast of Plymouth, NC, constitutes the remaining portion of the river basin (13%) and is located in the coastal plain (Rulifson and Manooch 1991, USDOC and USDOI 1992). The Albemarle Sound is oriented east to west with seven major embayed lateral estuaries: the Chowan, Perquimans, Little Pasquotank, North, Scuppernong, and Alligator Rivers (Copeland et al. 1983). The Albemarle Sound itself is the drowned portion of the Roanoke River and its extensive floodplain, containing approximately 900 square miles (575,757 acres; 233,100 ha) of water (Copeland *et al*. 1983). The Sound is enclosed by barrier islands, with flow into the ocean limited to the Oregon Inlet. With a large freshwater inflow/Sound volume ratio, the Albemarle Sound is intermittently brackish (oligohaline) throughout its entire area (Copeland *et al*. 1983).

Albemarle Sound and Roanoke River

As noted above, three dams altered the natural flow of the Roanoke River, and the flow conditions to sustain striped bass were not initially considered when the dams were constructed (Rulifson 1989, USDOC and USDOI 1992). Later studies suggested that these hydropower and/or flood control measures caused a number of negative impacts to striped bass: sub-optimal oxygen concentrations in the lower Roanoke River and western portions of the Albemarle Sound in certain seasons; cessations or delays in spawning activity; adverse distributions of larvae as a result of flood control releases; and adult mortality due to sudden flow reductions (USDOC and USDOI 1992). Since the 1990s, however, hydropower discharge in the Roanoke River has been altered to mimic natural flow (Rulifson and Manooch 1993), and it is often cited as the key management measure in the stock's recovery in the 1990s.

In general, the salinity of the Albemarle Sound changes seasonally, based on discharge flows from the Roanoke River and the other seven tributaries, as well as the rate of evaporation

within the Sound (highest during the summer). A few studies have reported on the annual variations in salinity with the Albemarle Sound. Sampled surface salinities throughout the Albemarle Sound and found that salinities varied from 0 to 29 ppt on an annual basis (Bowden and Hobbie 1977 in Giese *et al*. 1979). During the spring (April) surface salinities ranged from 0 – 2 ppt throughout the Sound, while summer salinities (July) ranged between 26 and 29 ppt. Fall (November) and winter (January) salinities ranged from 1 – 5 ppt and 7 – 10 ppt, respectively. Other surveys report that the Albemarle Sound is essentially oligohaline (0.5 – 8.0 ppt) throughout the year, with the western portion of the Sound being essentially fresh water and the eastern-most portions of the Sound typically having salinities less than 8.0 ppt (Epperly 1984, Stanley 1992, Mohan 2009). The Pamlico Sound, which is separated from the Albemarle Sound by the Pamlico peninsula, exhibits slightly higher salinity levels (5 – 10 ppt; low mesohaline). Stanley (1992) noted that salinities are generally lower in the Albemarle Sound compared to the Pamlico Sound for two reasons: 1) the ratio of freshwater input to Sound volume is greater in the Albemarle Sound, which effectively blocks saline water intrusion, and 2) saline water that reaches the Albemarle Sound has already been diluted by the Pamlico Sound.

While year round salinity levels are not readily available for the Albemarle Sound, the United States Geological Survey (USGS) has been monitoring the salinity of the Pamlico Sound since 1989. The monthly average salinity level ranged between 0.7 and 15.4 ppt. Similarly, sampling by the University of North Carolina ModMon program noted that salinity levels are relatively constant through the year at 12.0 ppt (approximations based on salinity and depth profiles), increasing slightly to 18.0 ppt during the fall (September – November). These data from the Pamlico Sounds suggest that the Albemarle Sound salinity levels on average are less than 12 to 15 ppt throughout much of the year. Salinity data provided by Mohan (2009)

corroborate this conclusion as he found that salinity ranged between 0.1 and 8.0 ppt during the months of July through September of 2008 when salinity levels were expected to be at their highest.

Water temperature and dissolved oxygen data are lacking for much of the Albemarle Sound. Haeseker et al. (1996) reported the summer water temperature and dissolved oxygen concentrations of the Albemarle Sound for 1994. The average water temperature for the Sound was 21°C in May and increased to 28°C by mid June. Throughout June, July and August, temperatures remained between 25°C and 29°C. By late September water temperatures had declined to 22°C. Almost identical trends were observed by Mohan (2009) in 2008, who observed water temperatures declining from ~28.0°C in July to ~21°C in September in the Albemarle Sound. Similar trends in water temperature were also observed at the mouth of the Pamlico River (located in Washington, NC), averaging 22°C in May, increasing to 29°C in July, and declining to 25°C in September (between 1999 and 2009). Therefore, it is likely that water temperature profiles of the Albemarle Sound mimic those recorded in the Pamlico River that average 7.0°C in January and increases to 28.7°C in July.

Haeseker *et al*. (1996) reported that dissolved oxygen levels remained relatively constant throughout the summer of 1994, ranging from 6 to 10 mg/L. Dissolved oxygen only dropped below 6 mg/L for a two-week period in June. Mohan (2009) reported similar observations, with dissolved oxygen increasing from ~5.0 ppt in July to ~8.0 ppt in September during 2008. Dissolved oxygen sampling within the Pamilco Sound (via ModMon) also produced similar results during the summer months (May to September) varying between 7 and 8 mg/L (an approximation based on DO profiles versus water depth). Dissolved oxygen is assumed to be

lowest during the summer months, increasing during the other seasons when water temperatures are lower and dissolved oxygen saturation is higher.

The ambient strontium concentrations within the Albemarle Sound were reported by Mohan (2009), averaging 0.873 ppm ranging between 0.062 and 1.506 ppm. These concentrations are a magnitude higher than that reported by Woods *et al*. (2000), who observed that the Tar and Neuse Rivers Sr concentrations ranged between 0.04 and 0.05 ppm . The vast difference between the Sr concentrations of the Albemarle Sound and Tar and Neuse Rivers Sr are unexpected, given that both watersheds are fed by the same surficial and subterrain aquifers (i.e., Chesapeake, Castle Hayne, Pee Dee, and Potomac) (Trapp and Horn 1997). It is unknown if these differences are in fact real, or the result of human or equipment error.

Another aspect of abiotic impacts that could influence Sr uptake into fish otoliths is the rarely-reviewed ambient concentration of calcium. It is generally assumed that Ca concentrations within estuaries and rivers are constant, and that only variations of Sr are expected (Reviewed in Secor and Rooker 2000, Walther and Thorrold 2006). However, a recent study by Mohan (2009) found that high Ca concentrations in the eastern portion of the Albemarle Sound caused Sr:Ca ratios to max out at ~20.0 in salinities of just 5 ppt, where Sr:Ca ratios of 20.0 is usually equivalent to marine waters (35 ppt salinity). Even though Sr concentrations were highly correlated with salinity, the varying Ca concentrations caused Sr:Ca concentration to only be useful for tracking salinities between 0 and 5 ppt. Attempts to corroborate the findings of Mohan (2009) have been unsuccessful, as Ca concentrations observed in aquifers along the Pamlico Peninsula (i.e., the Alligator River) found that Ca concentrations were depleted or lower in the region (Woods *et al*. 2000a, 2000b).

Regardless of whether Ca concentrations are higher or lower in the eastern sound, it appears that Ca concentrations are not constant throughout the sound, which makes the use of Sr:Ca less useful for purposes of this study. Given that these findings were unknown at the beginning of dissertation research and that question is not settled, my approach in Chapter 4 is based on Sr:Ca ratio as a proxy for salinity. Within the results and discussion of Chapter 4, however, I will evaluate how my analysis could be affected by the new questions about Ca concentrations in the sound and provide alternative findings.

Oregon Inlet

Water quality conditions in the vicinity of Oregon Inlet differ from that of the Albemarle Sound proper, which as noted earlier is the most direct route for striped bass to enter and exit the Albemarle Sound. Only a few studies have reported on the water quality conditions of Oregon Inlet; thus, this review relies heavily on findings of Singer and Knowles (1975) who examined the hydrology and circulation patterns in the vicinity of Oregon Inlet. Oregon Inlet is located between the south end of Bodie Island and the north end of Pea Island, both barrier islands. The depth of this region is slightly deeper than the Albemarle Sound, ranging between 2.4 and 3.7 m. Dredged channels within the region are 3.0 to 3.7 m deep and 30.5 m wide (Singer and Knowles 1975), and are often re-dredged due to shoaling. Historically, the inlet gorge generally ranged in depth from 6.1 to 10.1 m and was nearly 0.8 km wide (Singer and Knowles 1975). However, due to the high levels of physical energy flowing into and out of the inlet, causing shoaling events, the main inlet migrated over time to the southern portion of the of inlet. Depth profiles of inlet and surrounding areas have likely changed substantially since 1975 when Singer and Knowles surveyed the area.

As reviewed by Singer and Knowles (1975), water temperatures ranged from 4°C in January to 21°C in August. Salinity at Oregon Inlet was observed at 8.5 ppt and 32.1 ppt within a single month, demonstrating that salinity did not simply follow seasonal fluctuations; rather it was dependent on the tide and wind direction. Water temperatures tended to track those observed in the Albemarle and Pamlico Sounds, which ranged from 5°C in January to 29°C in July (Reviewed in Singer and Knowles, 1975). A literature review was unable to identify any studies of dissolved oxygen or Sr levels observed in or near Oregon Inlet. Therefore, the assumption is made that DO and Sr levels should be in between levels observed in the Albemarle Sound and the Atlantic Ocean.

Atlantic Ocean – nearshore habitat

As noted above, striped bass entering the Atlantic Ocean normally stay within eight kilometers of shore and occupy waters ranging from Cape Hatteras, NC to Maine; however, striped bass are occasionally observed to migrate as far north as the St. Lawrence Bay, Canada. Water temperature data collected by the National Oceanic and Atmospheric Administration's National Oceanic Data Center (NODC) appear to remain relatively constant throughout the mid-Atlantic regions where striped bass regularly migrate (i.e., Mid-Atlantic Bight [Maryland – New York], Southern New England [Connecticut – Massachusetts]). Water temperatures in these areas, on average, range from 2.8°C in January to a high of 22.8°C in August. However, water temperatures in the vicinity of Cape Hatteras, NC and the Gulf of Maine vary significantly from waters in the Mid-Atlantic. In the coastal waters off of Cape Hatteras, NC water temperature are much warmer throughout the year, ranging from 7.8°C in February to 26.7°C in August. Within the Gulf of Maine, water temperatures are much colder throughout the year, ranging from 1.7°C in February to 16.1°C in August.

The regional differences in water temperature are related to the two main oceanic currents, the Gulf Stream and Labrador Current, which parallel the Atlantic coastline, merging near Oregon Inlet. Originating from the convergence of the warm water Loop and Antillies Currents near the Florida Keys, the Gulf Stream flows north along the eastern coastline of Florida (also referred to as the Florida Current). Once the Gulf Stream reaches the vicinity of Cape Hatteras, NC it turns (or is deflected) eastward from the continental shelf and flows in a northeastern path towards the Grand Banks off Newfoundland (Kelly 1991; Frankignoul *et al*. 2001). There, the Gulf Stream forms two main branches: a northern branch called the North Atlantic Current and a southern branch called the Azores Current (Krauss 1986; Hogg 1992).

The Labrador Current is a cold-water current that originates from the merging of the Baffin Island Current and a branch of the West Greenland Current (Fratantoni and Pickart 2007). The merging zone is located between Baffin Island, Canada and Greenland flowing southward along the coastline of Labrador, Canada (Thompson *et al*. 1986; Reynaud *et al*. 1995; Fratantoni and Pickart 2007). As the current continues to flow southward, it branches at two locations along the Grand Banks of Newfoundland. The first branching point is located at Flemish Pass, and the main branch continues southwestward while the minor branch merges with the warmer waters of the North Atlantic Current (Fratantoni and Pickart 2007). The second branching point is just south of Flemish Pass, at a location called the Tail of the Banks. At this point, the main branch of the current continues westward along the coastline of Nova Scotia, Canada and the minor branch turns eastward merging again with the North Atlantic Current (Fratantoni and Pickart 2007). The Labrador Current continues to flow on a southwestward path along the Scotian shelf and into the Mid-Atlantic Bight, finally ending inshore of the Gulf Stream off Cape Hatteras, North Carolina (Fratantoni and Pickart 2007).

Salinity levels remain relatively constant throughout the year in the Atlantic ocean, ranging between 33.6 and 35.0 ppt in the shallow shelf waters (0 – 200 m in depth) from North Carolina to Newfoundland (Wright and Parker 1976). Wood *et al*. (1996) reported slightly lower levels of salinities taken from water depths of 0 to 30 meters off the coast of North Carolina, ranging from 30.5 and 32.8 ppt. Further north, in the vicinity of Newfoundland and Nova Scotia, sea surface salinities are likely to range between 27.7 and 31.5 ppt (Lazier and Wright 1993).

Sr concentrations within the Atlantic Ocean were evaluated by de Villiers (1999). Readings taken along the approximate mid-point between North America and Europe ranged between 86.97 μM and 87.95 μM, which represents Sr:Ca ratios ranging from 8.519 mmol/mol to 8.605 mmol/mol. Sr levels taken from oceans around the world do not vary substantially from those observed in the Atlantic, and range between 86.92 μM and 88.98 μM. Therefore, it is reasonable to assume that Sr levels along the Atlantic coastline likely range between 8.5 and 8.6 mmol/mol or ppm, which is 170 times that of the Albemarle Sound.

Summary

For the purposes of this study, Sr concentrations in the otolith of striped bass are a proxy for determining the salinity of water inhabited by the fish during its life span. Salinity is strongly correlated to Sr concentration (Secor and Rooker 2000) and is considered the primary function controlling the uptake of Sr in fish ototliths. As discussed in the introduction in this chapter, several studies have shown that the incorporation of Sr into the otolith matrix of fish can be influenced by abiotic and biotic factors including water temperatures, ambient concentrations of Sr in freshwater habitat, diet of the fish, and maternal contribution to the yolk sac larvae. The

majority of this chapter reviewed the specific abiotic and biotic characteristics for AR striped bass.

Within the Albemarle Sound and Roanoke River, it does not appear that ambient concentrations of Sr are an issue for this study's purposes: concentrations range in the Sound from 0.062 to 1.506 ppm, whereas in marine waters the range is between 8.5 and 8.6 ppm.

Because different prey species uptake different amounts of Sr, then it follows that a variable striped bass diet would cause varying levels of Sr in the fish. However, striped bass have been found to consume mostly one type of prey: clupeids. Since clupeid species would be expected to uptake Sr at comparable rates, the effect of diet on the uptake of Sr in striped bass is probably small. Whether striped bass are feeding in estuaries or in the open ocean, several studies revealed that one certain clupeid, Atlantic menhaden, was the preferred prey item during the summer, fall, and winter months. During the spawning season when striped bass are found within their native river, their diet favored different clupeids, namely blueback or alewife herring. Since diet accounts for only 10-20% of variation observed Sr uptake, the effect of secondary and tertiary prey items on the Sr uptake in striped bass would be even more insignificant (Reviewed in Campana 1999).

Spawning behavior of female striped bass may affect Sr uptake for developing yolk-sac larvae, because the metabolism of the mother is expressed in the characteristics of the yolk-sac. Gravid females that overwinter in the ocean and gather in an oceanic staging area and quickly migrate up the river to spawn will create a more saline yolk-sac with concomitantly higher concentrations of Sr, compared to gravid females that do not overwinter in the ocean, gather in oceanic staging areas, or run quickly up the river to spawn. The larvae use the energy reserves from the yolk-sacs for the first 3 to 9 days of their lives before they have used up its contents.

The Sr uptake levels for a larva carrying a saline yolk-sac would suggest the individual was within marine waters. However, since this phenomenon is known, it would not be expected to introduce error in interpreting where the individual lived.

The seasonal changes in water temperature may affect Sr uptake. Compared to the Sound, seasonal temperature changes are slightly larger in the ocean, given the much larger latitudinal range encompassed there. Campana (1999) reported that Sr:Ca ratios increase 0.1 mmol/mol per 1°C change in water temperature. This would translate to an average of a ± 2.2 mmol/mol variance of the Sr:Ca ratio for resident striped bass that remain within the Roanoke River or Albemarle Sound throughout the year. Striped bass that participate in marine migrations could display Sr:Ca variances of ± 2.5 mmol/mol, assuming they migrated to the cold waters of Maine and Nova Scotia. Tagging data, however, suggest that the majority of migratory striped bass remain in the Mid-Atlantic or New York Bight waters, which means the average variance of Sr:Ca ratios would be ± 1.5 mmol/mol.

Campana (1999) did not specifically limit his temperature-uptake equation to striped bass. However, Secor et al. (1995) undertook laboratory and field studies of Sr uptake for striped bass otoliths and found that an average variance in the Sr:Ca ratio of 0.01 mmol/mol per 1°C change in water temperature – an order of magnitude smaller than Campana (1999) found. Applying this equation would translate to a Sr:Ca ratio variance of ± 0.22 mmol/mol for Sound residents and ± 0.25 mmol/mol for striped bass making the largest possible oceanic migration.

Regardless of whether Secor *et al*. (1995) or Campana's (1999) equation is applied to the sample studied here, the possibility of seasonal temperature variances affecting the interpretation of Sr uptake would be minimal. This is for two reasons: first, the variances due to water temperature fluctuations are cyclical with the seasons, and therefore predictable; and second,

because the magnitude of the effect, even with Campana's (1999) higher estimate, is much smaller than the effect of migrating from the Sound to the ocean or vice-versa. Fluctuations of Sr uptake caused by seasonal temperature changes could be considered background noise at a quiet level, while migration from Sound to the ocean or vice-versa would manifest as a louder and stronger signal.

Ambient concentrations of Ca are generally not considered a bias on Sr uptake into fish otoliths, because Ca concentrations are usually assumed to be relatively constant (although Ca is correlated with salinity). However, a recent study of striped bass migration patterns within the Albemarle Sound using otolith microchemistry techniques found that ambient Ca concentrations varied greatly between eastern and western portions of the sound (Mohan 2009). However, this result has not been replicated, and only one other study (Woods *et al*. 2000a, 2000b) has recorded relevant results on Ca concentrations. This study found that Ca concentrations in aquifers feeding the Alligator River, an eastern tributary of the Albemarle Sound, were lower than that of the western sound. This is the opposite of what Mohan's study would suggest for this area. Although conclusions or explanations are far from firm, the limited study on Ca concentrations in the Albemarle Sound sugges ts they are not constant, and this makes using Sr or Sr:Ca to predict salinity levels questionable.

The following chapter will discuss the results of otolith analysis and will consider whether maternal behavior, water temperature fluctuations, or ambient Ca concentrations affected Sr uptake in the examined samples.

Literature cited

Able, K. W. and T. M. Grothues. 2007. Diversity of striped bass (*Morone saxatilis*) estuarine movements: synoptic examination in a passive, gated estuarine observatory. Fisheries Bulletin 105: 426-435.

Bergey, L. L., R. A. Rulifson, M. L. Gallagher, and A. S. Overton. 2003. Variability of Atlantic coast striped bass egg characteristics. North American Journal of Fisheries Management 23: 558-572.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. Fisheries Bulletin, United States Fish and Wildlife Service 53, Washington D.C.

Boreman, J., and R. R. Lewis. 1987. Atlantic coastal migration of striped bass. American Fisheries Society Symposium 1: 331-339.

Buckel, J. A., B. L. Sharach, and V. S. Zdanowicz. 2004. Effect of diet on otolith composition in *Pomatomus saltatrix*, and estuarine piscivore. Journal of Fish Biology 64: 1469-1484.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263-297.

Chapoton, R. B., and J. E. Sykes. 1961. Atlantic coast migration of large striped bass an evidenced by fisheries and tagging. Transactions of the American Fisheries Society 90: 13-20.

Clark, J. 1968. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. Transactions of the American Fisheries Society 97: 320-343.

Cooper, J. E., R. A. Rulifson, J. J. Isely, and S. E. Winslow. 1998. Food habits and growth of juvenile striped bass, *Morone saxatilis*, in Albemarle Sound, North Carolina. Estuaries 21: 307-317.

Copeland, B. J., R. G. Hodson, S. R. Riggs, and J. E. Easley, Jr. 1983. The ecology of Albemarle Sound, North Carolina: an estuarine profile. Report FWS/OBS – 83/01 to the National Coastal Ecosystems Team, Division of Biological Services, Fish and Wildlife Service, U. S. Department of the Interior, Washington, D.C.

Coutant, C. C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Transactions of the American Fisheries Society 114: 31-61.

Coutant, C. C. 1986. Thermal niches of striped bass. Scientific American 255: 98-104.

de Villiers, S. 1999. Seawater Sr and Sr/Ca variability in the Atlantic and Pacific oceans. Earth and Planetary Science Letters 171: 623-634.

Dorazio, R. M., K. A. Hattala, C. B. McCollough, and J. E. Skjeveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Transactions of the American Fisheries Society 123: 950-963.

Elsdon, T. S., and B. M. Gillanders. 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. Canadian Journal of Fisheries and Aquatic Sciences 59: 1796-1808.

Epperly, S. P. 1984. Fishes of the Pamlico-Albemarle peninsula, N.C. area utilization and potential impacts. Special Scientific Report No. 42, North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, NC. 129 p.

Frankignoul, C., G. de Coetlogon, T. M. Joyce, and S. F. Dong. 2001. Gulf stream variability and ocean-atmosphere interactions. Jounral of Physical Oceanography 31: 3516-3529.

Fratantoni, P. S. and R. S. Pickart. 2007. The western north Atlantic shelfbreak current system in summer. Journal of Physical Oceanography 37: 2509-2533.

Giese, G. L., H. B. Wilder, and G. G. Parker, Jr. 1979. Hydrology of major estuaries and sounds of North Carolina. U.S. Geological Survey, Water Resources Investigations 79-46. 175 pp.

Greene, K. E., J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission Habitat Management Series No. 9, Washington, D.C.

Grothues, T. M., K. W. Able, J. Carter, and T. W. Arienti. 2009. Migration patterns of striped bass through nonnatal estuaries of the U.S. Atlantic Coast. American Fishery Society Symposium 69: 135-150.

Haeseker, S. L., J. T. Carmichael, J. E. Hightower. 1996. Summer distribution and condition of striped bass within Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 125: 690-704.

Hassler, W. W., N. L. Hill, and J. T. Brown. 1981. The status and abundance of striped bass, *Morone saxatilis*, in the Roanoke River and Albemarle Sound, North Carolina, 1956-1980. Special Scientific Report No. 38, North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, NC. 156 p.

Hill, J., J. W. Evans, and M. J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic): striped bass. United States Fish and Wildlife Service, Biological Report No. 82 (11.118), and U. S. Army Corps of Engineers Report No. TR EL-82-4, Washington, D. C.

Hogg, N. G. 1992. On the transport of the Gulf Stream between Cape Hatteras and the Grand Banks. Deep-Sea Research 39: 1231-1246.

Holland, B. F., Jr., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sports Fisheries, Special Scientific Report No. 24, Morehead City, North Carolina.

Kelly, K. A. 1991. The meandering Gulf Stream as seen by the Geosat altimeter: surface transport, position and velocity variance from 73° to 46° W. Journal of Geophysical Research 96: 16721-16738.

Kennedy, B. P., J. D. Blum, C. L. Folt, and K. H. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. Canadian Journal of Fisheries and Aquatic Sciences 57: 2280-2292.

Kernehan, R. J., M. R. Headrick, and R. E. Smith. 1981. Early life history of striped bass in the Chesapeake and Delaware Canal and vicinity. Transactions of the American Fisheries Society 110: 137-150.

Koo, T. S. Y. 1970. The striped bass fishery in the Atlantic states. Chesapeake Science 11: 73-93.

Krauss, W. 1986. The North Atlantic Current. Journal of Geophysical Research 91: 5061-5074.

Lazier, J. R. N., and D. G. Wright. 1993. Annual velocity variations in the Labrador Current. Journal of Physical Oceanography 23: 659-678.

Manooch, C. S., III. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. Chesapeake Science 14: 73-86.

May, P. G. 2001. Genetic and morphological characterization of striped bass *Morone saxatilis* collected from the Roanoke River, North Carolina during the 1999 spawning season. Master's Thesis. East Carolina University, Department of Biology, Greenville, North Carolina.

McDowall, R. W. 1992. Diadromy: origins and definitions of terminology. Copeia 1992: 248-251.

Merriman, D. 1937. Notes on the life history of the striped bass, *Roccus lineatus*. Copeia 15-36.

Merriman, D. 1941. Studies on the striped bass of the Atlantic coast. Fishery Bulletin 50: 1-77.

Meyers, G. S. 1949. Usage of anadromous, catadromous and allied terms for migratory fisheries. Copeia 1949: 89-97.

Milton, D. A. and S. R. Chenery. 1998. The effect of otolith storage methods on the concentrations of elements detected by laser-ablation ICPMS. Journal of Fish Biology 53: 785-794.

Mohan, J. 2009. Habitat utilization of juvenile striped bass *Morone saxatilis* in Albemarle Sound inferred from otolith and water chemistries. Master Thesis, Department of Biology, East Carolina University, Greenville, NC.

Morris, Jr., J. A., R. A. Rulifson, J. A. Babaluk, P. G. May, and J. L. Campbell. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry 34: 301-305.

NCDMF (North Carolina Division of Marine Fisheries). 2003. North Carolina Fishery Management Plan, estuarine striped bass, Albemarle Sound Area, Central/Southern Area. North Carolina Division of Marine Fisheries, Morehead City, NC. 363 p.

NCSBSMG (North Carolina Striped Bass Study Management Board). 1991. Report on the Albemarle Sound-Roanoke River stock of striped bass. U.S. Fish and Wildlife Service, National Marine Fisheries Service, North Carolina Division of Marine Fisheries, North Carolina Wildlife Resources Commission, Virginia Department of Natural Resources, and U.S. Army Corps of Engineers. 56 p + appendices.

Nelson, G. A., B. C. Chase, and J. Stockwell. 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. Northwest Atlantic Fisheries Science 32: 1-25.

Patrick, W. S. 2002. Genetic structure of striped bass, *Morone saxatilis*, populations from the Roanoke, Tar, and Neuse Rivers of North Carolina. Master's Thesis. East Carolina University, Department of Biology, Greenville, North Carolina.

Patrick, W. S. and R. A. Rulifson. 2003. The seasonal food habits of striped bass in the Albemarle Sound, North Carolina. Final Report to North Carolina Sea Grant, Project Number 00-EP14, Raleigh, North Carolina.

Pearson, J. C. 1938. The life history of the striped bass, or rockfish, *Roccus saxatilis* (Walbaum). United States Bureau of Fisheries Bulletin 49: 825-851.

Raney, E. C. 1952. The life history of the striped bass, *Roccus saxatilis* (Walbaum). Bulletin of the Bingham Oceanographic Collections at Yale University 14: 5-97.

Reynaud, T. H., A. J. Weaver, and R. J. Greatbatch. 1995. Summer mean circulation of the northwestern Atlantic Ocean. Journal of Geophysical Research 100: 779-816.

Rudershausen, P. J., J. E. Tuomikoski, J. A. Buckel, and J. E. Hightower. 2005. Prey selectivity and diet of striped bass in western Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 134: 1059-1074.

Rulifson, R. A. 1984. Food and feeding of young striped bass in western Albemarle Sound, North Carolina. East Carolina University, Institute for Coastal and Marine Resources Technical Report No. 84-07 for North Carolilna Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, North Carolina.

Rulifson, R. A. 1989. Abundance and viability of striped bass eggs spawned in the Roanoke River, North Carolina, in 1988. East Carolina University, Institute for Coastal and Marine Resources Technical Report 89-03 for North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Albemarle-Pamlico Estuarine Study Project No. APES 90-03, Morehead City, North Carolina.

Rulifson, R. A. and C. S. Manooch, III (eds.). 1991. Roanoke River Water Flow Committee Report for 1988 and 1989. NOAA Technical Memorandum NMFS-SEFSC-256. 209 p.

Rulifson, R. A. and C. S. Manooch, III (eds.). 1993. Roanoke River Water Flow Committee report for 1991 – 1993. Albemarle-Pamlico estuarine study, Project APES 93-18, Raleigh, North Carolina.

Rulifson, R. A., and S. A. McKenna. 1987. Food of striped bass in the upper Bay of Fundy, Canada. Transactions of the American Fisheries Society 116: 119-122.

Schaefer, R. 1970. Feeding habits of striped bass from the surf waters of Long Island. New York Fish and Game Journal 17: 1-17.

Secor, D. H., A. Henderson-Arzapalo, and D. M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology 192: 15-33.

Secor, D. H. and J. R. Rooker. 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fisheries Research 46: 359-371.

Singer, J. J. and C. E. Knowles. 1975. Hydrology and circulation patterns in the vicinity of Oregon Inlet and Roanoke Island, North Carolina. University of North Carolina Sea Grant Program Publication UNC-SG-75-15, Raleigh, NC. 171 p.

Stanley, D. W. 1992. Historical trends: water quality and fisheries, Albemarle-Pamlico Sounds with emphasis on the Pamlico River estuary. University of North Carolina Sea Grant College Program Publication UNC-SG-92-04. Institute for Coastal and Marine Resources, East Carolina University, Greenville, NC. 215 p.

Talbot, G. B. 1966. Estuarine environmental requirements and limiting factors for striped bass. Transactions of the American Fisheries Society 95: 37.

Thompson, K. R., J. R. N. Lazier, and B. Taylor. 1986. Wind-forced changes in Labrador Current Transport 91: 14261-14268.

Trapp, Jr., H. and M. A. Horn. 1997. U.S. Geological Survey, hydrologic atlas 730-L. http://pubs.usgs.gov/ha/ha730/ch_l/L-text3.html

Trent, W. L. and W. W. Hassler. 1966. Feeding behavior of adult striped bass, *Roccus saxatilis*, in relation to stages of sexual maturity. Chesapeake Science 7: 189-192.

Trent, W. L. and W. W. Hassler. 1968. Gill net selection, migration, size and age composition, sex ratio, harvest efficiency, and management of striped bass in the Roanoke River, North Carolina. Chesapeake Science 9: 217-232.

USDOC and USDOI (United States Department of Commerce and United States Department of Interior). 1992. Emergency striped bass research study. Report for 1990. Washington, District of Columbia. 31 p.

Vladykov, V. D., and D. H. Wallace. 1952. Studies of the striped bass with special reference to the Chesapeake Bay region during 1936-1938. Bulletin of the Bingham Oceanographic Collections, Yale University 14: 132-177.

Volk, E. C., A. Blakley, S. L. Schroder, and S. M. Kuehner. 2000. Otolith chemistry reflects migatory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and freshwaters. Fisheries Research 46: 251-266.

Walter, III, J. F., A. S. Overton, K. H. Ferry, and M. E. Mather. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. Fisheries Management and Ecology 10: 349-360.

Walther, B. D., and S. R. Thorrold. 2006. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Marine Ecology Progress Series 311: 125-130.

Winslow, S. E. 2002. Summary of North Carolina striped bass tagging programs (NC DMF) January 1980 – September 2001. North Carolina Division of Marine Fisheries, Northern District, Elizabeth City, NC.

Wirgin, I. I., R. Proenca, and J. Grossfield. 1989. Mitochondrial DNA diversity among populations of striped bass in the southeastern United States. Canadian Journal of Zoology 67: 891-907.

Wood, A. M., N. D. Sherry, and A. Huyer. 1996. Mixing of chlorophyll from the Middle Atlantic Bight cold pool into the Gulf Stream at Cape Hatteras in July 1993. Journal of Geophysical Research 101: 20579-20593.

Woods, T. L., E. G. Beck, D. T. Tolen-Mehlhop, R. Troiano, and J. K. Whitley. 2000a. Geochemical tracers of groundwater movement between the Castle Hayne and associated coastal plain aquifers. Final Report to Water Resources Research Institute of the University of North Carolina, Project Number 70148. 237 p.

Woods, T. L., P. D. Fullagar, R. K. Spruill, and L. C. Sutton. 2000b. Strontium isotopes and major elements as tracers of ground water evolution: example from the Upper Castle Hayne Aquifer of North Carolina. Ground Water 38: 762-771.

Wright, W. R., and C. E. Parker. 1976. A volumetric temperature/salinity census for the Middle Atlantic Bight. Limnology and Oceanography 21: 563- 571.

Table 1 – Summary of NCDMF tagging data from 1980 to 2002, noting striped bass that were recaptured in the Albemarle Sound, Pamlico Sound, and Atlantic Ocean.

	Albemarle Sound		Pamlico Sound		Atlantic Ocean		Total tagged in year and recaptured at later date
Year	Number	%	Number	%	Number	%	
1988-1992	204	97.6%	4	1.9%	1	0.5%	209
1993	257	99.6%	1	0.4%		0.0%	258
1994	157	100.0%		0.0%		0.0%	157
1995	109	98.2%	2	1.8%		0.0%	111
1996	140	96.6%	2	1.4%	3	2.1%	145
1997	241	95.6%	10	4.0%	1	0.4%	252
1998	202	94.0%	7	3.3%	6	2.8%	215
1999	224	96.1%	5	2.1%	4	1.7%	233
2000	186	94.9%	9	4.6%	1	0.5%	196
2001	162	96.4%	4	2.4%	2	1.2%	168
2002	1942	99.9%			2		1944
Totals	3824	98.4%	44	1.1%	20	0.5%	3888

Figure 1. A map of the Albemarle and Pamlico Sounds, North Carolina. Courtesy of ArcGIS.

CHAPTER 4: AN INVESTIGATION OF ROANOKE RIVER STRIPED BASS MIGRATORY BEHAVIORS USING GENETIC AND MICRO-PIXE ANALYSES

Introduction

The migratory patterns of striped bass based largely on tag-recapture studies have been well documented, with some of the earliest studies from the 1930s, 40s and 50s summarizing the movements of striped bass populations from the Gulf of Mexico to the Gulf of St. Lawrence (Reviewed in Collette and Klein-MacPhee 2002). The multitude of life history studies conducted since then indicates that Atlantic Coast striped bass migrate between their river and the estuary or between the river and marine environment. Populations located south of Cape Hatteras, North Carolina rarely emigrate into the marine environment, migrating only between riverine and estuarine environments. Thus, they complete the entire life cycle in the fresh and brackish waters of the natal watershed (Merriman 1941, Coutant 1985). Juvenile striped bass north of Cape Hatteras generally inhabit fresh/brackish water habitat until mature, at which time they emigrate to the ocean and become part of a larger migratory population that consists of multiple spawning populations that do not necessarily congregate with one another (Merriman 1941, Dorazio *et al*. 1994). The migratory population uses habitats ranging from coastal and estuarine waters of North Carolina to Atlantic Canada (Pearson 1938, Chapoton and Sykes 1961, Holland and Yelverton 1973, Boreman and Lewis 1987). It is generally believed that marine migratory adults return to natal rivers to spawn in the spring, only to return to the marine environment in later months.

Although different life history strategies of striped bass are observed between southern and northern populations, some populations located at the transition zone exhibit a mixed

migratory behavior. The Albemarle Sound/Roanoke River (AR) population located just north of the Cape Hatteras traditionally has been viewed as estuarine, though a portion of the population is believed to participate in marine migrations (Boreman and Lewis 1987, Haeseker *et al*. 1996, Winslow 2002, Greene *et al*. 2009). Dorazio *et al*. (1994) demonstrated through tag-recapture data that the probability of striped bass emigrating to marine waters depends on size or age class. In their study, Chesapeake Bay striped bass measuring ~800 mm total length (TL) had a 50% probability of emigrating into marine waters, and striped bass measuring ~950 mm TL striped bass had a 95% probability of emigration. Fishery managers and scientists believe that the current rate of marine migrations, which is based on tag-recapture data, in the AR striped population is low (0% to 3%; Winslow, 2002) because of the population's depleted age structure, a result of overfishing during the 1970s and 80s (see Chapter 1). As the AR striped bass age structure expands, fishery managers speculate that the rate of marine migrations will increase.

Morris *et al*. (2005) posited that a greater percentage of striped bass may emigrate into marine waters than previous tag-recapture data suggest. Morris et al.'s otolith microchemistry study examined the strontium (Sr) levels of six AR striped bass, since Sr concentrations in the otolith serve as a proxy for salinity levels a striped bass encounters over its life span (Reviewed in Secor and Rooker 2000). The six striped bass in the study were selected based on their age (e.g., 5+), sex (3 males and 3 females) and haplotype (I, II, and III). The combined genetic/otolith microchemistry study found that neither males nor females of haplotypes I and II had gone to sea up to the time of capture, but both the male and female of haplotype III had gone to sea and back at ages 4 and 5, prior to capture (Figure 1). Since haplotype III striped bass make up ~10% of the AR spawning population, Morris *et al*. (2005) suggested that the occurrence of marine migrations may also be as high as 10%. Their study further suggests that

there may be two AR subpopulations, differentiated by their migratory patterns: an estuarine group (freshwater to estuarine) and an anadromous group (freshwater to marine).

Morris *et al*. (2005) acknowledged that their study should be considered preliminary, since only a limited number of samples were analyzed, and that additional analysis is needed to confirm their observations. They suggested that confirmation could reveal insights into the contribution AR striped bass make to the marine migratory population, the control genetics exerts on migration for striped bass, and the need to protect genetic diversity of striped bass populations.

This chapter attempts to validate Morris *et al*.'s observations by analyzing an additional 120 samples from haplotypes I, II, and III. The primary objectives of this analysis were to: 1) estimate the percentage of striped bass that participate in marine migrations, 2) determine the age at which this behavior is initiated, and 3) determine if marine migration is correlated to a specific genetic subgroup of AR striped bass.

Methods

Albemarle Sound/Roanoke River haplotypes

May (2001) and Patrick (2002) identified, through sequencing of 370 base pairs in the mtDNA d-loop region, six distinct haplotypes in three North Carolina striped bass spawning populations, which included the AR population. While the populations exhibited heterogeneity, all three rivers shared the same three dominant haplotypes – I, II and III – which represented over 96% of the haplotype variation sampled in each population. Minor haplotypes specific to populations were also found within the AR (IV) and Neuse River (VI). Within the AR population, haplotype I represented 60% of the samples, haplotype II represented 24% of the

samples, and haplotype III represented 12% of the samples. The rest of the haplotypes (IV-V) made up the remaining 4% of the sample.

Data collection

Given a sequencing success rate of 60 to 80% documented in Patrick (2002) and the 12% rate of occurrence for haplotype III, it was necessary to collect around 470 AR striped bass to have a reasonable chance of obtaining greater than 30 haplotype III striped bass, which would provide a sufficient number of specimens to achieve a statistically significant distribution of the three haplotypes to test hypotheses concerning the influence of genetics on behavior. Based on the work of Dorazio *et al*. (1994), I also collected an additional 30 large striped bass (> 800 mm TL) to test whether larger/older striped bass participate in marine migrations more often than smaller larger striped bass, which may have biased the findings of Morris *et al*. (2005) because the fish they sampled ranged between 412 and 529-mm TL.

Sampling was conducted in 2004 and 2005. In 2004, sampling was focused on collecting 30 large striped bass (>800 mm TL) from the Roanoke River spawning grounds during the spawning season (March – June). These large fish were provided by two sources: 1) the North Carolina Wildlife Resources Commission (NCWRC) Watha Fish Hatchery, which collected the striped bass using electro-fishing boats in 2004 and used them that year as broodstock for their hatchery operations; and 2) a recreational fishing guide (George Beckwith, Jr., Down East Guide Service) who received special permission from the NCWRC to take up to 3 large fish (686 – 800 mm TL or 27 – 31 inches TL) per day until 18 fish were collected. Otolith and muscle tissue samples were obtained from the heads of the sampled fish.

In 2005, striped bass were captured by recreational fishers between the months of March and May. Sampling was conducted at various Roanoke River boat access areas throughout the

fishing season. Most of these fish were 18 – 22 inches (457 – 559 mm) TL, the slot limit for the recreational fishery, though fishers were allowed to keep one striped bass over 27 inches (686 mm) TL. Occasionally, a fisher donated one of these larger fish to the study. Like the large fish collected in 2004, only the fish heads of striped bass were needed for analysis; the remaining fish carcasses were kept by the recreational fishers.

All fish were measured for total length (TL), weighed (nearest ¼ pound or 0.1134 kg), and sexed, before the heads of the fish were removed. Fish heads that were collected at boat ramps were preserved on ice and then dissected within 48 hours in the lab to excise the otoliths and collect muscle tissue for genetic analysis. Fish heads that were provided by the NCWRC and recreational fishing guide had been frozen, so that all of the samples could be collected at once. All otoliths were rinsed with deonized water, wrapped in a paper towel, and stored at room temperature in a 5-mL plastic sample jar. Tissue samples for mtDNA analysis were obtained from muscle within the head or opercular region and stored at -20° C in a 5-mL plastic sample jar.

Genetic analysis

May (2001) and Patrick (2002) provide a detailed description of the methodology used to sequence the mtDNA d-loop fragment of striped bass. In brief, for this study, approximately 20 mg of tissue was sub-sampled from the stored tissue and extracted for genomic DNA. The d-loop region of mtDNA was amplified from the genomic DNA by the polymerase chain reaction (PCR), using mitochondrial DNA d-loop specific PCR primers (Table 1). The final amplification product was approximately 1.6 kilobases in length, of which about 400 base pairs were sequenced using mtDNA d-loop specific primers and fluorescence-based Sanger sequencing technology. The products obtained from DNA sequencing reactions were analyzed

on an Applied Biosystems 377 Model automated DNA sequencer. Raw sequencing data were edited and both the forward and reverse strands for each sample were assembled using Autoassembler software (Applied Biosystem, Foster City, California). The final d-loop DNA sequences were compared to each other using both the Sequence Navigator software program from Applied Biosystems and the Pileup software program from GCG (University of Wisconsin, Genetics Computer Group). After aligning sequences from all the fish collected, the DNA sequences were grouped according to haplotype based on the pattern of shared nucleotide differences.

Otolith microchemistry analysis

After tissues were genetically typed, 30 randomly selected otolith samples from each haplotype (I, II, and III), and all otoliths from the larger (>800 mm TL) striped bass were analyzed for Sr concentrations. Otoliths were prepared for proton-induced x-ray emission microprobe analysis (micro-PIXE) analysis by sectioning the focus or core of each otolith using a low speed Buehler saw, resulting in a 0.8-mm otolith section. Six sectioned otoliths were placed into a 25.4-mm diameter Lucite® disc probe mount, and backfilled with cold cure epoxy. After curing, the face of each otolith was sanded and polished using aluminum oxide lapping films. The first two grades of polishing (30 and 12 μm) were performed by hand, and the last step of polishing (9 μm) employed a rotary polisher. After polishing, the samples were cleaned thoroughly with deionized water, dried with a Chem® wipe, and shipped for final preparation to John Babaluk at Fisheries and Oceans Canada, Winnipeg, Manitoba. Final stages of preparation included a 2-3 minute ultrasonic wash in Buehler Ultramet Sonic Cleaning Solution (1 part cleaner to 20 parts deionized water), followed by 2-3 minutes in distilled/deionized water only,

and then followed by 2-3 minutes in 95% ethyl alcohol. Samples were then air-dried and immediately coated with carbon.

Carbon-coated otolith discs were shipped to Dr. Ian Campell at the University of Guelph to be scanned using a micro-PIXE machine. Each otolith was examined using the University of Guelph proton microprobe. A one-dimensional line-scan of the Sr K x-ray intensity for each otolith was obtained by scanning a transect of the otolith from the core area to the dorsal edge of the otolith, incorporating all annuli. The beam diameter was ~10 μm and each data point along the transect was spaced at 4 μm. All measurable Sr data were analyzed using GUPIX software (Maxwell *et al*. 1995). For a detailed description of micro-PIXE analysis, refer to Morris et al. 2005.

Based on a review of strontium to calcium ratios (Sr:Ca), Morris *et al*. (2005) conservatively estimated Sr concentrations in freshwater habitat to be < 2,000 mg kg^{-1}, estuarine habitat to range between 2,000 – 4,000 mg kg^{-1}, and marine habitat to contain > 4,000 mg kg^{-1}. These Sr ranges correspond with Secor *et al*.'s (1995) equation for estimating salinity that relies on Sr:Ca ratios:

$$\text{Estimated Salinity} = 40.302\ (1 + 56.337\ EXP^{-1523.31*\text{Sr:Ca Ratio}})^{-1}$$

To estimate calcium concentration within the otolith, I used a reference amount of 1,000,000 mg kg^{-1} from Campana's (1999) meta-analysis of elemental concentrations of otoliths. Using Secor *et al*.'s salinity conversion equation, the Sr concentration ranges of Morris et al. (2005) equate to 0 – 11 ppt (< 2,000 mg kg^{-1}), 11 - 35 ppt (2,000 – 4,000 mg kg^{-1}), and > 35 ppt (> 4,000 mg kg^{-1}). Sr:Ca ratios were calculated for each data point along the one-dimensional

line-scan and then converted to estimated salinity levels in parts per thousand (ppt). Estimates of salinity levels were then superimposed on a digital image of the cross-sectioned otolith to determine how salinity levels varied over the lifetime of each individual.

The conversion of Sr concentrations to salinity profiles are estimates and may not reflect the true salinity inhabited by the fish. While the Secor *et al*. (1995) salinity conversion equation has a maximum salinity estimate of 40 ppt based on its logarithmic shape at high Sr:Ca ratios, a striped bass is unlikely to inhabit waters with salinities higher than 35 ppt, since maximum salinities in the Atlantic Ocean where striped bass have been captured are 35 ppt (see Chapter 3). The salinity profiles are better viewed relative to other habitat profiles chemically imprinted on the otolith, to indicate a change to markedly more saline habitat.

Age calculations and other related analysis

To validate the age of fish, two otolith readers separately determined the age of each fish examined by micro-PIXE analysis. Any disagreement in age classifications resulted in the disqualification of that otolith for age analysis. To examine how Sr levels and fish length (mm) varied among age classes, each annulus was examined to document the starting and ending point for Sr analysis and provide a reference point for back-calculating fish lengths.

Statistical analyses

Various descriptive and inferential statistics were performed on the data collected. Using both Microsoft Excel and SPSS software, descriptive statistics including means, minimums, maximums, and percentages were calculated for age, sex, fish length, migratory types, and salinity estimates. A Kruskal-Wallis statistical test was performed to determine if haplotypes

were related to migratory behavior types (measured as period of time spent in marine waters; based on # Sr counts above 4,000 ppm compared to total number of Sr counts).

Kruskal-Wallis statistical tests (SPSS software) were performed on the following data groupings to determine if there was a significant difference between groups. If significant differences occurred, a Mann-Whitney post hoc test was performed to determine which variables were significantly different:

1. Length of Fish at Age X versus Haplotype
2. Length of Fish at Age X versus Migratory Type
3. Initial Sr Concentration versus Haplotype
4. Initial Sr Concentration versus Migratory Type
5. Mean Sr Concentration at Age X versus Haplotype
6. Mean Sr Concentration at Age X versus Migratory Type
7. Max Sr Concentration at Age X versus Haplotype
8. Max Sr Concentration at Age X versus Migratory Type

Results

Overall, 536 striped bass were collected during the 2004 (*N = 34*) and 2005 (*N = 502*) sampling season. The mean total length of fish collected in 2004 was 782 mm TL (range 433-1025 mm TL). Nineteen of the 34 fish collected in 2004 were donated by the NCWRC Fish Hatchery in Watha, NC, the majority of which (*N = 13*) were 750+ mm TL adults. The remainder of the 34 fish was captured by the George Beckwith, Jr. Guide Service, and all measured approximately 800 mm TL. In 2005, sampling began in March; however, striped bass did not enter the Roanoke River to spawn until mid-April. Therefore, all fish were collected over

a two-and-a-half week period from April 14th to May 1st, when the recreational striped bass fishery closed. The mean length of fish collected in 2005 was 503 mm TL (range 409-908 mm TL).

Two hundred and thirty-six (44%) of the 536 tissue samples collected in 2004 and 2005 were successfully haplotyped; all failures came from 2005 collections. It is unknown what caused the 2005 tissue samples to have such a low DNA amplification success rate.

The genotypic distribution of 2004 collection, consisting of 34 mainly 800 mm TL fish, was: 50% haplotype I (N = 17), 32% haplotype II (N = 11), and 18% haplotype III (N = 6). The 2005 collection saw successful amplification of 202 samples from the 502 tissue samples collected that year (40%). The haplotype distribution of striped bass collected in 2005 was 63% haplotype I (N = 128), 21% haplotype II (N = 42), 14% haplotype III (N = 29), and 2% haplotype V (N = 3).

Haplotype IV fish were likely present in the sample, but due to a new sequence primer set that sequences a smaller portion of the mtDNA d-loop, the portion of the mtDNA d-loop that contains the mutation identifying haplotype IV was not sequenced. Since haplotype IV share a common mutation event with haplotype II fish, a small portion of haplotype II fish could actually be haplotype IV. However, since May (2001) and Patrick (2002) indicate that haplotype IV is relatively rare (~5%), this outcome would not likely skew results significantly.

Of the 236 haplotyped fish, 122 had their otoliths prepared for micro-PIXE analysis. This included all 34 large fish (> 750 mm TL) collected in 2004, a random sample of 30 fish each from haplotype I and II collected in 2005, and all 29 haplotype III fish collected in 2005. One hundred and ten otoliths were successfully analyzed by micro-PIXE, with corresponding genetic data. Twenty-nine of these otoliths were obtained from fish more than 6 years old.

A total of 115 otoliths were aged. The 18-22 inch slot limit skewed age distribution toward age-5 fish (Table 2). Back calculations of fish length found many age classes overlapping, indicating a wide range of growth rates in striped bass (Figure 2). The majority (60%) of haplotypes examined came from the 2000 year class, as expected based on the skewed sampling of age-5 fish in this slot-based fishery. Because there were only about ~30 random samples of haplotypes I, II, and III (as opposed to random sampling by year class), the sample size was not large enough to allow for statistical analysis to determine if haplotype frequencies varied among year classes. However, Patrick (2002) noted that there were no qualitatively observable differences in haplotype frequencies and year classes.

Migratory behaviors as inferred from otolith Sr:Ca ratios

Overall, 87% of Roanoke River striped bass exhibited signs of anadromy, if only for a short period of their life time (Table 3). The majority (79%; n=89) of adult striped bass spawning in the Roanoke River appear to have migrated to marine habitat during their first year of life (i.e., young-of-year (YOY). However, strontium levels suggest that these migrations were short in duration, such that most (80%; n=72) of YOY returned to estuarine habitat before forming the first annulus. In subsequent years of life, the occurrence of marine migrations decreases to 40% of fish at age 2, and 19% by age 5 (Table 4). Age-6 and older fish did not appear to enter marine waters, except for one fish at age 8. None of the 115 striped bass exhibited potential signs of maternal Sr contributions, which would have been identified as initial Sr readings at the core of the otolith above 4,000 ppm (>35 ppt estimated salinity), followed by a quick decline to concentrations of 1,000 to 2,000 pm within 30 μm (~10 days).

Unlike observations by Morris *et al*. (2005), there was no indication that haplotype III AR striped bass participated in marine migrations more often than haplotype I or II striped bass.

A Kruskal-Wallis test comparing haplotype I, II, and III striped bass to the period of time spent in the marine waters found no significant differences ($P = 0.612$). Kruskal-Wallis statistical test also found no significant differences between the frequency distributions of marine migrants versus sex ($P = 1.000$).

Further examination of migratory movements revealed that AR striped bass display one of four major migratory behaviors in the first year of life. YOY striped bass migrating into the western Albemarle Sound from their riverine spawning grounds spend their first year as: 1) a stager, 2) a sprinter, 3) an estuarine resident or 4) mixed behavior. The word "stager" refers to those fish that moved into different habitats in consecutive stages, first staying in oligo- or mesohaline habitat ($Sr < 2{,}000$ ppm) , then moving to a meso- or polyhaline habitat ($2{,}000$ ppm $< Sr < 4{,}000$ ppm) for some length of time, then finally moving into the marine habitat ($Sr > 4{,}000$ ppm) near the end of their first year (Figure 3). The designation "sprinter" refers to those fish that moved quickly from an oligo- or mesohaline habitat into the marine habitat (Figure 4). Estuarine residents never moved into the marine waters during the first year of life, although they may have inhabited high salinity waters (~32 ppt) similar to that of the Croatan, Pamlico, or Roanoke Sounds, or Oregon Inlet (Figure 5; see Chapter 3). The fourth behavior, mixed, displayed unusually high initial Sr concentrations (averaging 4,700 ppm) that either gradually declined to concentrations similar to that of the estuarine waters or mimicked other marine migratory behaviors described above (Figure 6). These four distinct and clear-cut behaviors were observable only in the first year of life. The frequency of occurrence for these different migratory behaviors was dominated by mixed (36%), followed by sprinters (28%), residents (23%) and stagers (13%).

