Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass Morone saxatilis*

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Management of Chesapeake Bay and coastal striped bass *Morone saxatilis* fisheries is affected by migration of large Chesapeake adults into coastal waters. Tagging studies during the 1930s and 1950s indicated that a small percentage of Chesapeake striped bass contribute to the coastal fishery (Vladykov and Wallace 1952, Mansueti 1961, Massman and Pacheco 1961). However, work on age- and sex-specific migration patterns (Chapoton and Sykes 1961, Kohlenstein 1981) suggested that about half of the females aged 3+ migrate out of the Bay. The current consensus appears to be that young striped bass remain in or near the tributary in which they were spawned for 2 or 3 years; thereafter most males remain in the Bay, while a substantial number of females migrate out of the Bay and remain in coastal waters until sexually mature (Chapman 1987, Setzler-Hamilton and Hall 1991). Although facultative anadromy is suggested by tagging studies, age- and sex-specific rates of anadromy remain largely unknown (ASMFC 1990).

Wave-length dispersive electron microprobe analysis of strontium/calcium ratio (Sr/Ca) in otoliths has recently been employed as a method for distinguishing between freshwater and marine life-history phases

of individual fishes (Casselman 1982, Radtke et al. 1988, Kalish 1990). Sr is substituted for Ca into the lattice of aragonitic calcium carbonate (Kinsman and Holland 1969), and in otoliths the rate of substitution is in proportion to its abundance in the endolymph (Kalish 1989). Sr concentration in seawater is more than one order of magnitude greater than in freshwater (Bagenal et al. 1973, Radtke et al. 1988, Kalish 1990, Ingram and Sloan 1992). Therefore, Sr levels in otoliths of fish exposed to seawater should be substantially higher than those exposed to freshwater.

Sr/Ca ratio in otoliths of anadromous striped bass was analyzed to determine its usefulness in charting individual migratory histories. In a prospectus, Coutant (1990) suggested a similar application to investigate patterns of estuarine use by Chesapeake Bay and Roanoke River striped bass. Here, I looked for a seasonal pattern in otolith Sr/Ca ratios that was consistent with anadromous behavior. An annual cycle of low Sr/Ca ratios during spring (exposure to Sr-poor freshwater) and high ratios during fall and winter (exposure to Sr-rich saltwater) was expected in large adults. If such a pattern existed, then further research and application would be justified. Analysis of Sr/Ca composition could be applied to problems of migratory behavior, spawning, hatchery contribution to coastal stocks, definition of life-

history traits, environmental degradation (Coutant 1990), and consequences of anadromy to recruitment (e.g., Kalish 1990).

In this investigation, I related Sr/Ca ratios to annuli which are assumed to form in spring (see Discussion). I used a less traditional definition for annulus, "...a ridge or a groove in or on the [hard] structure..." (Wilson et al. 1987), because opaque and translucent zones did not adequately describe the microstructure observed under scanning electron microscopy or light microscopy.

Methods

Sr/Ca ratios were examined for five large adults from the Chesapeake Bay and South Carolina (Table 1). Adults from the Chesapeake were presumed to be anadromous based on their size (Setzler-Hamilton and Hall 1991); the South Carolina population is a freshwater population, resident to the Santee-Cooper watershed (Secor et al. 1992). Chesapeake Bay fish (*n* 3) were collected by charterboat fisherman from Solomons, Maryland during the May 1991 "Maryland Trophy Season", presumably caught in upper Bay waters. South Carolina fish were collected at a 1989 fishing tournament. Otoliths were removed, cleaned in 10% sodium hypochlorite solution (bleach), and rinsed with deionized water. They were embedded in Spurr epoxy, sectioned in a transverse plane with a Buehler Isomet saw, and mounted on a glass slide. Otoliths were polished (see Secor et al. 1991) until all annuli were visible with transmitted light on a compound microscope. Otolith sections were further polished with 3 µm alumina to limit any surface structure that could cause artifacts

Table 1

Striped bass *Morone saxatilis* from Chesapeake Bay (MD and Juv) and Santee-Cooper (SC) populations used in electron microprobe analyses.

ID	Population	Sex	Age	TL (cm)	Weight (kg)
MD-1	Chesapeake	Female	21	119	15.5
MD-2	Chesapeake	?	8	94	7.3
MD-3	Chesapeake	?	9	93	8.1
SC-1	Santee-Cooper