The otoliths sampled from the fish that exhibited these four migratory behaviors were significantly different in both mean ($P = 0.001 – 0.048$) and maximum Sr concentrations ($P = 0.001 – 0.050$) observed in the first, second, and fifth year of growth (Table 5). Migratory behaviors also had significantly different ($P < 0.001$) initial Sr concentrations. Mann-Whitney post-hoc test revealed that the behavior category mixed had significantly higher Sr concentrations than all other behaviors observed ($P < 0.001$). A Kruskal-Wallace test did not find migratory behaviors to be correlated with specific haplotypes ($P = 0.760$).

Migratory behavior and growth as inferred from otolith Sr:Ca ratios

On a post hoc basis, I further investigated why it appeared that only a portion of AR striped bass participated in marine migrations (i.e., exhibited partial migration – see Kerr et al. 2009). One possible reason is that marine waters offer better foraging habitat or less competition compared to the Albemarle Sound; to test this, I compared growth rates among migratory behavior groups. The mean length (TL mm) of each migratory type versus age was plotted to display differences in growth in relationship with time (Figure 7). Stagers, sprinters, and mixed behaviors displayed significantly lower growth rates than resident striped bass ($P < 0.029$) at ages 2 through 5 (Table 6) (I was unable to compare ages 6 – 14 because of insufficient data for statistical tests). The differences observed between migratory behaviors and growth was quite large. At age 2, stagers, sprinters, and mixed striped bass were on average 75 to 79 mm smaller than estuary resident striped bass (~434 mm TL), respectively. And by age five, stagers, sprinters, and mixed striped bass were on average 90 to 105 mm smaller than estuary resident striped bass, who were on average 625 mm TL. Beginning at age-6, however, these differences in growth were no longer observed, likely due to the low sample size (N=29).

Albemarle Sound/Roanoke River YOY striped bass were divided into four salinity groupings, based on Secor et al.'s (1995) conversion equation and the mean salinity value in their first year of life (regardless of migratory type), to determine if there was an optimal salinity in which YOY striped grew. The salinity groupings included: 0 – 10 ppt; 11 – 20 ppt; 21 – 30 ppt; and > 30 ppt (Figure 8). ANOVA and Tukey post hoc tests revealed AR YOY striped bass in the 11-20 ppt salinity grouping were significantly larger (mean = 295 mm TL) than fish in 21-30 ppt ($P = 0.043$; mean = 249 mm TL) and > 30 ppt ($P < 0.001$; mean = 250 mm TL) salinities. Sample sizes for the 0-10 ppt salinity grouping was small (n=7, mean TL = 242 mm), and its size was not found to be significantly different ($P = 0.116$ to 0.936) from any of the other salinity grouping.

Discussion

Management of the Albemarle-Roanoke striped bass stock can be difficult, because the population is located at the transition zone differentiating resident and anadromous striped bass, and therefore the life history strategies of this spawning population are not clear. Most of the life history strategies known about striped bass come from anadromous populations, in particular the two largest striped bass populations, which are found in the Chesapeake Bay (multiple spawning stocks) and the Hudson River.

Migratory patterns and comparison to other studies

The findings here suggest that AR striped bass do not follow the paradigm described by Dorazio *et al*. (1994), in which the marine migration of Chesapeake Bay striped bass is positively correlated with age or length. Instead, the salinity proxy (Sr concentration in the

otolith and related salinity equation) used here suggests that AR striped bass are more likely to go to sea briefly at age 1 than at later ages.

NCWRC's tagging-recapture studies of adult spawners between 1988-2001 saw few recaptured in the ocean (Winslow 2002). Between those years, 20,520 adult striped bass were tagged in the riverine spawning grounds (average per year = 1,465) and ~2,000 were recaptured. Only 1% (20) of the recaptured fish were found in the ocean. The true recapture rate in the ocean could actually be 2% or higher, since fishermen report capture of tagged fish only about half the time (Poulsen 1957; Aires-da-Silva 2009; Kurota 2009). There are other factors that could have influenced this low number, including that most of the recaptured fish are found within a short time (30 days) of being tagged (Winslow 2002), which means a large portion of the recaptured fish may not have had much time to migrate away from the tagging site. Additionally, those fish that do migrate to the ocean only spend a portion of the year there, which affects the chance of their recapture at sea. Finally, there may be more recapture effort applied in the estuary than in the ocean, since the estuary is a smaller and more accessible place for many fishermen. These tagging-recapture findings are not necessarily inconsistent with the findings described in this study, which found that likelihood of migrating to the ocean declined with age (Table 4).

The observation that some proportion of YOY striped bass migrate into the marine waters is not unique to the AR population. Although Dorazio *et al*. (1994) found no evidence of YOY migrating to the ocean, others studying Hudson River and Chesapeake Bay striped bass did find this behavior (Zlokovitz *et al*. 2003; Secor and Piccoli 2007). Zlokovitz *et al*. (2003) consistently observed juvenile striped bass using polyhaline habitats (i.e., 19-35 ppt salinity) during the first year of life. Zlokovitz *et al*.'s (2003) observations are supported by Hurst and

Conover (2002), who found that YOY striped bass may reduce over-wintering mortality by seeking higher salinity waters. Hurst and Conover's (2002) one- and two-week simulated overwintering laboratory experiments observed the lowest mortality rates for striped bass (i.e., ~10% to 30%) to be in 15 to 25 ppt saline waters, with 30 to 35 ppt saline waters often having the second lowest mortality rates (i.e., ~20 to 30%). Freshwater (0 ppt) and slightly brackish waters (5 ppt) had the highest mortality rates (i.e., ~50% to 100%) during those one- and two-week trials. In their four-week trial experiments, 35 ppt saline waters caused higher mortality rates (~80%) than 5 ppt saline waters (40% mortality), and they concluded the discrepancy between the survival of fish in 30-35 ppt saline water in one- and two-week trials versus the four week trial was likely due to the cumulative effects of exposure.

Hurst and Conover's (2002) findings also may explain why a majority (80%; n=72) of YOY AR striped bass examined in this study presumably returned from marine waters prior to the overwintering period – a change observable on the otolith as occurring just before the annuli is created during the winter (Schramm 1989; Beckman and Wilson 1995). Of the 72 AR striped bass returning to the estuary – 74% (n=53) of them inhabited waters with a mean of 25 ppt estimated salinity (95% Confidence Interval = +/- 7 ppt), which Hurst and Conover (2002) identified as the salinity range associated with the lowest mortality rates (i.e., ~10%) in their four-week trial experiment. In sum, AR striped bass that presumably use marine habitat in the first year of life could return to estuarine waters to overwinter, because survival is higher there than in marine or freshwater areas.

The findings that marine migrants (i.e., stagers and sprinters) display significantly slower growth rates than resident AR striped bass may also be related to habitat use. Bogadanov *et al*. (1967; reviewed in Greene *et al*. 2009), described the optimal salinity conditions for YOY

striped bass survival as between 10 and 20 ppt. Assuming that survival is a proxy of growth since the growth rate would likely be higher for less-stressed fish, it is plausible that AR YOY striped bass migrating to marine waters do not grow as fast as estuary resident striped bass inhabiting waters optimal for survival. My study found that YOY AR striped bass in waters with mean salinity values between 11 and 20 ppt exhibited significantly higher growth rates compared to those in waters with mean salinity values between 20-30 ppt ($P = 0.043$) and higher than 30 ppt ($P < 0.001$) (Figure 8).

Other possibilities explaining the differences in growth of marine migrants versus residents in both the first year and subsequent years could include: 1) naturally slow growers; 2) poor food availability, thus burning up more energy and slowing growth rate; 3) normal or faster-growing fish potentially targeted more by predators; and 4) migrants may be less effective predators after returning from marine waters, compared to estuarine residents accustomed to that habitat.

Some salmonid studies have shown that slower-growing fish have a tendency to migrate more than the faster growing residents (Nordeng 1983; Jonsson and Jonsson 1993; Naslund *et al*. 1993). However, the opposite trend was observed in white perch (*Morone americana*), a sister taxon of striped bass (Kerr *et al*. 2009).

The condition of the habitat within the Albemarle Sound may also cause YOY striped bass to migrate into marine environments, traditionally referred to as the random escapement hypothesis (Tsukamoto *et al*. 2009). If a particular habitat is not productive, fish may expend high amounts of energy moving from one habitat to the next which can lead to exhaustion, stress, and increased risk of infection (McCleave and Edeline 2009). Mohan (2009) demonstrated that YOY striped bass that frequently moved between tributaries within the Albemarle Sound had

slower growth rates compared to those that remained within a single tributary or embayment during its first year of life.

Predation rates on YOY in shallow-water estuaries (like the Albemarle Sound) are usually lower than in deepwater habitat, because shallow-water estuaries have better refugia for these young fish (e.g., marsh grass) and fewer large piscivorous fish (Paterson and Whitfield 2000). If this assumption applies in the Albemarle Sound (see Sheaves 2001), it is possible that marine migrants may be susceptible to higher predation rates. However, the predation rate would have to be selective of striped bass that have average or above average growth rates (and thus are not available to be sampled), compared to slower growing marine migrants who survived the first year of migration and were later captured and analyzed for this study.

The disproportionately low growth of AR striped bass participating in marine migration during the first year of life carries through to subsequent years, but these comparatively low growth rates do not appear to be linked to a specific haplotype examined in this study. Another alternative for the disproportionately low growth in subsequent years could also be explained by competition. Patrick and Moser (2001) reviewed the competitive interactions of striped bass and hybrid striped bass in the Cape Fear River, NC and suggested faster-growing hybrid striped bass (similar to faster-growing estuary resident striped bass) likely out-compete the slower-growing striped bass for food and refugia.

The above findings and suggestions provide supportive evidence as to why AR striped bass exhibit partial migration into marine habitat and varying growth rates. However, a more recent study by Mohan (2009) suggested that the application of Secor's salinity equation may bias interpretation of the results, as he found that Sr:Ca ratios from four of the nine tributaries within the Albemarle Sound were not correlated with salinity (the other five tributaries were not

sampled in his study). Mohan (2009) did observe a high correlation between Sr and salinity in the Albemarle Sound, but unexpectedly higher concentrations of Ca in the eastern portion of the Sound caused Sr:Ca ratios to max out at 20.0 to 21.0 at salinities of just 5 ppt (Figure 9). These Sr:Ca ratio values are more than twice those observed in marine waters (~9.0), which means that Sr uptake into the otolith is governed by the concentration of Ca in the water as opposed to the concentration Sr or the salinity of the water in the Albemarle Sound. Mohan's (2009) findings, however, do not align well with Woods et al. (2000a, 2000b), who examined the micro-elements of ground and surficial waters in the Pamlico Sound and observed a low concentration of Ca in wells located along the Pamlico Peninsula (i.e., the Alligator River). If Mohan's findings are correct, and the Albemarle Sound has very unique Sr:Ca ratios that exceed those of 98% of the 507 locations reviewed in Kraus and Secor (2004), then Sr concentrations within otolith are only useful for identifying freshwater and oligohaline habitats within the Albemarle Sound (Sr < 1,500 ppm),

Regardless of the degree of correlation between Sr:Ca and salinity in the Albemarle Sound, it is still possible to observe that AR striped bass with Sr concentrations greater than 4,000 ppm exhibited staging and sprinting behaviors, and had slower growth rates compared to AR striped bass that did not exhibit these migratory behaviors. Although not described in Mohan (2009), analysis of his appendix shows that stager, sprinter, resident, and mixed behaviors were present: 80%, 10%, 0%, and 10%, respectively. Mohan (2009) described migratory behaviors as resident and transient YOY AR striped bass, defining residents as YOY striped bass that reside within a particular habitat for the first year of life, and transients as YOY striped bass that exhibited different habitat signatures the last few weeks before capture, compared to the period before.

Resident fish displayed higher growth rates than compared to transients, which Mohan (2009) suggested was due to transients expending energy searching for better habitat. A large portion of the residents (46%) and transients (67.7%) observed in Mohan's study, however, exhibited otolith Sr concentrations above 4,000 ppm. The high percentage of transients exhibiting mixed concentrations is expected, but findings here would not predict the same for residents. The finding here, that YOY AR striped bass entering mesohaline waters (Sr > 4,000 ppm, originally believed to be marine waters) exhibit lower growth than striped bass remaining in waters less than 5 ppt, is contradicted by Mohan's (2009) findings, and requires further validation.

Migratory behaviors and genetics

The main purpose of this study was to validate the preliminary findings of Morris et al. (2005), who suggested that the AR stock of striped bass may consist of two subpopulations – a "resident" group and an "anadromous" group. Morris *et al*.'s (2005) findings were based on the observation that haplotype III striped bass exhibited signs of anadromy (based on Sr concentrations > 4,000 ppm), while haplotype I and II did not. The findings here do not corroborate Morris et al.'s findings, because there were no significant differences observed among haplotype I, II, or III striped bass and Sr concentrations ($P = 0.948$). Instead, Sr concentrations greater than 4,000 ppm and the period of time spent in these waters was randomly distributed among all three haplotypes. The differences observed between the two studies are likely due to sample size: Morris *et al*. (2005) evaluated 6 otoliths (2 from each haplotype), while this study evaluated 115 otoliths, 29 of which were haplotype III striped bass. It is plausible that migratory patterns of striped are genetically linked, but were not detected in this study due to the type of genetic markers examined. As described in Chapter 2, the mtDNA haplotype markers

used here are the same as those used by Morris et al. These markers are based on the highly mutable mtDNA d-loop region, and are not linked with a discernable phenotypic trait. Instead the DNA sequences characteristic of a particular haplotype, which I designated as either I, II, or III are purely a reflection of individual maternal lineages that can be differentiated from one another based on the inheritance of mtDNA d-loop sequence differences. As of yet, these sequence differences have not been linked to any phenotypic difference among the lineages they represent. Therefore, it is feasible that there is marine migratory sub-population of AR striped bass, but based on the best available science this claim is not supported at this time.

Abiotic and biotic effects on strontium uptake

As described above (Migratory patterns and comparison to other studies) and in Chapter 3, several studies have shown that the incorporation of Sr into the otolith matrix can be influenced not only by the salinity of the water, but also water temperature, ambient concentration of Sr and Ca in the water, diet, and maternal contributions to the developing yolk-sac larvae. All of these influences could potentially affect the results of this analysis. Complications due to ambient concentrations of Sr and Ca in the Albemarle Sound have already been discussed previously (Migratory patterns and comparison to other studies – Mohan (2009) discussion). Maternal contributions of Sr and water temperatures were identified as potential hurdles that would need to be overcome in this analysis in Chapter 3. Each of these two factors, however, was easily identifiable because the effects on Sr uptake were known and observable. Maternal contributions were not observed.

A 1°C increase in water temperature can cause an increase in Sr:Ca uptake of 0.01 to 0.1 mmol/mol (Secor *et al.* 1995, Campana 1999). Since Sr:Ca levels are a proxy for salinity, and given the range of water temperatures in the Albemarle Sound, salinity estimates could therefore

be skewed by as little as 1 ppt (0.01 mmol/mol) or as much as 18 ppt (0.1 mmol/mol). Since this study found no evidence of cyclic variations of Sr:Ca levels that followed seasonal cycles of water temperature in the sound, Secor *et al*.'s lower estimates of the effect of temperature on Sr:Ca uptake are more reliable. For example, one striped bass examined showed a constant estimated salinity profile of approximately 2 ppt throughout its entire life, with the variability in salinities ranging from 1 ppt to 4 ppt (Figure 10). The largest change in estimated salinity profile occurred in the first year of life, when salinity ranged from 2 ppt and 4 ppt. Knowing that water temperature in the Albemarle Sound and Roanoke River changed by 20° C during that period, this striped bass would have had to find thermal refugia repeatedly, an unlikely occurrence (see Haeseker et al. 1996). Therefore, the significant effect of water temperature on Sr:Ca uptake reported by Campana (1999) probably does not apply to AR striped bass.

Conclusions

My findings suggest Roanoke River striped bass exhibit four migratory behaviors during their first year of life: residents, stagers, sprinters, and mixed. Residents remain in waters less than 4,000 ppm Sr, while stagers and sprinters enter waters with Sr concentrations higher than 4,000 ppm for a short period of time. Mixed striped bass show unusually high Sr concentrations (> 4,000 ppm) during the first several months of development and then display a mixture of resident, stager, and sprinting behaviors. Approximately 82% of the YOY striped bass that enter 4,000 ppm Sr waters return to lower concentrations of Sr just before overwintering. Subsequent migrations into 4,000 ppm Sr waters occur at a lower frequency until age 6, when the likelihood of migration into these water falls to 0% to 4%. Young-of-year that migrate into high Sr water (> 4,000 ppm) appear to have slower growth rates than resident striped bass, and differences in

growth are significantly different at age 2. Despite returning to waters with lower Sr levels (usually by age 1), growth rates continue to be slower for migrants compared to residents: age-5 migrants are 90–105 mm smaller than resident fish of the same age. The different migratory behaviors are not related to known striped bass haplotypes, as was previously hypothesized by Morris *et al.* (2005).

The management implications of this study are several. First, this study indicates that as many as 87% of Roanoke River striped bass may migrate into marine waters, which is much higher than the previous estimate of 0-3%, which was based on tag-recapture studies focused on older fish. To address this, more studies could be done on juvenile fish, especially in the higher-salinity Roanoke, Croatan and Pamlico Sounds.

This study also found that Albemarle Sound striped bass show different behaviors than the striped bass of other estuaries, like the Chesapeake Bay. Managers should be careful about applying life history data from studies on striped bass of other estuaries. North Carolina may have a much higher percentage of striped bass that are part of the oceanic migratory stock, compared to other estuaries. If so, North Carolina may consider increasing their role within the Atlantic States Marine Fisheries Commission when it comes to managing this migratory stock.

With more than 80% of juveniles going to sea during their first year, Roanoke River striped bass may be good candidates for areas that are seeking to improve their striped bass populations in the face of sub-prime habitat in the estuary (such as in the Gulf of Mexico). This marine migration behavior could mean that Roanoke River striped bass would have higher survivability than other striped bass extirpated there. However, it is also possible that the high rate of juvenile migration for Roanoke River striped bass is itself a reaction to sub-optimal

habitat in the Albemarle Sound, and that habitat restoration and improvement there could increase the health of the population.

Finally, with these findings demonstrating a significantly different rate of growth among fish exhibiting different migration behaviors, stock assessments may be improved by taking into account these varying growth rates.

The findings here leave a number of unanswered questions. Principal among these is the cause of the difference in growth rates among fish exhibiting different migration behaviors. One possibility is that this difference is related to selective predation on faster growing migrant striped bass (e.g., Lee's Phenomenon).

Another unanswered question is the cause for the different migration behaviors themselves. This study found it is not genetically linked, based on the genetic markers used, but it could be driven by density-dependence (e.g., Random Escapement Hypothesis, Basal Theory), or it could be an evolutionary tactic to protect against threats like natural disasters (e.g., hedge-betting). If the latter, the behavior could be genetically based, but linked to other portions of the genome than those studied here.

Another puzzle concerns contradictory findings about the Sr:Ca ratio in the Albemarle Sound. Mohan (2009) found the Albemarle Sound Sr:Ca ratio to be twice that of marine waters, making the Albemarle Sound an anomaly among estuaries in the U.S (see Kraus and Secor 2004). This uniqueness could present a problem for scientists using the Sr:Ca ratio in a fish otolith as a proxy for salinity, but could provide a way to conclusively trace fish caught elsewhere that show extraordinarily high Sr:Ca ratios to their origin in the Albemarle Sound.

Literature cited

Aires-da-Silva, A. M., M. N. Maunder, V. F. Gallucii, N. E. Kohler, and J. J. Hoey. 2009. A spatially structured tagging model to estimate movement and fishing mortality rates for the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Marine and Freshwater Research 60: 1029-1043.

Beckman, D. W. and Wilson, C. A. (1995). Seasonal timing of opaque zone formation in fish otoliths. In *Recent Developments in Fish Otolith Research* (Secor, D. H., Dean,J. M. & Campana, S. E., eds), pp. 27–43. Columbia: University of South Carolina Press.

Boreman, J. and R. R. Lewis. 1987. Atlantic coastal migration of striped bass. American Fisheries Society Special Symposium 1: 331-339.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263-297.

Chapoton, R. B., and J. E. Sykes. 1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. Transactions of the American Fisheries Society 90: 13-20.

Collette, B. B., and G. Klein-MacPhee (eds.). 2002. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, DC.

Coutant, C. C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Transactions of the American Fisheries Society 114: 31-61.

Dorazio, R. M., K. A. Hattla, C. B. McCollough, and J. E. Skjeveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Transactions of the American Fisheries Society 123: 950-963.

Greene, K., E. J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate. 2009. Altantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission Habitat Management Series No. 9, Washington, D.C.

Haeseker, S. L., J. T. Carmichael, J. E. Hightower. 1996. Summer distribution and condition of striped bass within Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 125: 690-704.

Holland, B. F., Jr., and G. F. Yelverton. 1973. Distribution and biological studies of anadromous fishes offshore North Carolina. North Carolina Department of Natural and Economic Resources, Special Scientific Report Number 24. 132 pp.

Hurst, T.P., Conover, D.O., 2002. Effects of temperature and salinity on survival of young-of-year Hudson river striped bass (*Morone saxatilits*): implications for optimal overwintering habitats. Can. J. Fish. Aquat. Sci. 59, 787–795.

Kerr, L. A, D. H. Secor, and P. M. Piccoli. 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. Fisheries 34: 114-123.

Kraus, R. T., and D. H. Secor. 2004. Incorporation of strontium into otoliths of an estuarine fish. Journal of Experimental Marine Biology and Ecology 302: 85-106.

Kurota, H., M. K. McAllister, G. L. Lawon, J. I. Nogueria, S. L. H. Teo, and B. A. Block. 2009. A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic bluefin tuna (*thunnus thynnus*). Canadian Journal of Fisheries and Aquatic Sciences 66: 321-342.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

Maxwell, J. A., W. J. Teesdale, J. L. Campbell. 1995. Nuclear Instrument Methods B 95: 407.

May, P. G. 2001. Genetic and morphological characterization of striped bass (*Morone saxatilis*) collected from the Roanoke River, North Carolina during the 1999 spawning season. Master's thesis. Department of Biology, East Carolina University, Greenville, North Carolina.

McCleave, J. D., and E. Edeline. 2009. Diadromy as a conditional strategy: patterns and drivers of eel movements in continental habitats. American Fisheries Society Symposium 69: 97-119.

Merriman, D. 1941. Studies on the striped bass (*Roccus saxatilis*) of the Atlantic coast. United States Fish and Wildlife Service Fishery Bulletin 50: 1-77.

Mohan, J. 2009. Habitat utilization of juvenile striped bass *Morone saxatilis* in Ablemarle Sound inferred from otolith and water chemistries. Master Thesis, Department of Biology, East Carolina University, Greenville, NC.

Morris, Jr., J. A., R. A. Rulifson, J. A. Babaluk, P. G. May, and J. L. Campbell. 2005. Use of micro-PIXE to investigate otolith Sr distributions of the anadromous striped bass, *Morone saxatilis*. X-Ray Spectrometry 34: 301-305.

Näslund, I., G. Milbrink, L. O. Eriksson, and S. Holmgren. 1993. Importance of habitat productivity differences, competition, and predation for the migratory behavior of Arctic char. Oikos 66: 538-546.

Nordeng, H. 1983. Solution to the "char problem" based on Artic char (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 1372-1387.

Paterson, A. W., and A. K. Whitfield. 2000. Do shallow-water habitats function as refugia for juvenile fishes? Estuarine Coastal and Shelf Sciences 51: 359-364.

Patrick, W. S. 2002. Genetic structure of striped bass, *Morone saxatilis*, populations from the Roanoke, Tar, and Neuse Rivers of North Carolina. Master's thesis. East Carolina University, Department of Biology, Greenville, North Carolina.

Patrick, W. S., and M. L. Moser. 2001. Potential competition between hybrid striped bass (*Morone saxaitlis* x *M. americana*) and striped bass (*M. saxatilis*) in the Cape Fear River Estuary, North Carolina. Estuaries 24: 425-429.

Pearson, J. C. 1938. The life history of the striped bass, or rockfish, *Roccus saxatilis*,(Walbaum). Bulletin of the Bureau of Fisheries 48: 825-851.

Poulsen, E.M. 1957. Defects in the recovering of tagged fish. International Commision for Northwest Atlantic Fisheries Series No. 439, Issue 4.

Schramm, H. L. Jr (1989). Formation of annuli in otoliths of bluegills. *Transactions of the American Fisheries Society* **118,** 546–555.

Secor, D. H., A. Henderson-Arzapalo, and D. M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology 192: 15-33.

Secor, D. H. and P. M. Piccoli. 2007. Oceanic migration rates of Upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. Fishery Bulletin 105: 62-73.

Secor, D. H. and J. R. Rooker. 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fisheries Research 46: 359-371.

Sheaves, M. 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Marine Ecology-Progress Series 222: 279-290.

Tsukamoto, K., M. J. Miller, A. Kotake, J. Aoyama, and K. Uchida. 2009. The origin of fish migration: the random escapement hypothesis. American Fisheries Society Symposium 69: 45-61.

Winslow, S. E. 2002. Summary of North Carolina striped bass tagging programs (NC DMF) January 1980 – September 2001. North Carolina Division of Marine Fisheries, Northern District, Elizabeth City, NC.

Woods, T. L., E. G. Beck, D. T. Tolen-Mehloop, R. Troiano and J. K. Whitley. 2000a. Goechemical tracers of groundwater movement between the Castle Hayne and associated coastal plain aquifers. University of North Carolina Water Resources Research Institute, Project Number 70148, Chapel Hill, North Carolina. 237 pp.

Woods, T. L., P. D. Fullagar, R. K. Spruill, and L. C. Sutton. 2000b. Strontium isotopes and major elements as tracers of ground water evolution: example from the Upper Castle Hayne Aquifer of North Carolina. Ground Water 38: 762-771.

Zlokovitz, E. R., D. H. Secor, and P. Mo. Piccoli. 2003. Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fisheries Research 63: 245-259.

Table 1. Synthetic oligonucleotide primers (GibcoBRL registered trademark) used for PCR amplification and sequencing.

Name	Utility	Concentration	Sequence 5' - 3'
sbmt 107-130	PCR amplication	15 pmols	CGACCACTCGCTCCCAAGCCAGC
sbmt 1642-1620	PCR amplification	15 pmols	GGTTGTCTCGGGGTATTGTAGGG
	Sequencing	15 pmols	
sbmtds	Sequencing	15 pmols	ACAGGCCCCCATAAAACCCC

Table 2. Age distribution of striped bass age for the 2004 and 2005 collections. One hundred and twelve of these fish were analyzed for Sr concentrations

Age	Number	Percentage (%)
3	1	0.9
4	16	13.9
5	64	55.7
6	2	1.7
7	4	3.5
8	7	6.1
9	6	5.2
10	5	4.3
11	4	3.5
14	6	5.2
Total	115	100

Table 3. Periodicity of marine migrations, categorized by age at capture, haplotype, and migratory behavior. Periodicity was calculated as a ratio, using the number of Sr counts above 4,000 ppm compared to total number of Sr counts during micro-PIXE analysis. Counts refer to a sample point along the micro-PIXE transect line of the otolith, which were spaced 4 μm apart.

		Ratio of number of Sr counts above 4,000 ppm : total number of Sr counts		
Category	Number	Minimum	Average	Maximum
Age at capture				
3	1	0.021	0.021	0.021
4	16	0.005	0.175	0.510
5	64	0.000	0.271	0.575
6	2	0.017	0.172	0.328
7	4	0.000	0.062	0.194
8	7	0.014	0.051	0.164
9	6	0.000	0.004	0.017
10	5	0.000	0.012	0.032
11	4	0.000	0.038	0.125
14	6	0.000	0.001	0.006
Haplotype				
I	47	0.000	0.165	0.575
II	34	0.000	0.189	0.540
III	29	0.000	0.205	0.482
Migratory behavior				
Stager	15	0.001	0.179	0.382
Sprinter	32	0.003	0.232	0.458
Resident	27	0.000	0.010	0.056
Mixed	41	0.001	0.267	0.575

Table 4. Estimates of the number and percentage of striped bass that entered the marine environment at different ages.

		Exhibiting marine migatory behavior	
Age	Sample size	Number	Frequency
1	112	89	79.5%
2	111	44	39.6%
3	110	21	19.1%
4	109	24	22.0%
5	93	18	19.4%
6	29	0	0.0%
7	27	0	0.0%
8	23	1	4.3%
9	16	0	0.0%
10	10	0	0.0%
11	5	0	0.0%
12	1	0	0.0%
13	1	0	0.0%
14	1	0	0.0%

Table 5. Frequency of occurrence (%) of migratory behaviors observed in the first year of life for Roanoke River striped bass. Migratory patterns are stagers (1), sprinters (2), and residents (3).

Migratory behavior	Number	Frequency
Stager	15	13.0%
Sprinter	32	27.8%
Resident	27	23.5%
Mixed	41	35.7%
Total	115	100.0%

Table 6 – Kruskal-Wallace and Mann-Whitney Post Hoc test of migratory types and growth. Within the Post Hoc Test, 1 refers to sprinters, 2 stagers, 3 residents, and 4 mixed migratory types.

Age	Mean Sr concentrations			Maximum Sr concentrations		
	Kruskal-Wallace *P* -value	Post Hoc Comparison	Mann-Whitney *P* -value	Kruskal-Wallace *P* -value	Post Hoc Comparison	Mann-Whitney *P* -value
1	< 0.001	1 ≠ 3 2 ≠ 3 3 ≠ 4	< 0.001 < 0.001 < 0.001	< 0.001	1 ≠ 3 2 ≠ 3 3 ≠ 4	< 0.001 < 0.001 < 0.001
2	0.001	1 ≠ 3 2 ≠ 3 3 ≠ 4	< 0.001 0.006 0.002	0.026	1 ≠ 3 2 ≠ 3 3 ≠ 4	0.013 0.005 0.033
3	0.76	-	-	0.11		
4	0.82	-	-	0.361		
5	0.048	2 ≠ 3	0.014	0.05	2 ≠ 3	0.010
6	0.228	-	-	0.103		
7	0.196	-	-	0.41		
8	0.318	-	-	0.089		

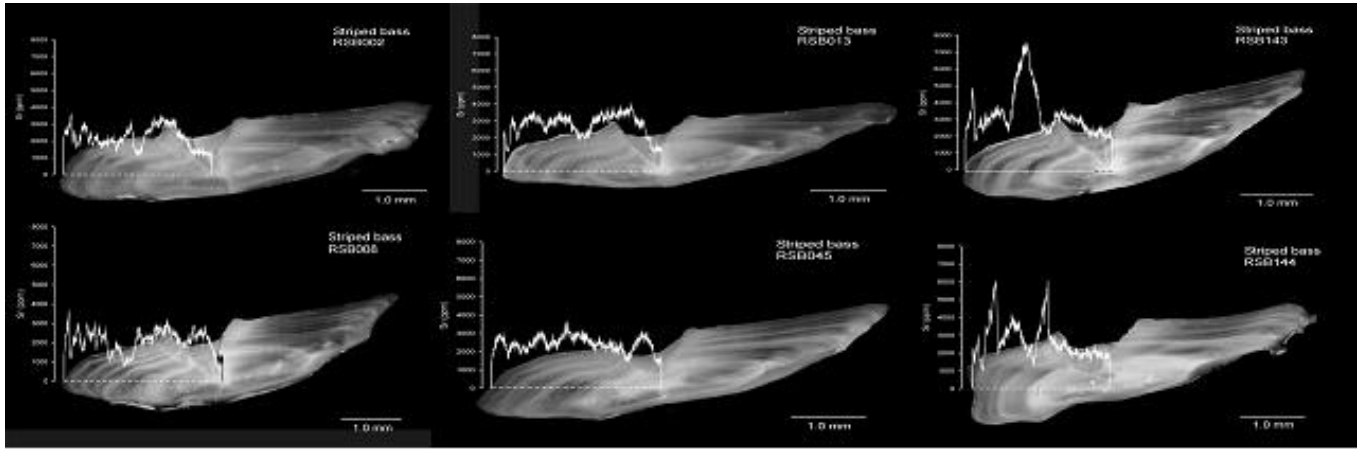


Figure 1. Linear/continuous micro-PIXE analysis of Sr concentrations from six striped bass collected in the Roanoke River during the 2000 spawning season. Haplotype I (left) and II (center) fish exhibit Sr patterns of an estuarine and freshwater migration, while haplotype III (right) fish exhibit distinct Sr spikes that are indicative of an oceanic migration (courtesy of James Morris (NOAA-NOS), Roger Rulifson (ECU), and John Babuluk DFO, Canada). For a better resolution photo see Morris et al. (2005).

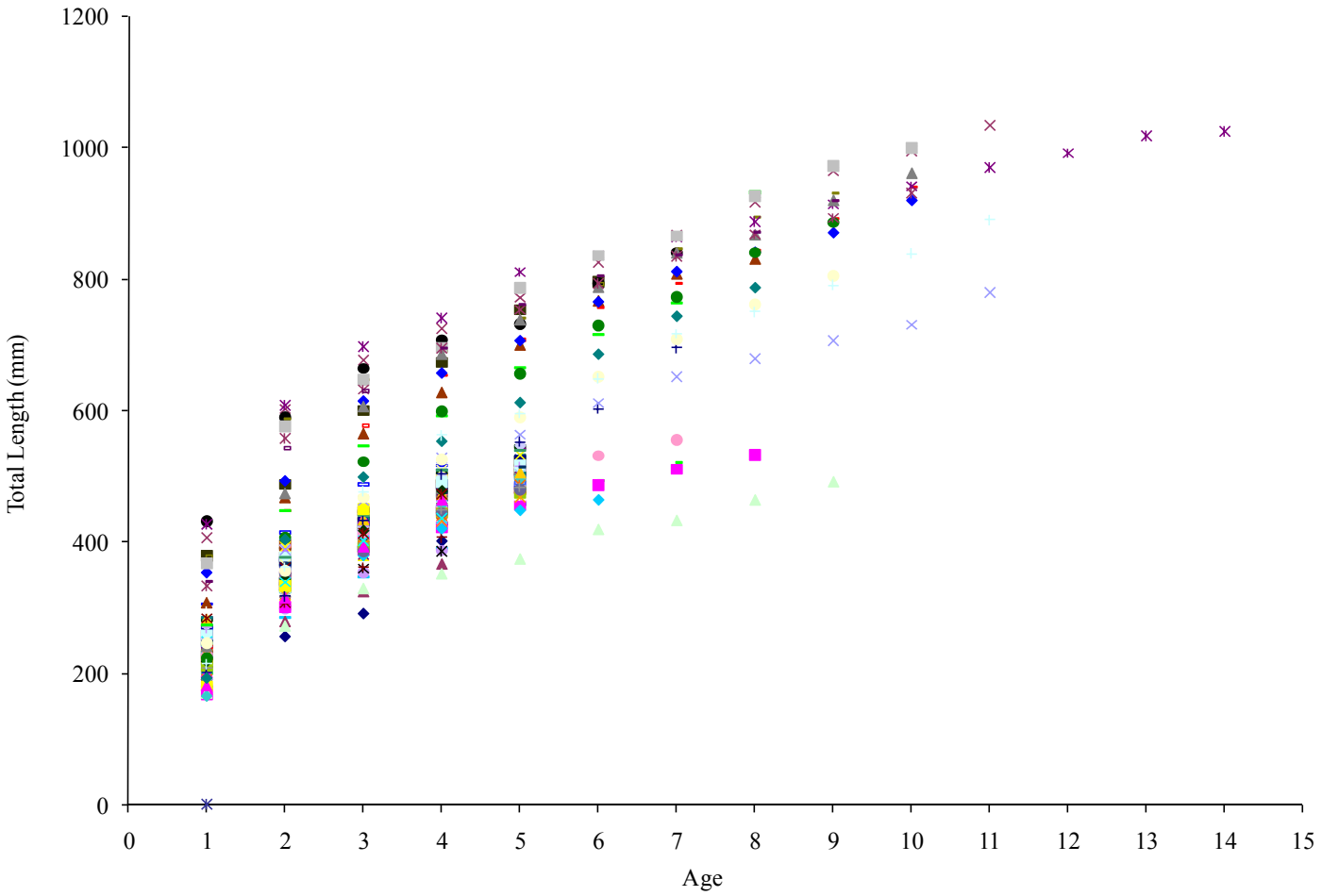


Figure 2. Scatter plot of total length versus age class of striped bass collected for the Roanoke River in 2004 and 2005. Each marker represents a unique fish.

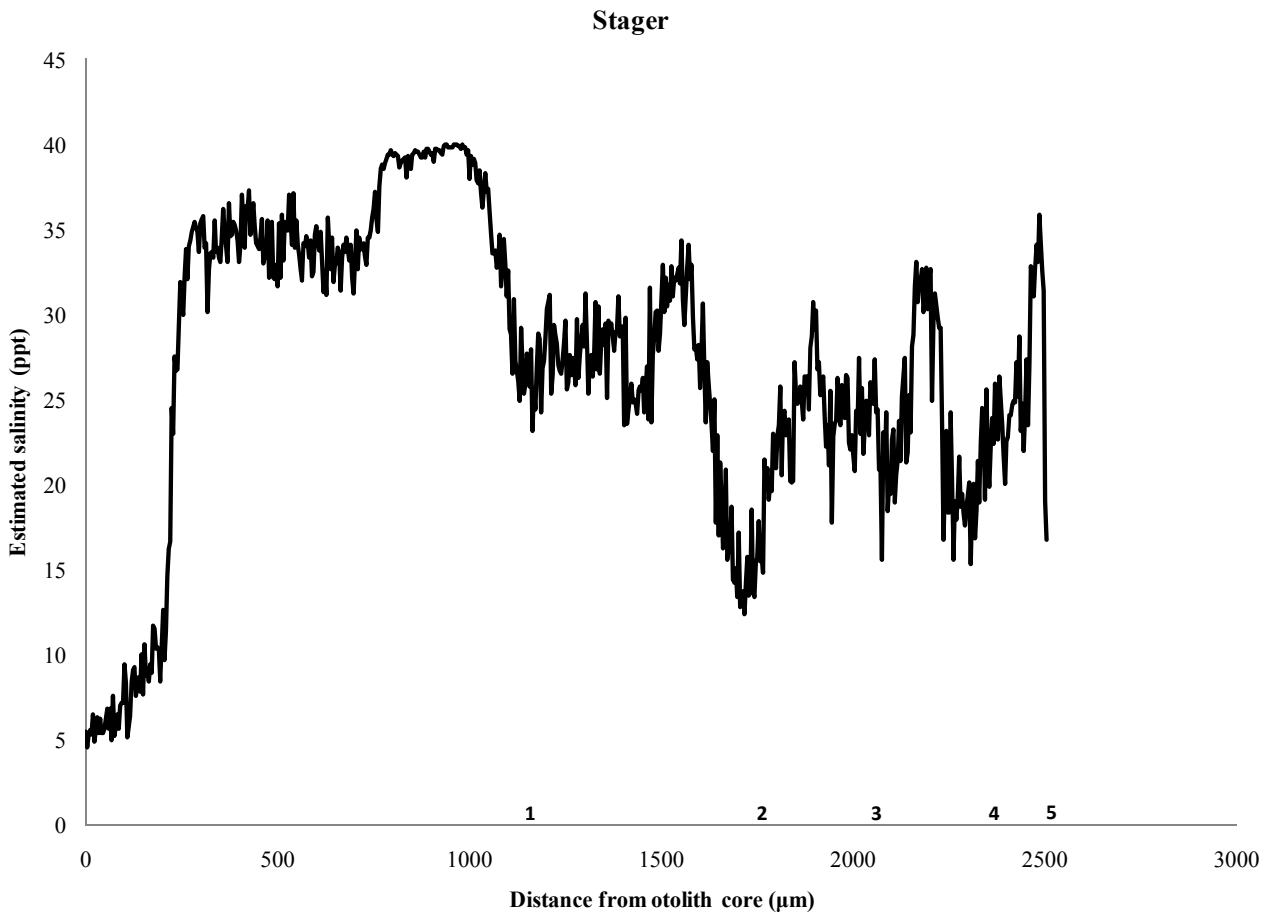


Figure 3. A "stager" striped bass, age 5, migrating from mesohaline (0.5 – 5 ppt) to euhaline (30 – 35 ppt) habitat, then to marine (> 35 ppt) habitat within the first year of life. Like the majority of other marine migrants, this fish returned to estuarine waters to overwinter in its first year of life. Subsequently, it remained in polyhaline (18 – 30 ppt) waters of the estuary until age-4, when it briefly entered marine waters and then returned.

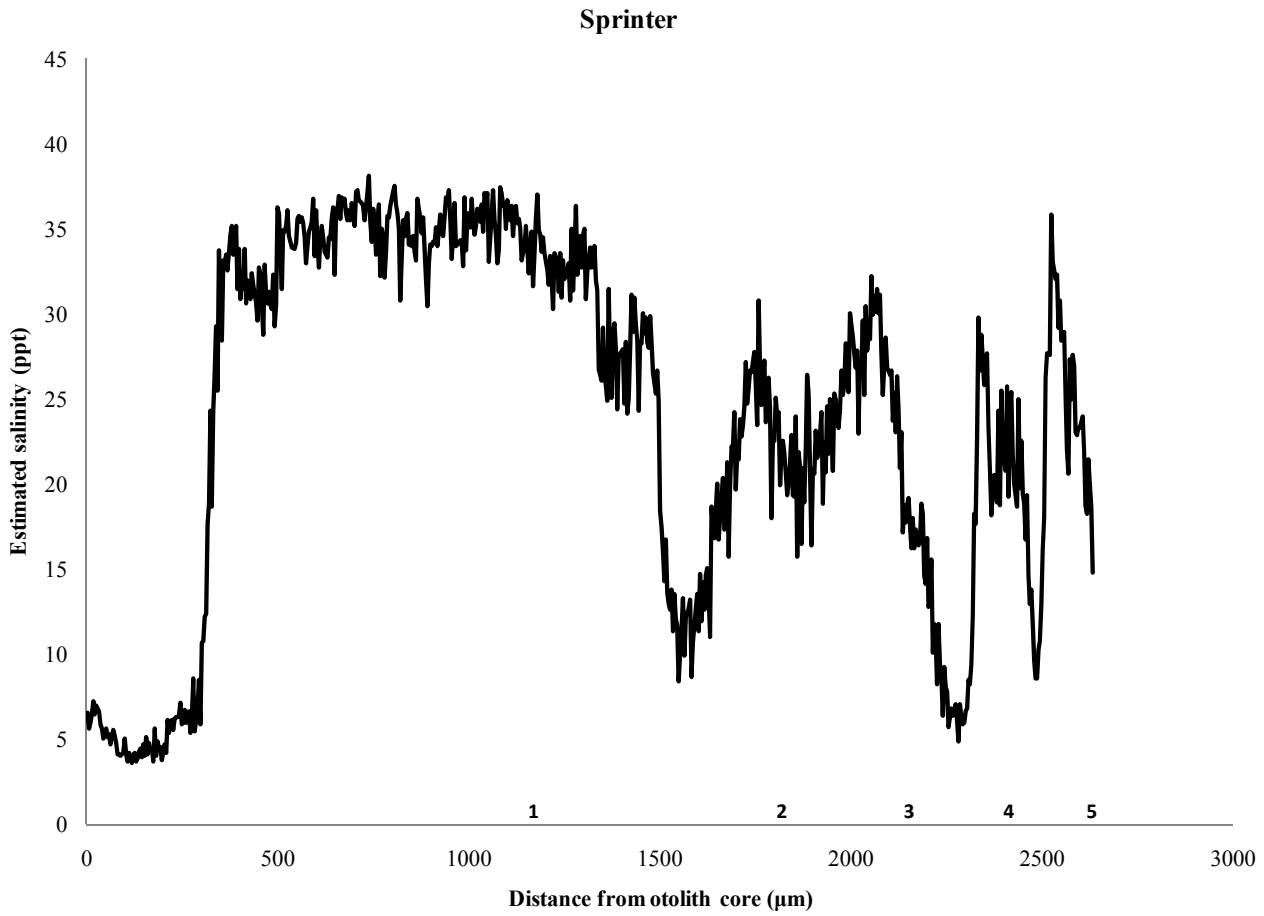


Figure 4. A "sprinter" striped bass, age 5, moving from oligohaline (0.5 – 5 ppt) directly into marine (> 35 ppt) habitat within the first year of life. Unlike the majority of marine migrants, this fish did not return to estuarine waters to overwinter in its first year of life, instead returning mid way through age-1. The striped bass moved between mesohaline (5 – 18 ppt) and polyhaline (18 – 30 ppt) habitats between the ages of 1 and 4, and entered marine habitat in its fourth year of life. .

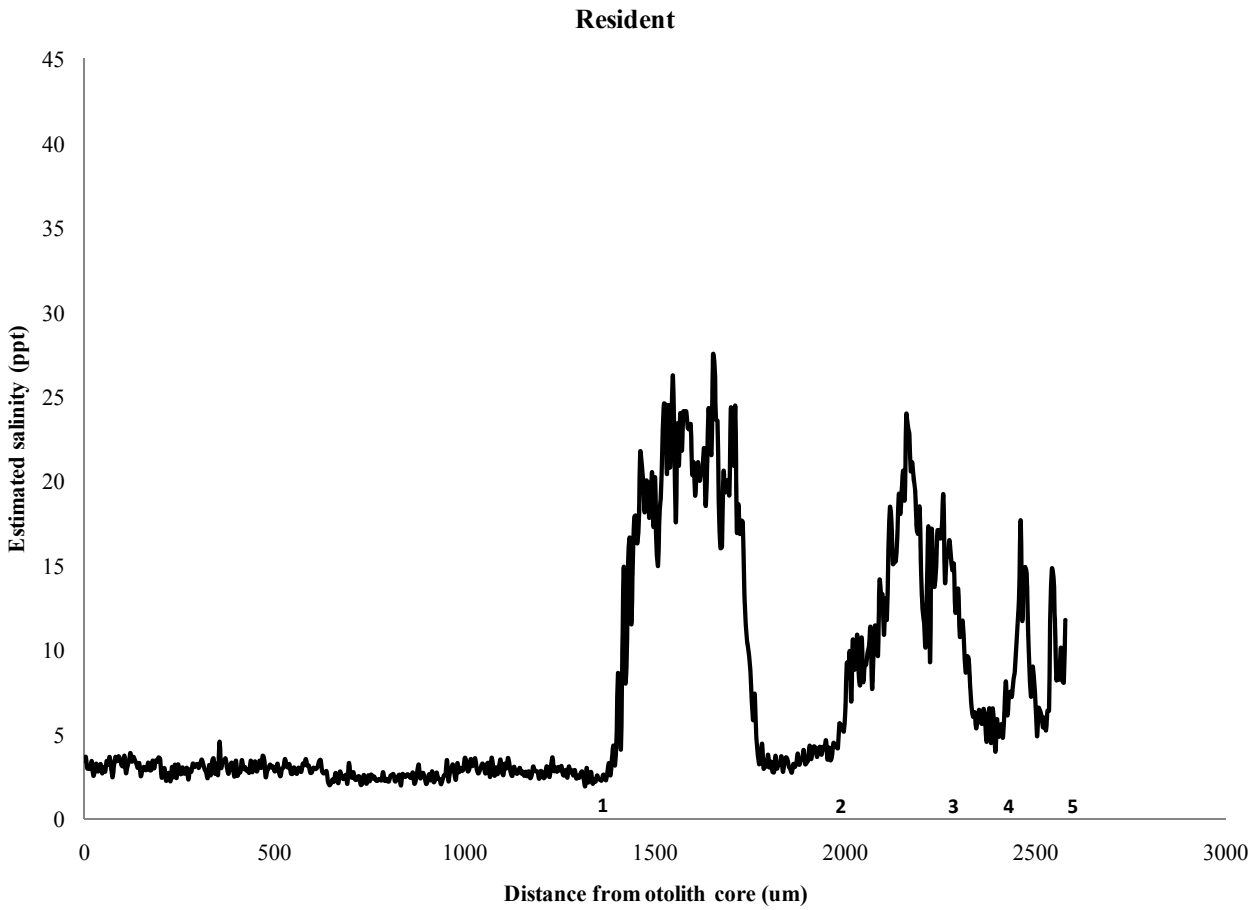


Figure 5. A "resident" striped bass, age 5, never leaving oligohaline (0.5 – 5 ppt) habitat during the first year of life. This bass moved in and out of mesohaline (5 – 18 ppt) and polyhaline (18 – 30 ppt) waters within the estuary at ages 1,2, 3, 4 and 5.

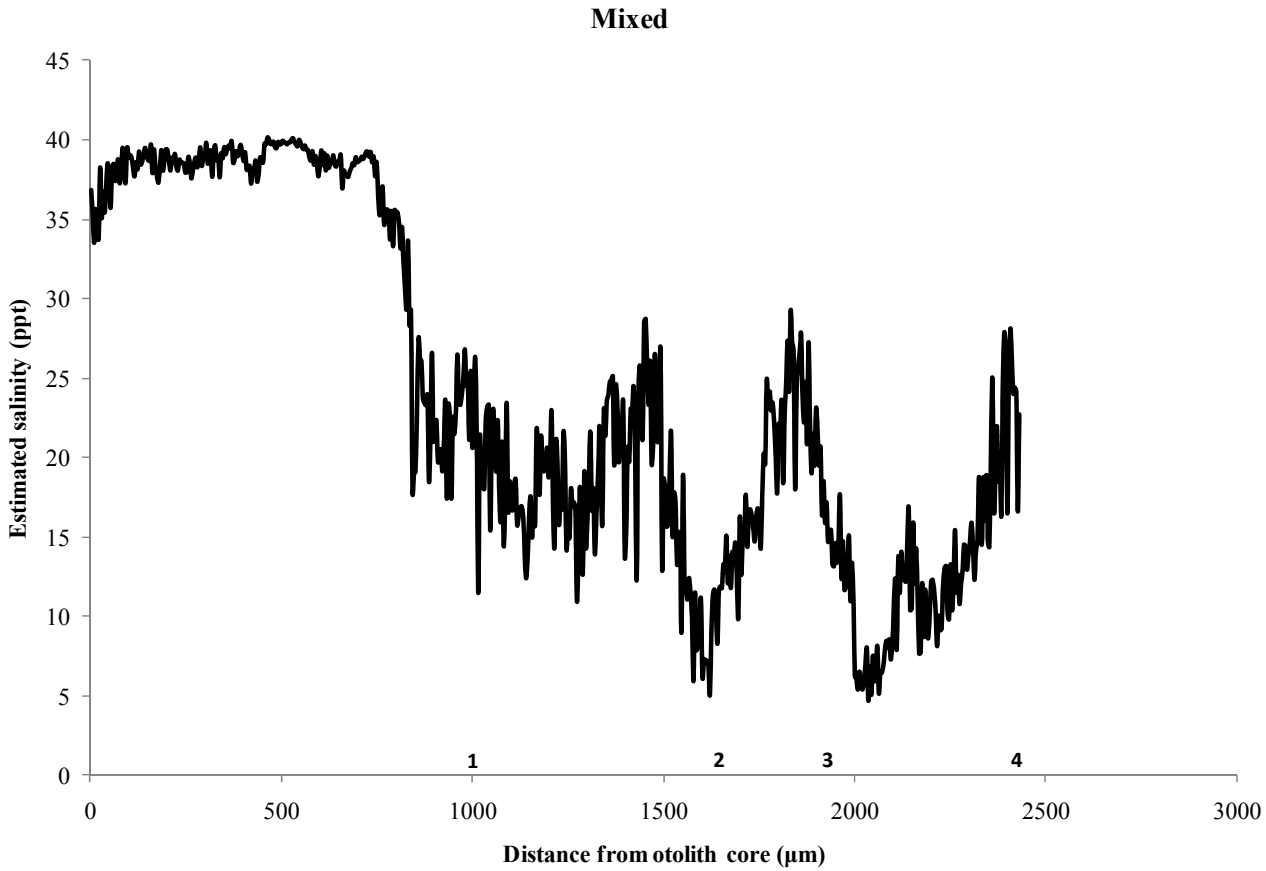


Figure 6. A "mixed" striped bass, age 4, with estimated salinities of 35 ppt throughout its first year of life. This bass moved in and out of mesohaline (5 – 18 ppt) and polyhaline (18-30 ppt) waters within the estuary at ages 2, 3, and 4.

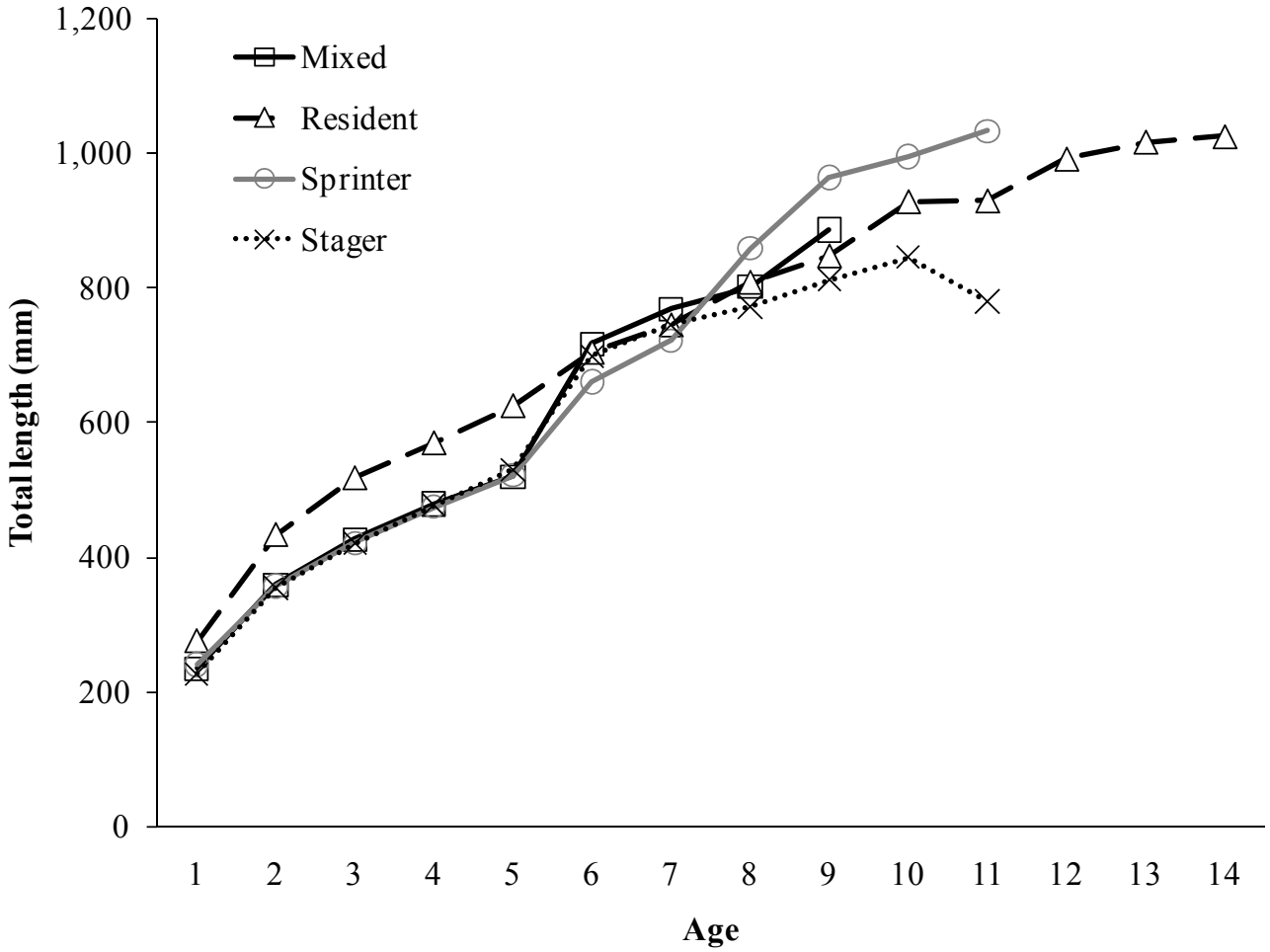


Figure 7. Comparison of growth and migratory behavior versus age class. Stager, sprinter, and mixed striped bass exhibited significantly slower growth rates than resident AR striped bass.

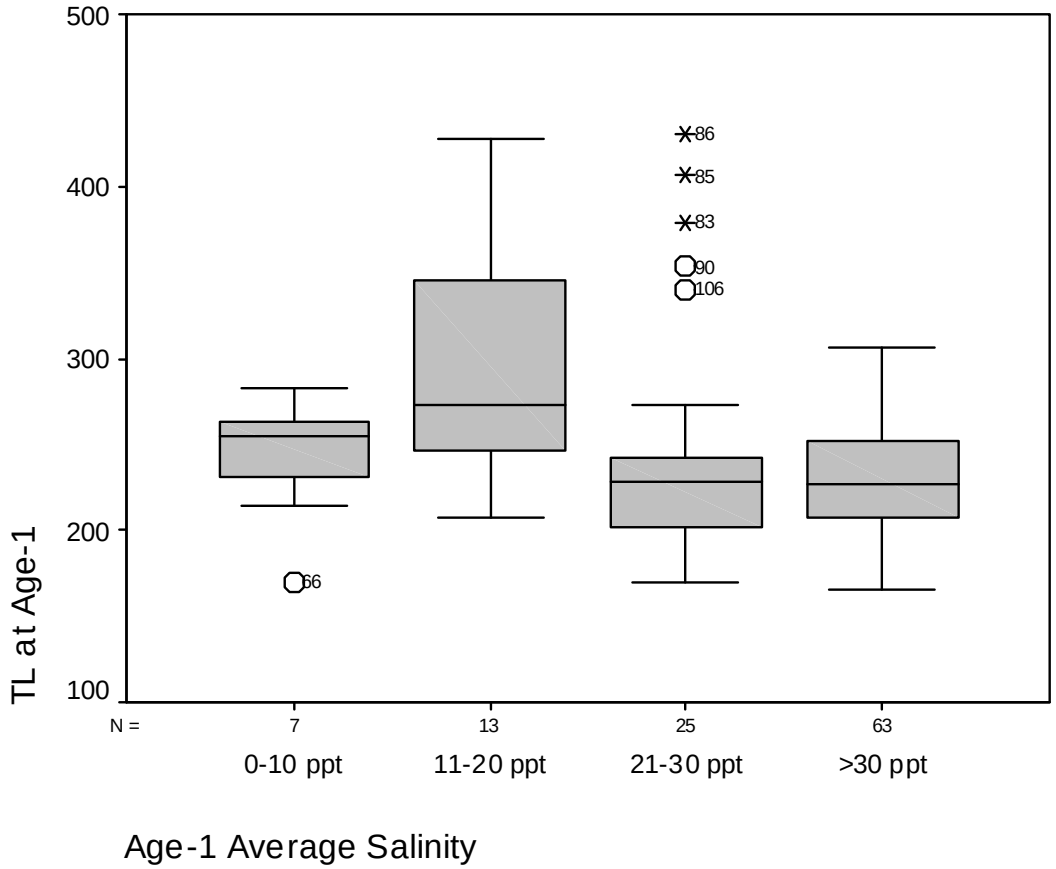


Figure 8. Comparison of growth (Total length) and average salinity of habitat occupied (based on Sr:Ca ratios) by Age-1 striped bass in the Albemarle Sound.

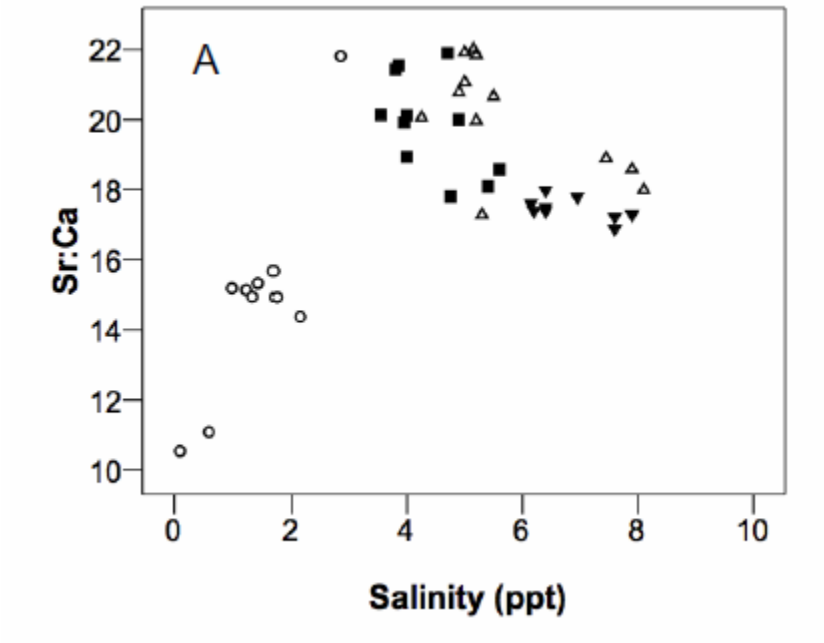


Figure 9. A scatter plot of Sr:Ca ratios versus salinity for each habitat sampled in Mohan (2009). Symbols used differentiate among the four areas sampled: open circle (Batchelor Bay); black square (Perquimans River); open triangle (Pasquotank River); black inverted triangle (Alligator River). Courtesy of Mohan 2009.

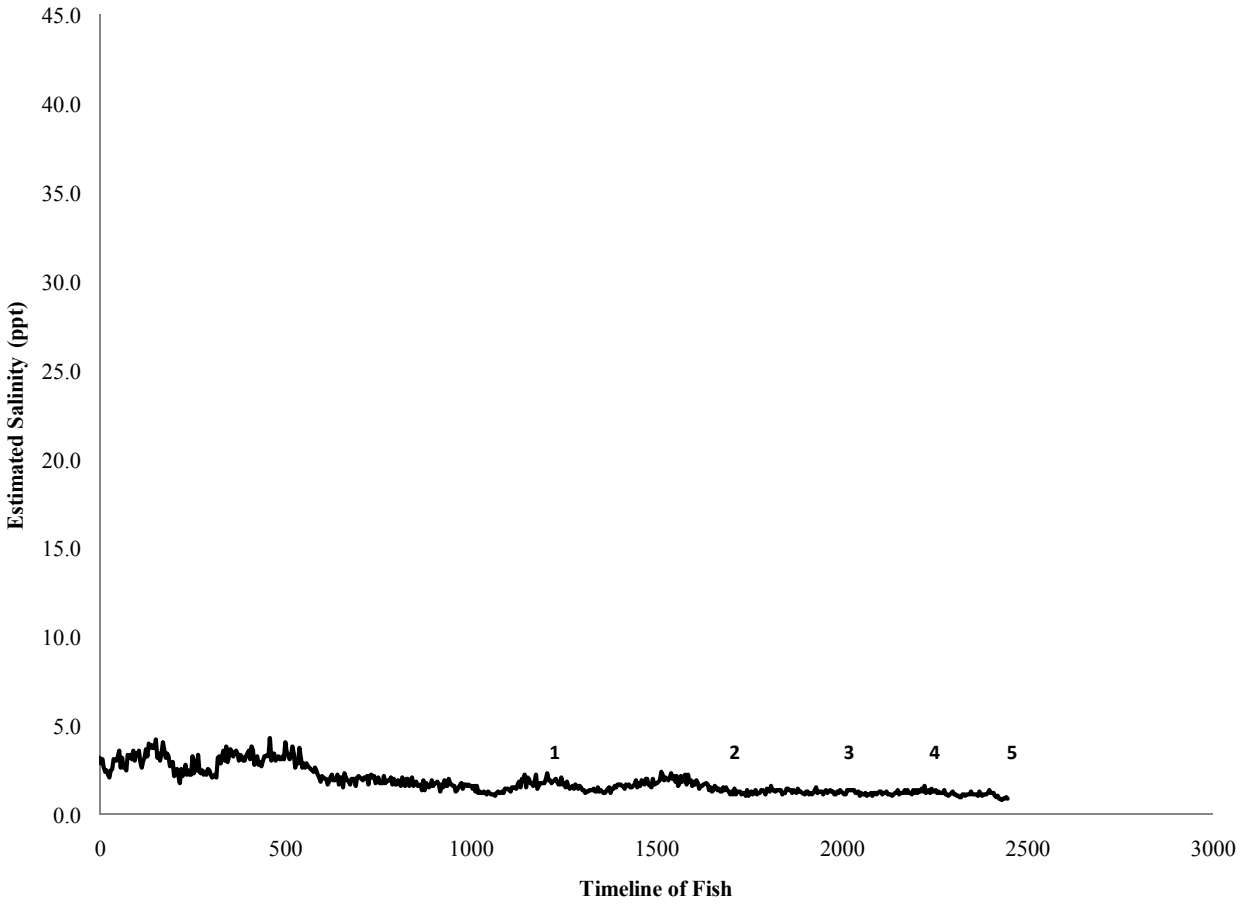


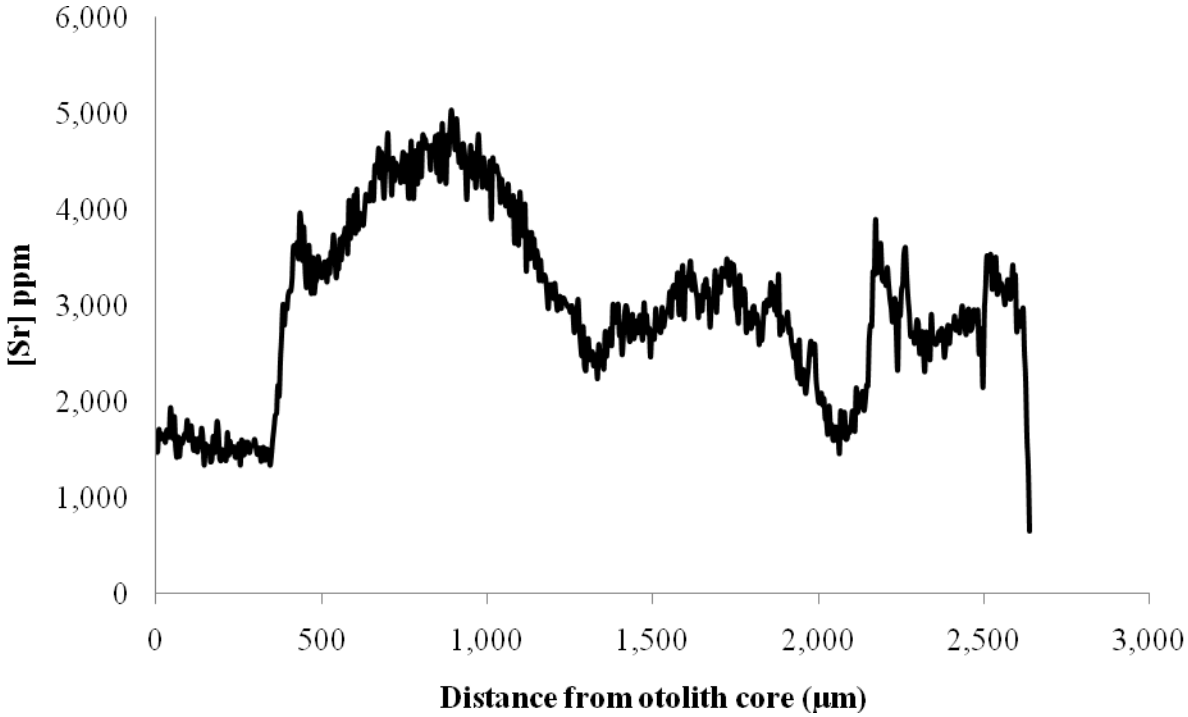
Figure 10. A "resident" striped bass, age 5, never leaving oligohaline (0.5 – 5 ppt) waters of the estuary. Salinity values varied between 1 ppt and 4 ppt throughout its life time, suggesting that the effect of temperature on Sr uptake is minimal.

APPENDIX A: STRONTIUM PROFILES OF STRIPED BASS EXAMINED

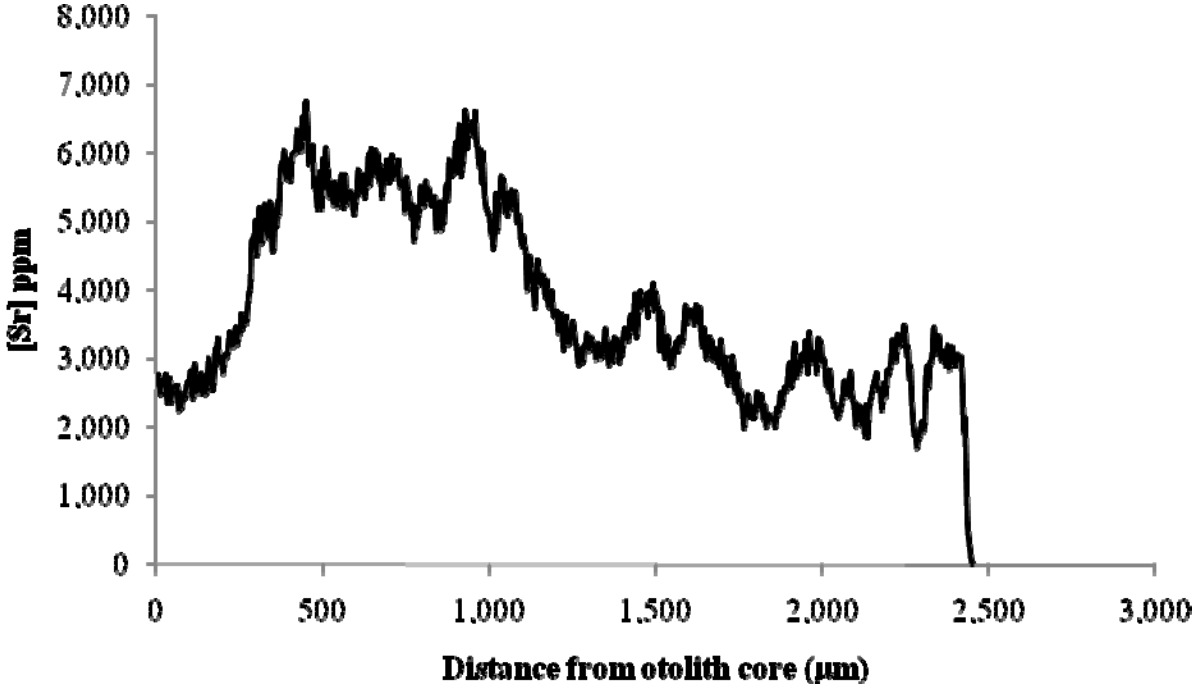
See attachment.

Fish ID: 1240; Disk 1 Otolith 1
High Sr

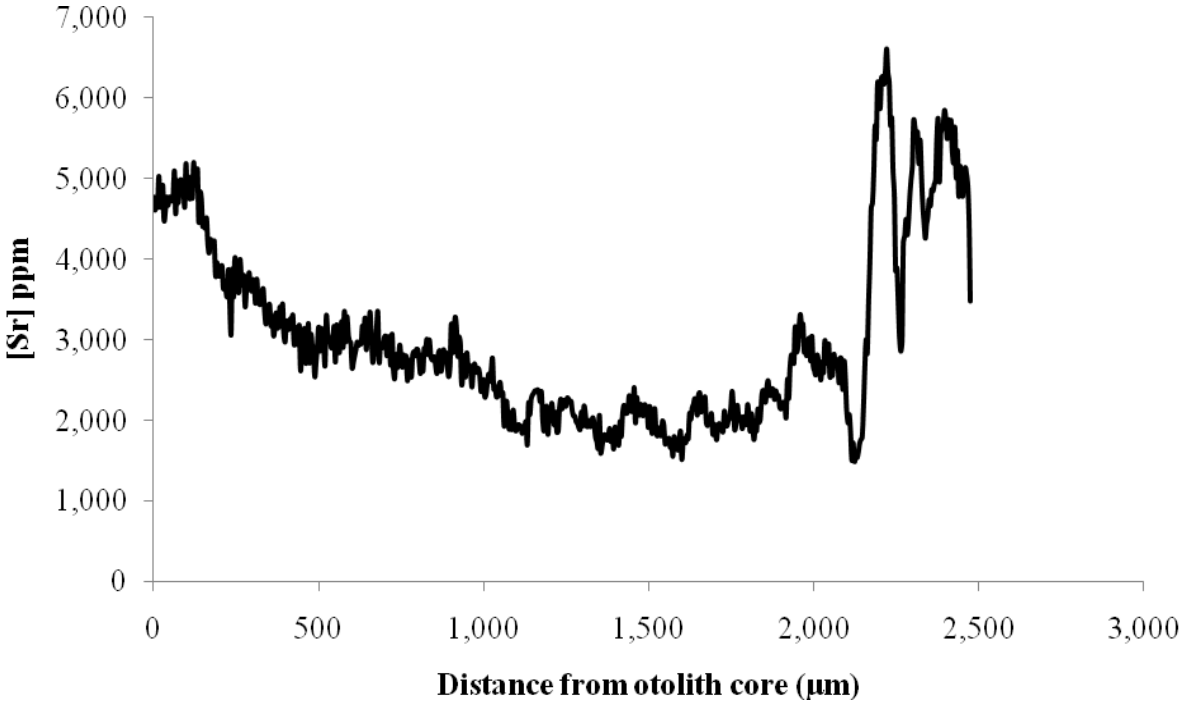
Fish ID: 1174; Disk 1 Otolith 2
Stager



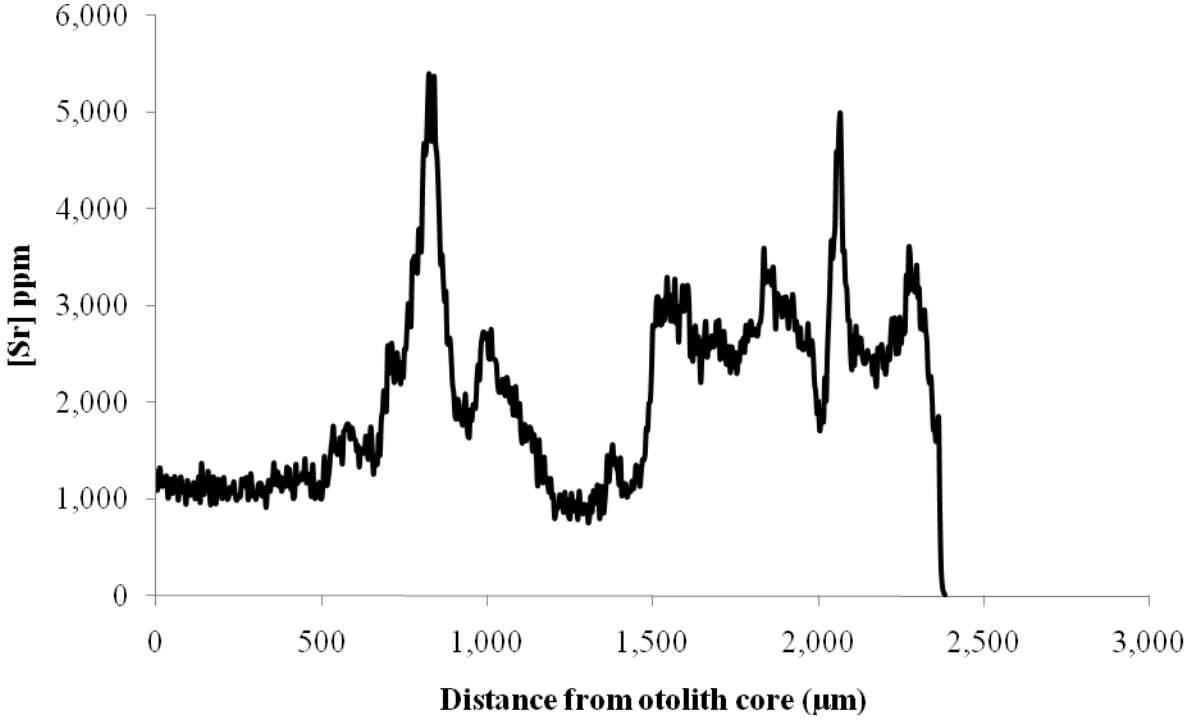
Fish ID: 1165; Disk 1 Otolith 3
Sprinter



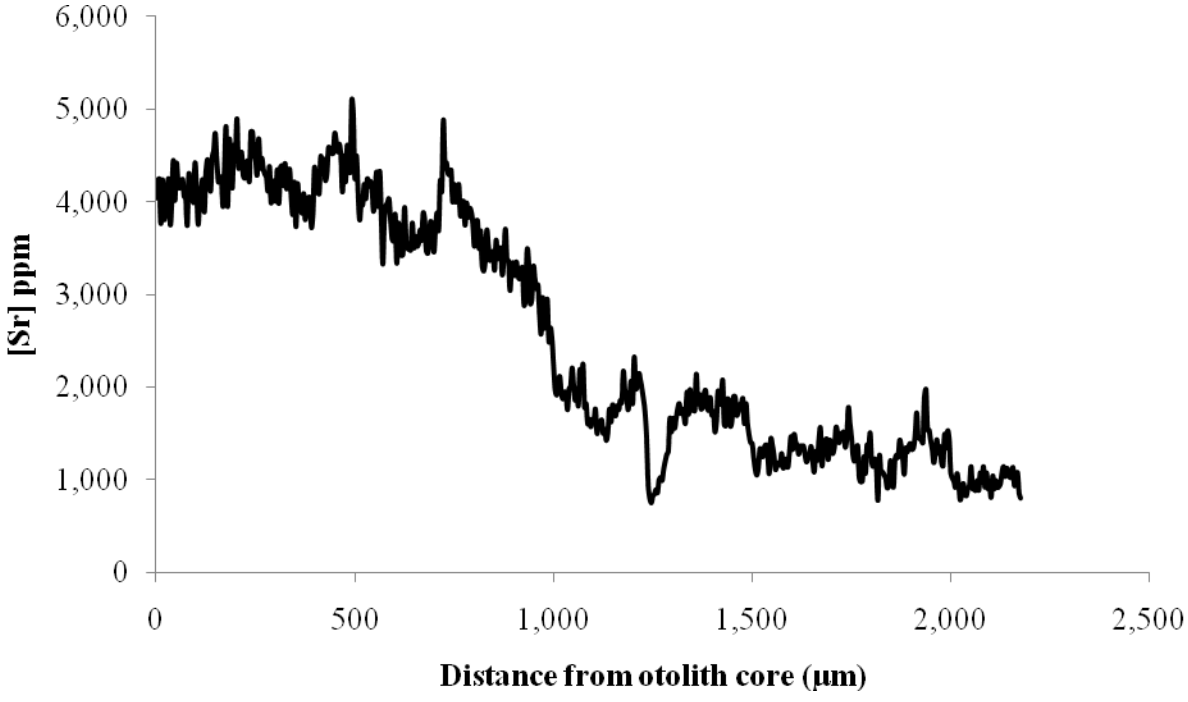
Fish ID: 1176; Disk 1 Otolith 4
High Sr



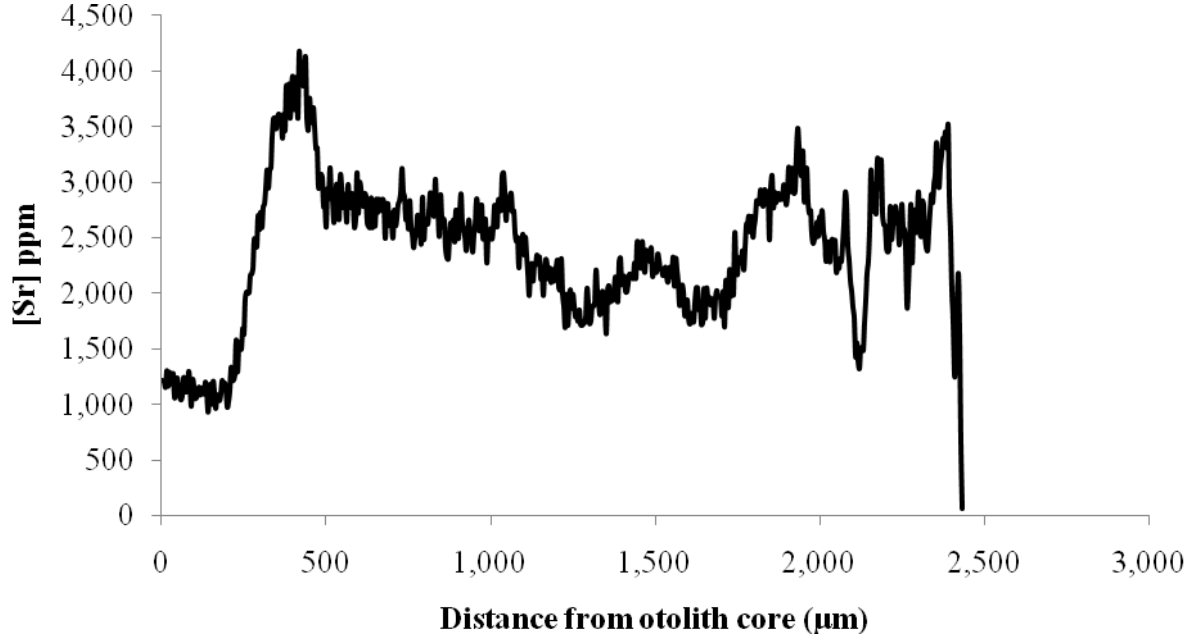
Fish ID: 482; Disk 1 Otolith 5
Sprinter



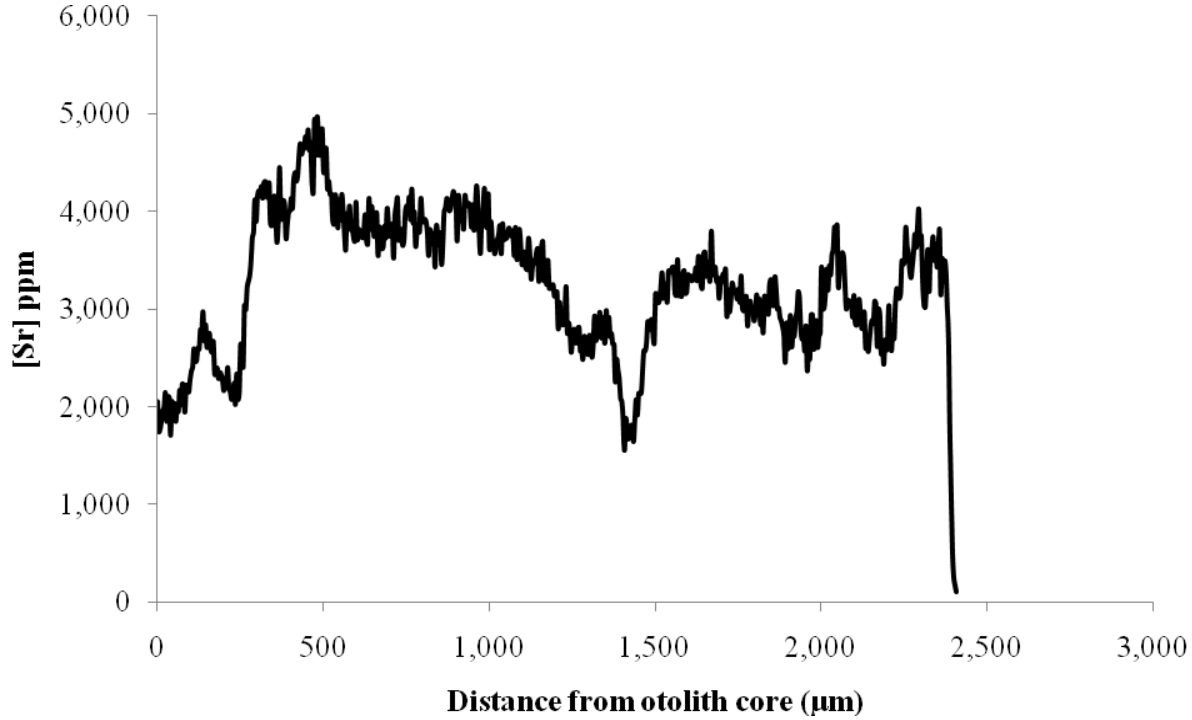
Fish ID: 1158; Disk 1 Otolith 6
High Sr



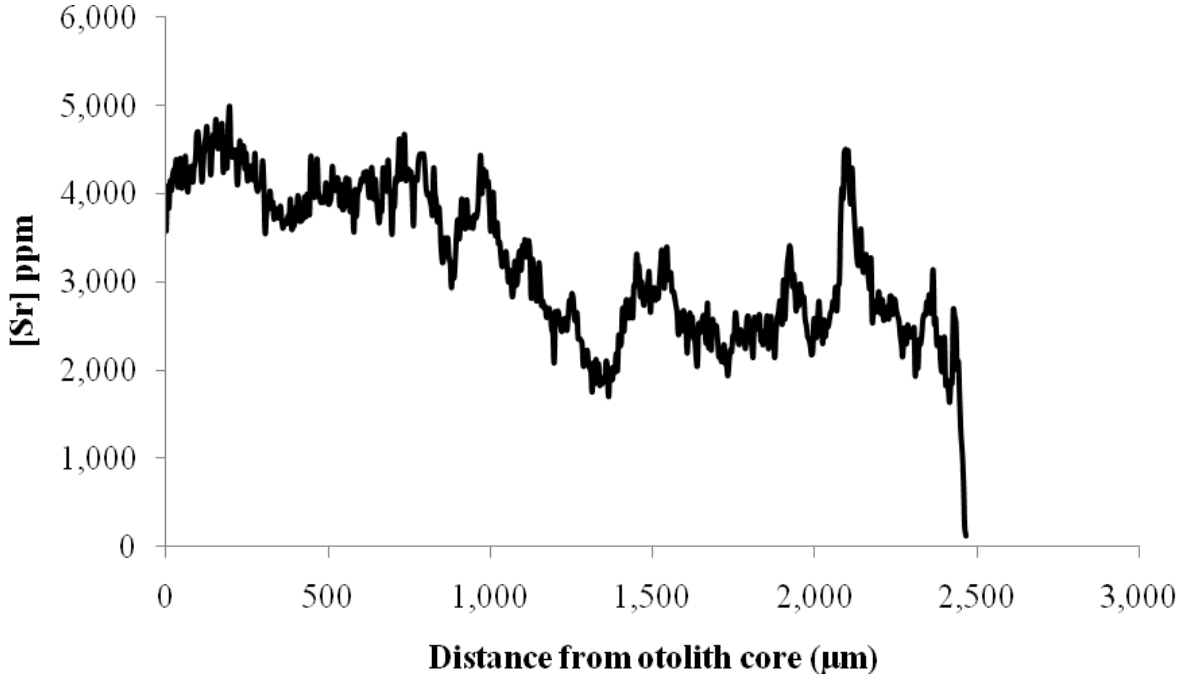
Fish ID: 1151; Disk 2 Otolith 2
Sprinter



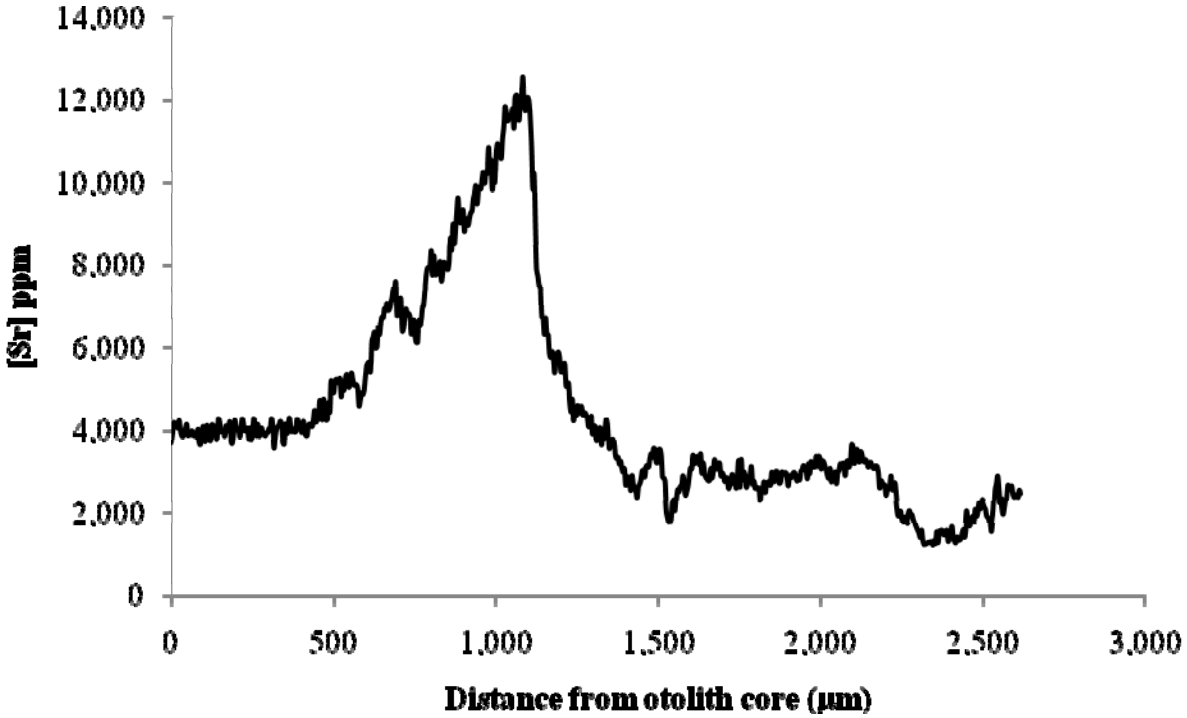
Fish ID: 1193; Disk 2 Otolith 2
Stager



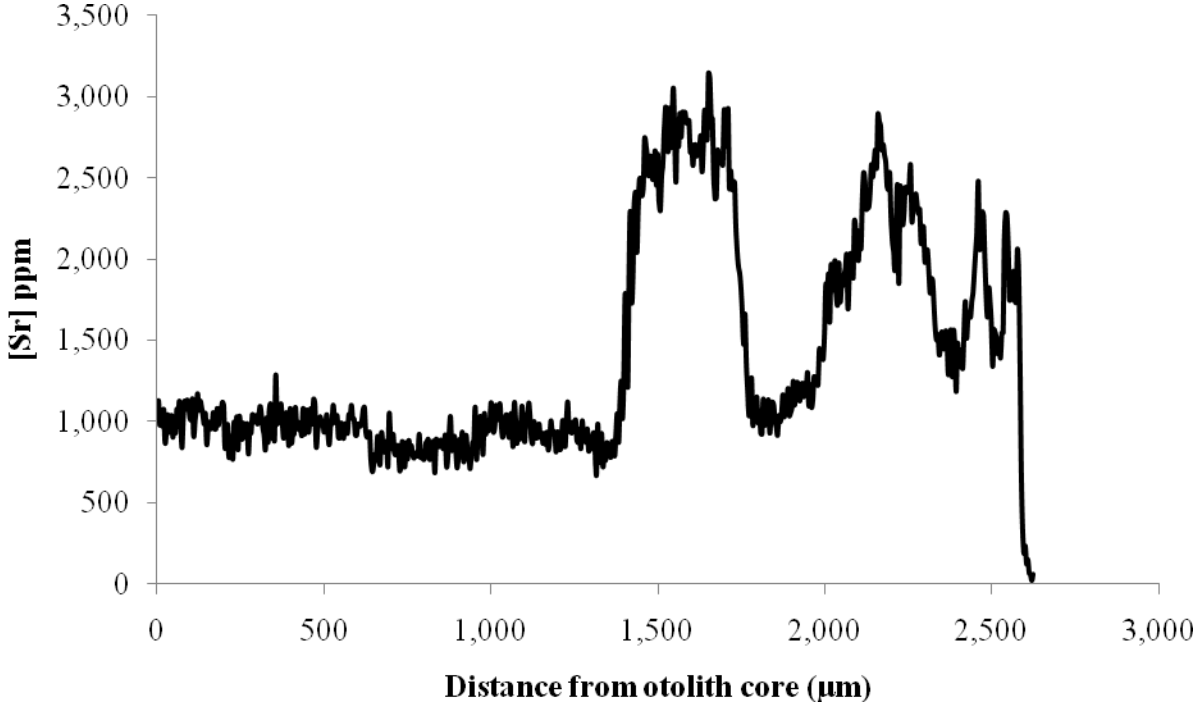
Fish ID: 1145; Disk 2 Otolith 3
High Sr



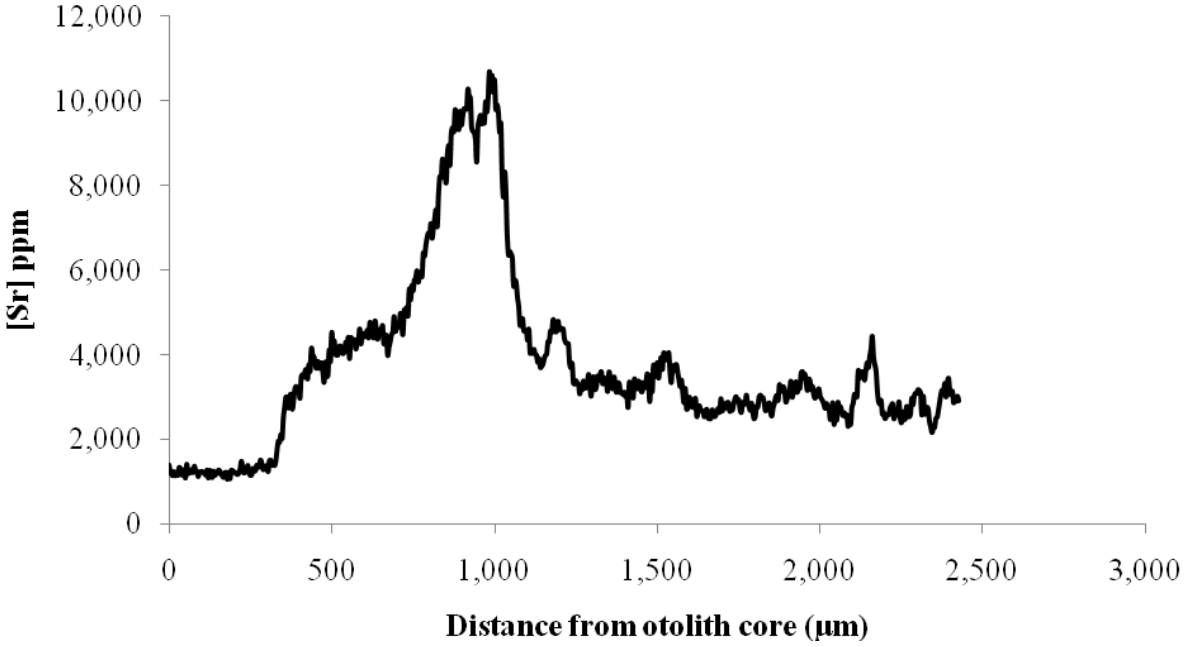
Fish ID: 1137; Disk 2 Otolith 4
High Sr



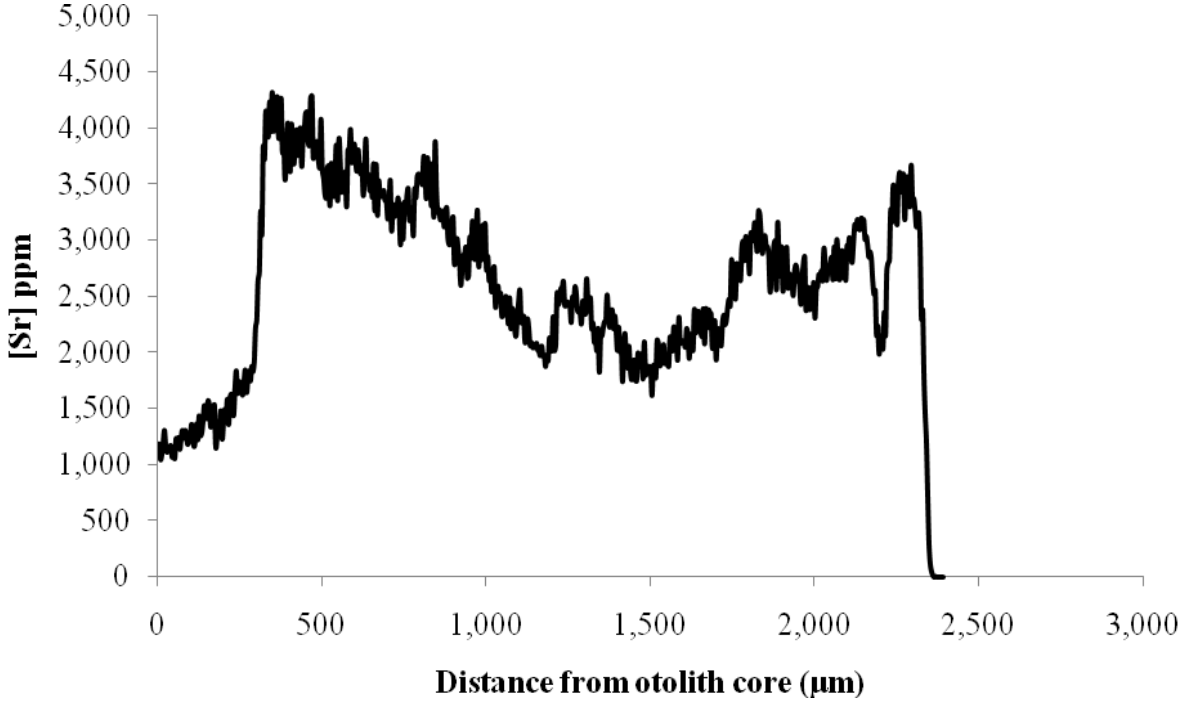
Fish ID: 1250; Disk 2 Otolith 5
Resident



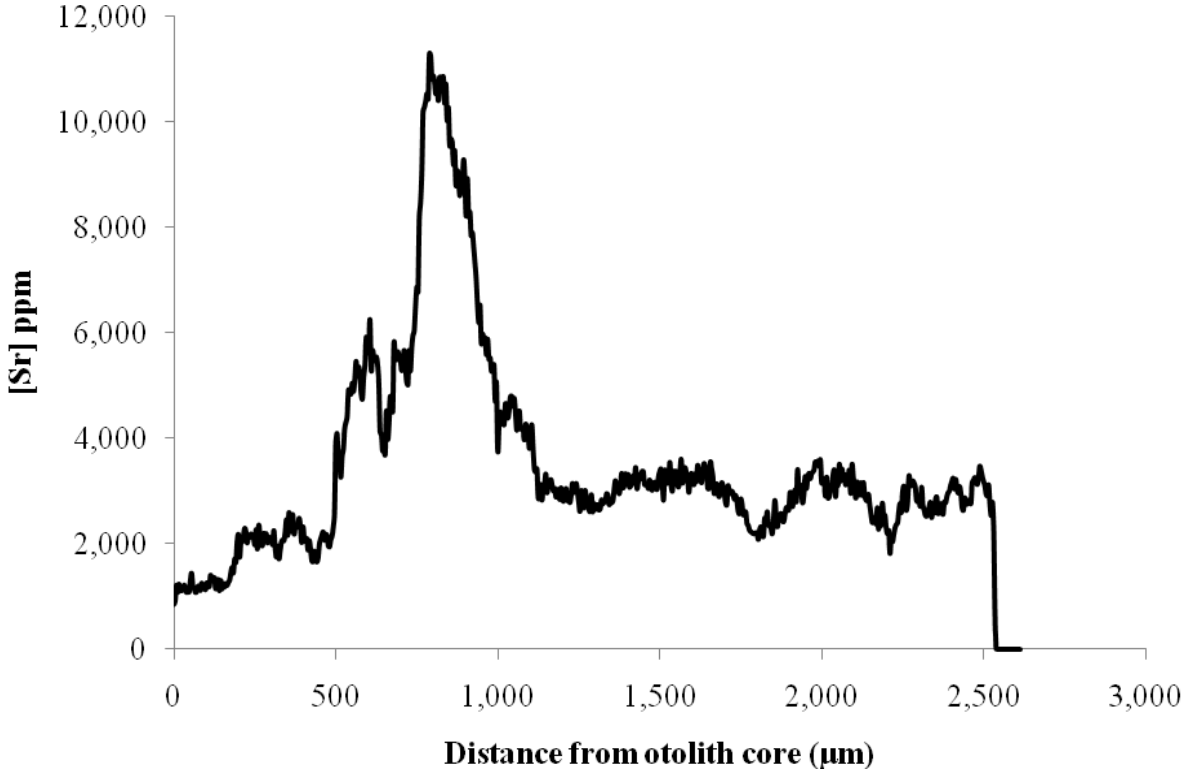
Fish ID: 1218; Disk 2 Otolith 6
Sprinter



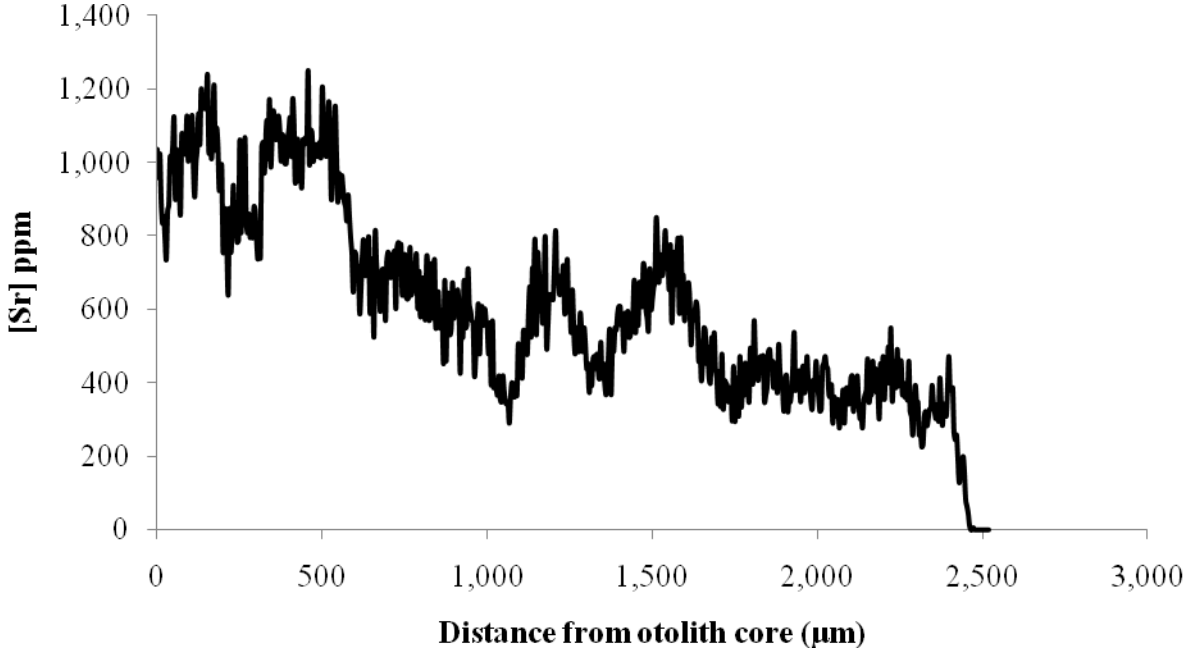
Fish ID: 1245; Disk 3 Otolith 1
Sprinter



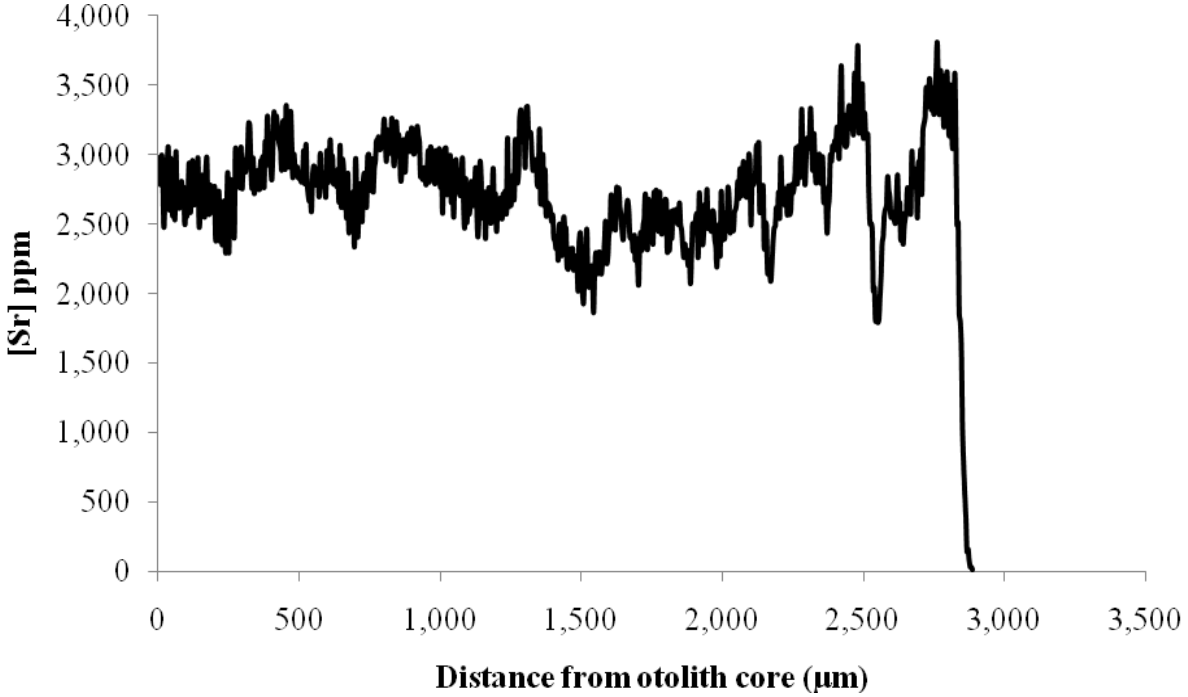
Fish ID: 1159; Disk 3 Otolith 2
Stager



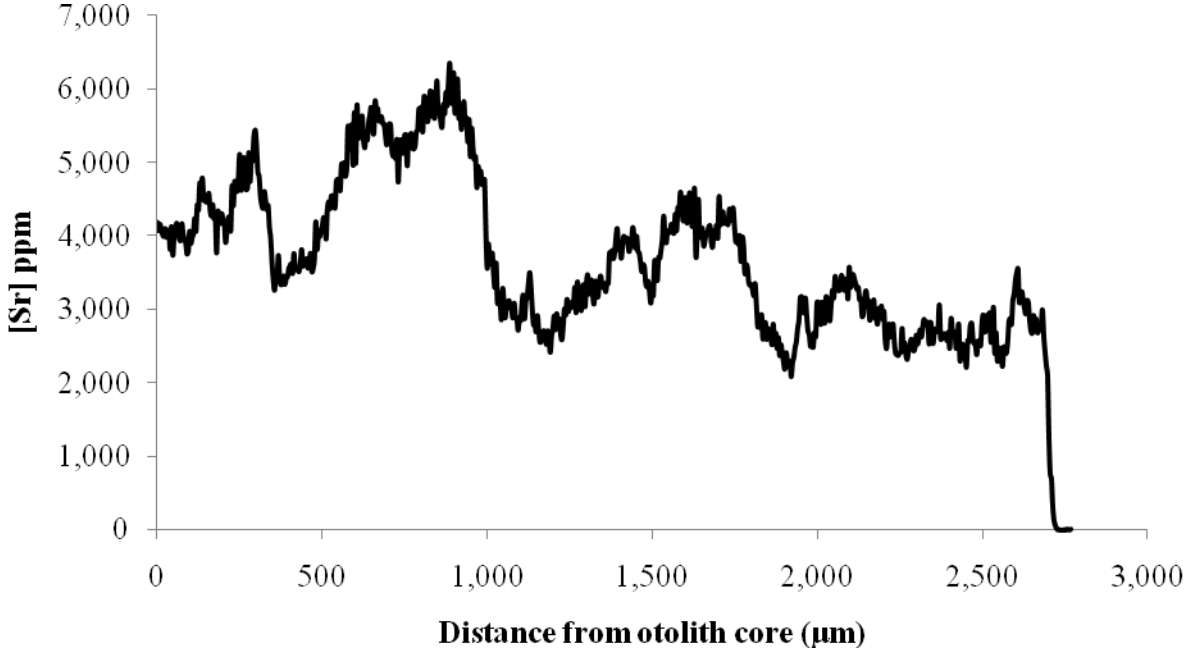
Fish ID: 1236; Disk 3 Otolith 3
Resident



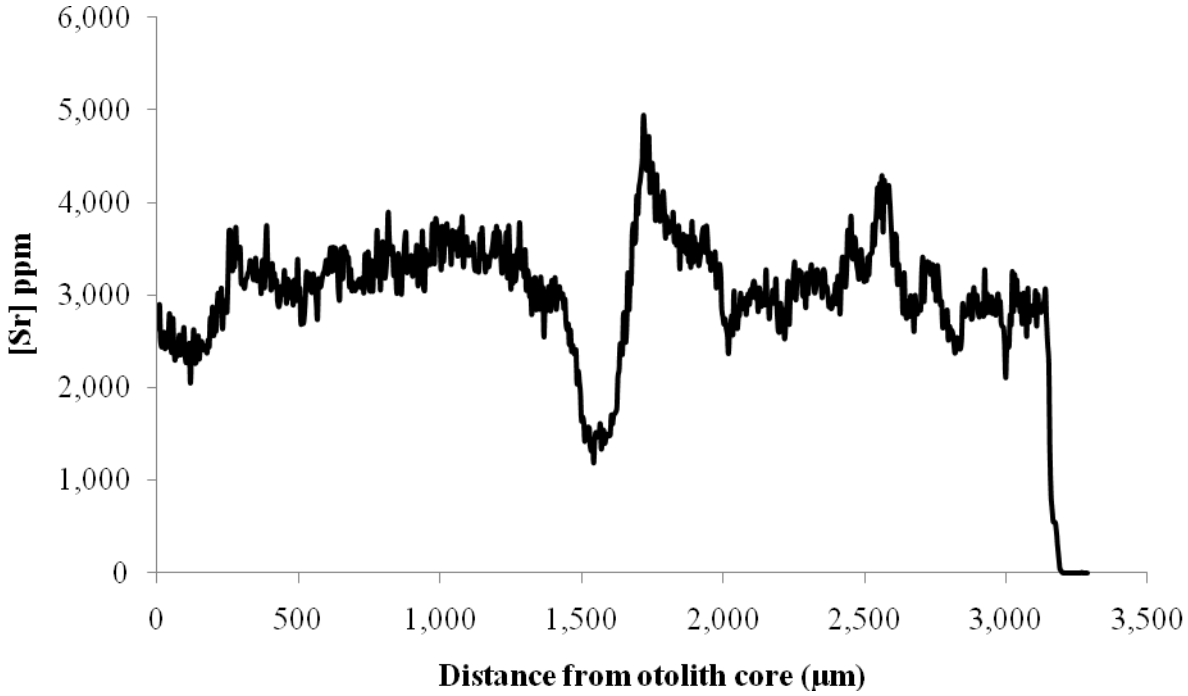
Fish ID: 367; Disk 3 Otolith 4
Resident



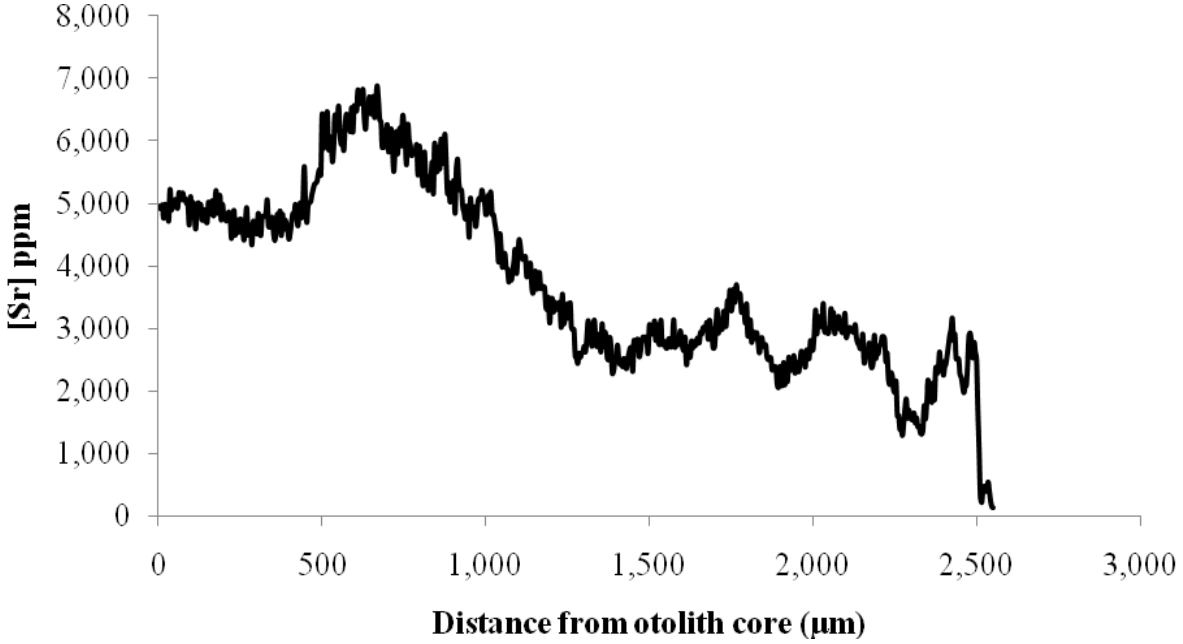
Fish ID: 330; Disk 3 Otolith 5
High Sr



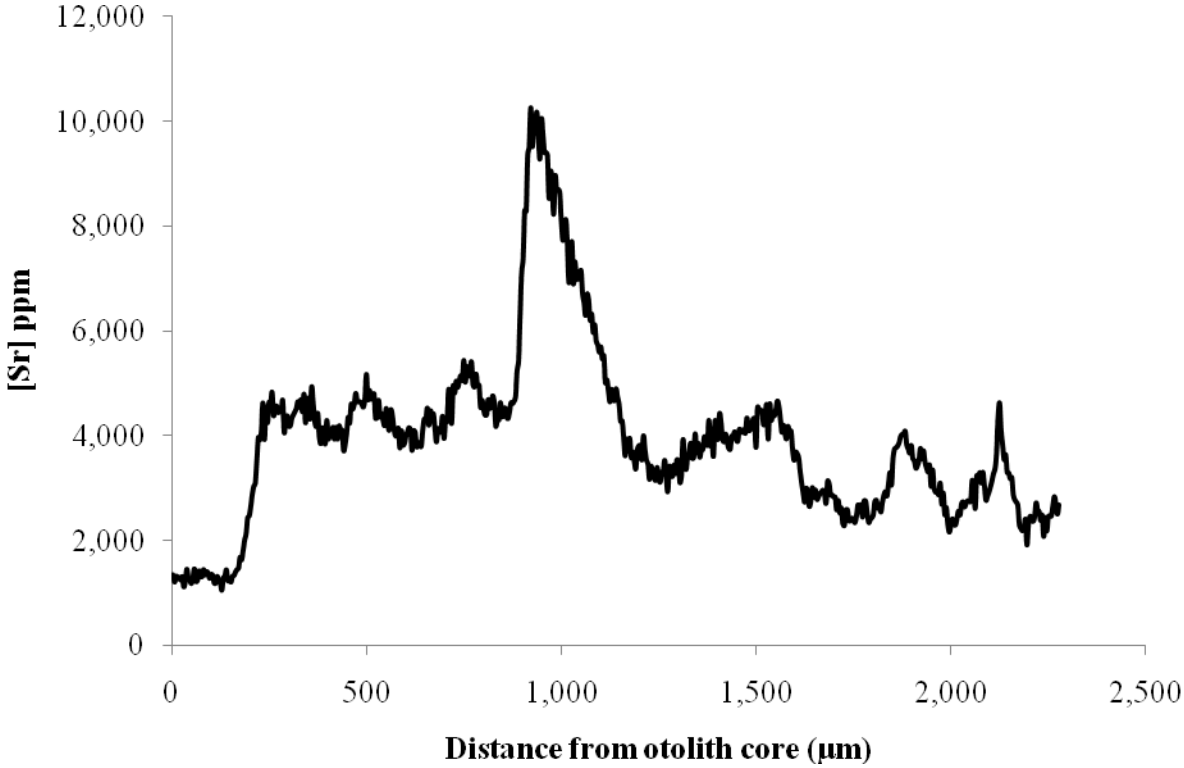
Fish ID: 385; Disk 3 Otolith 6
Resident



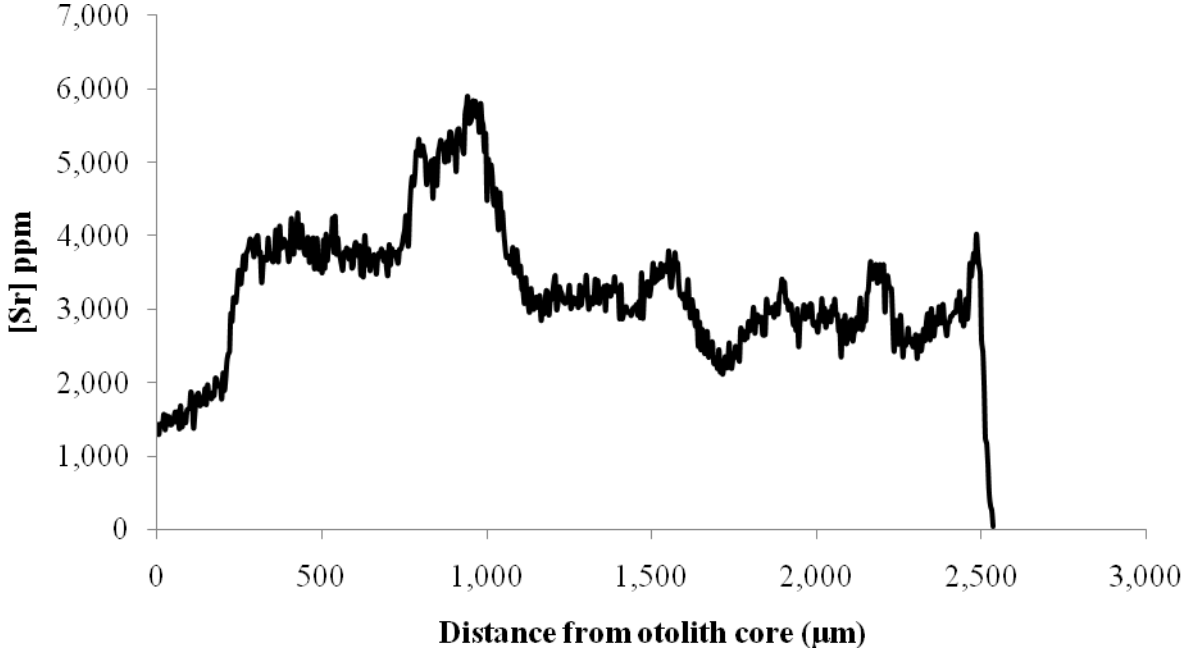
Fish ID: 351; Disk 4 Otolith 1
High Sr



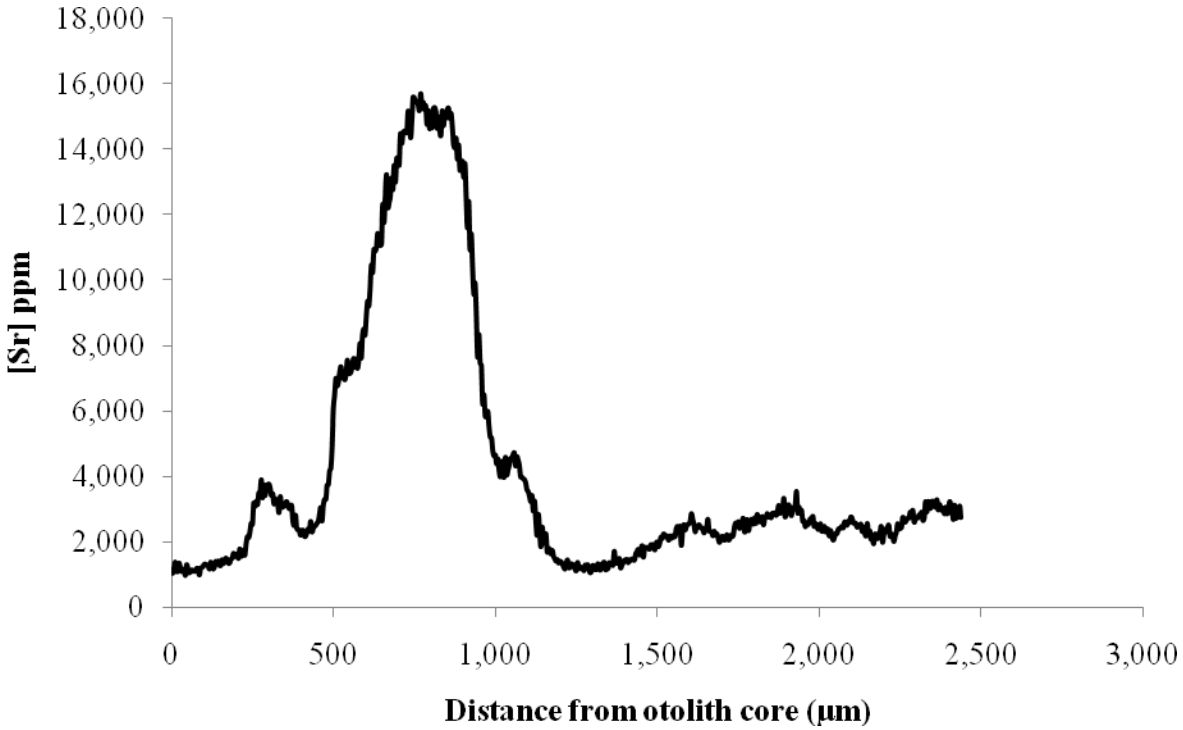
Fish ID: 328; Disk 4 Otolith 2
Sprinter



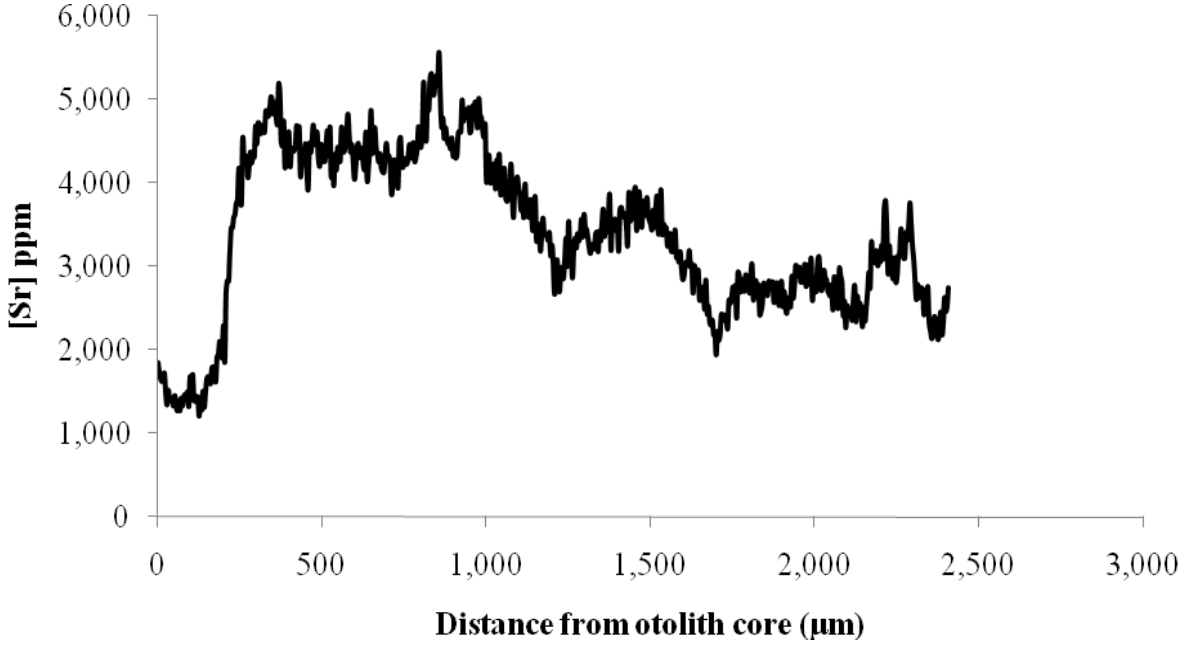
Fish ID: 1318; Disk 4 Otolith 3
Stager



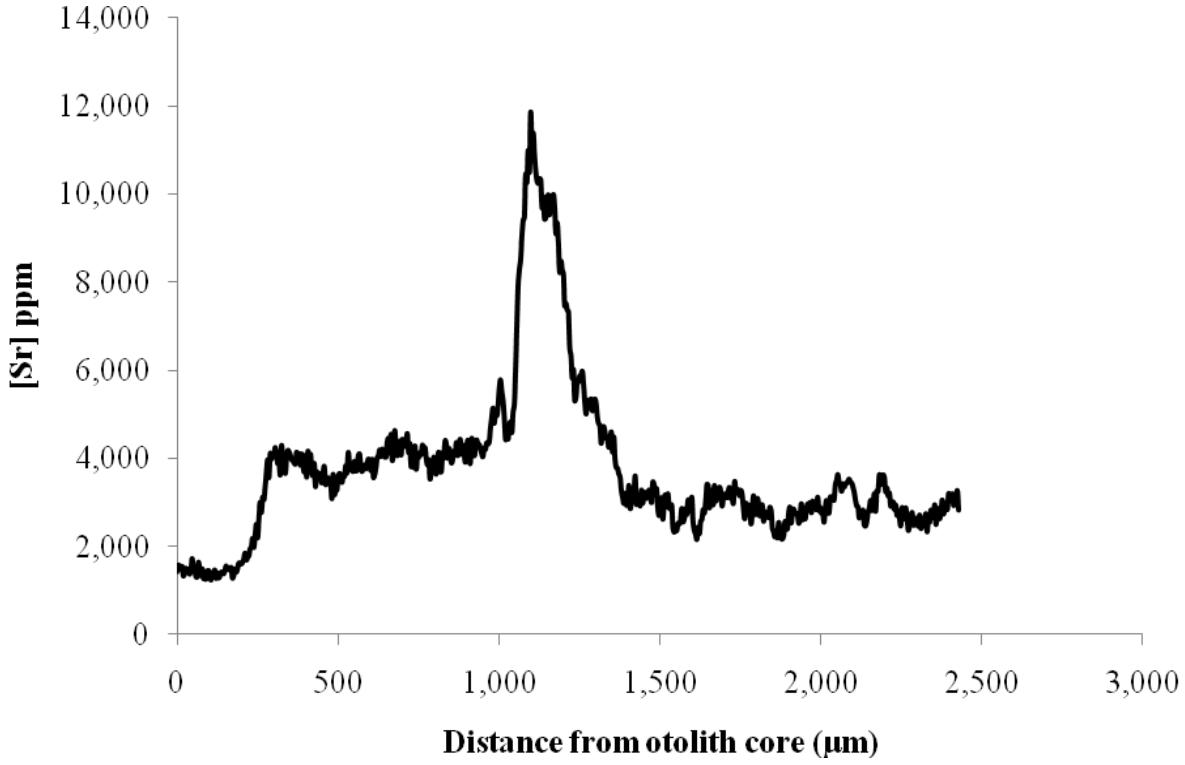
Fish ID: 359; Disk 4 Otolith 4
Stager



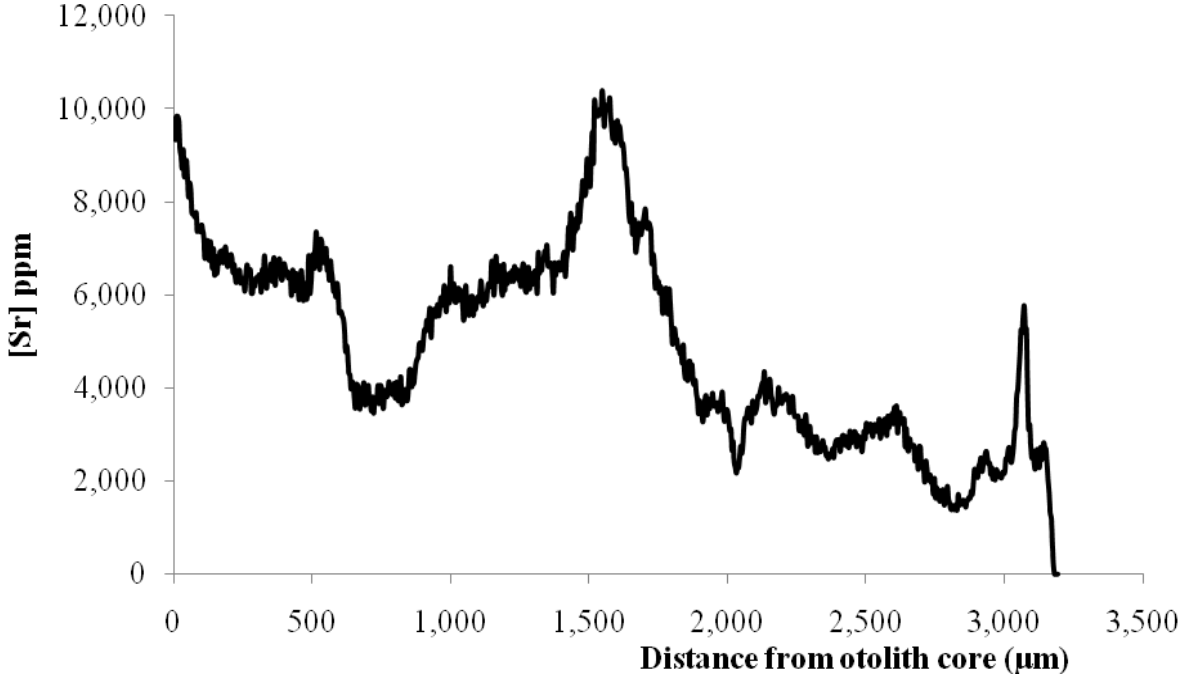
Fish ID: 1249; Disk 4 Otolith 5
Sprinter



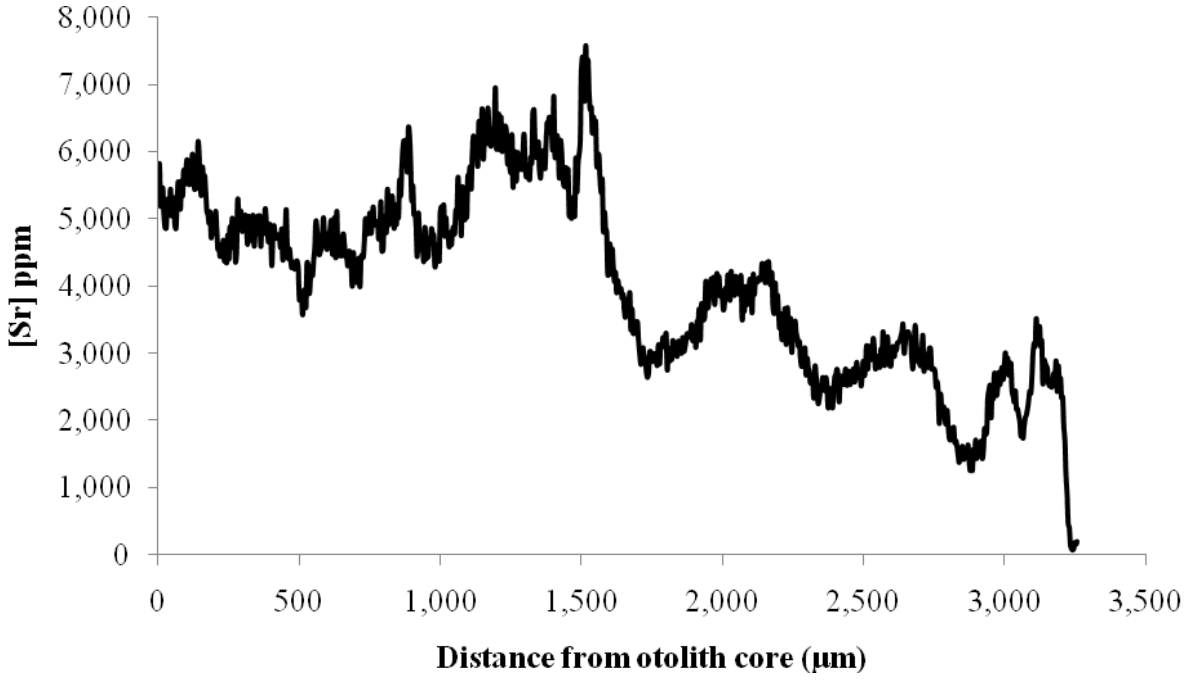
Fish ID: 1136; Disk 4 Otolith 6
Sprinter



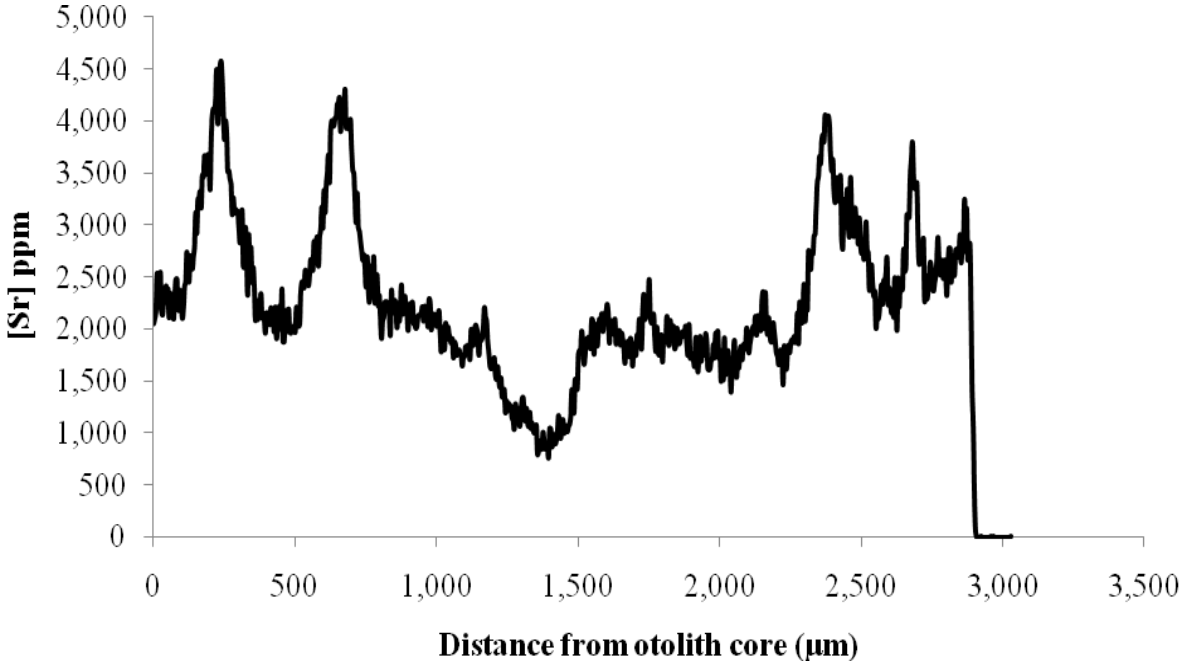
Fish ID: 1192: Disk 5 Otolith 1
High Sr



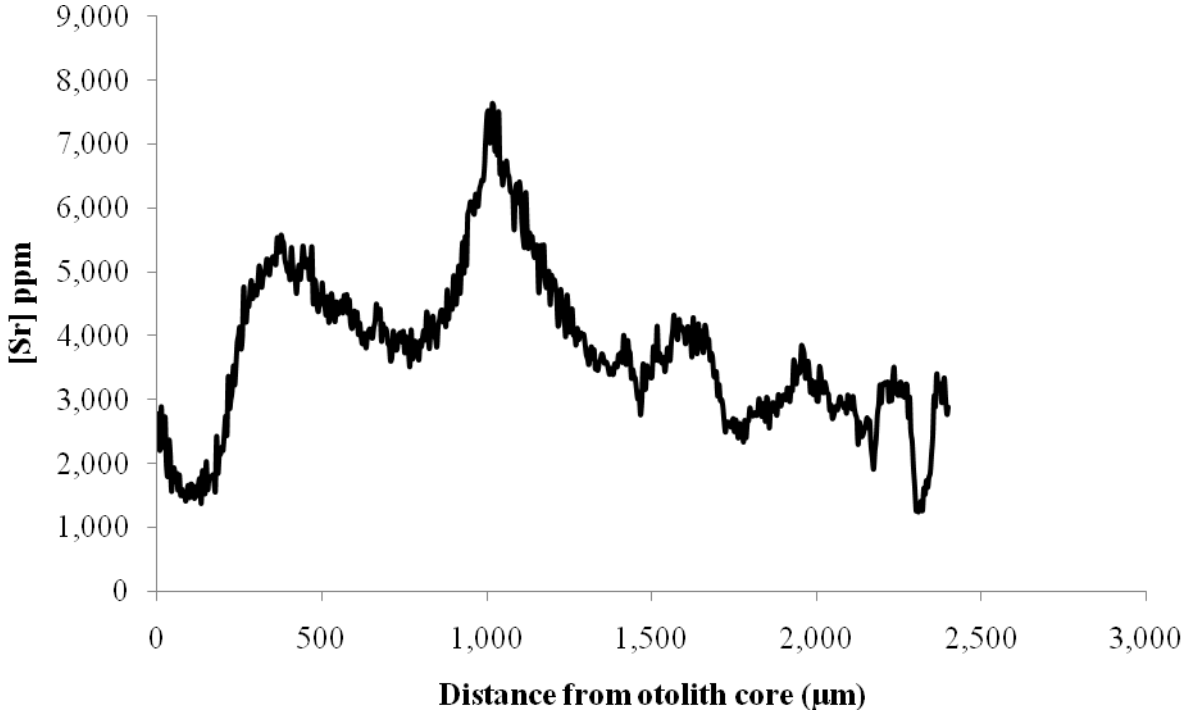
Fish ID: 1191; Disk 5 Otolith 2
High Sr



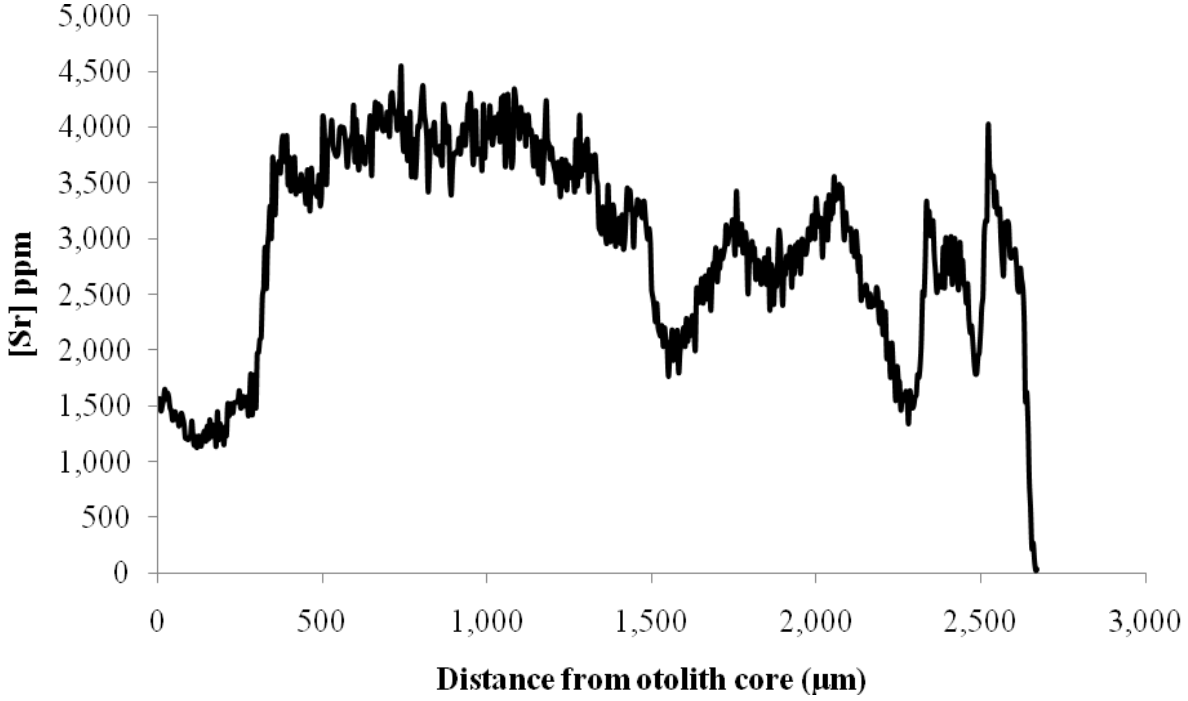
Fish ID: 1310; Disk 5 Otolith 3
Sprinter



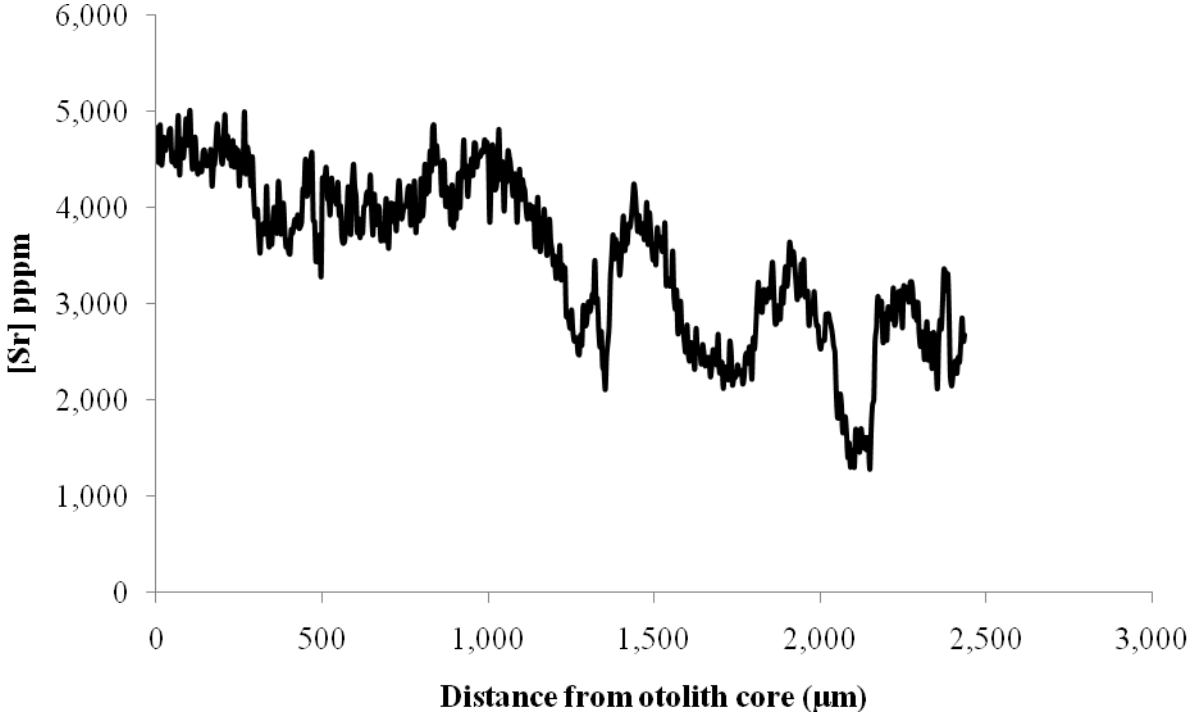
Fish ID: 466; Disk 5 Otolith 4
Sprinter



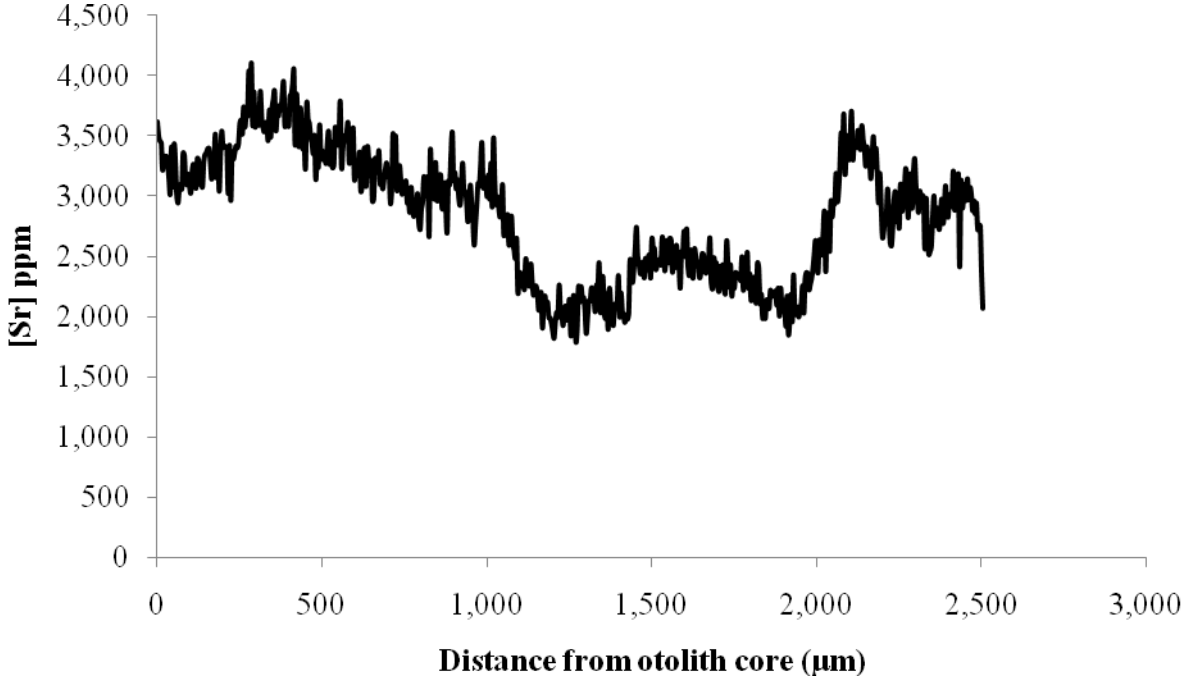
Fish ID: 461; Disk 5 Otolith 5
Sprinter



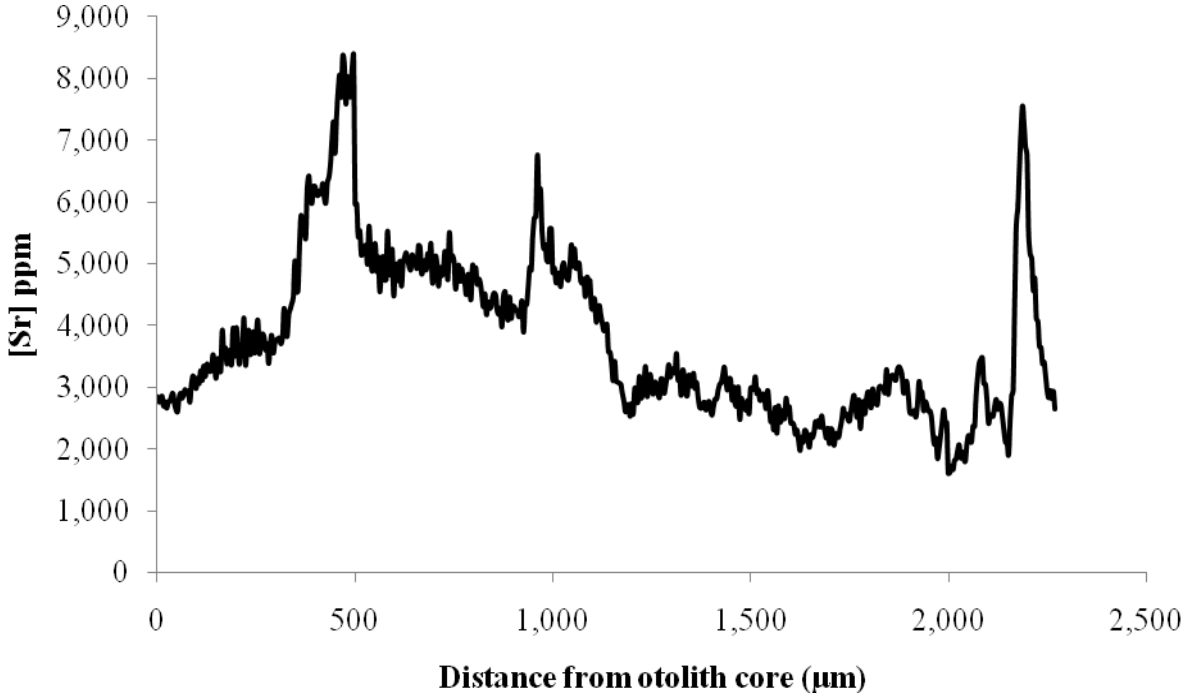
Fish ID: 430; Disk 5 Otolith 6
High Sr



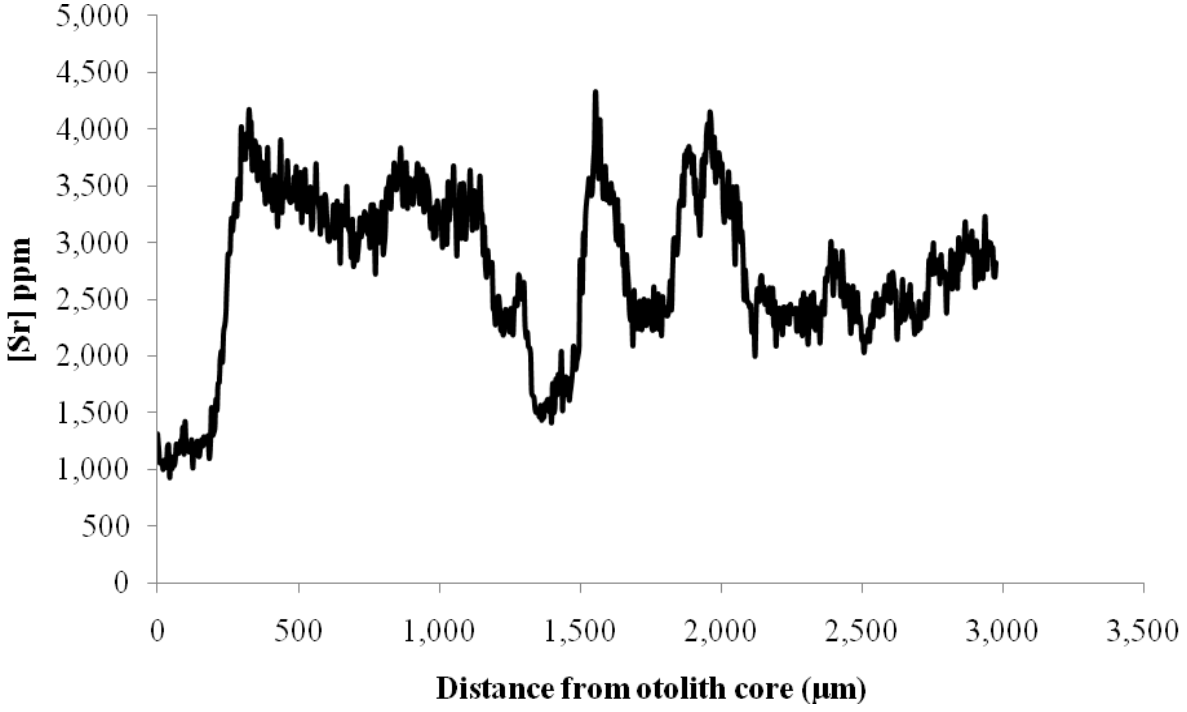
Fish ID: 468; Disk 5 Otolith 7
Resident



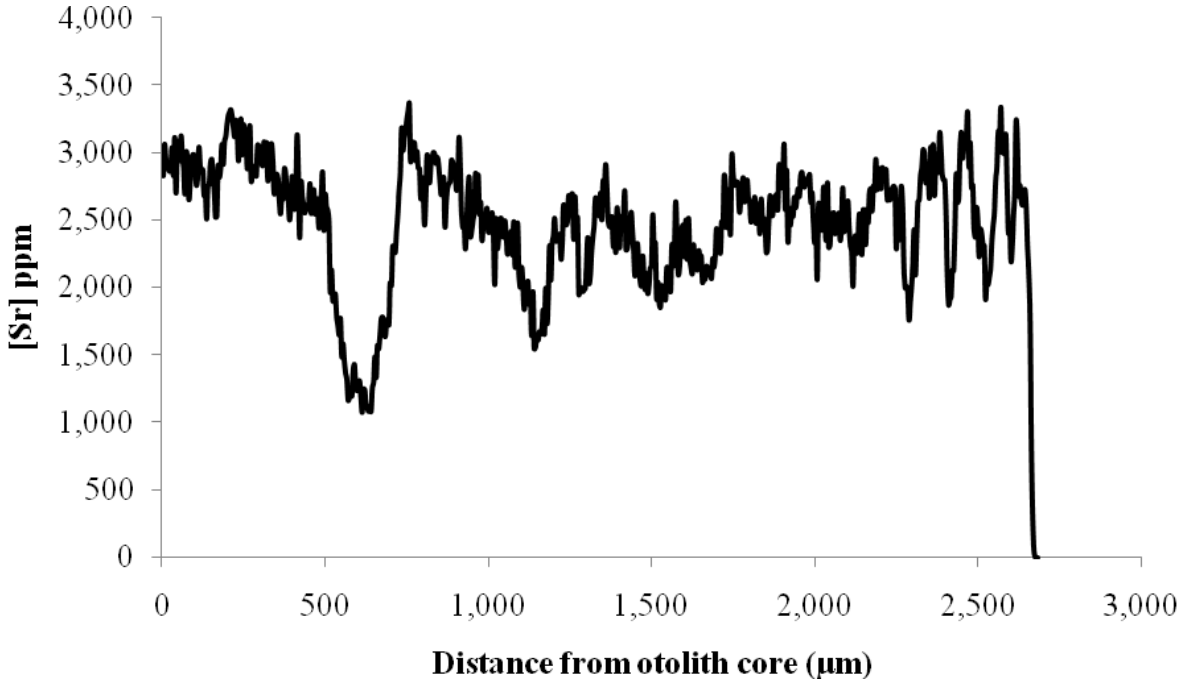
Fish ID: 361; Disk 5 Otolith 8
Stager



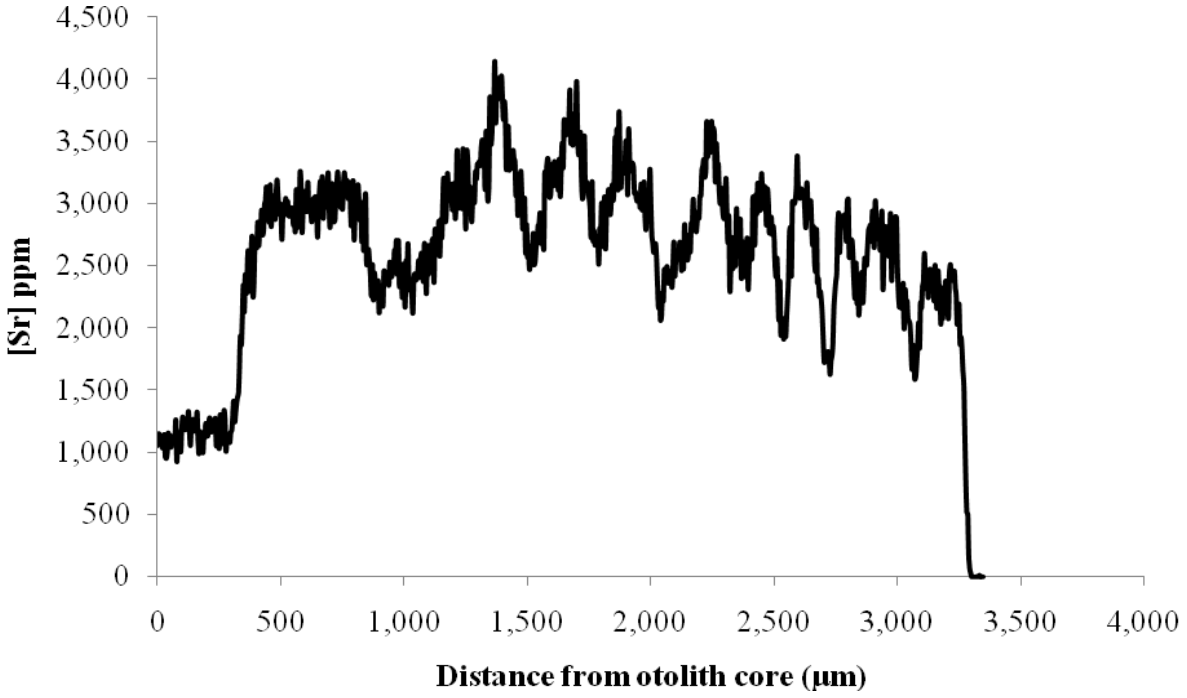
Fish ID: 5003; Disk 6 Otolith 1
Sprinter



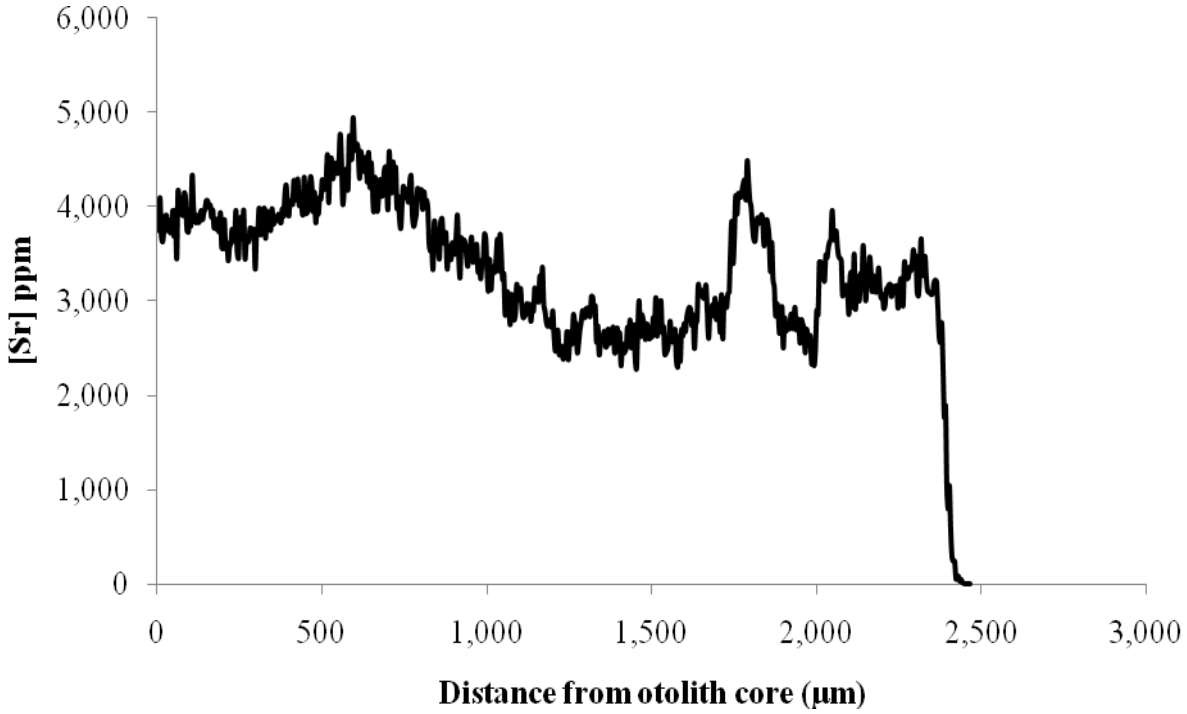
Fish ID: 6005; Disk 6 Otolith 2
Resident



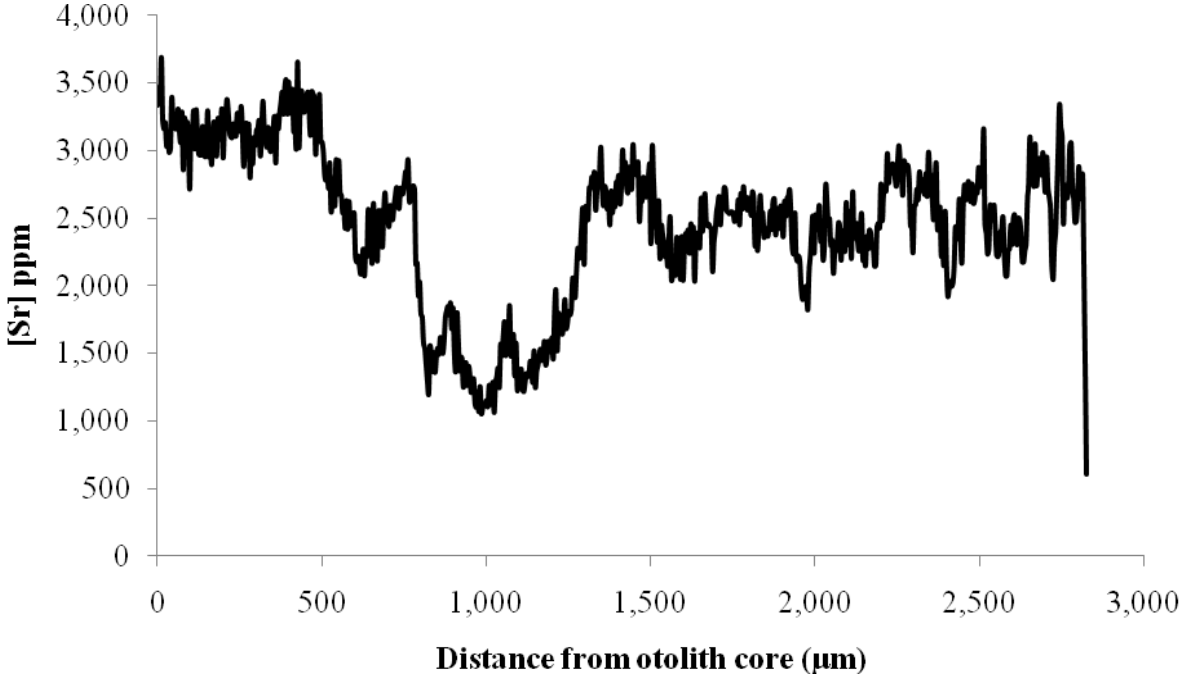
Fish ID: 110; Disk 6 Otolith 3
Resident



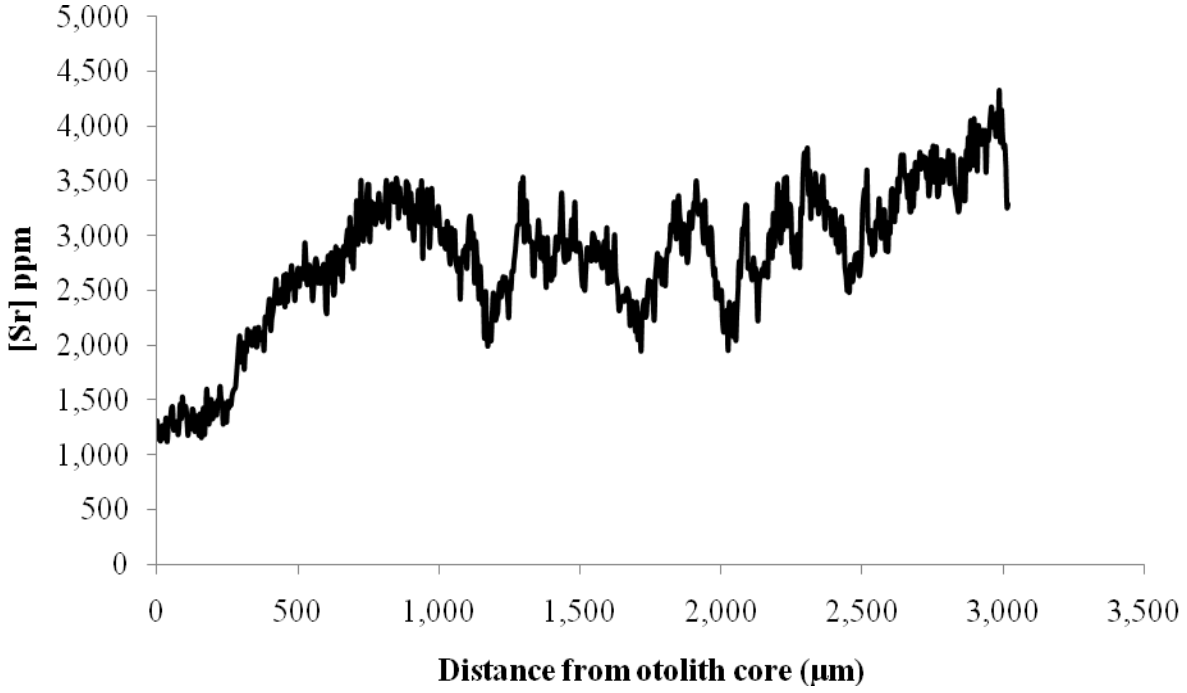
Fish ID: 1216; Disk 6 Otolith 4
High Sr



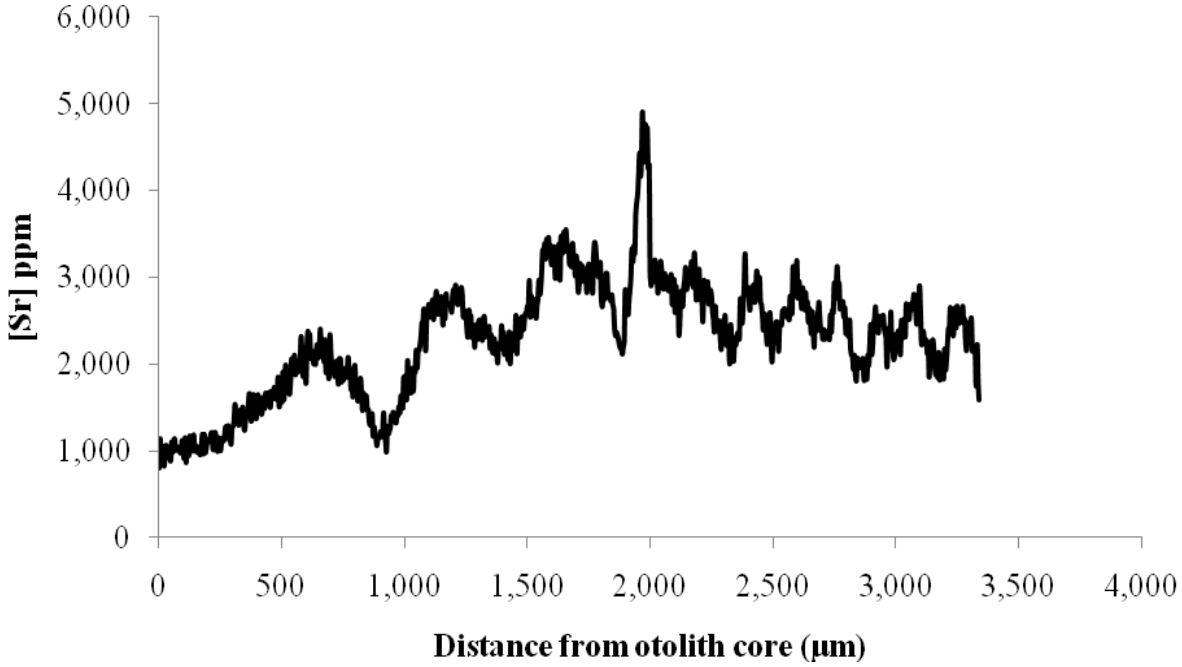
Fish ID: 6006; Disk 6 otolith 5
Resident



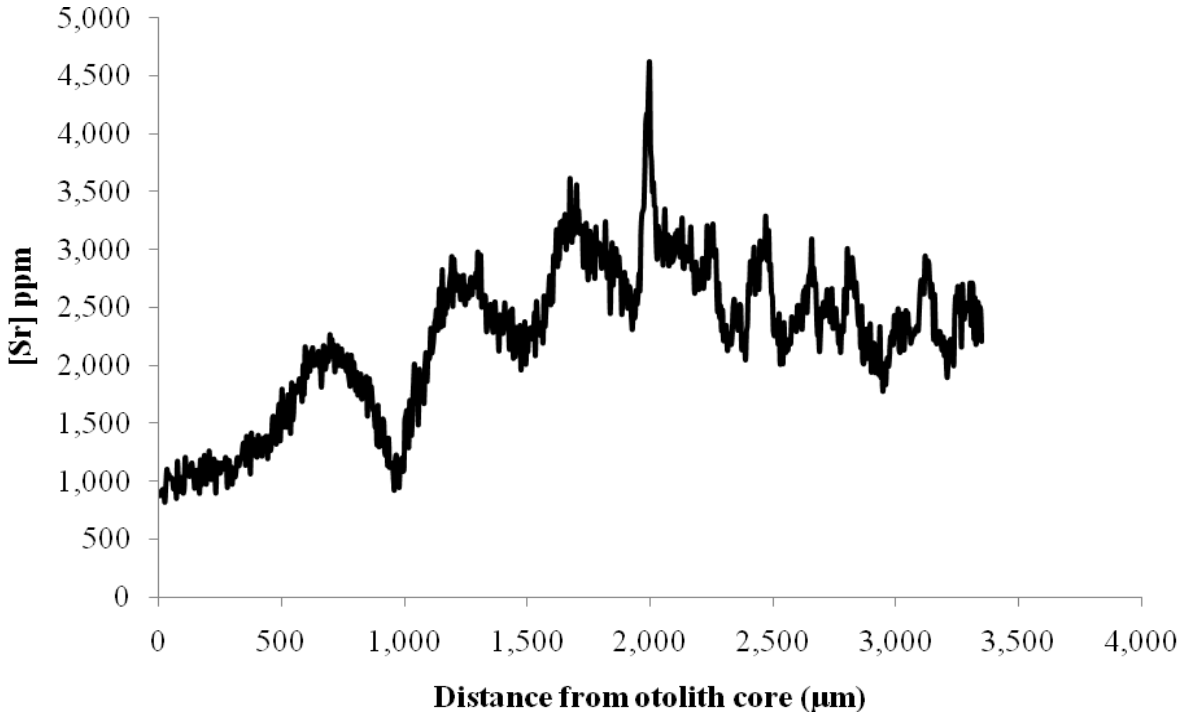
Fish ID: 5002; Disk 6 Otolith 6
Resident



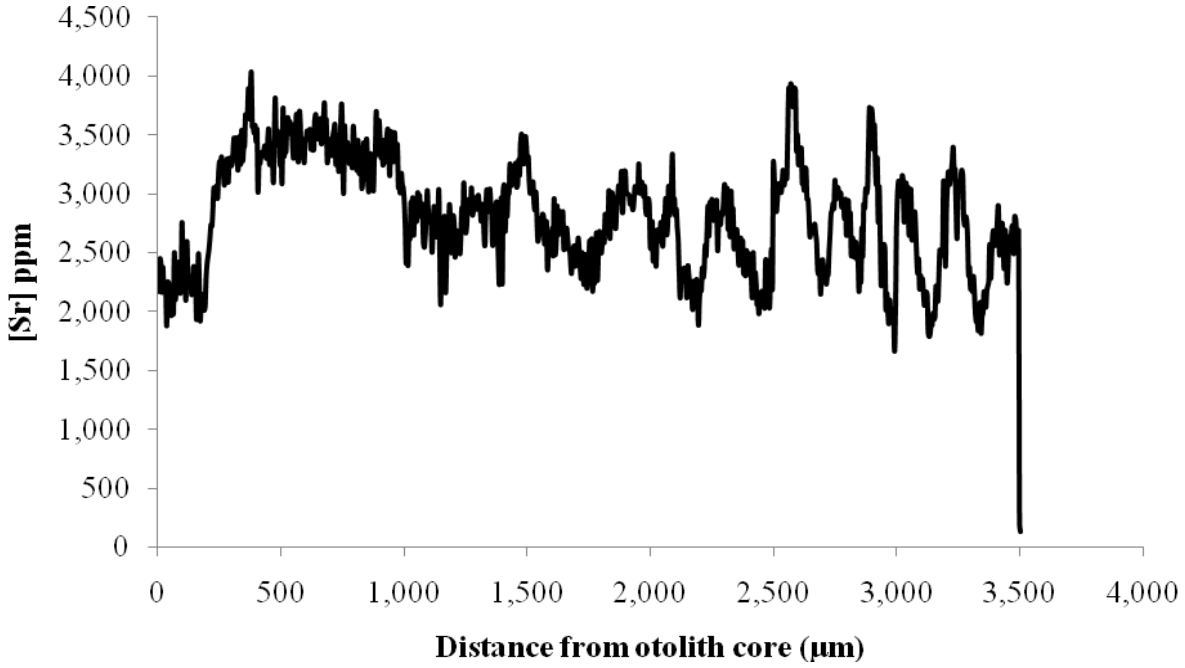
Fish ID: 111; Disk 7 Otolith 1
Resident



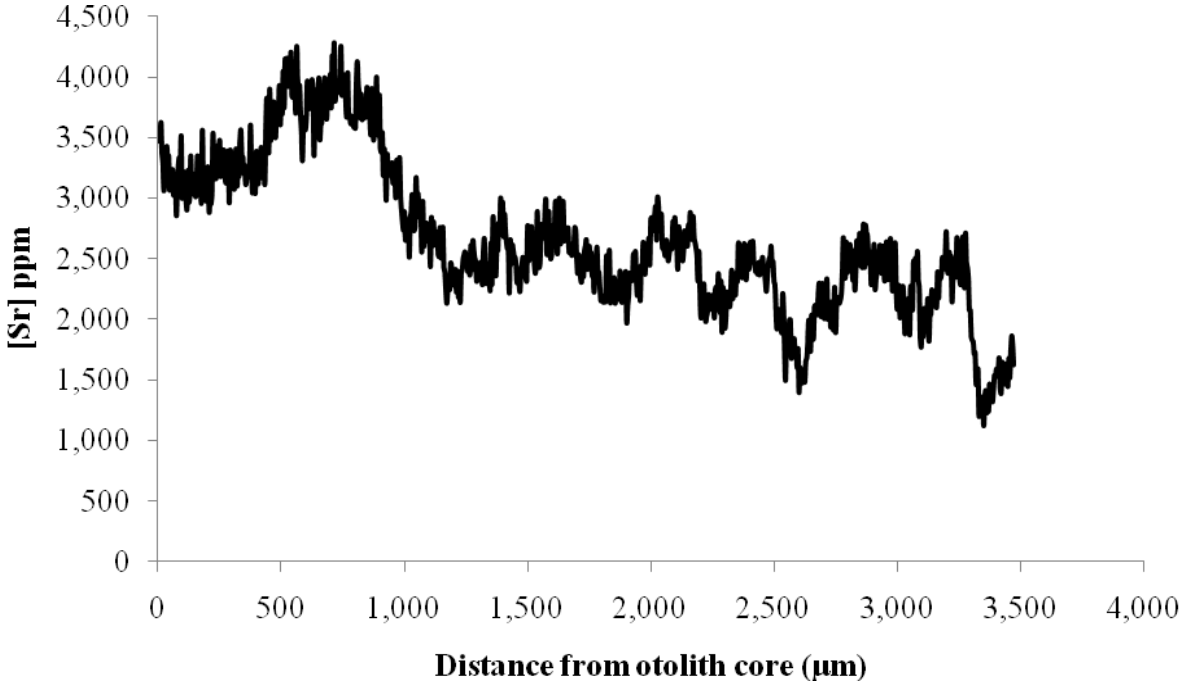
Fish ID: 6008; Disk 7 Otolith 2
Resident



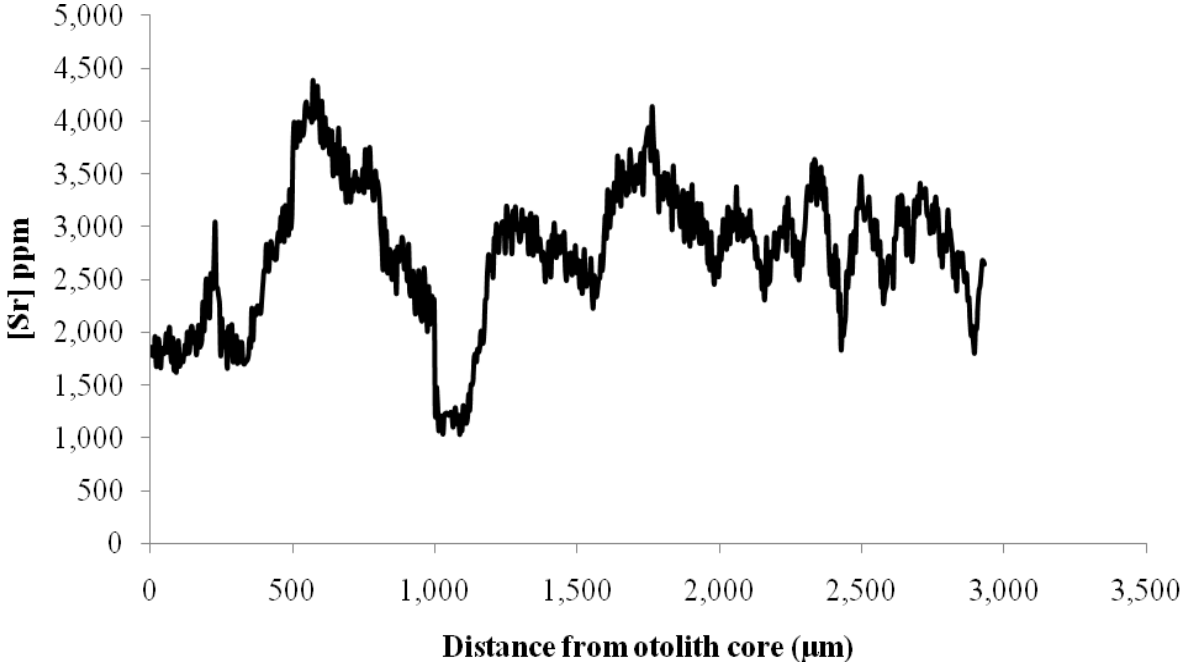
Fish ID: 107; Disk 7 Otolith 3
Stager



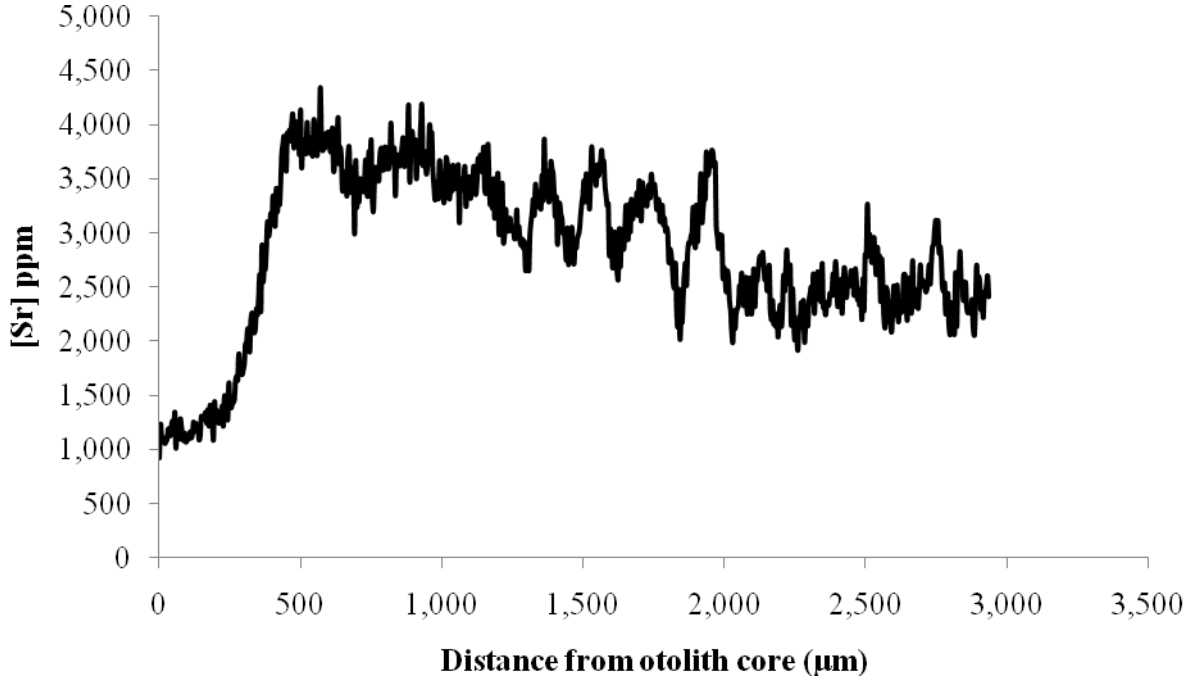
Fish ID: 105; Disk 7 Otolith 4
High Sr



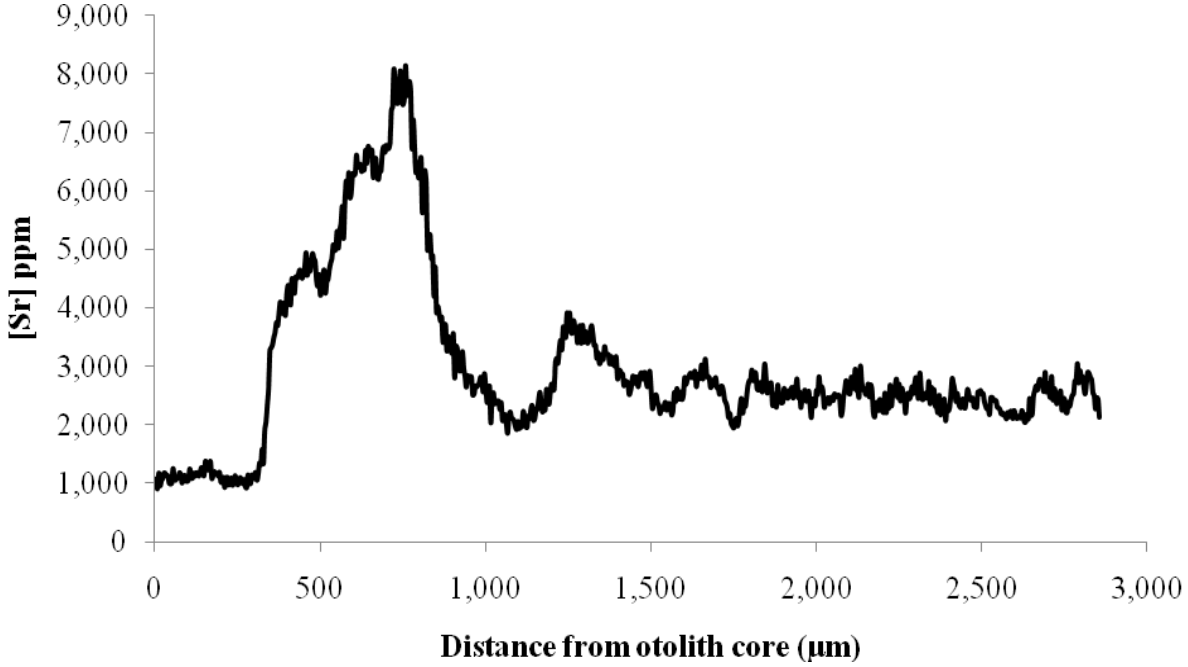
Fish ID: 102; Disk 7 Otolith 5
Sprinter



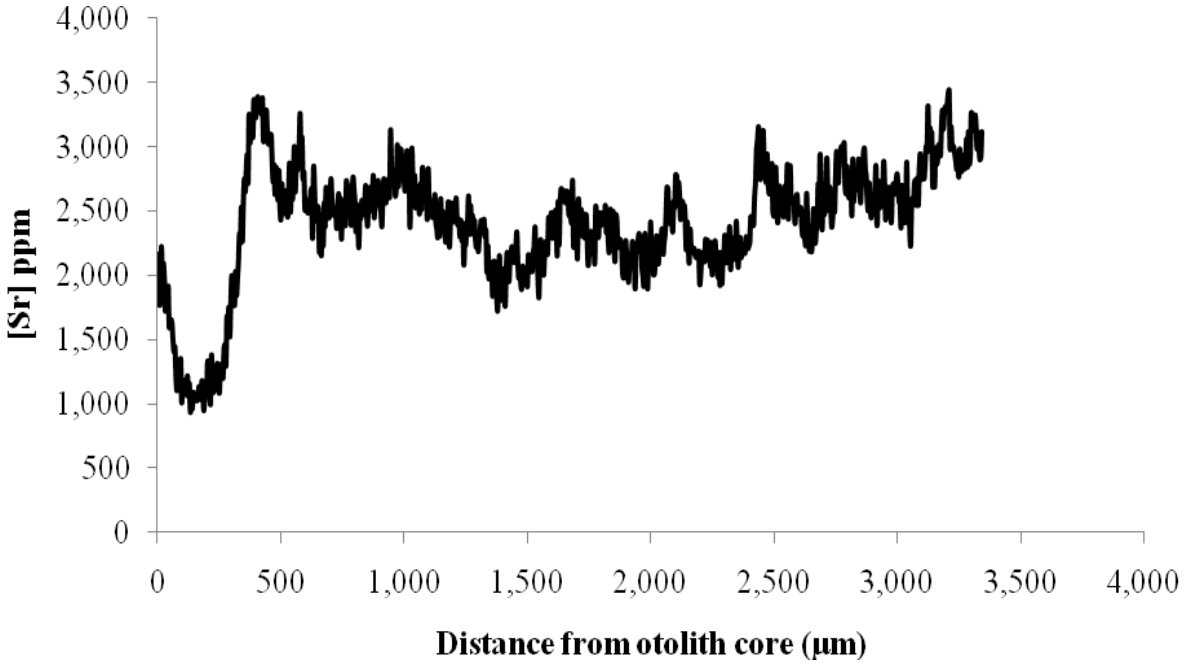
Fish ID: 5001; Disk 8 Otolith 2
Sprinter



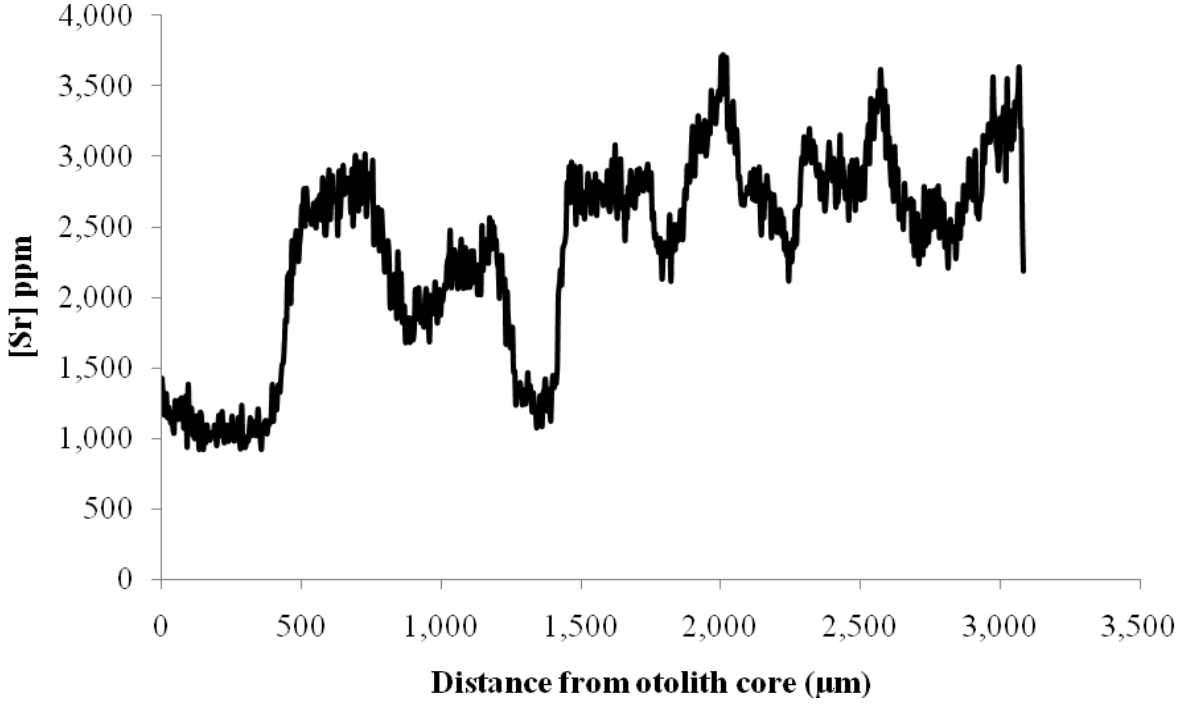
Fish ID: 3002; Disk 8 Otolith 3
Sprinter



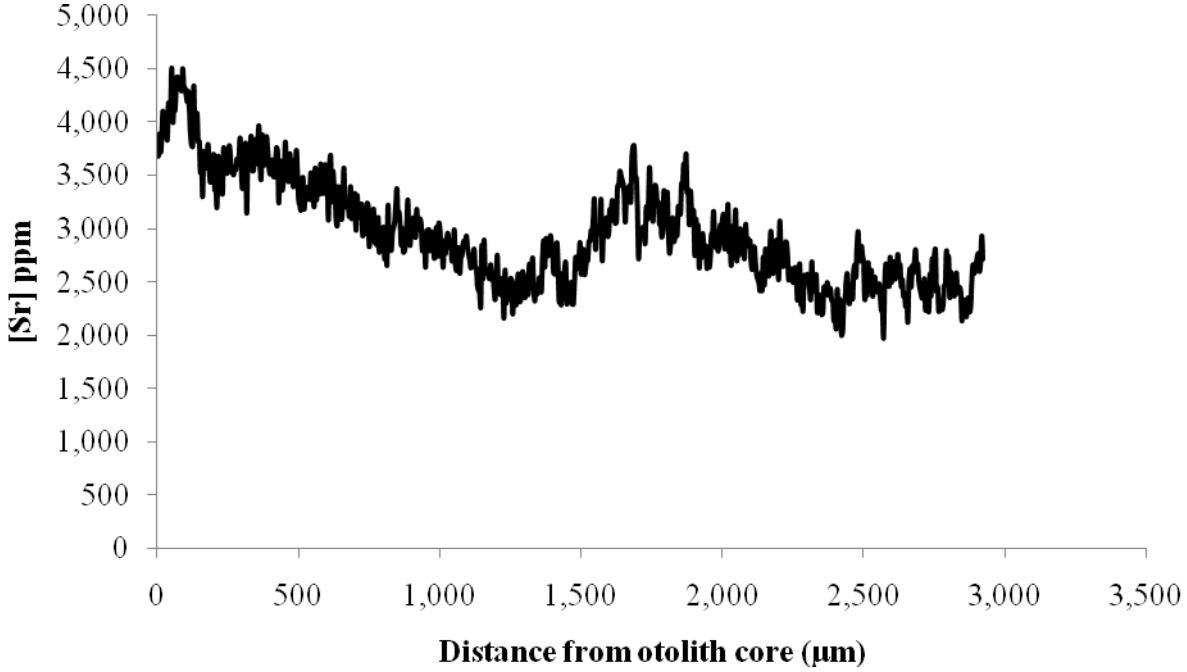
Fish ID: 6003; Disk 8 Otolith 4
Resident



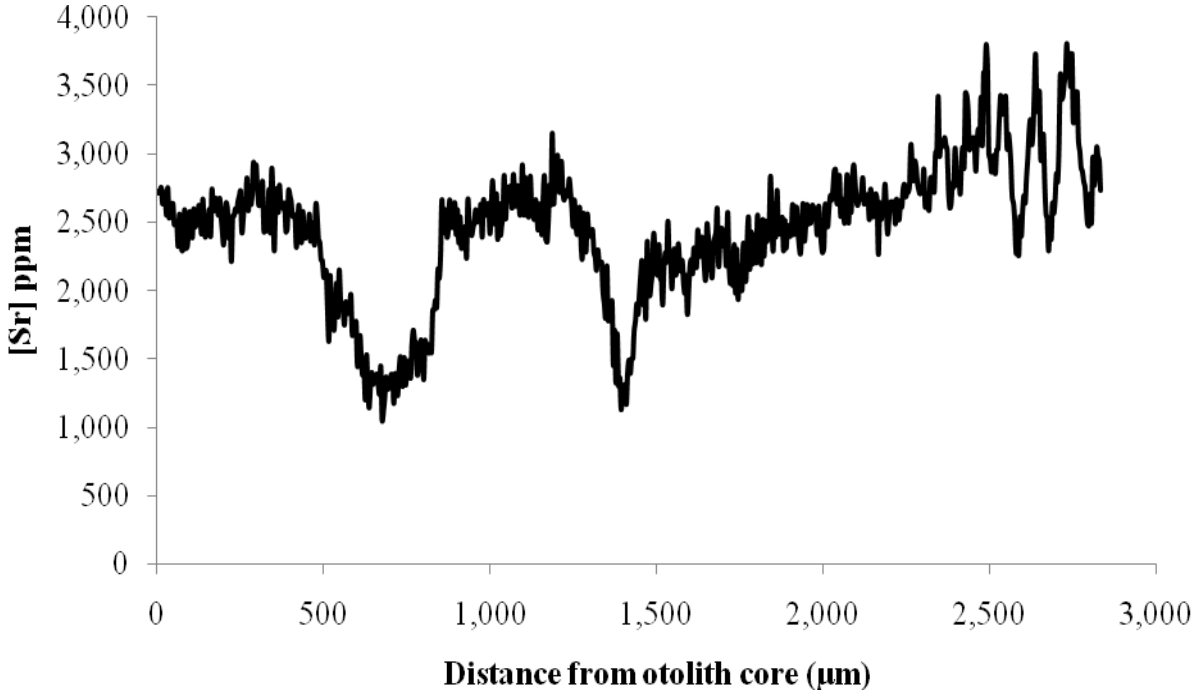
Fish ID: 6007; Disk 8 Otolith 5
Resident



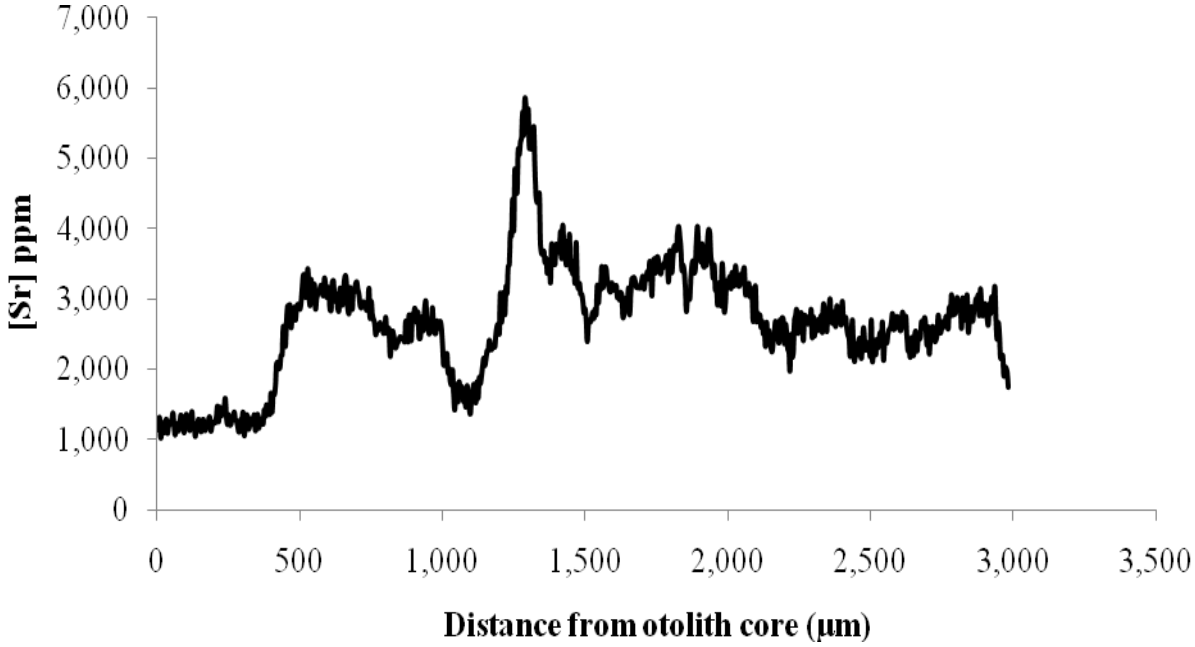
Fish ID: 5005; Disk 8 Otolith 6
High Sr



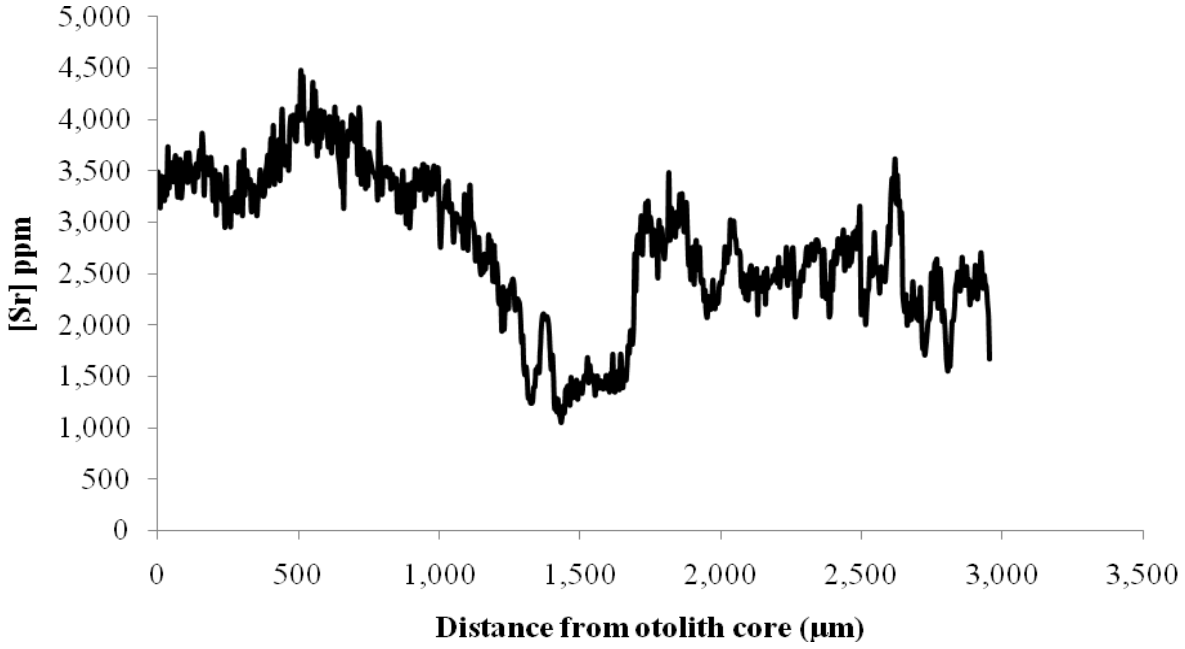
Fish ID: 104; Disk 9 Otolith 1
Resident



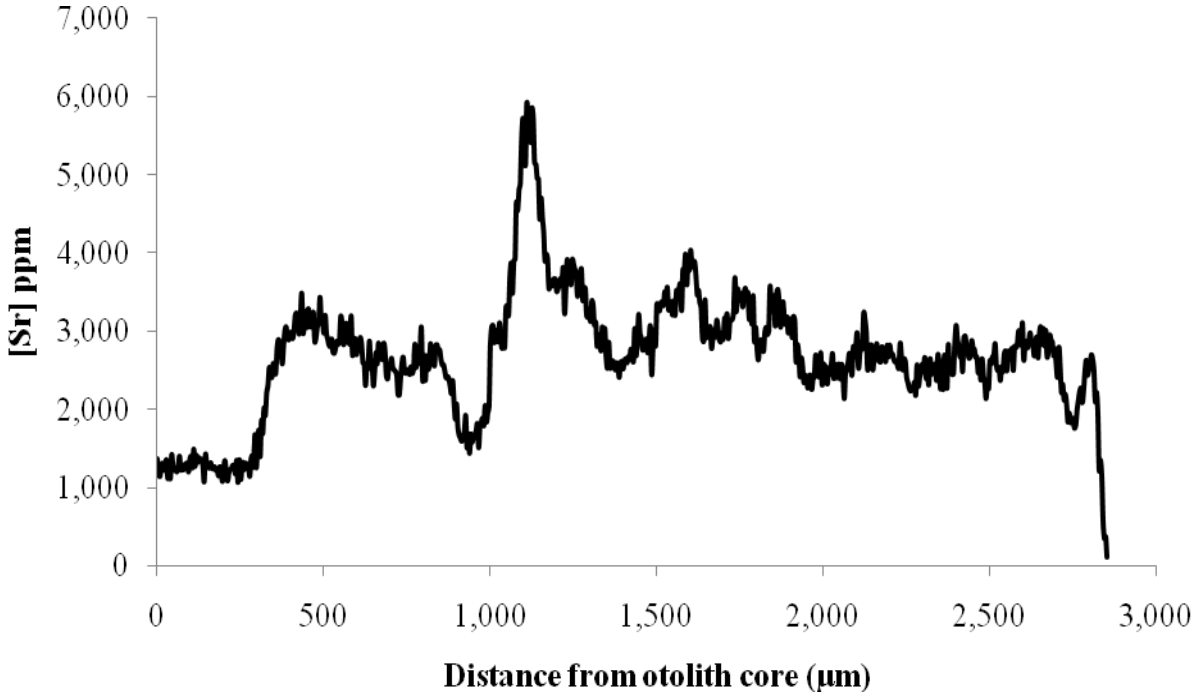
Fish ID: 3003; Disk 9 Otolith 2
Resident



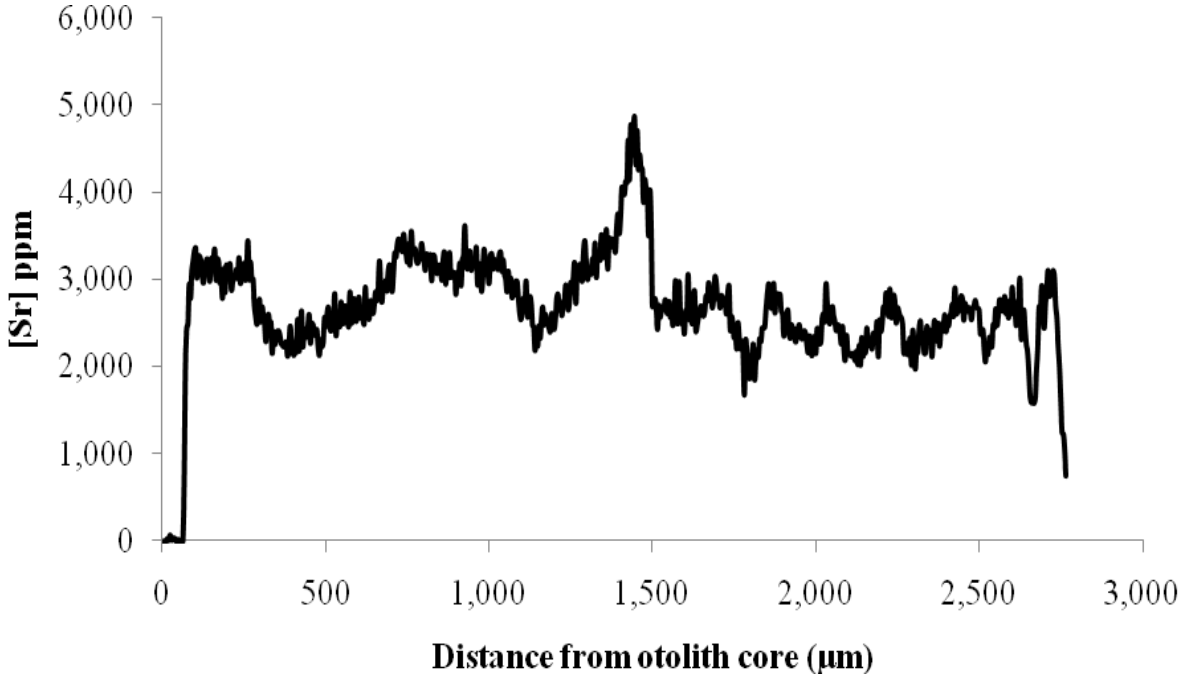
Fish ID: 5006; Disk 9 Otolith 3
High Sr



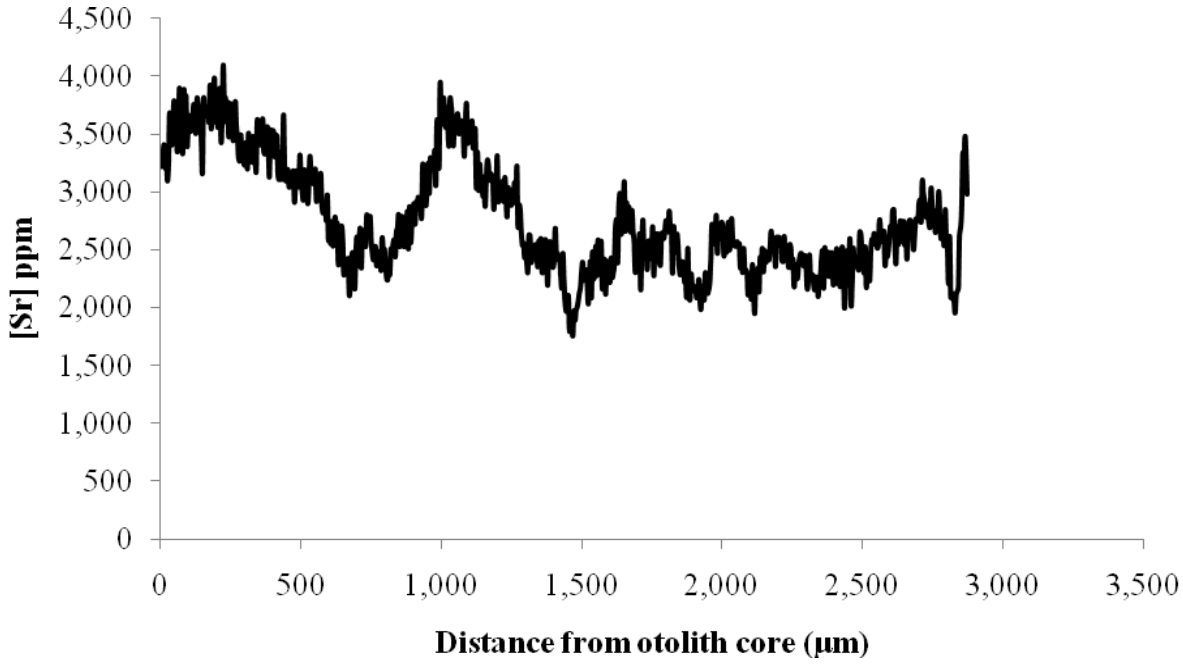
Fish ID: 106; Disk 9 Otolith 4
Resident



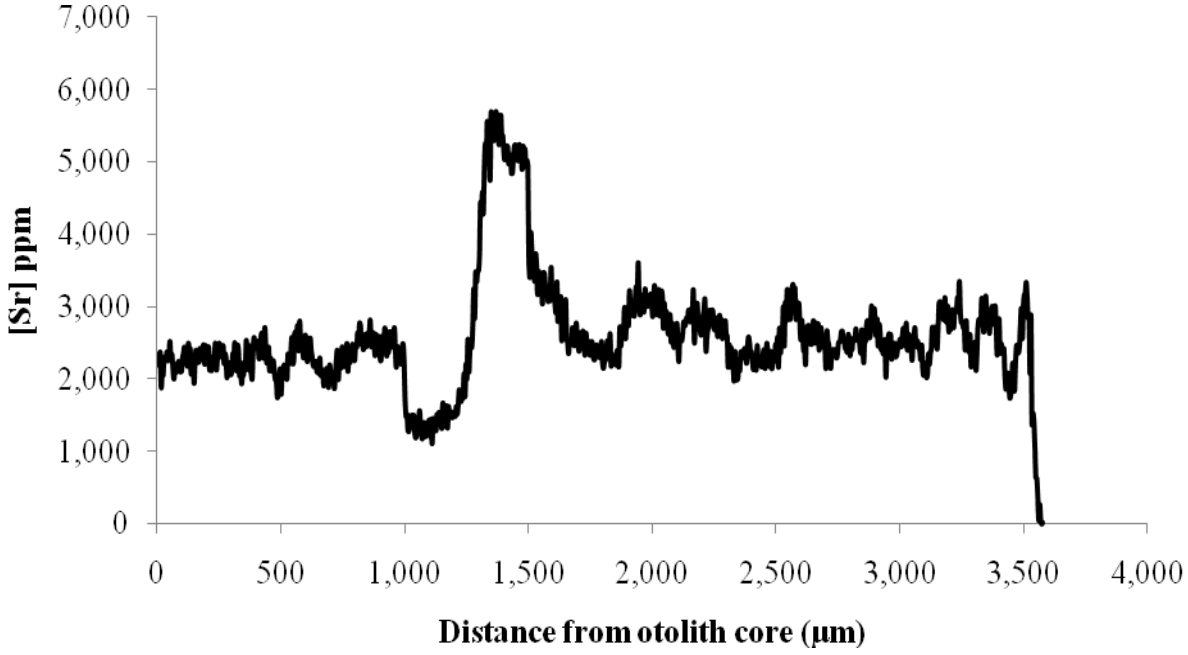
Fish ID: 5007; Disk 9 Otolith 5
Resident



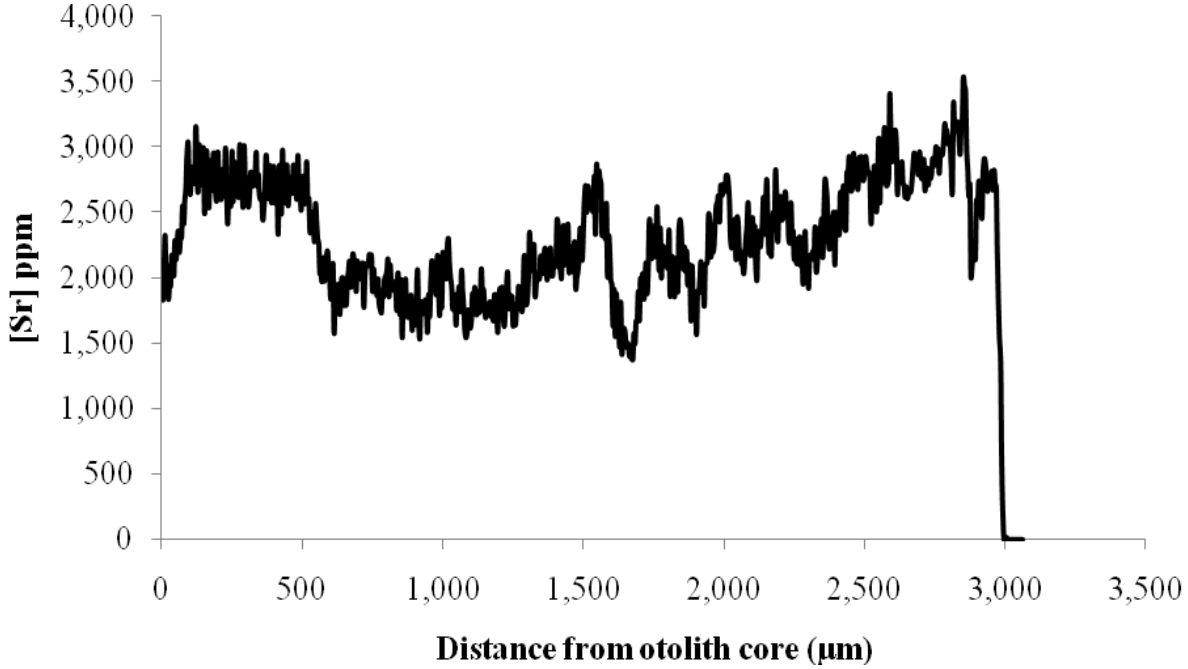
Fish ID: 101; Disk 9 Otolith 6
High Sr



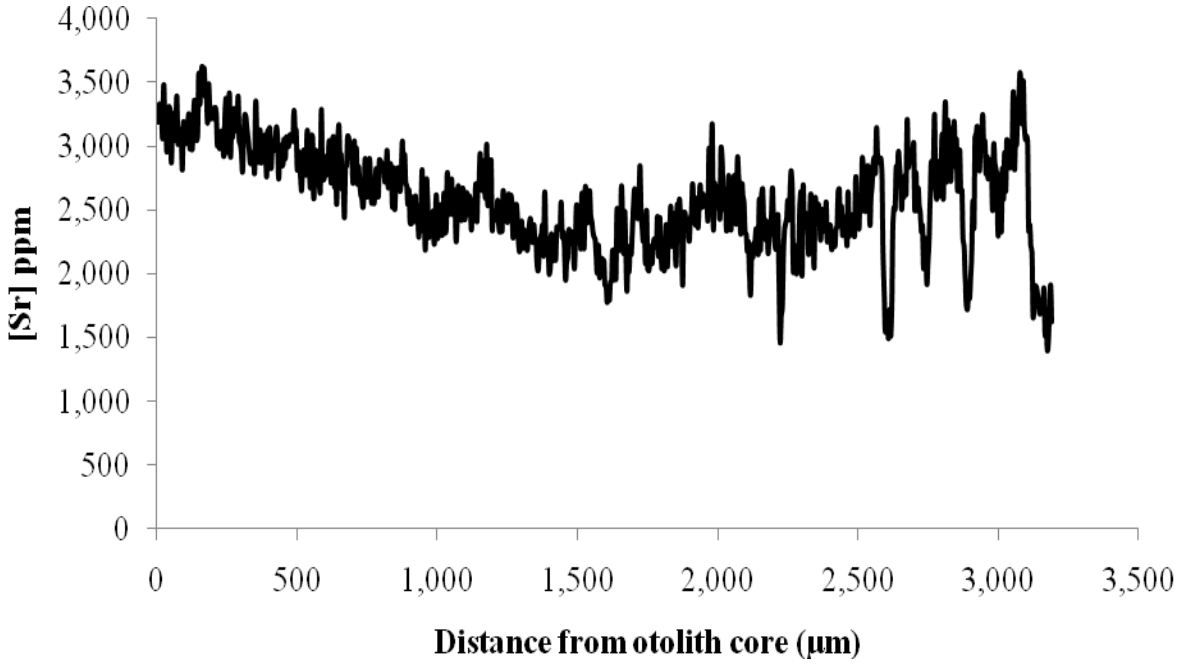
Fish ID: 5008; Disk 10 Otolith 1
Resident



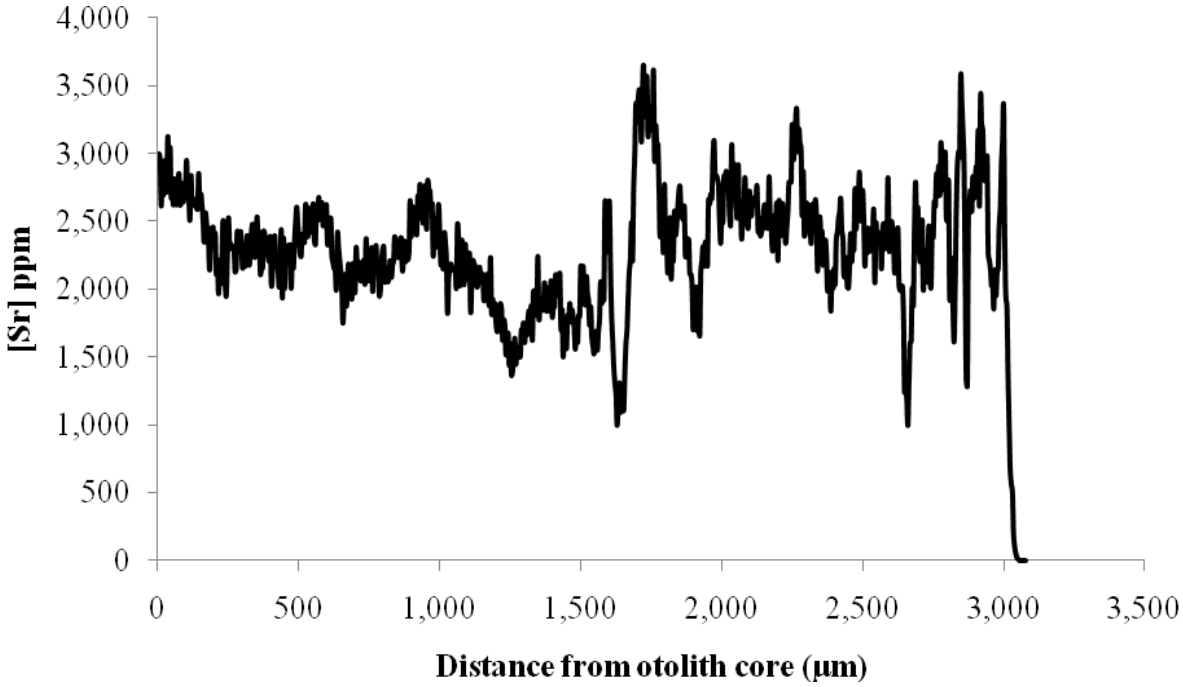
Fish ID: 5004; Disk 10 Otolith 2
Resident



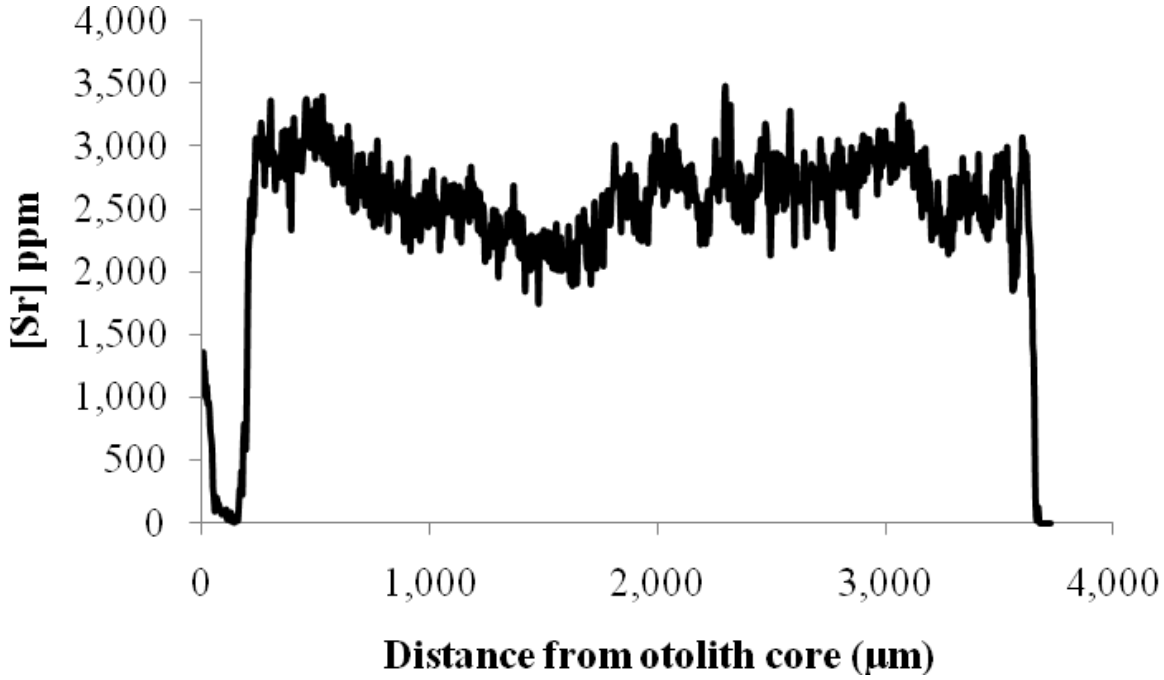
Fish ID: 112; Disk 10 Otolith 3
Resident



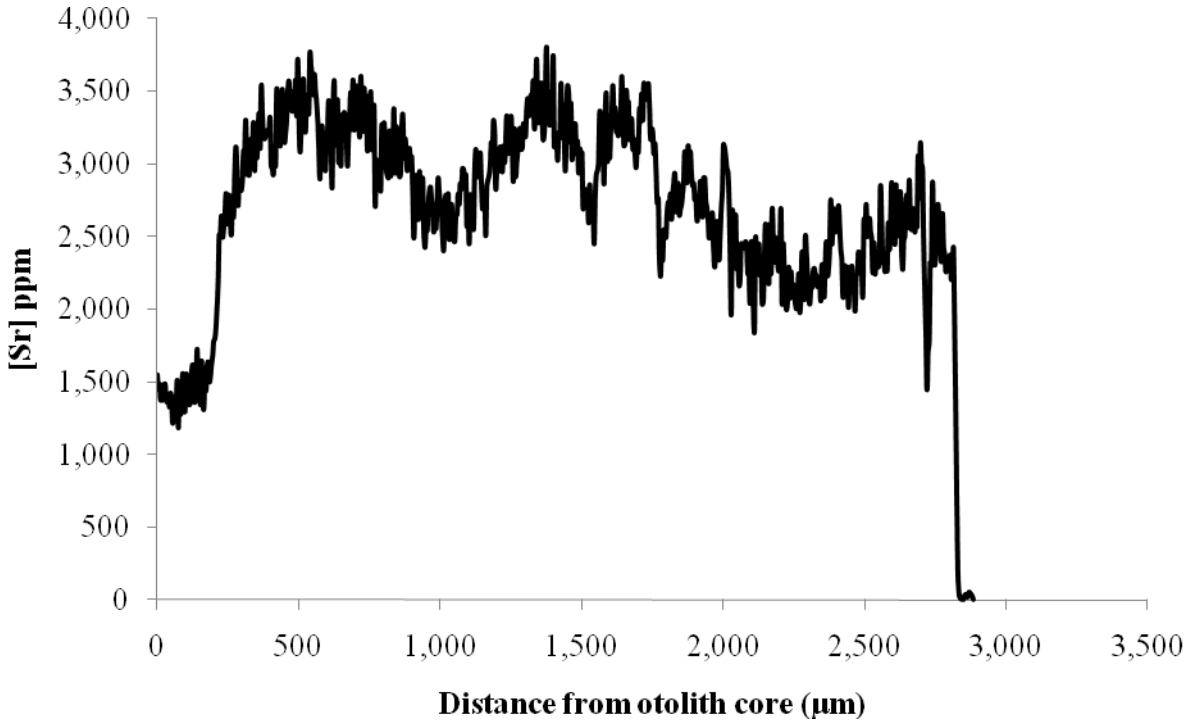
Fish ID: 109; Disk 10 Otolith 4
Resident



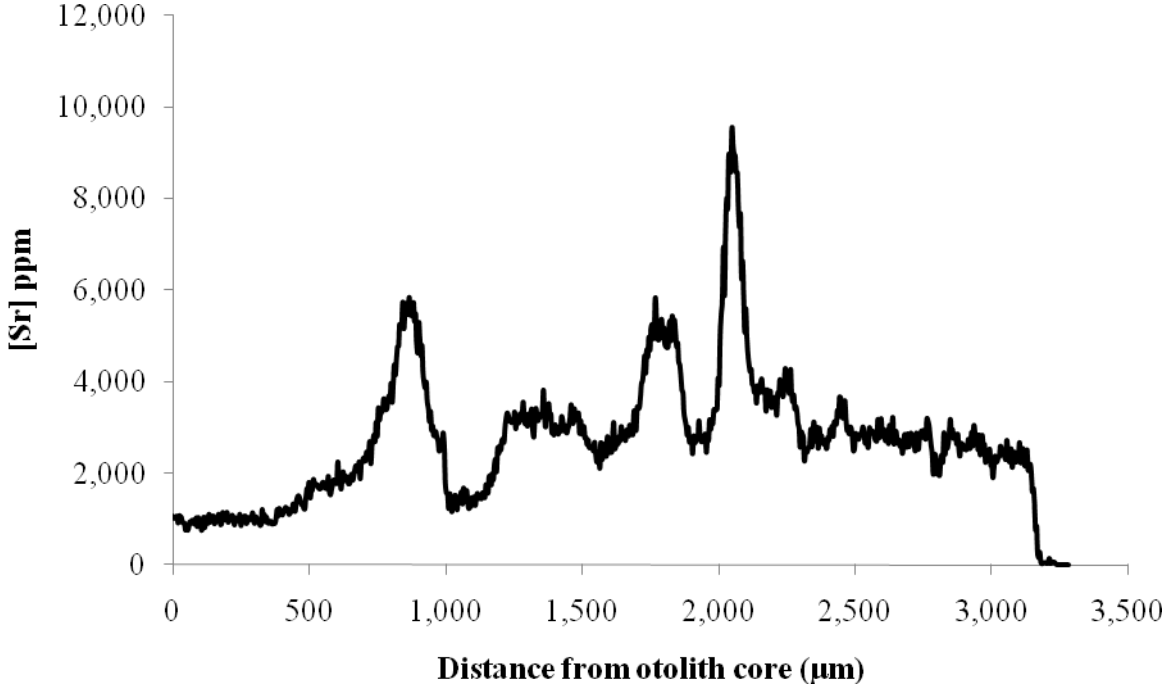
Fish ID: 103; Disk 10 Otolith 5
Resident



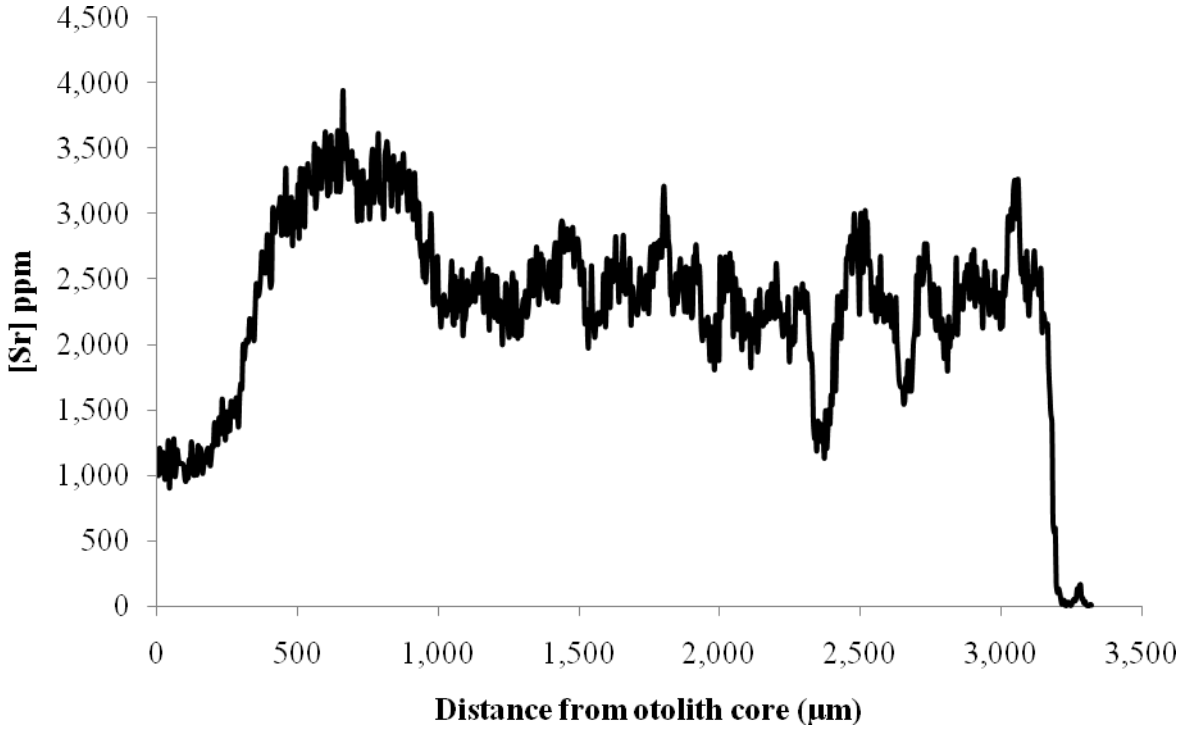
Fish ID 5009; Disk 10 Otolith 6
Resident



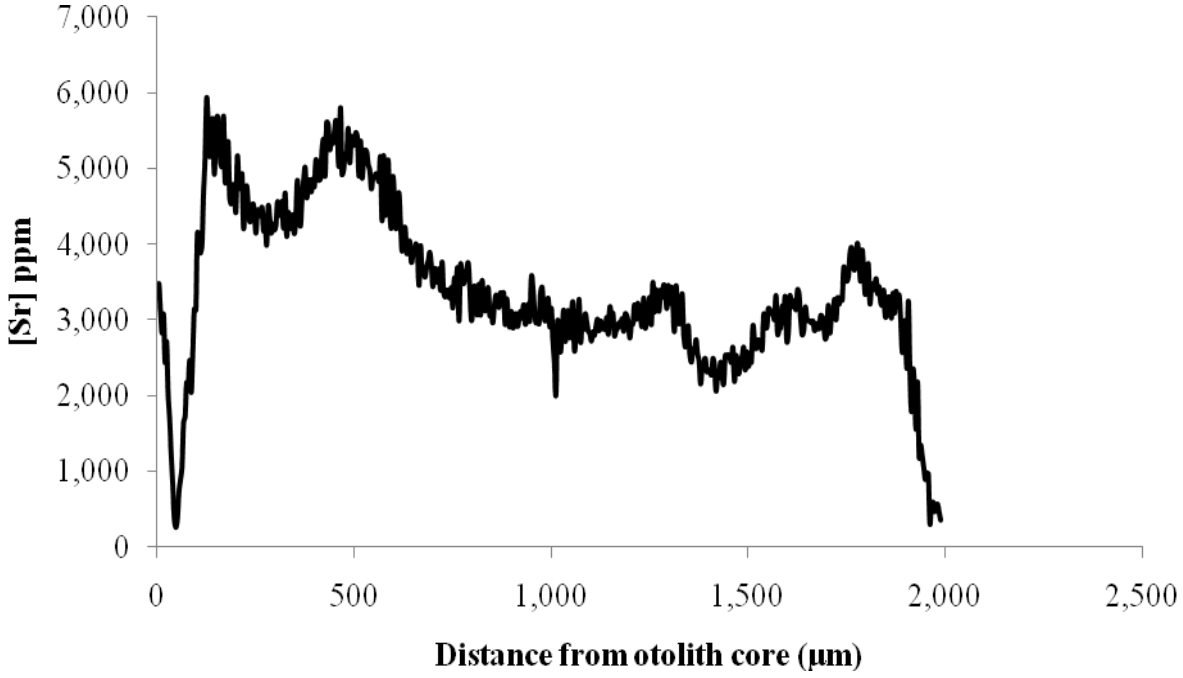
Fish ID: 108; Disk 11 Otolith 1
Stager



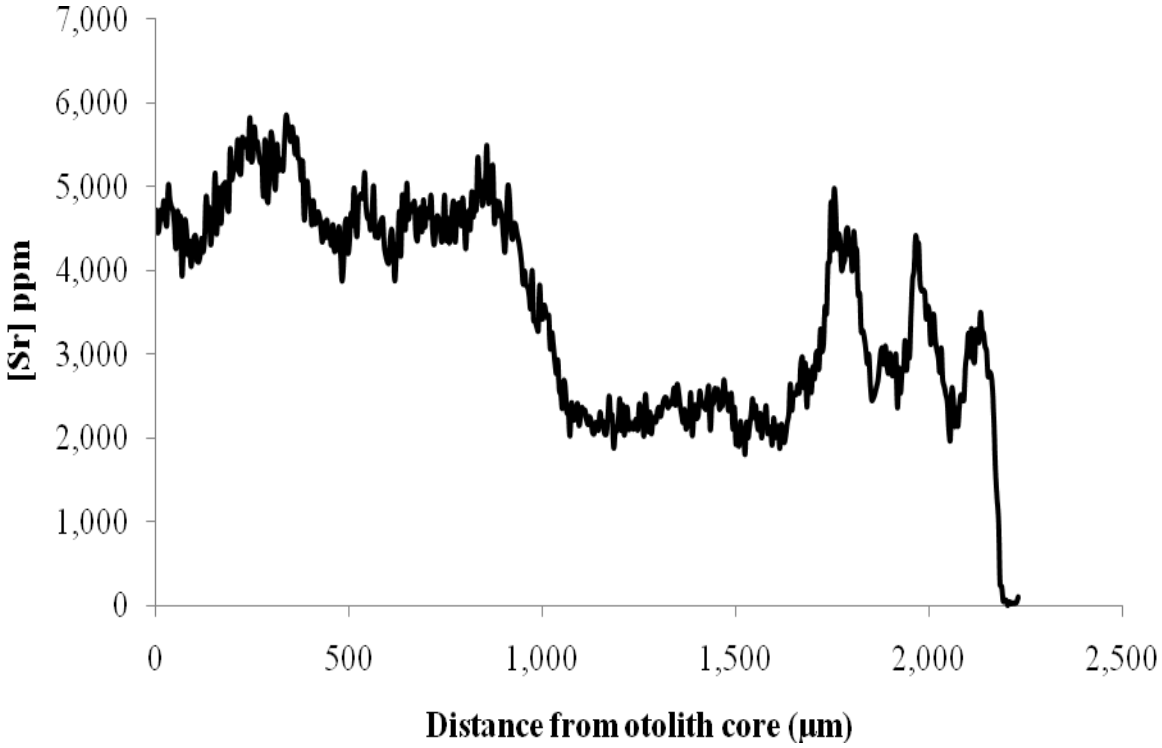
Fish ID: 6004; Disk 11 Otolith 2
Resident



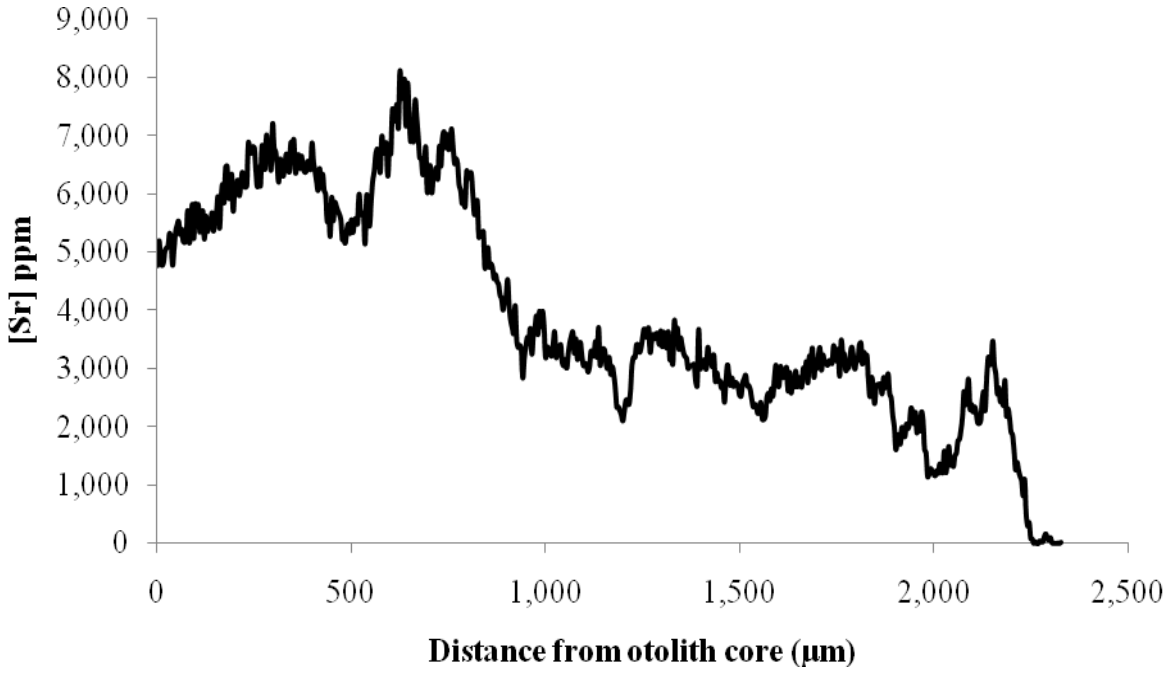
Fish ID: 4; Disk 11 Otolith 4
High Sr



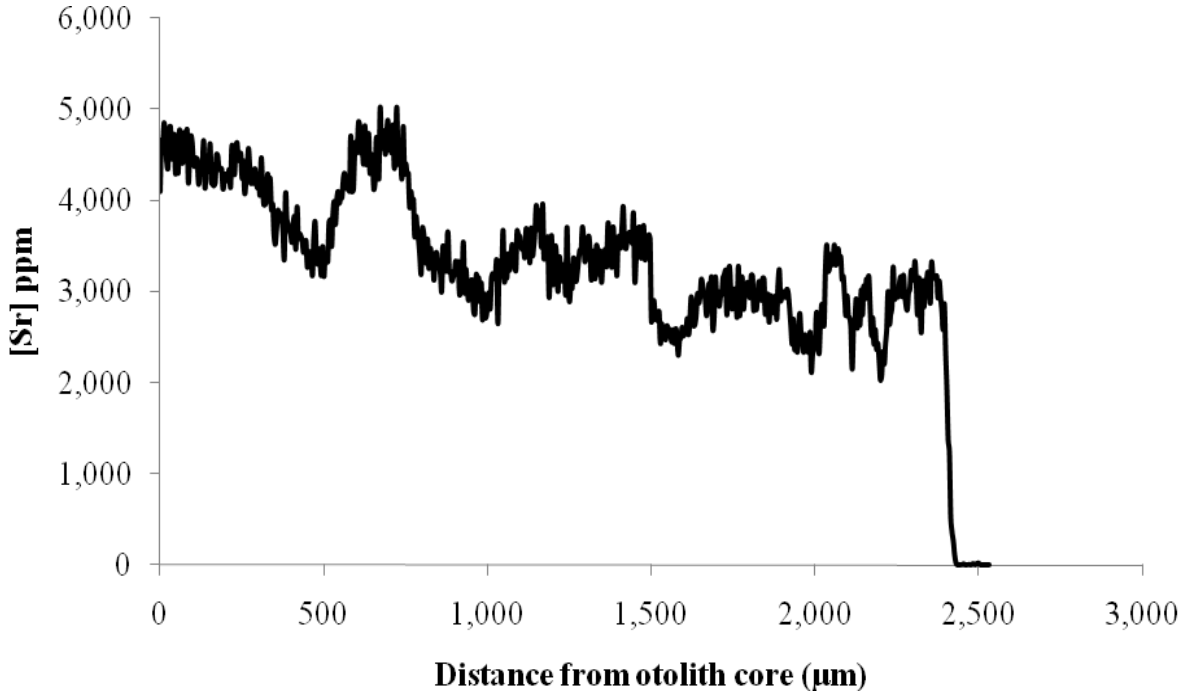
Fish ID: 1227; Disk 11 Otolith 5
High Sr



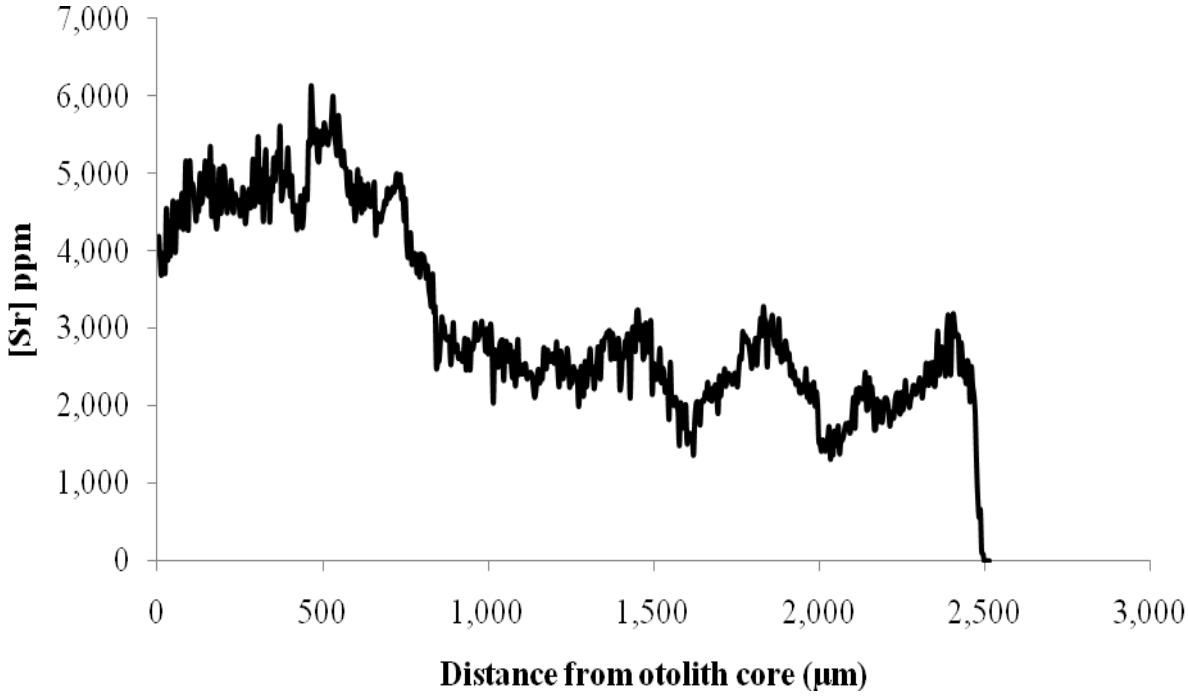
Fish ID: 1194; Disk 11 Otolith 6
High Sr



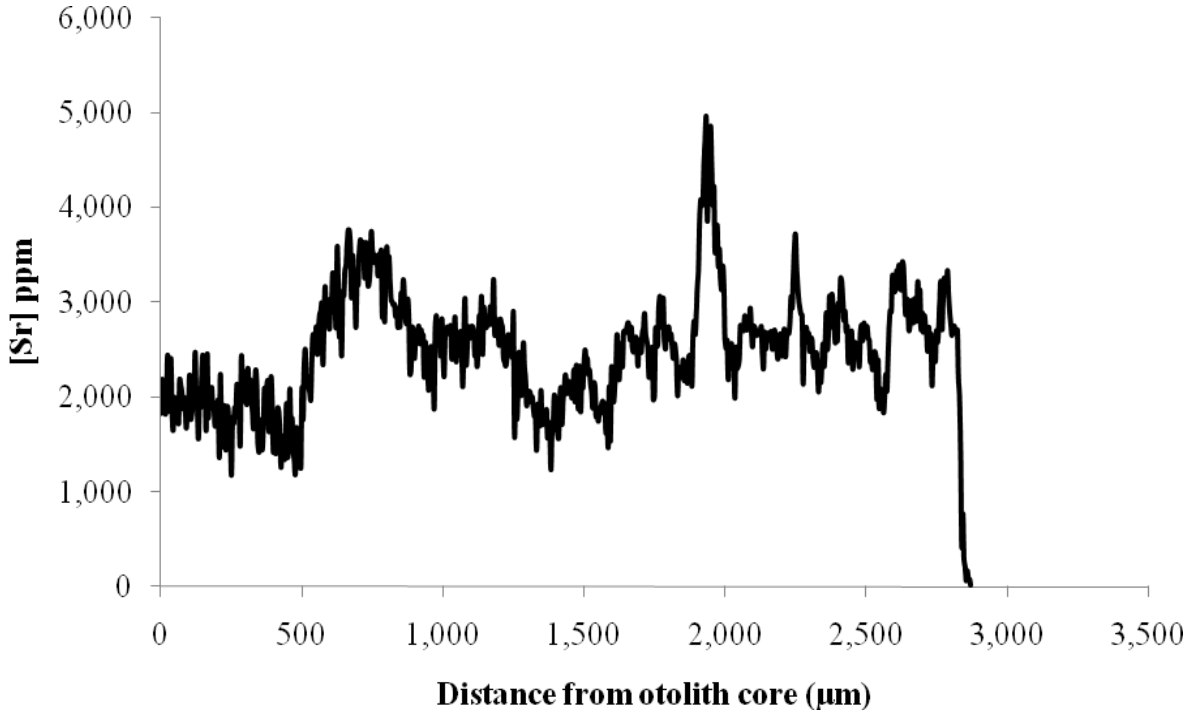
Fish ID: 1234; Disk 12 Otolith 1
High Sr



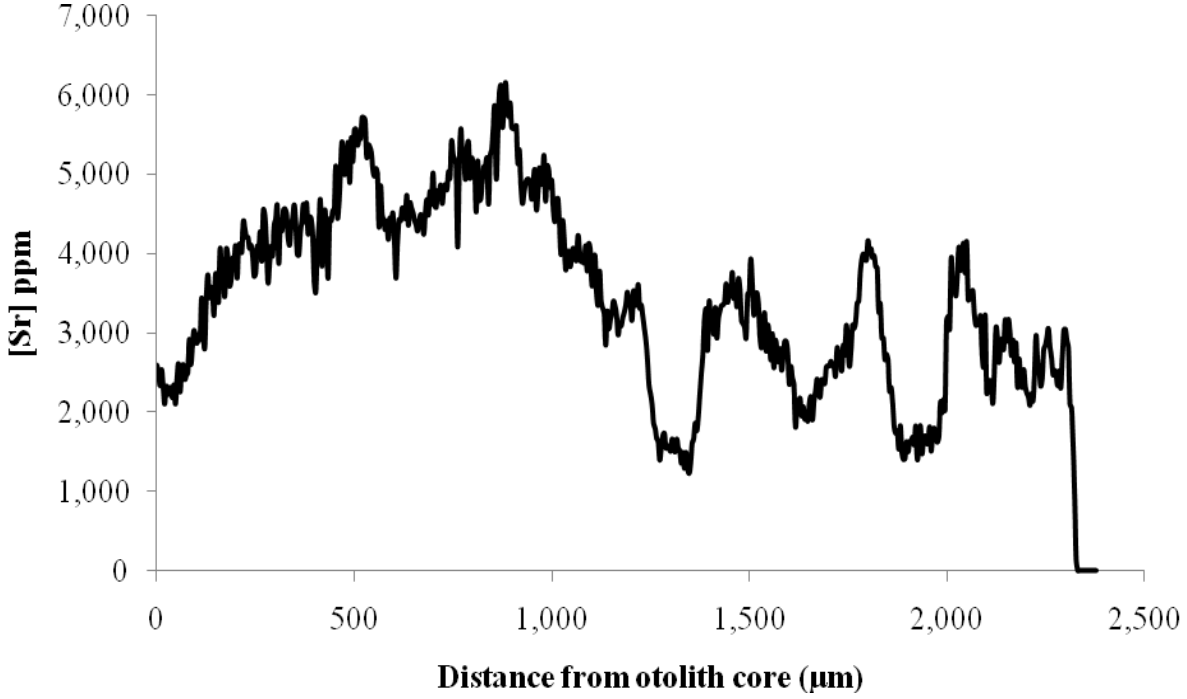
Fish ID: 1233; Disk 12 Otolith 2
High Sr



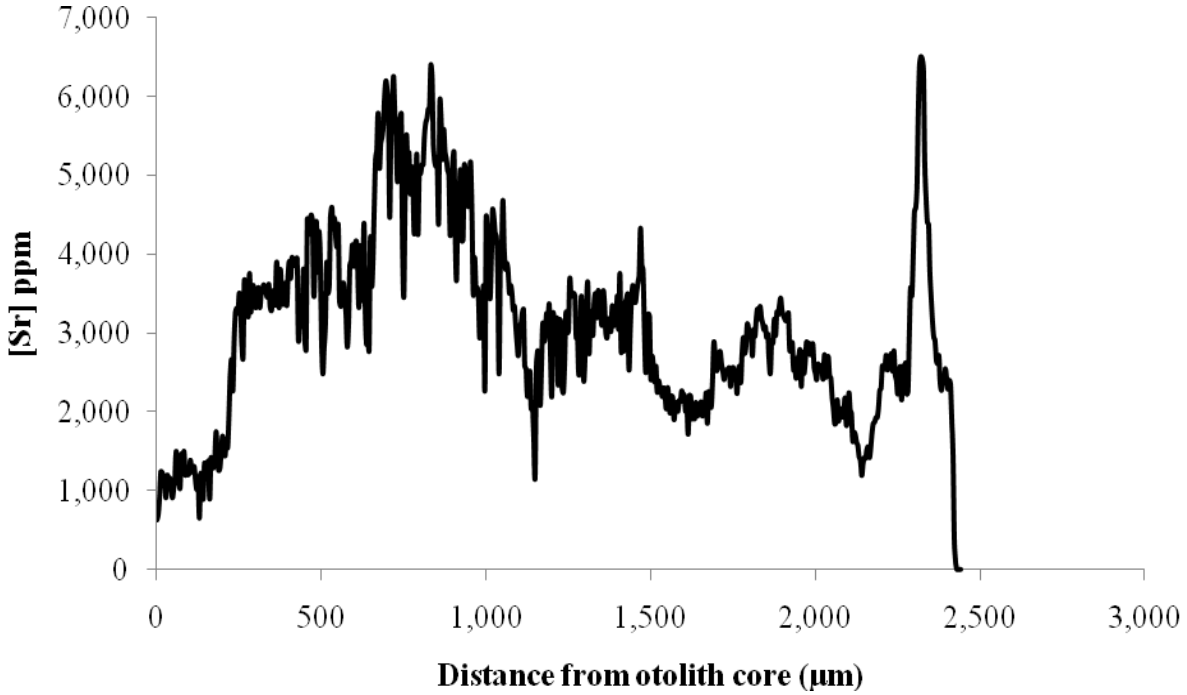
Fish ID: 1266; Disk 12 Otolith 3
Resident



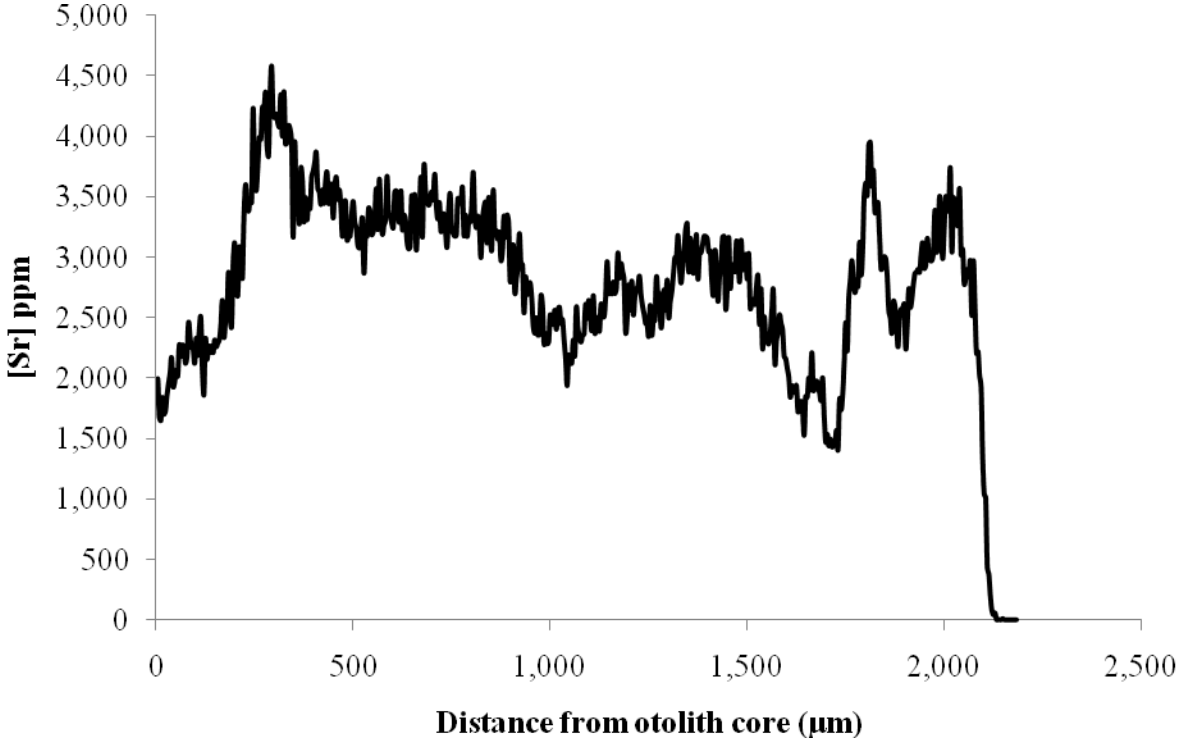
Fish ID: 1308; Disk 12 Otolith 4
Sprinter



Fish ID: 1202; Disk 12 Otolith 5
Stager

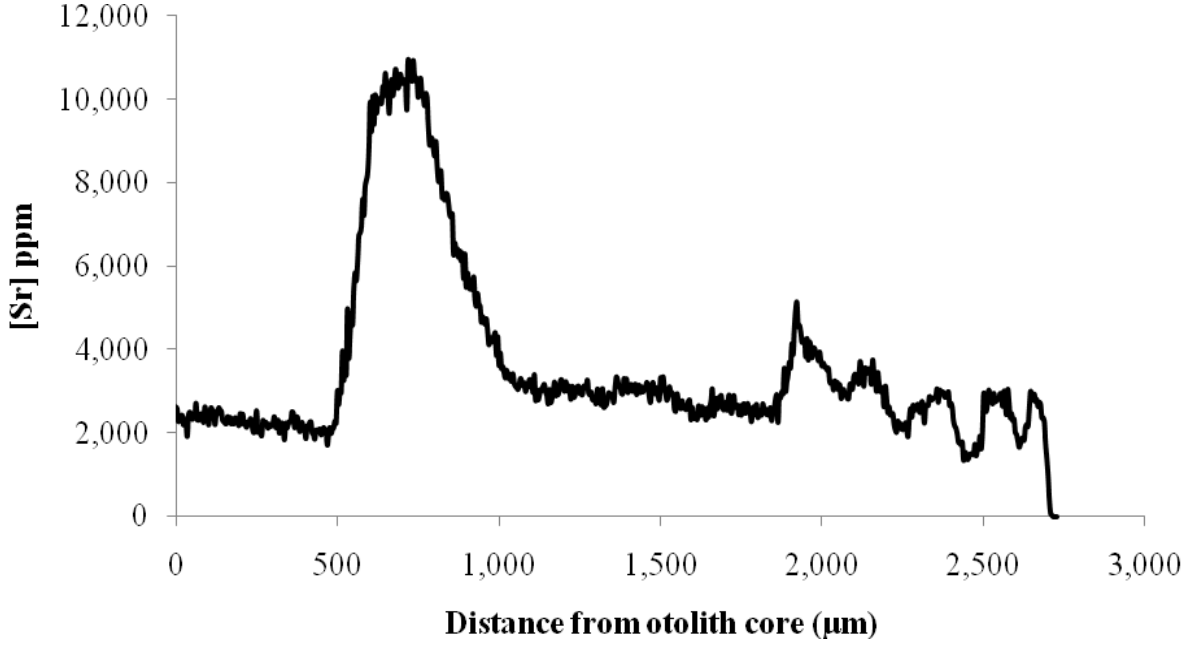


Fish ID: 1184; Disk 12 Otolith 6
Sprinter

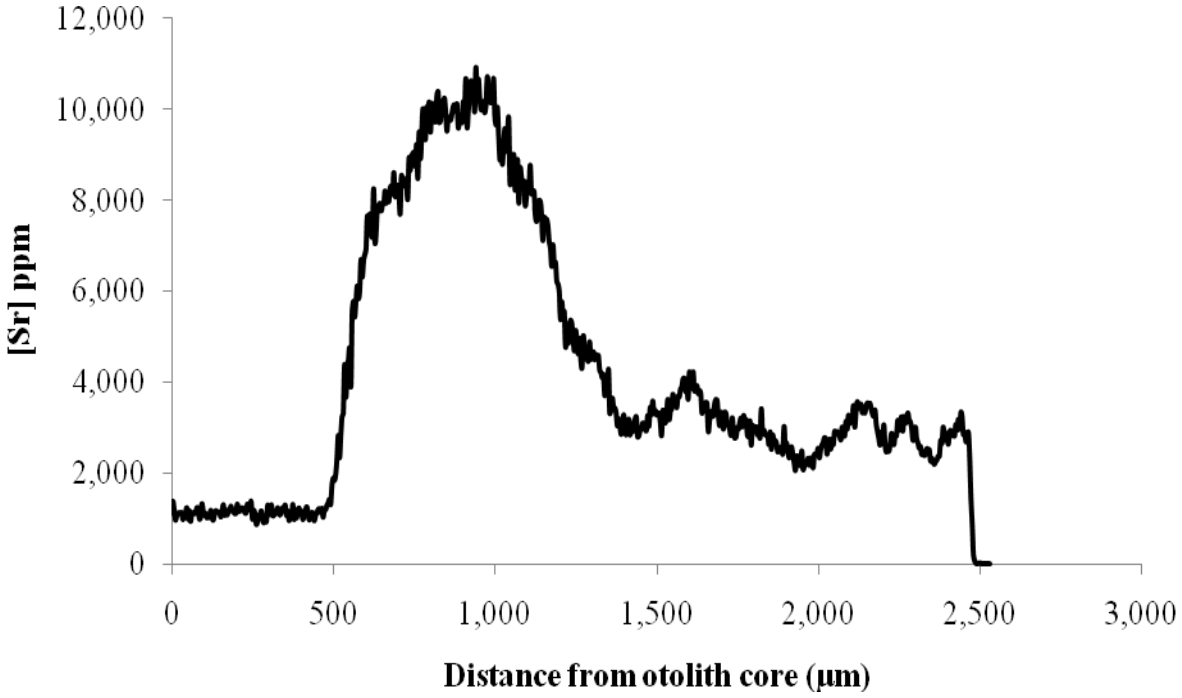


Fish ID: 1149; Disk 13 Otolith 1
High Sr

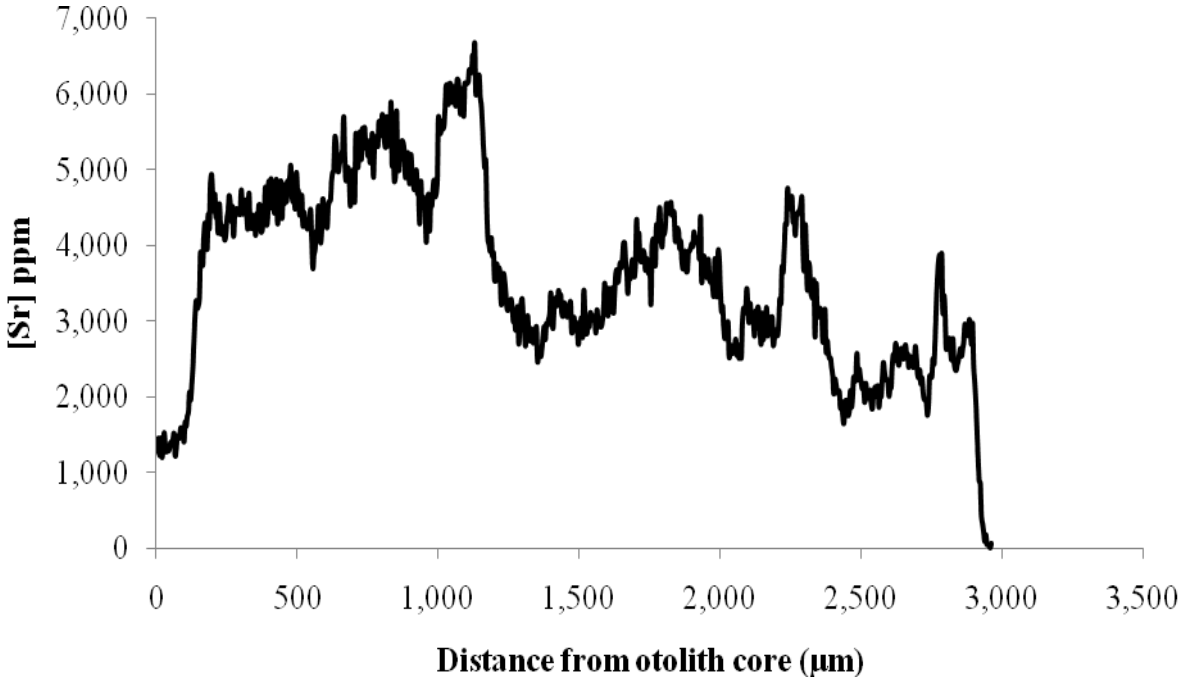
Fish ID: 1276; Disk 13 Otolith 2
Sprinter



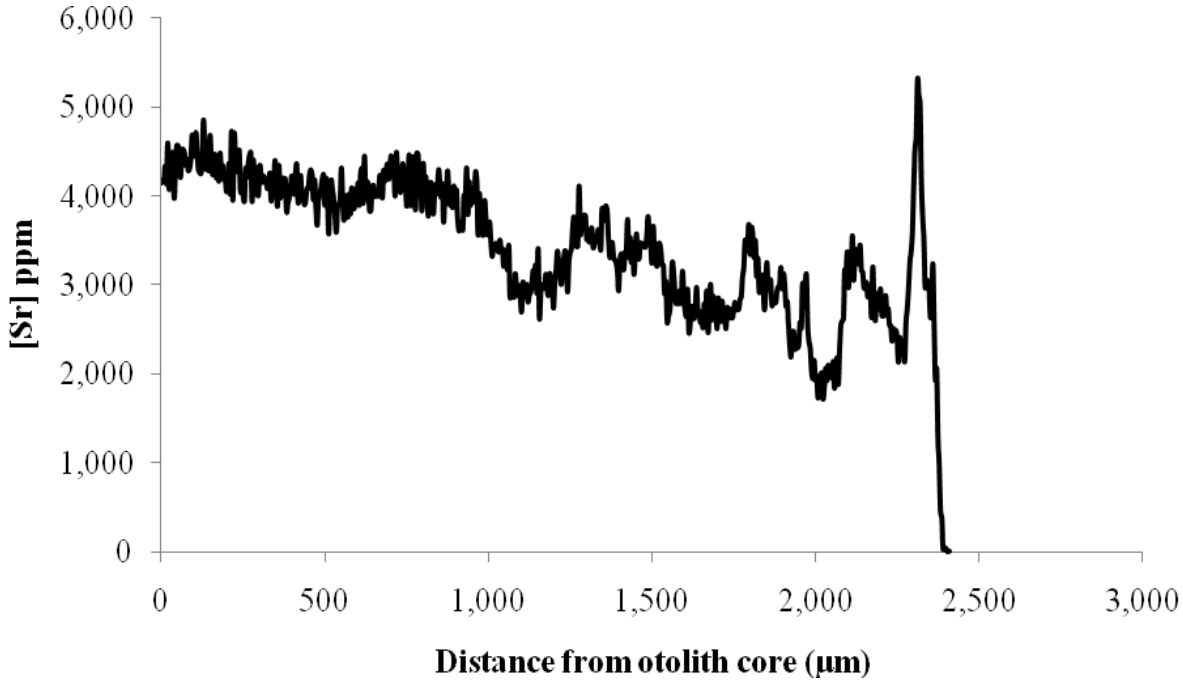
Fish ID: 1256; Disk 13 Otolith 3
Sprinter



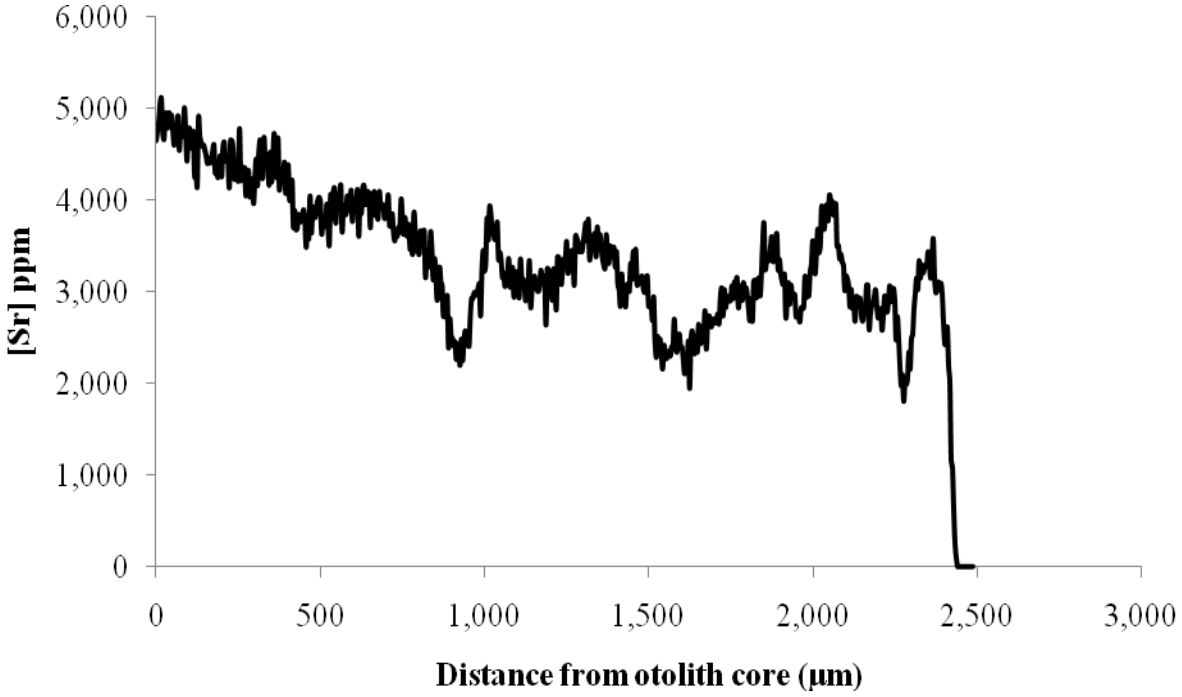
Fish ID: 437; Disk 13 Otolith 4
Sprinter



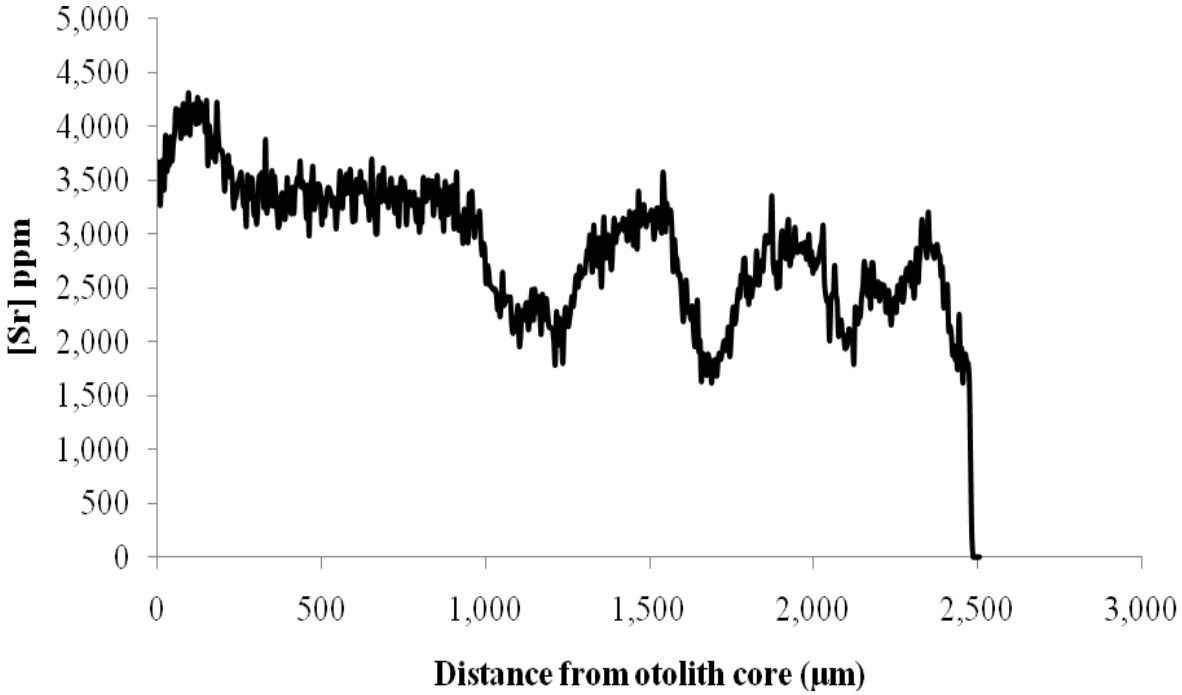
Fish ID: 1290; Disk 13 Otolith 5
High Sr



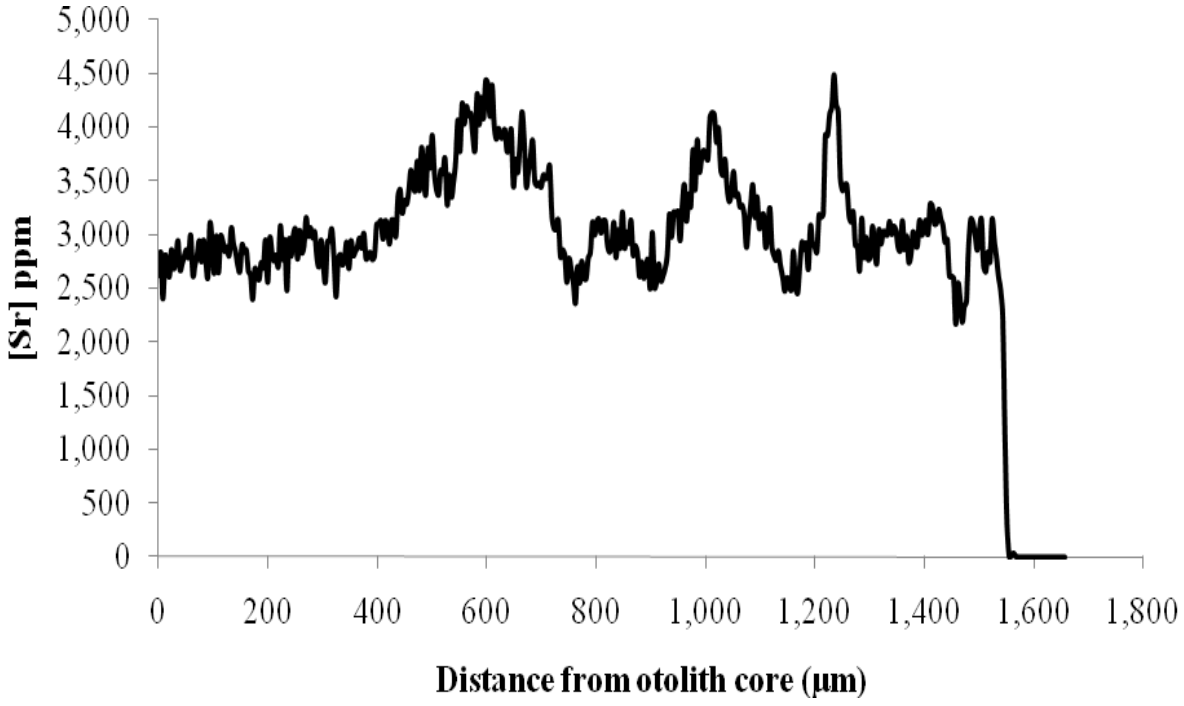
Fish ID: 1294; Disk 13 Otolith 6
High Sr



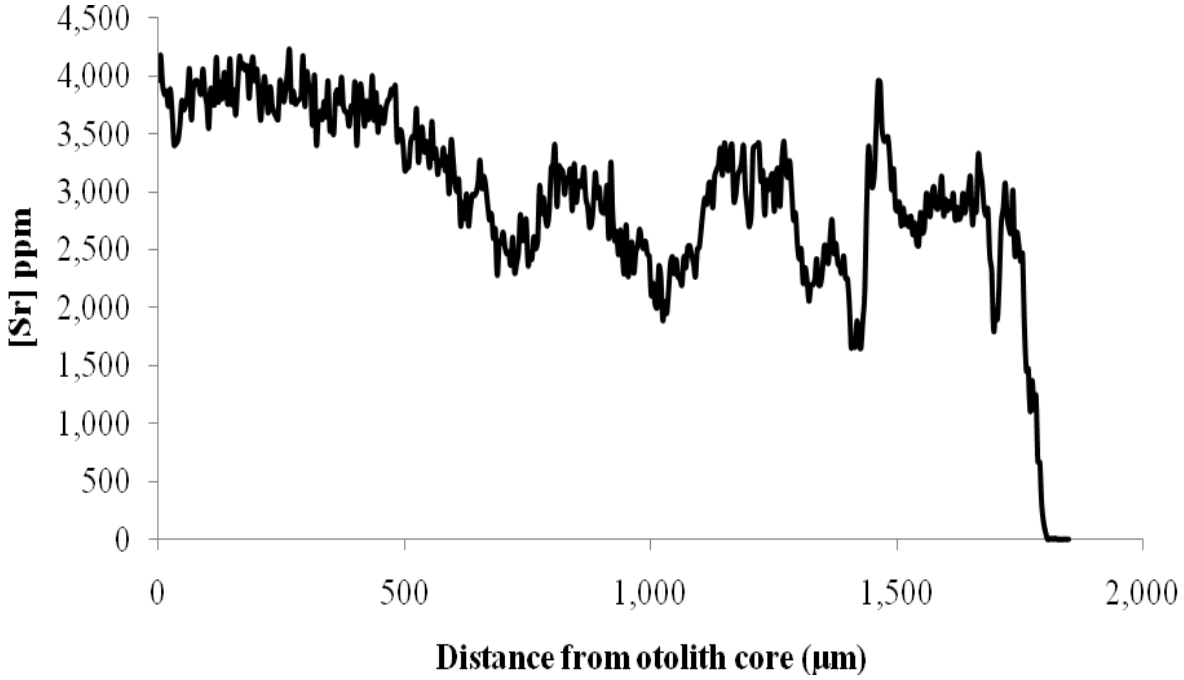
Fish ID: 1267; Disk 14 Otolith 1
High Sr



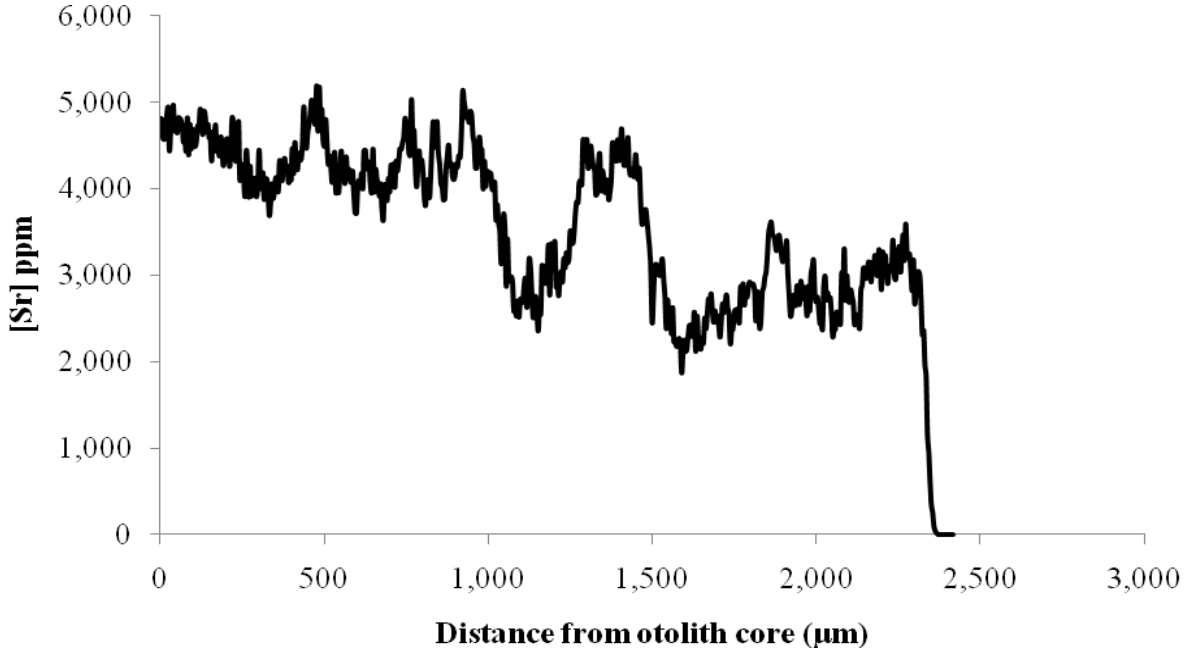
Fish ID: 411; Disk 14 Otolith 2
Stager



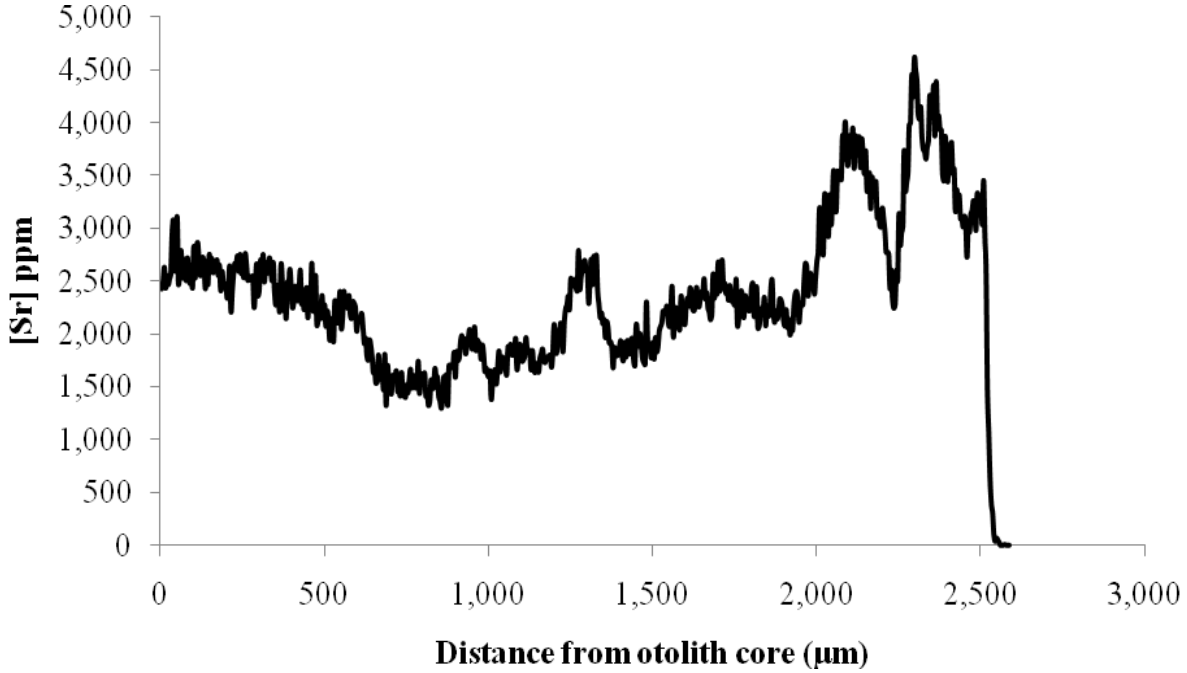
Fish ID: 484; Disk 14 Otolith 3
High Sr



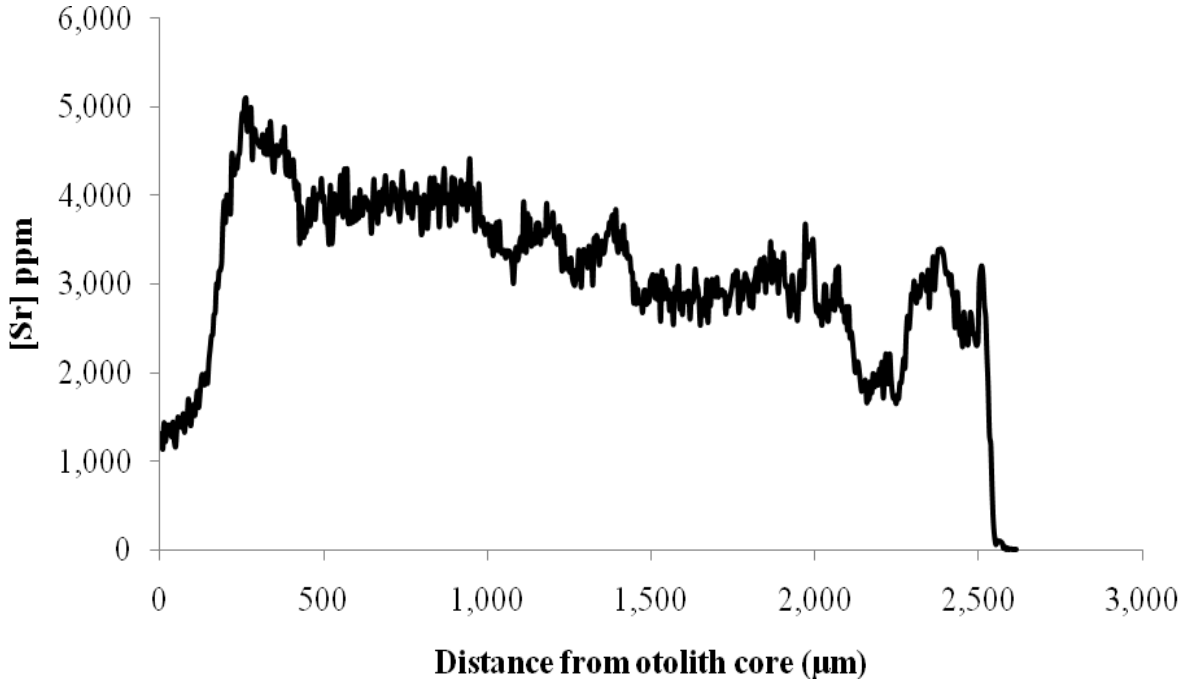
Fish ID: 415; Disk 14 Otolith 4
High Sr



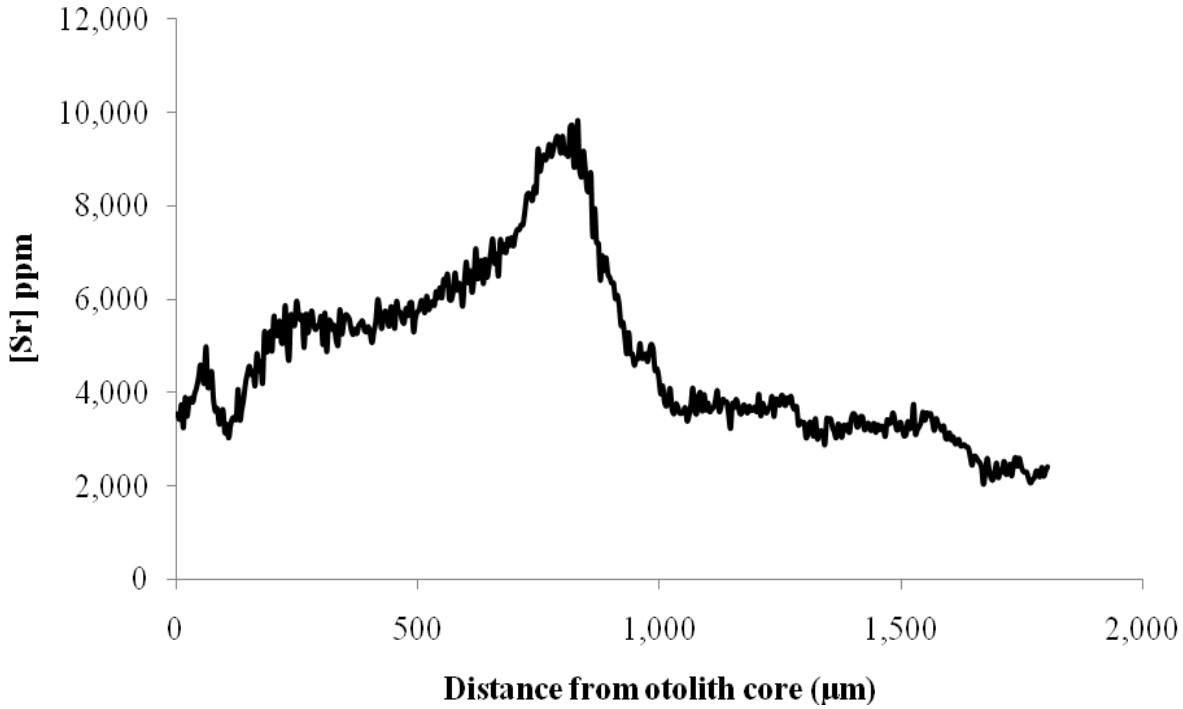
Fish ID: 493; Disk 14 Otolith 5
Resident



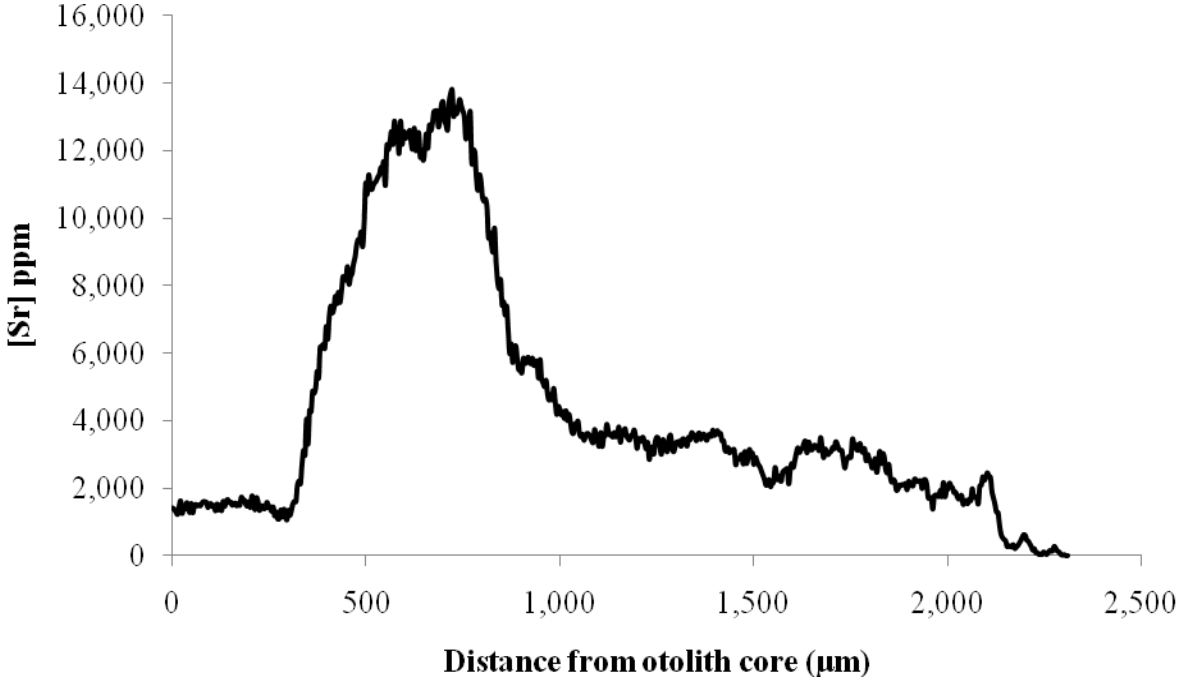
Fish ID: 498; Disk 14 Otolith 6
Sprinter



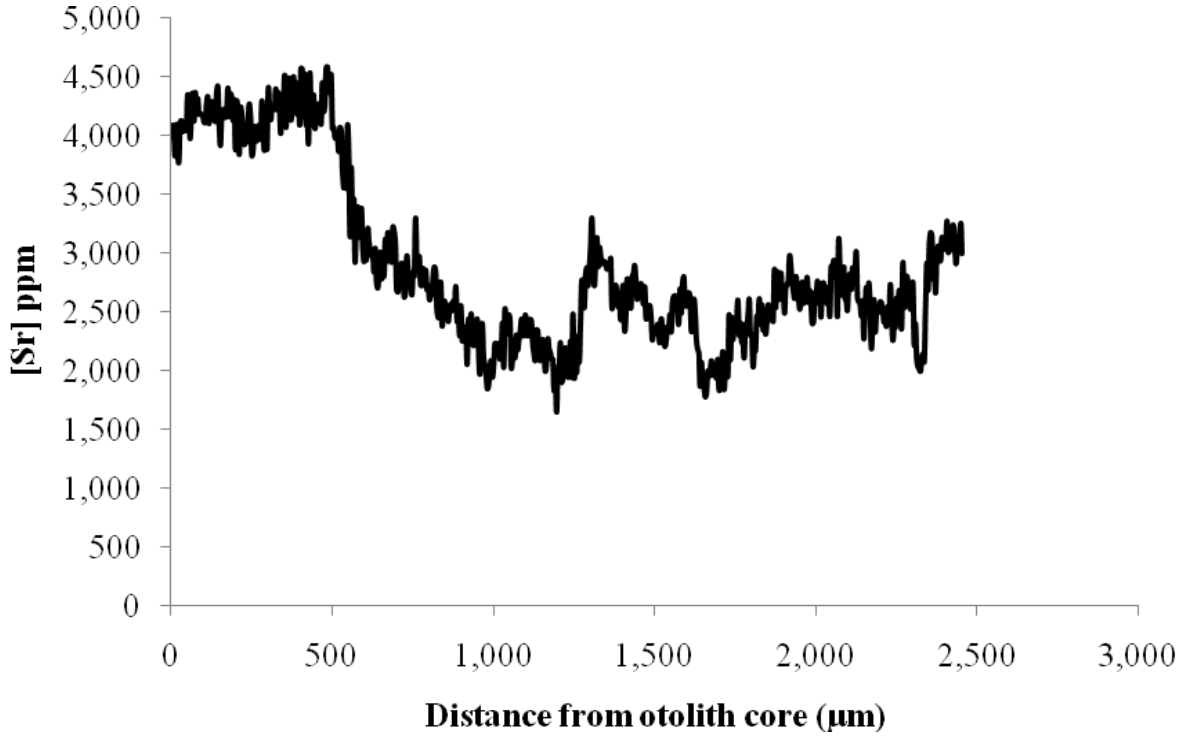
Fish ID: 1237; Disk 15 Otolith 2
High Sr



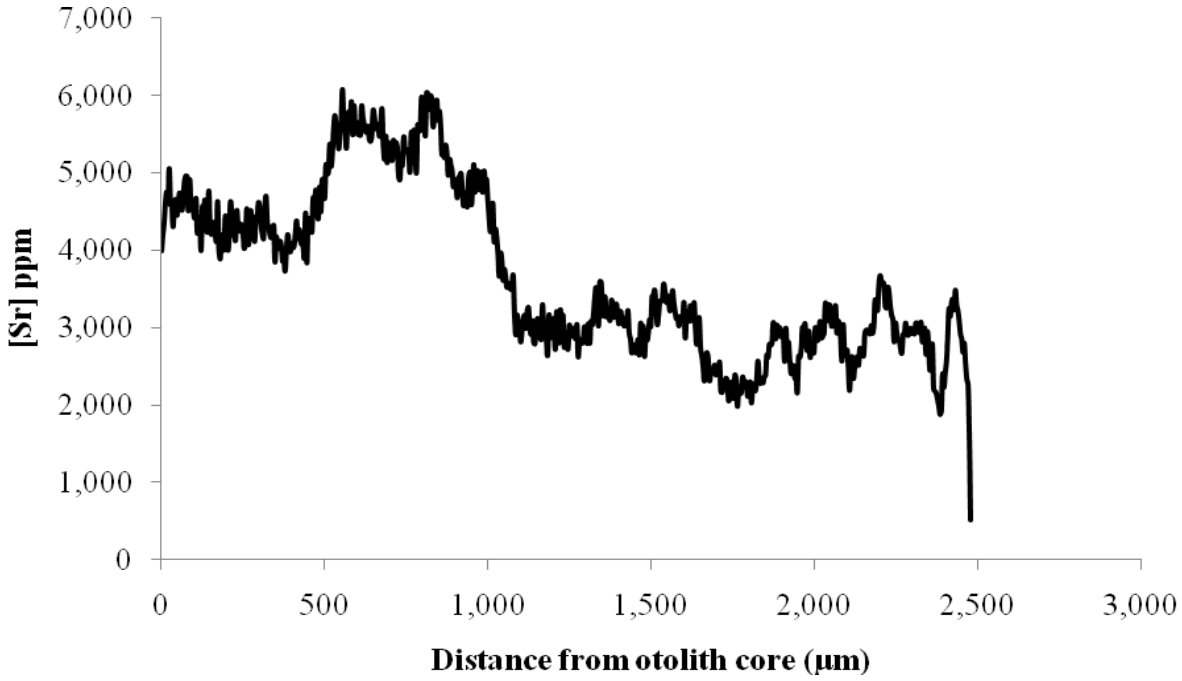
Fish ID: 391; Disk 15 Otolith 3
Sprinter



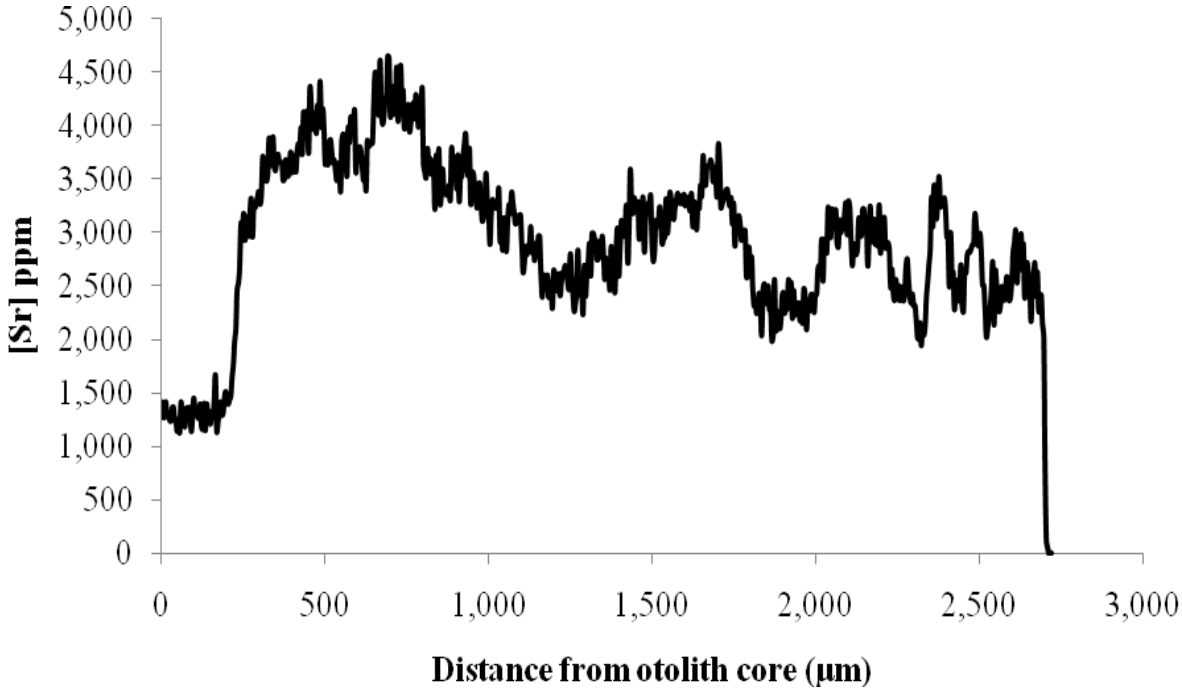
Fish ID: 398; Disk 15 Otolith 4
High Sr



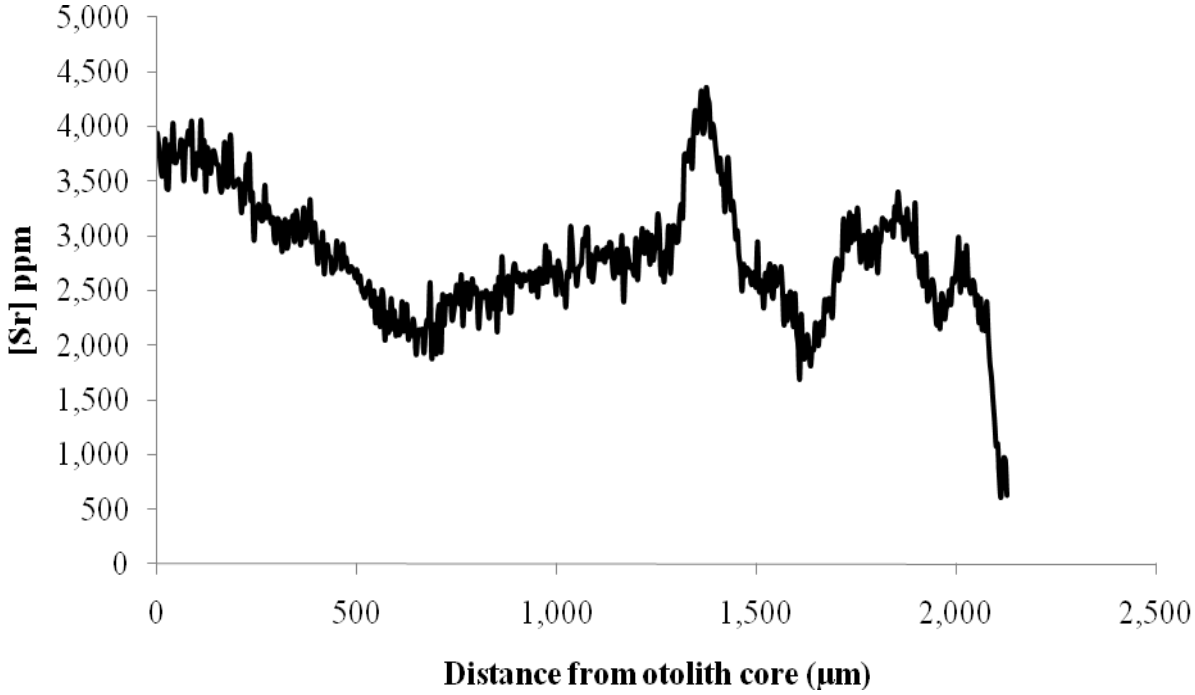
Fish ID: 1313; Disk 15 Otolith 5
High Sr



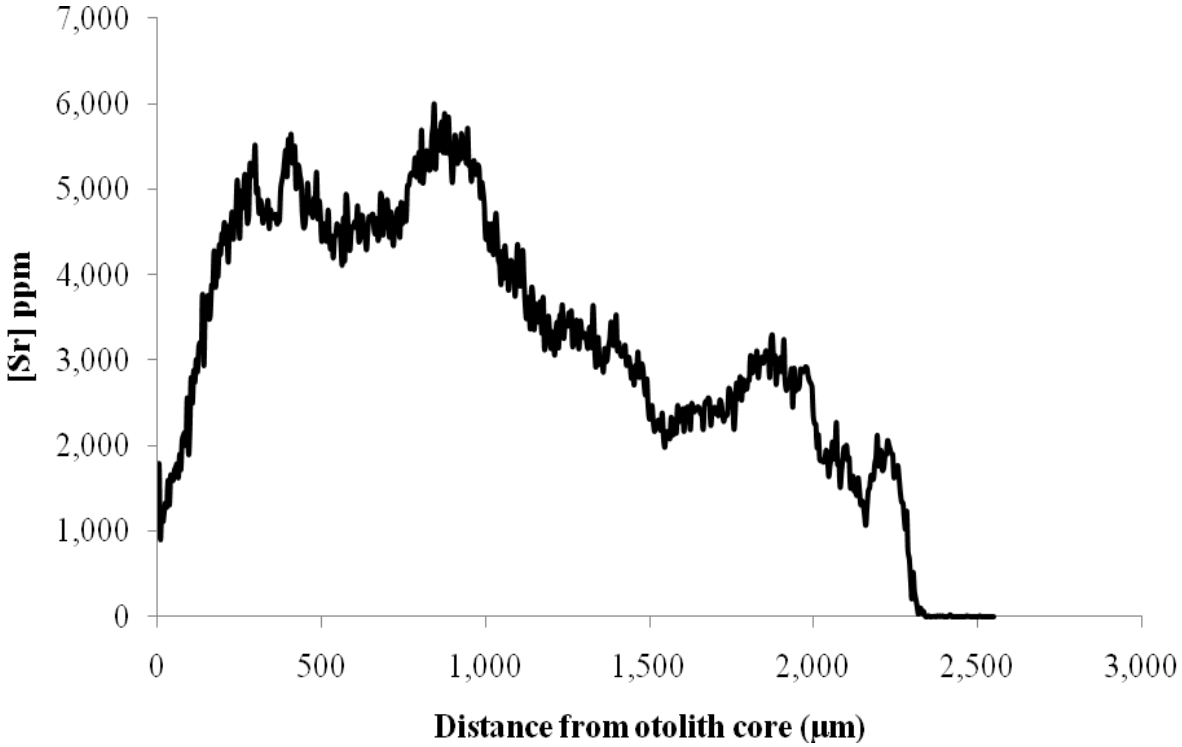
Fish ID: 363; Disk 15 Otolith 6
Stager



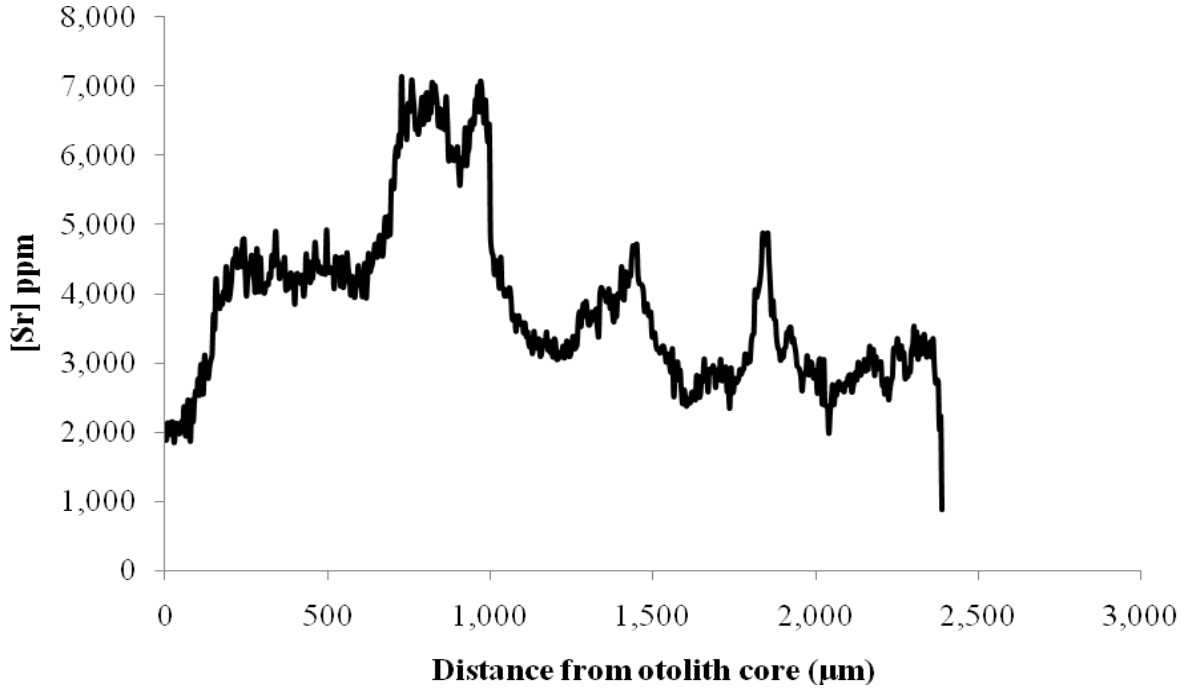
Fish ID: 1; Disk 16 Otolith 1
High Sr



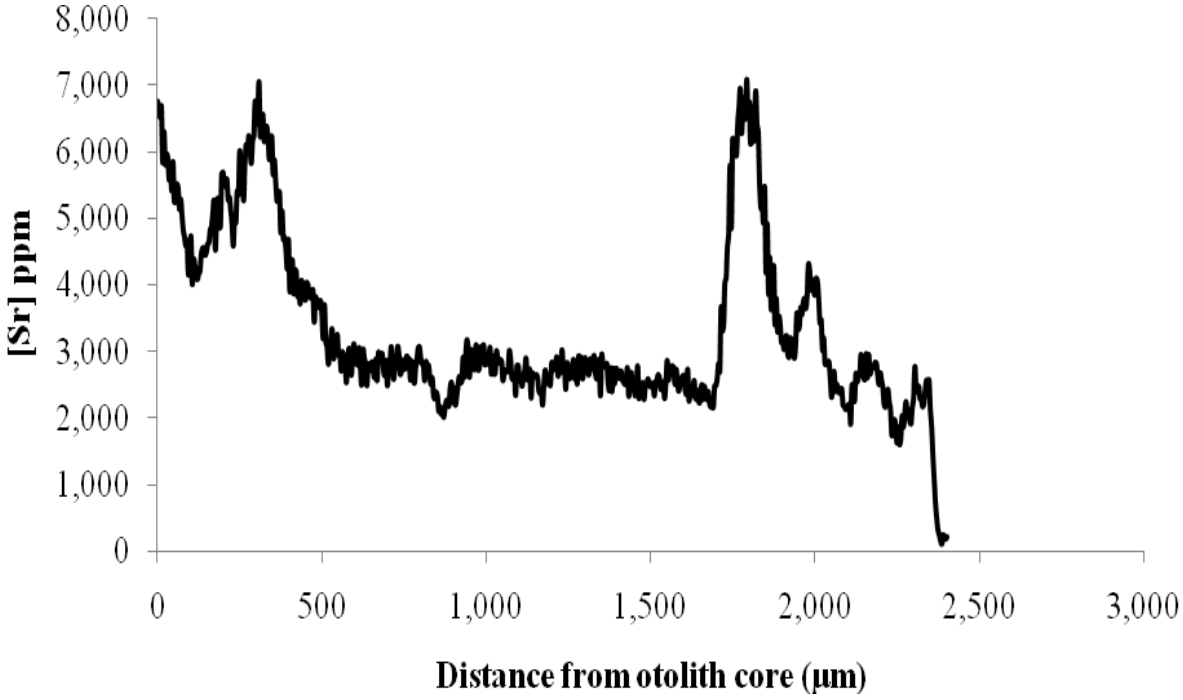
Fish ID: 3, Disk 16 Otolith 2
Sprinter



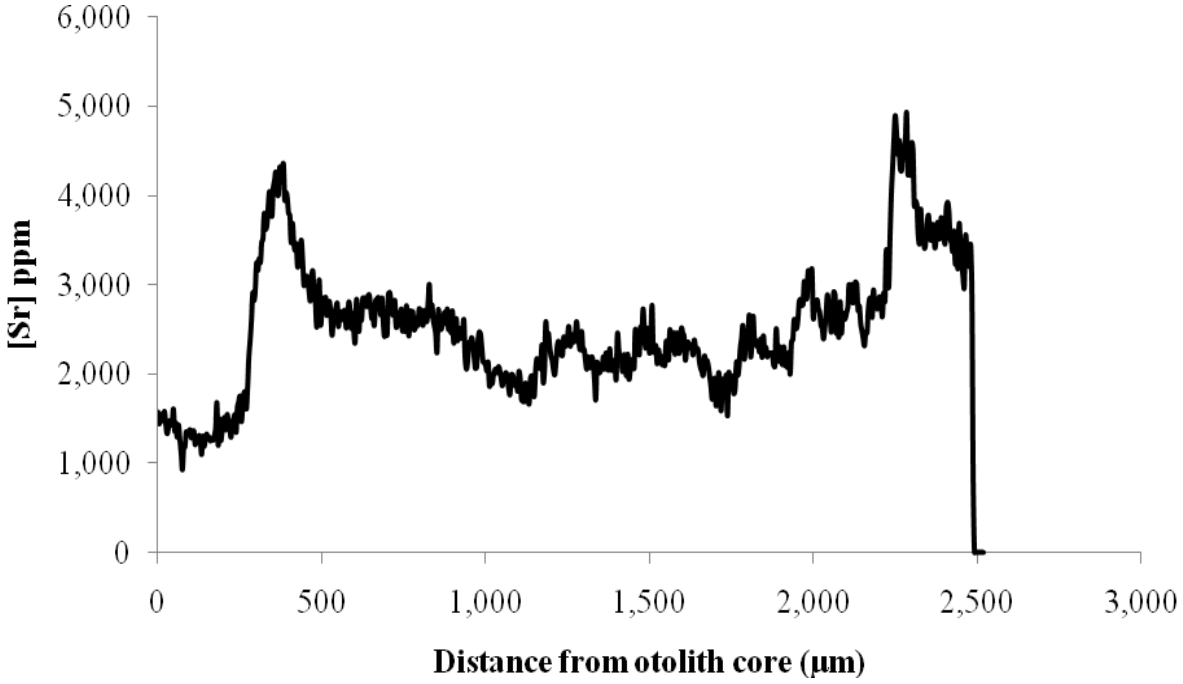
Fish ID: 1219; Disk 16 Otolith 3
Sprinter



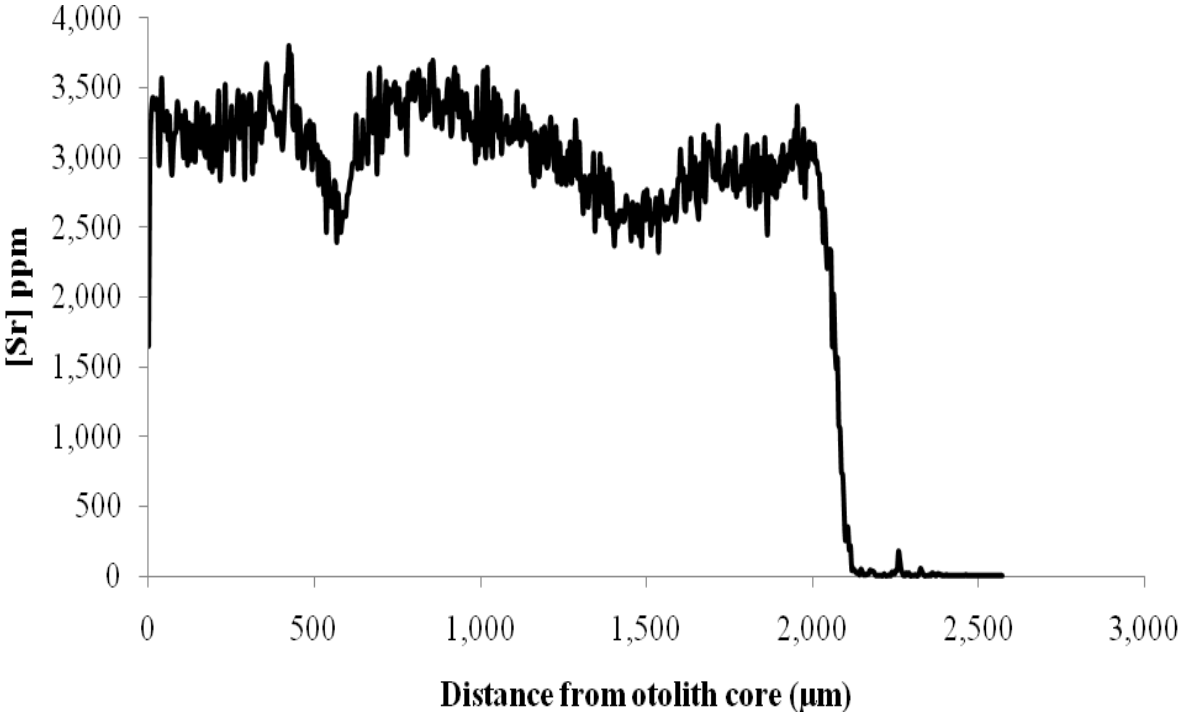
Fish ID: 1275; Disk 16 Otolith 5
High Sr



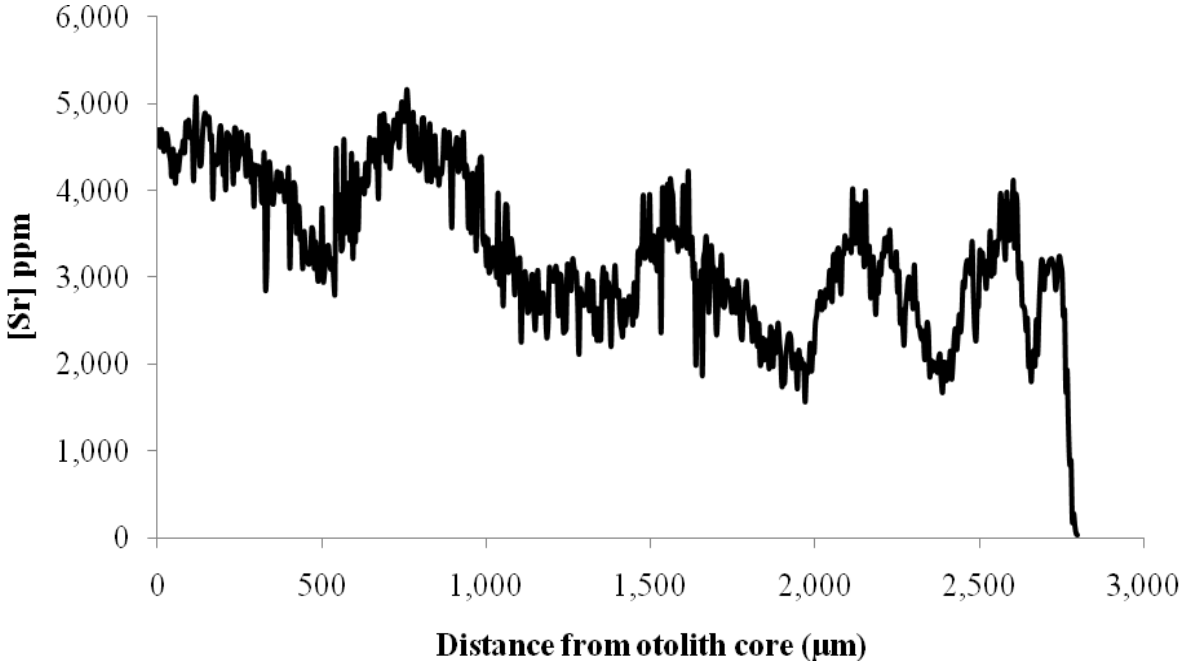
Fish ID: 1277; Disk 16 Otolith 6
Sprinter



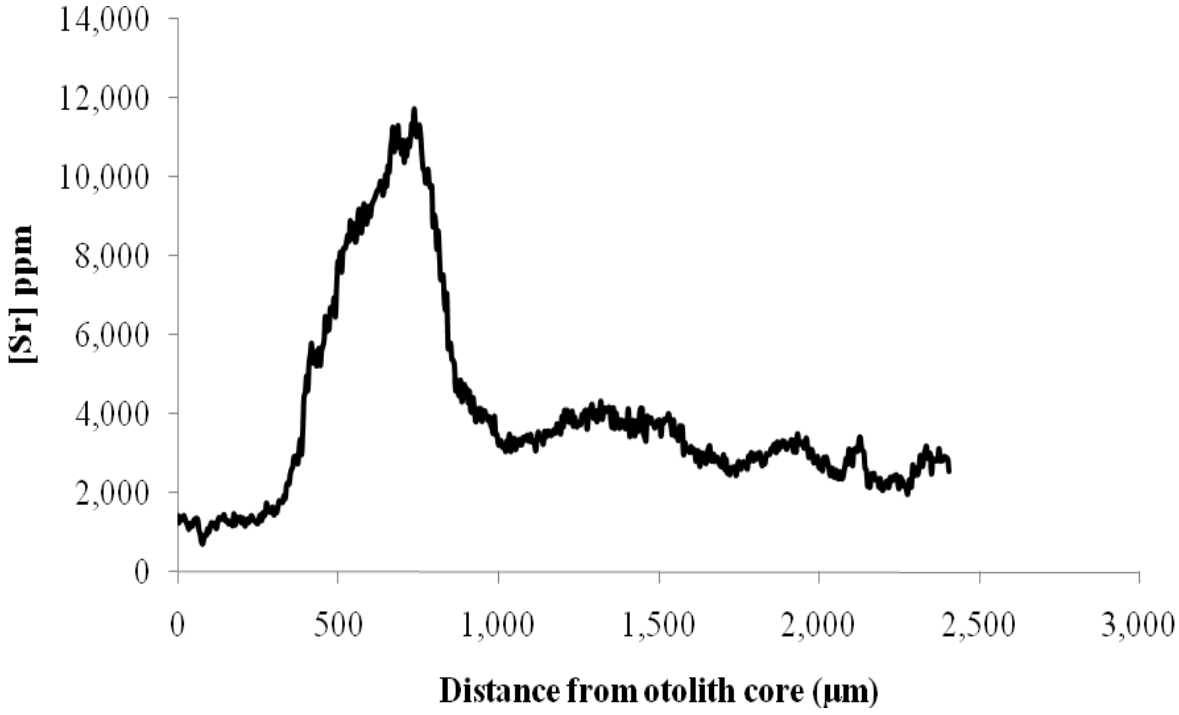
Fish ID: 1296; Disk 17 Otolith 1
Resident



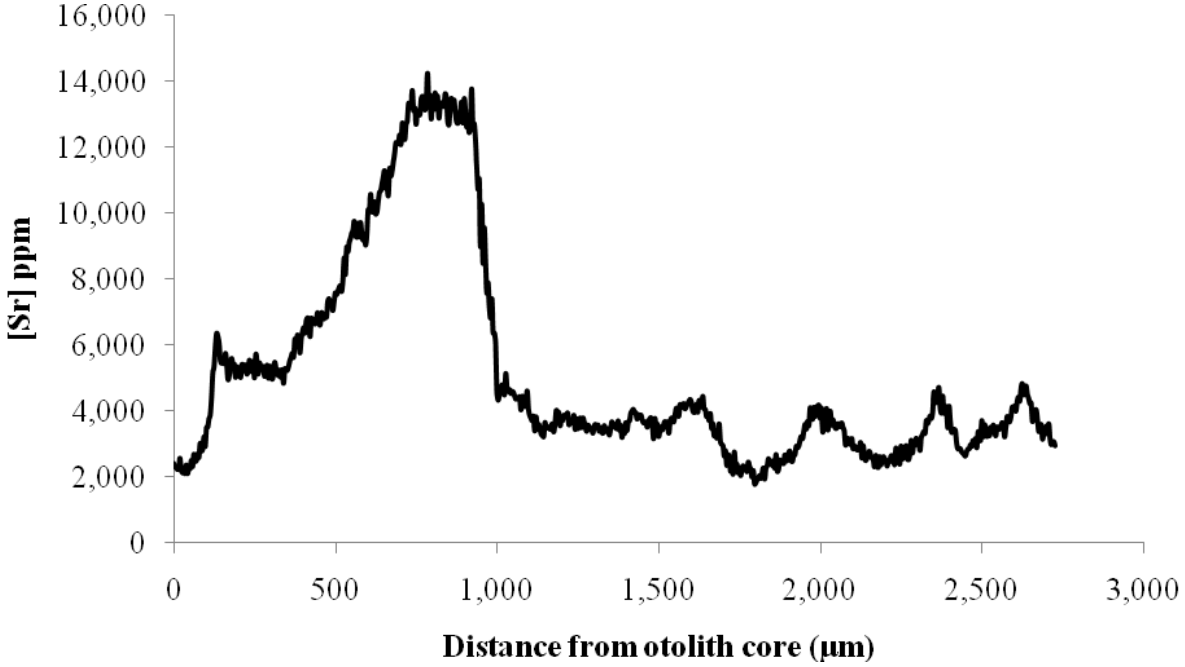
Fish ID: 1279; Disk 17 Otolith 2
High Sr



Fish ID: 1278; Disk 17 Otolith 4
Sprinter

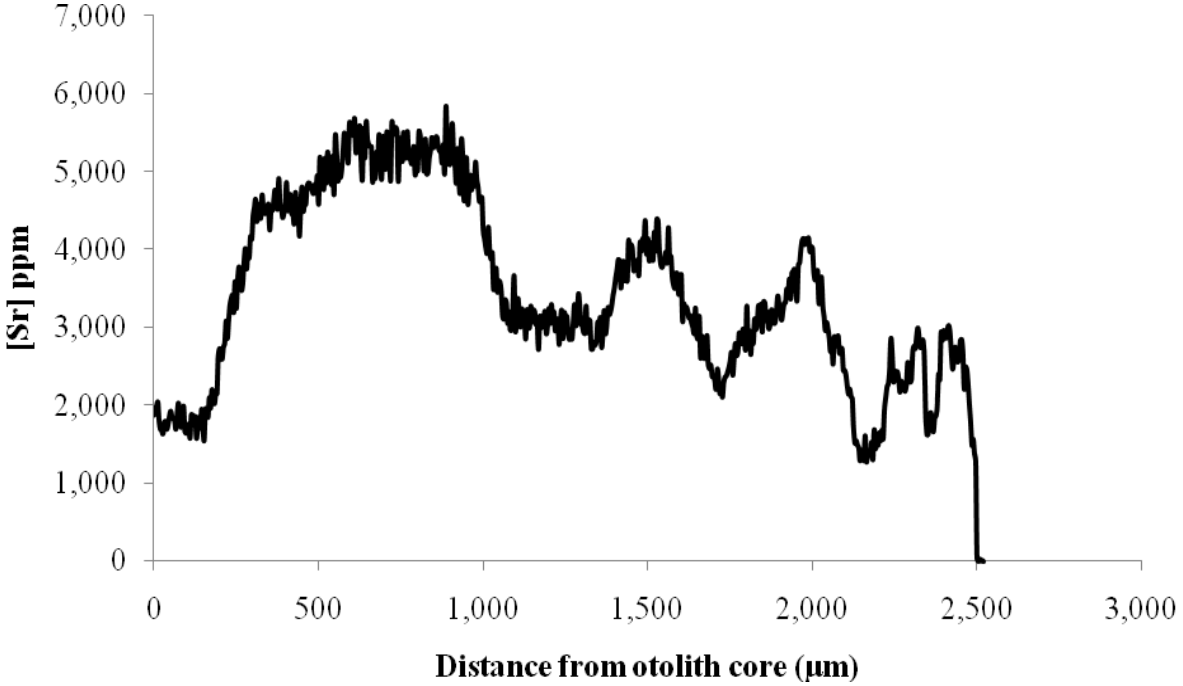


Fish ID: 360; Disk 17 Otolith 5
Sprinter

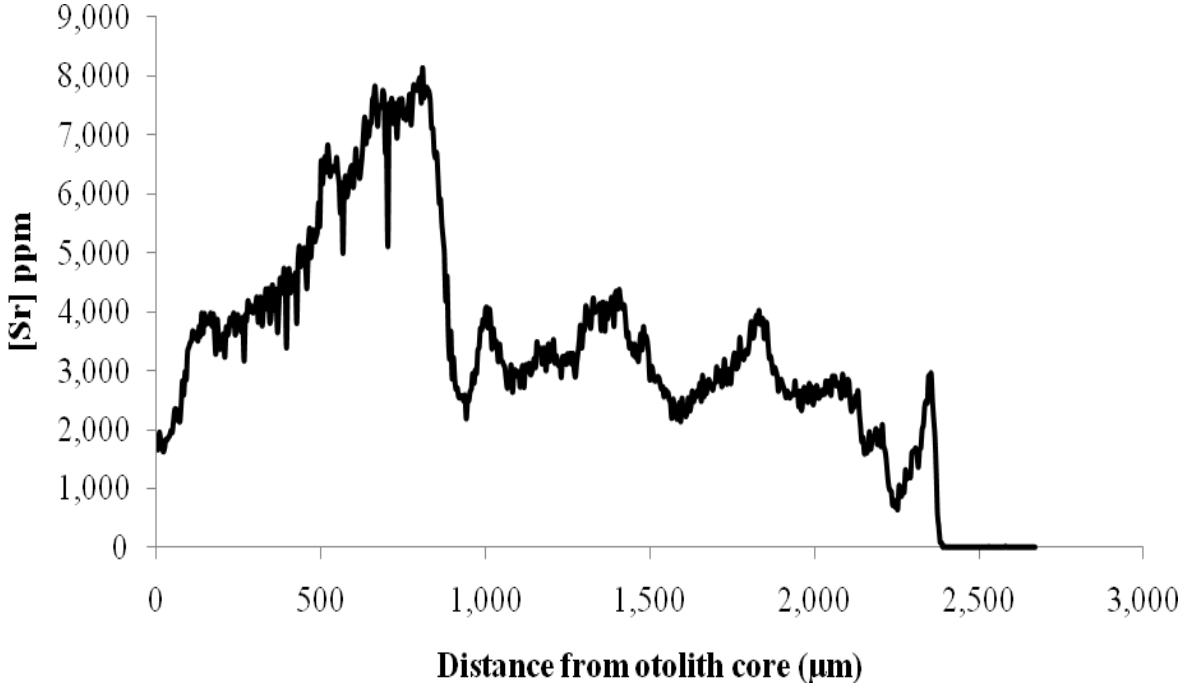


Fish ID: 1285; Disk 17 Otolith 6
High Sr

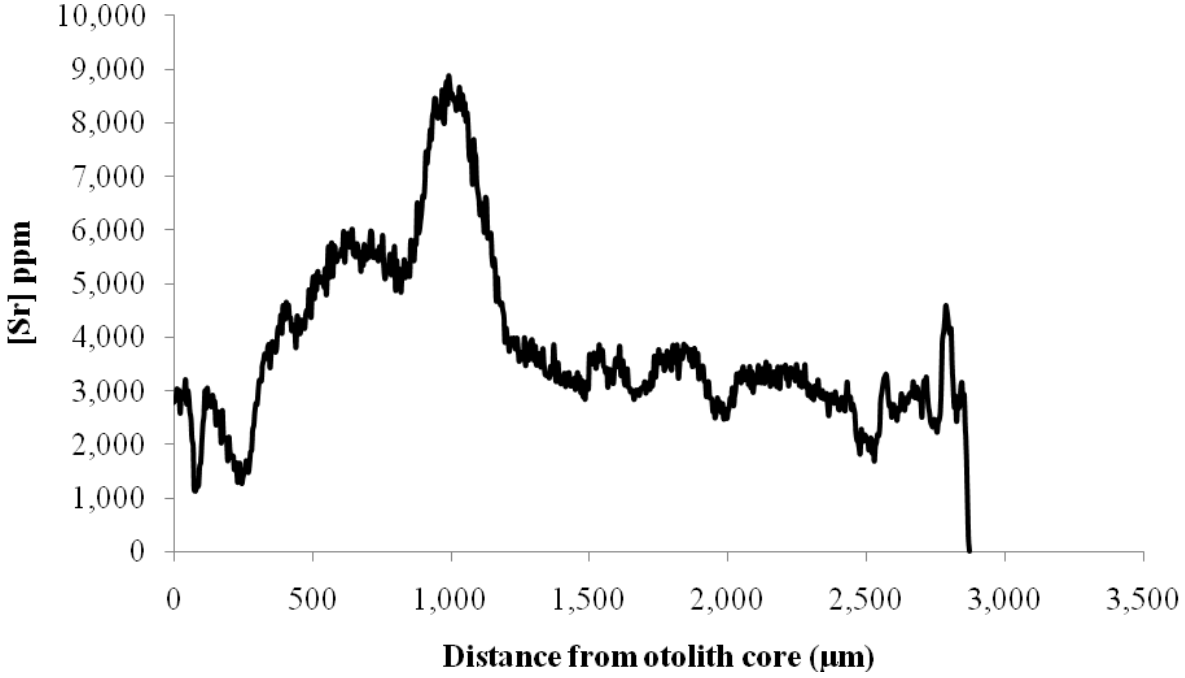
Fish ID: 1257; Disk 18 Otolith 2
Sprinter



Fish ID: 1264; Disk 18 Otolith 3
Stager

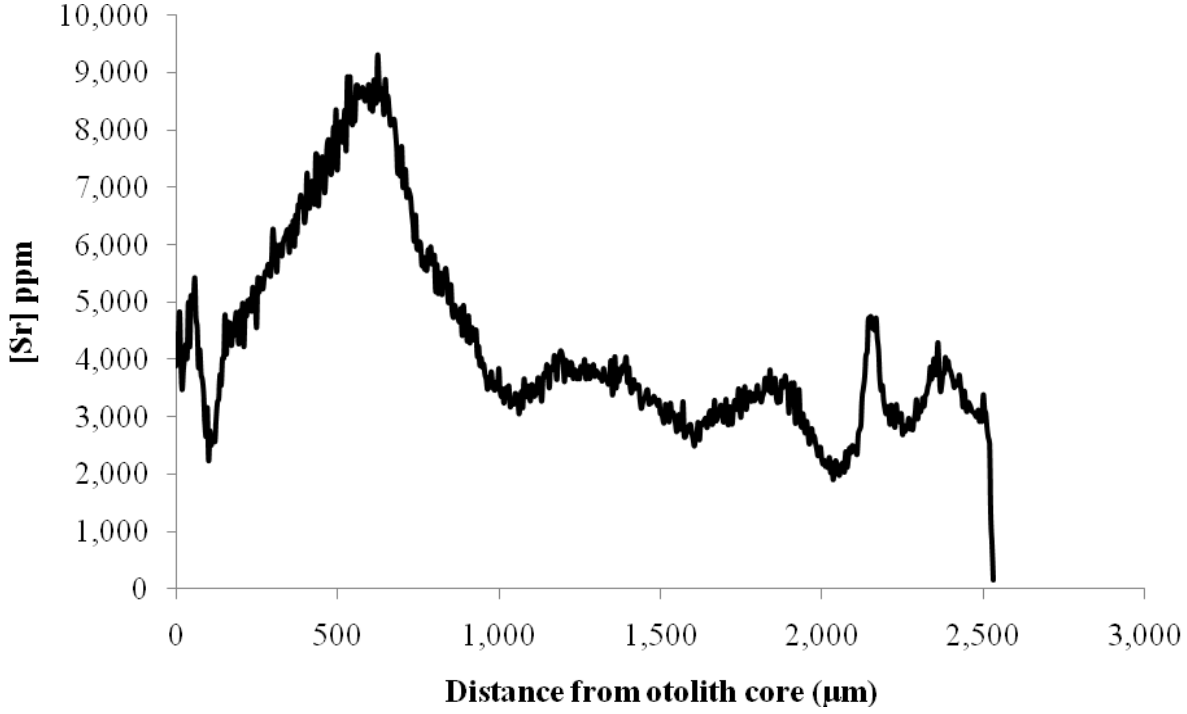


Fish ID: 365; Disk 18 Otolith 4
Sprinter

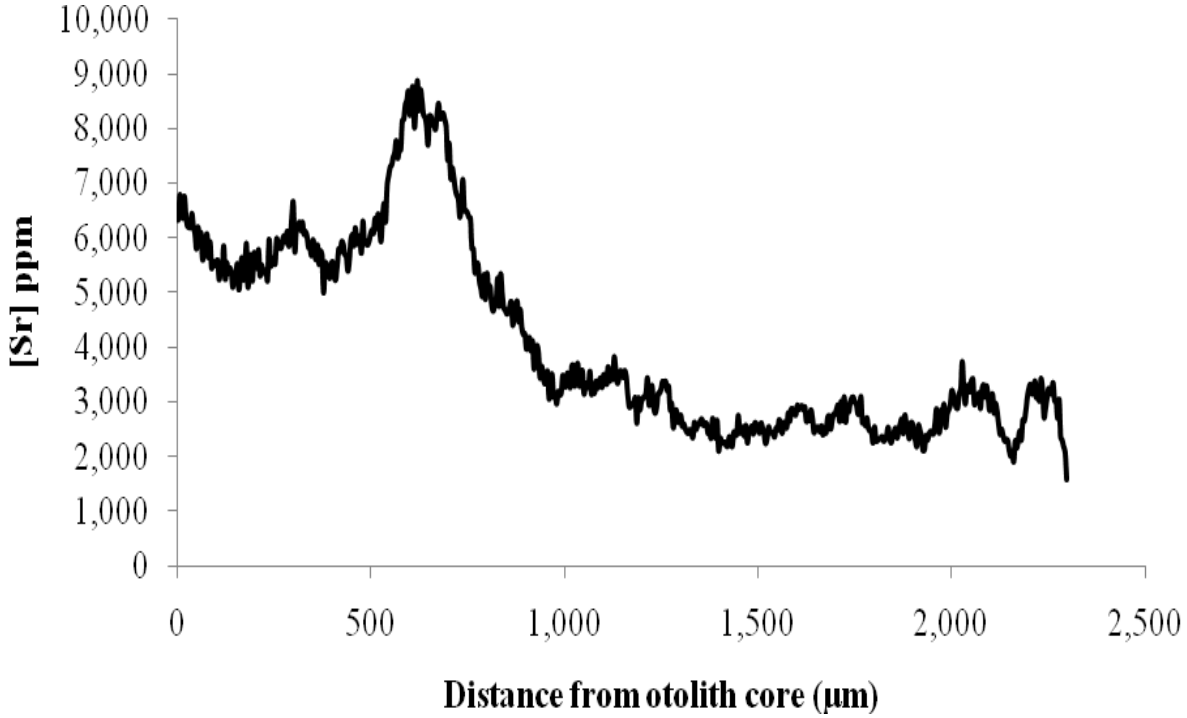


Fish ID: 417; Disk 18 Otolith 5
Stager

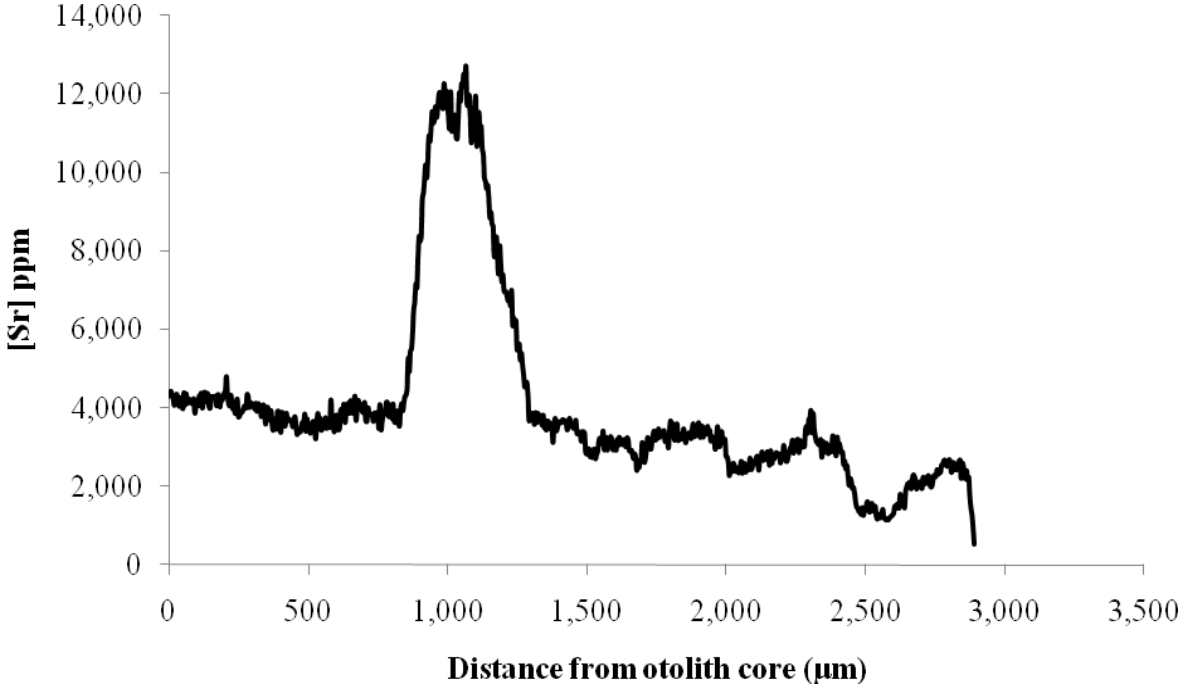
Fish ID: 487; Disk 18 Otolith 6
High Sr



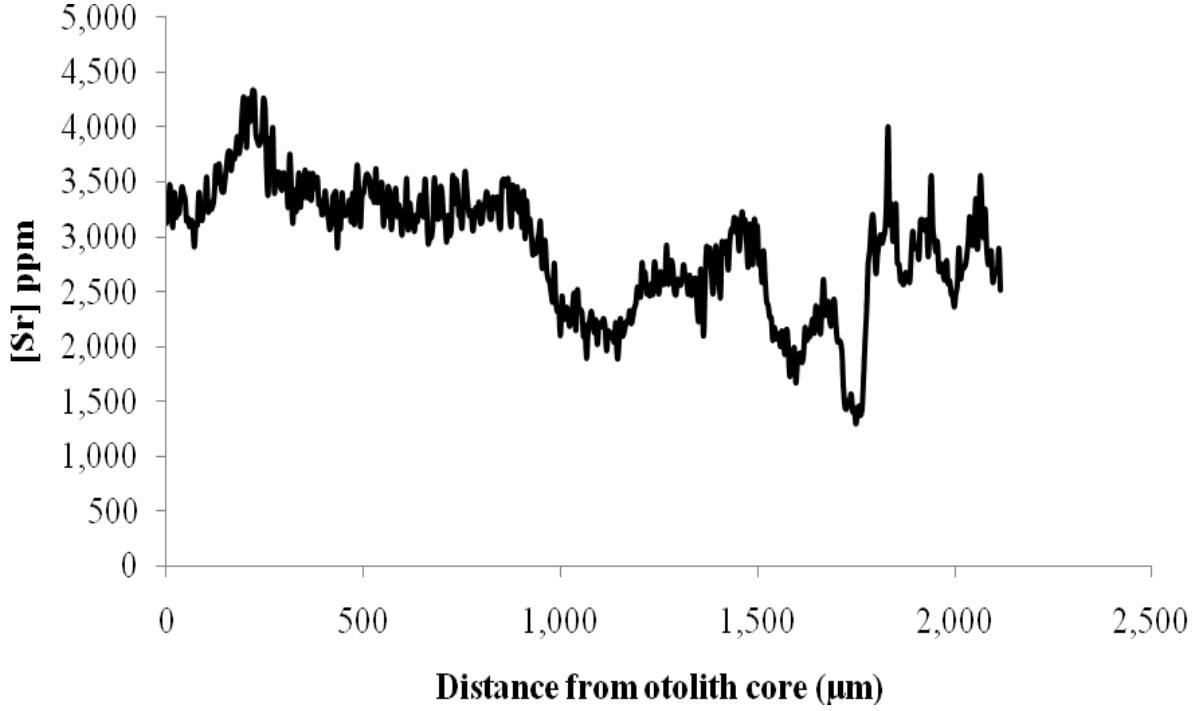
Fish ID: 503; Disk 19 Otolith 1
High Sr



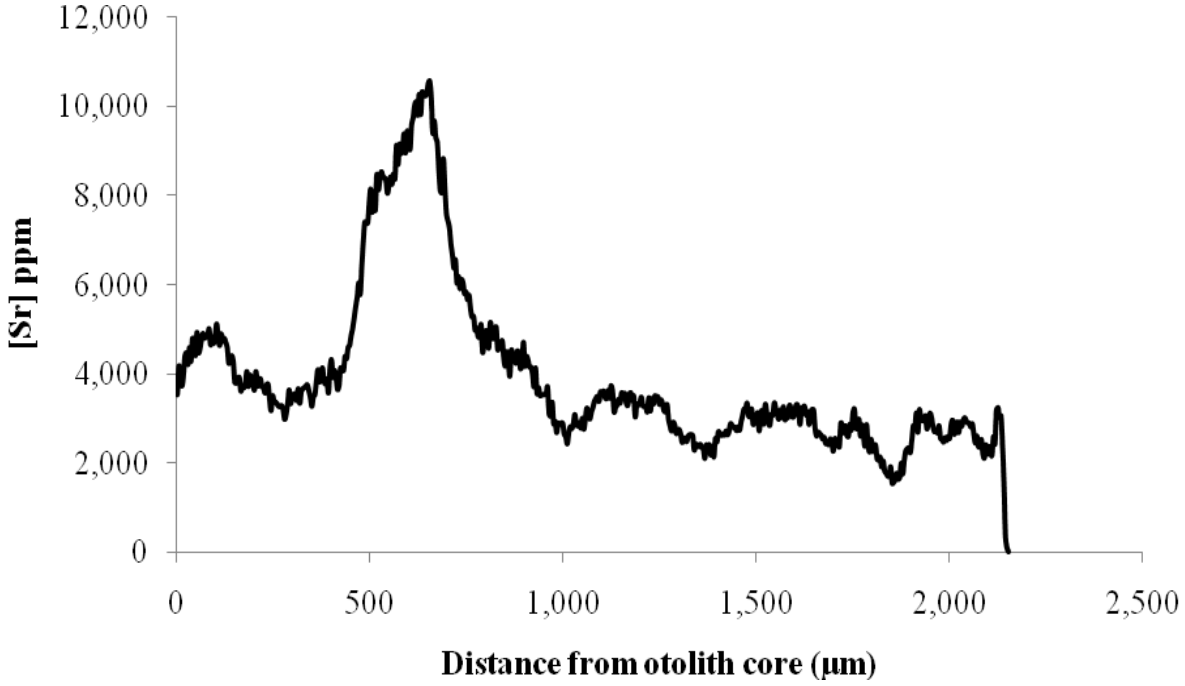
Fish ID: 454; Disk 19 Otolith 2
High Sr



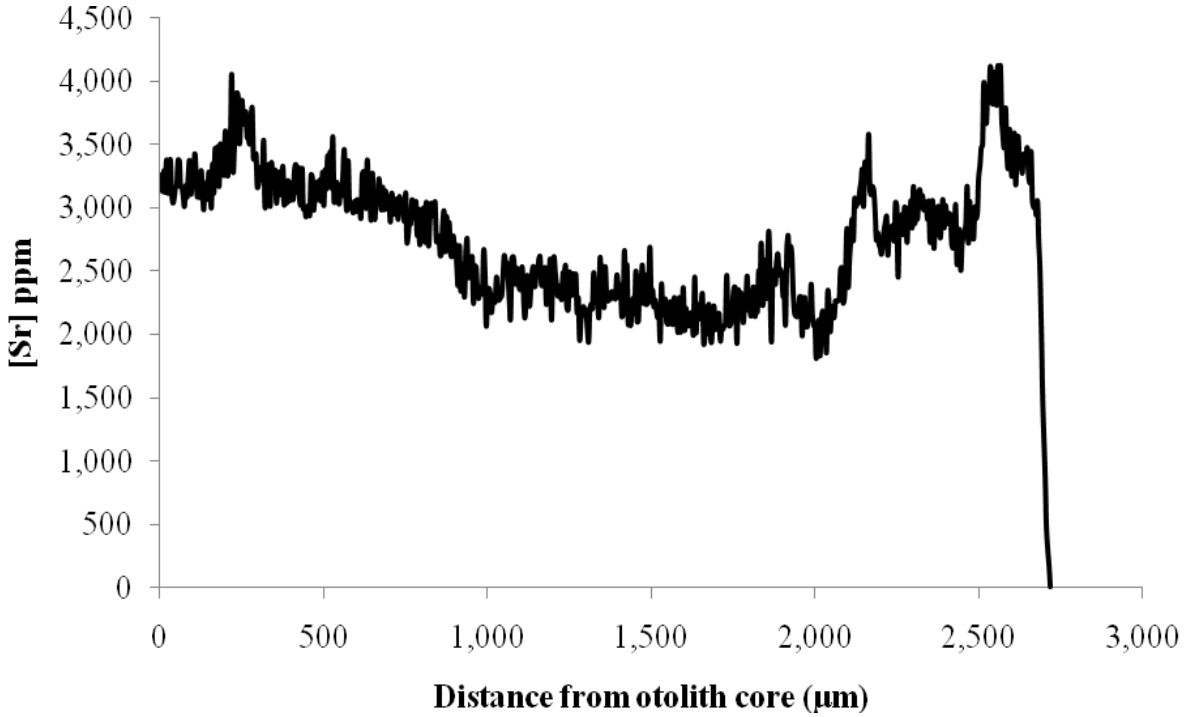
Fish ID: 1320; Disk 19 Otolith 3
High Sr



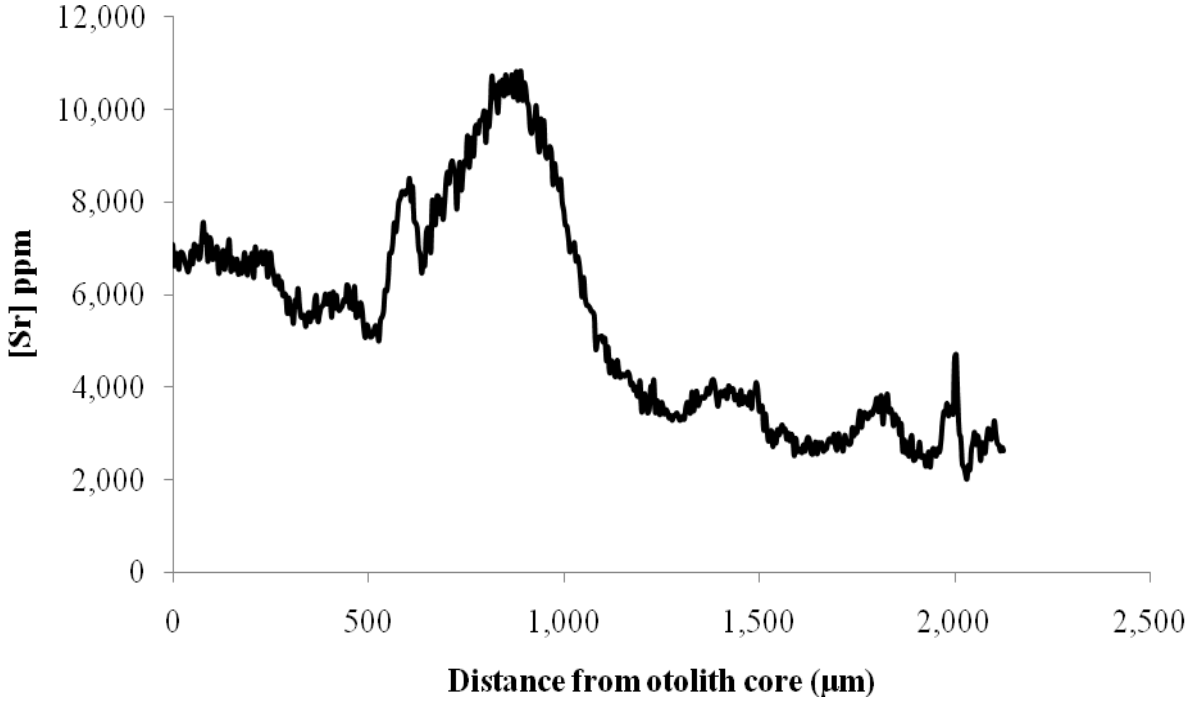
Fish ID: 404; Disk 19 Otolith 4
High Sr



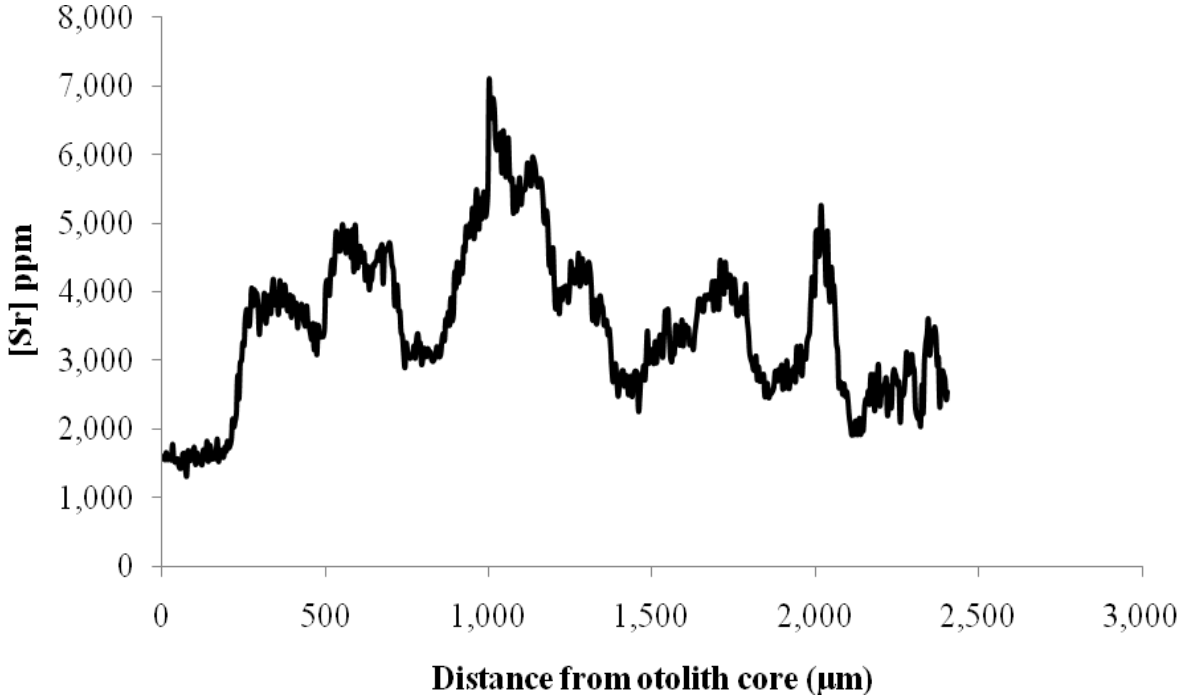
Fish ID: 2; Disk 19 Otolith 5
High Sr



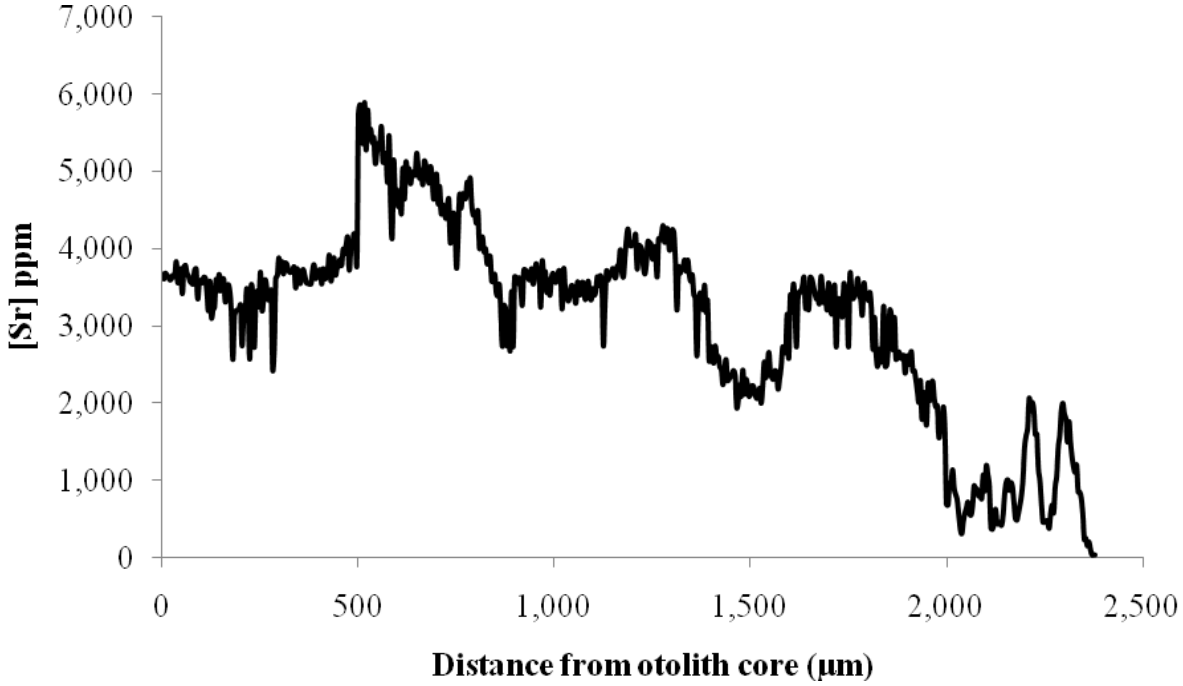
Fish ID: 373; Disk 19 Otolith 6
High Sr



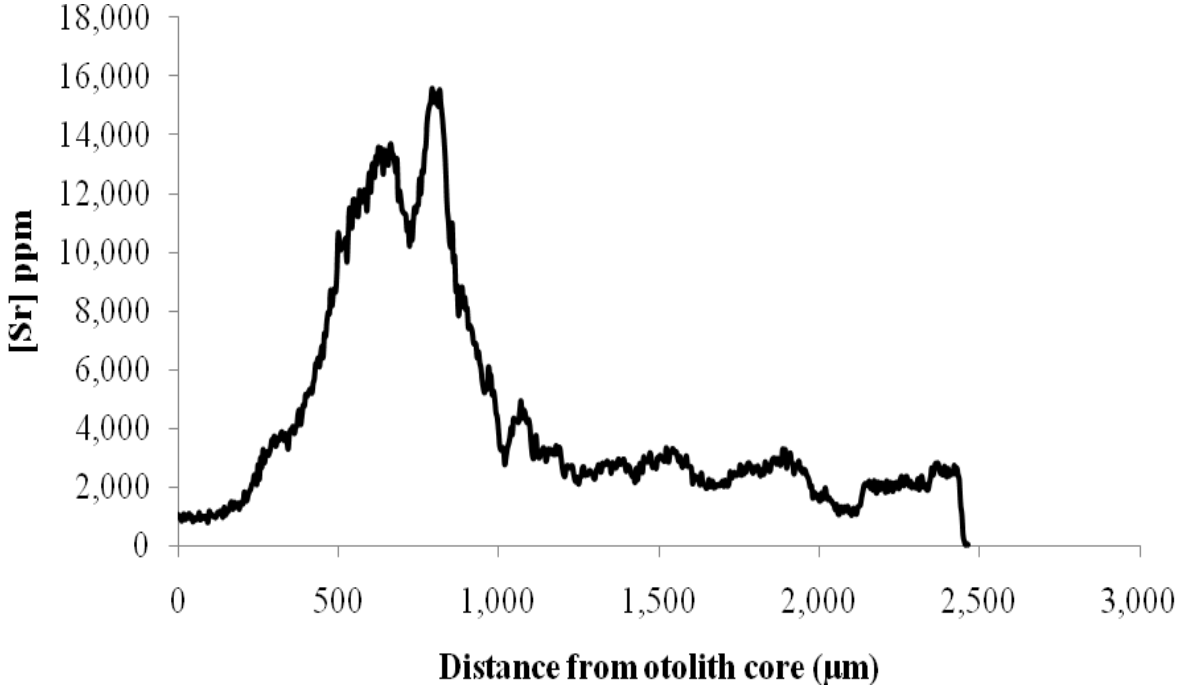
Fish ID: 379; Disk 20 Otolith 1
Stager



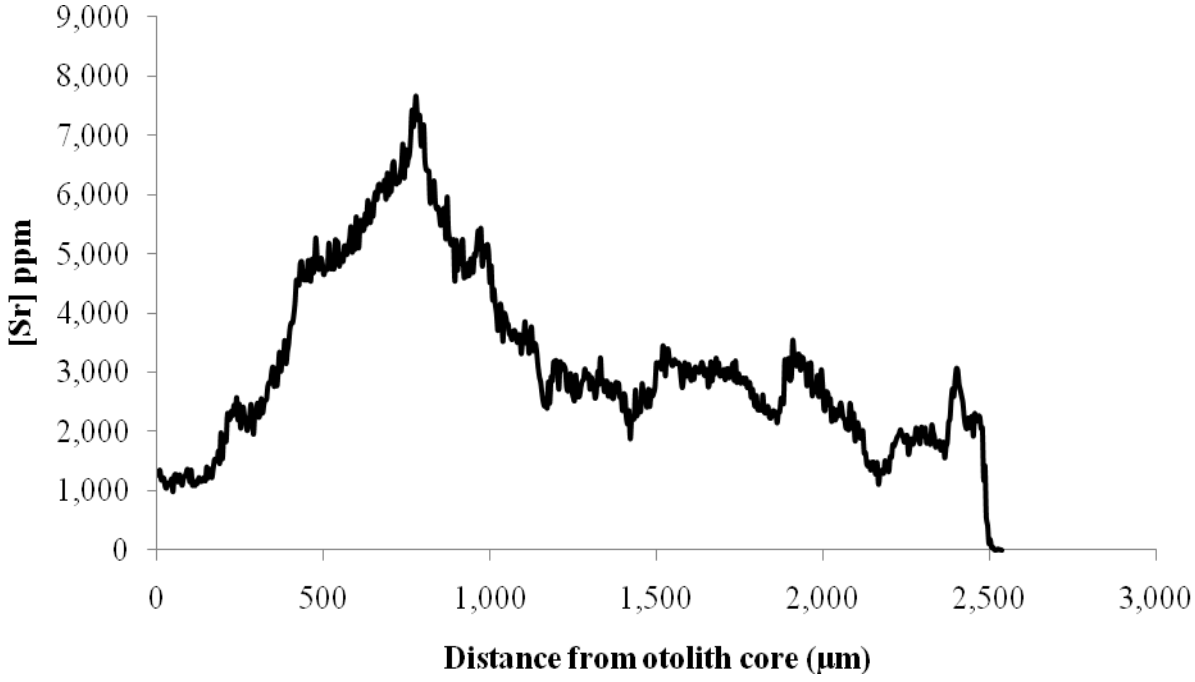
Fish ID: 1286; Disk 20 Otolith 2
Sprinter



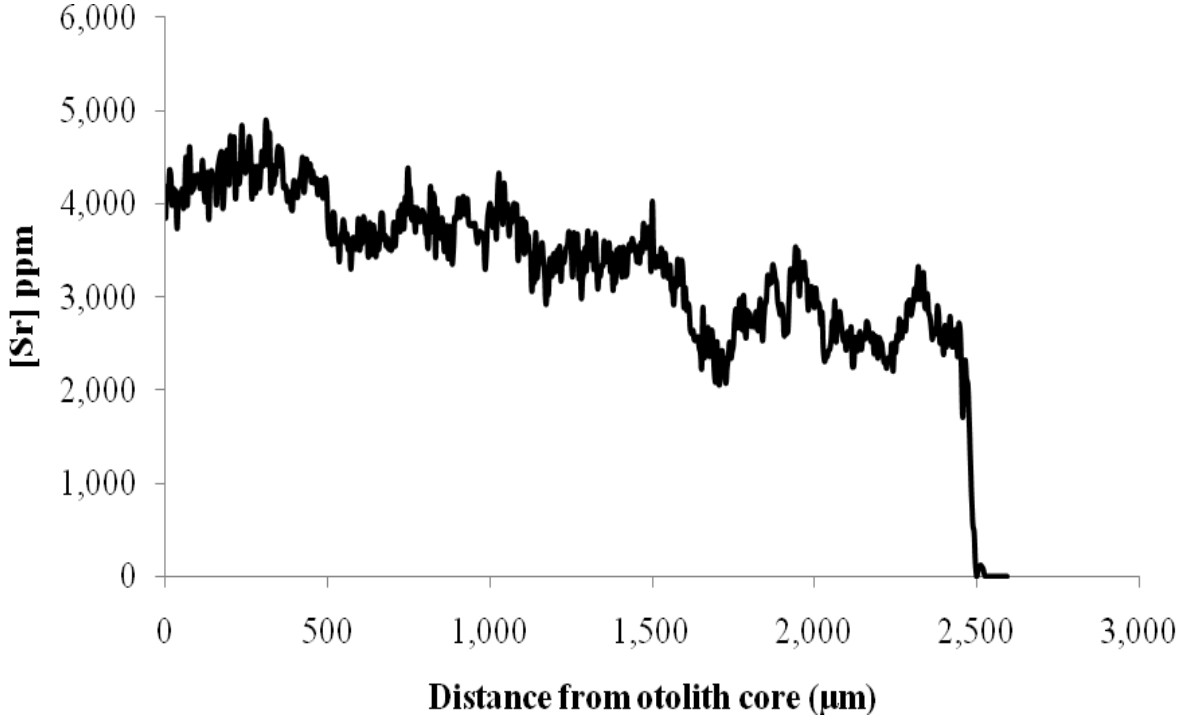
Fish ID: 1243; Disk 20 Otolith 3
Sprinter



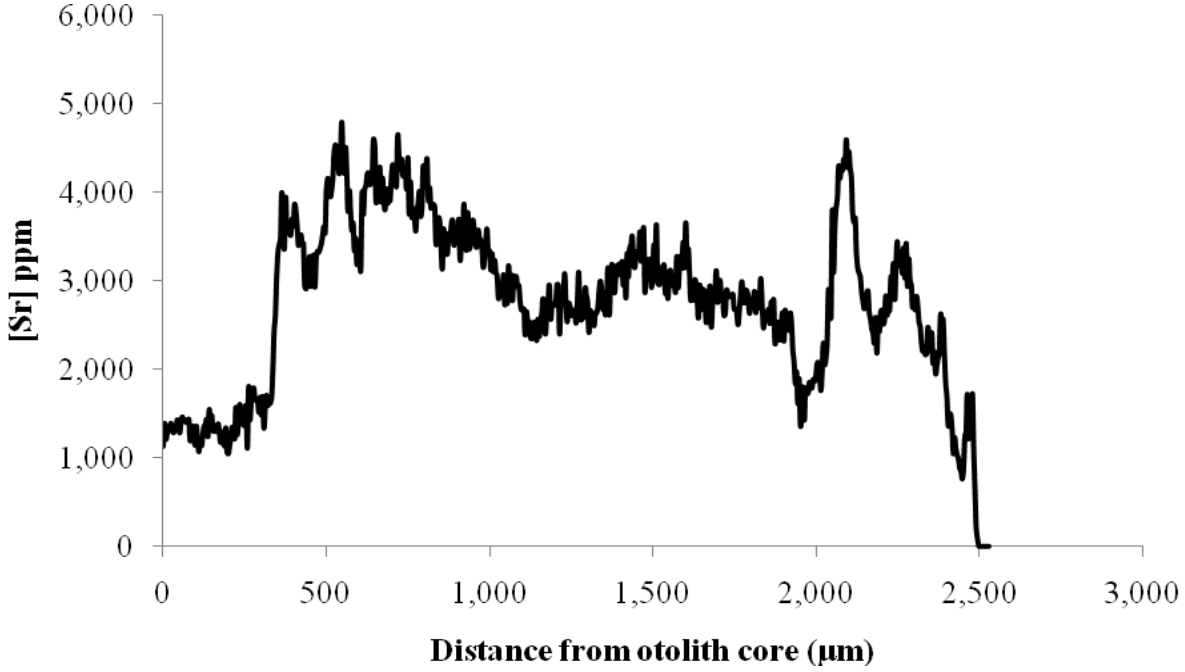
Fish ID: 453; Disk 20 Otolith 4
Stager



Fish ID: 450; Disk 20 Otolith 5
High Sr



Fish ID: 1222; Disk 20 Otolith 6
Stager



APPENDIX B: SAMPLING DATA, NOTING FISH IDENTIFICATION, DATE OF CAPTURE OR COLLECTION, TOTAL LENGTH (mm), WEIGHT (lbs), SEX, HAPLOTYPE, AND MIGRATION TYPE.

See attachment.

Fish number	Date of capture or collection	Total length (mm)	Weight (lbs)	Sex	Haplotype	Migatory type
1	4/19/2004	450	2.2	m	3	Mixed
2	4/19/2004	465	2.4	m	3	Mixed
3	4/19/2004	437	1.9	m	3	Sprinter
4	4/19/2004	473	2.5	m	2	Mixed
101	4/27/2004	886	19.3	f	3	Mixed
102	4/28/2004	695	8	f	1	Sprinter
103	4/28/2004	930	18.25	f	1	Resident
104	4/28/2004	1025	26.85	f	1	Resident
105	4/28/2004	786	12.3	f	1	Mixed
106	4/28/2004	1000	21.85	f	1	Resident
107	4/28/2004	960	20.55	f	1	Stager
108	5/12/2004	780	12.15	f	1	Stager
109	5/12/2004	930	18.65	f	2	Resident
110	5/12/2004	805	13.8	f	2	Resident
111	5/12/2004	890	17.5	f	1	Resident
112	5/12/2004	920	17.65	f	2	Resident
328	4/30/2005	545	4	f	3	Sprinter
330	4/30/2005	491	3.25	f	1	Mixed
351	4/30/2005	510	3	m	1	Mixed
359	4/30/2005	515	3.25	f	2	Stager
360	4/30/2005	526	3.5	f	1	Sprinter
361	4/30/2005	485	2.5	m	3	Stager
363	4/30/2005	515	3.25	m	2	Stager
365	4/30/2005	491	3	f	2	Sprinter
367	4/30/2005	521	4	m	3	Resident
373	4/30/2005	483	3	m	1	Mixed
379	4/30/2005	474	2.5	m	3	Stager
385	4/30/2005	533	4	m	1	Resident
391	4/30/2005	490	3	f	3	Sprinter
398	4/30/2005	486	3	m	1	Mixed
404	4/30/2005	502	3	m	1	Mixed
411	4/30/2005	501	3.25	m	2	Stager
415	4/30/2005	478	2.75	m	1	Mixed
417	4/30/2005	532	3.75	m	3	Sprinter
430	5/1/2005	497	3.25	f	1	Mixed
437	5/1/2005	517	3.5	f	1	Sprinter
450	5/1/2005	512	3	f	2	Mixed
453	5/1/2005	526	3.5	f	1	Stager
454	5/1/2005	514	3.25	m	3	Mixed
461	5/1/2005	508	3	f	2	Sprinter
466	5/1/2005	484	3.25	m	1	Sprinter
468	5/1/2005	482	3	f	3	Resident
482	5/1/2005	492	3	f	1	Sprinter
484	5/1/2005	487	3	f	3	Mixed
487	5/1/2005	503	3	f	2	Mixed
493	5/1/2005	524	3.75	m	1	Resident
498	5/1/2005	505	3	f	2	Sprinter
503	5/1/2005	484	3	f	3	Mixed
1136	4/22/2005	474	2.75	m	2	Sprinter

Fish number	Date of capture or collection	Total length (mm)	Weight (lbs)	Sex	Haplotype	Migatory type
1137	4/22/2005	482	3	m	1	Mixed
1145	4/22/2005	495	2.75	m	2	Mixed
1149	4/22/2005	518	3.75	f	3	Mixed
1151	4/22/2005	481	3	m	1	Sprinter
1158	4/22/2005	476	3	f	3	Mixed
1159	4/22/2005	485	3.25	m	2	Stager
1165	4/22/2005	458	2.5	m	1	Sprinter
1174	4/22/2005	485	3	f	1	Stager
1176	4/22/2005	502	3.5	m	2	Mixed
1184	4/22/2005	464	2.75	f	3	Sprinter
1191	4/23/2005	541	4.25	m	2	Mixed
1192	4/23/2005	529	4	f		Mixed
1193	4/23/2005	464	2.5	f	1	Stager
1194	4/23/2005	504	3	m		Mixed
1202	4/23/2005	495	3	f	1	Stager
1216	4/23/2005	474	3	m	1	Mixed
1218	4/23/2005	470	2.5	m	3	Sprinter
1219	4/23/2005	524	3.25	f	3	Sprinter
1222	4/23/2005	471	2.5	f	2	Stager
1227	4/23/2005	510	3.75	m	3	Mixed
1233	4/23/2005	510	3.5	m	1	Mixed
1234	4/23/2005	547	4.5	f	2	Mixed
1236	4/23/2005	524	3.5	m	3	Resident
1237	4/23/2005	470	2.5	m	2	Mixed
1240	4/24/2005	532	3.5	f	2	Mixed
1243	4/24/2005	494	3	f	2	Sprinter
1245	4/24/2005	511	3.25	m	1	Sprinter
1249	4/24/2005	487	2.5	m	2	Sprinter
1250	4/24/2005	505	3	m	2	Resident
1256	4/24/2005	517	4.25	m	1	Sprinter
1257	4/24/2005	464	2.5	f	3	Sprinter
1264	4/24/2005	516	3.5	m	1	Stager
1266	4/24/2005	492	3	m		Resident
1267	4/24/2005	510	3.25	m	3	Mixed
1275	4/24/2005	502	3	m	3	Mixed
1276	4/24/2005	556	4.25	m	1	Sprinter
1277	4/24/2005	515	3.25	m	3	Sprinter
1278	4/24/2005	484	3	m	2	Sprinter
1279	4/24/2005	490	3	m	2	Mixed
1285	4/24/2005	495	3	f	1	Mixed
1286	4/24/2005	475	2.5	m	2	Sprinter
1290	4/24/2005	505	3.25	m	1	Mixed
1294	4/24/2005	469	2.75	f	3	Mixed
1296	4/24/2005	487	3	f	3	Resident
1308	4/24/2005	480	3	m	2	Sprinter
1310	4/24/2005	483	3	m	1	Sprinter
1313	4/24/2005	514	4	f	2	Mixed
1318	4/24/2005	540	4	f	3	Stager
1320	4/24/2005	478	3	m	1	Mixed
3002	4/29/2004	800	17.25	f		Sprinter

Fish number	Date of capture or collection	Total length (mm)	Weight (lbs)	Sex	Haplotype	Migatory type
3003	4/23/2004	920	23	f		Resident
5001	4/21/2004	795	12.25	m	1	Sprinter
5002	4/23/2004	830	14.5	f	2	Resident
5003	4/27/2004	1033	29.5		1	Sprinter
5004					1	Resident
5005	4/21/2004	840	12.75	m	2	Mixed
5006	5/7/2004	779	13.25	f	1	Mixed
5007	5/3/2004	940	22.5	f	2	Resident
5008	4/25/2004	932	21.5	f	1	Resident
5009	8/22/2004	920	20	f	1	Resident
6003					2	Resident
6004					2	Resident
6005					1	Resident
6006					1	Resident
6007					3	Resident
6008					1	Resident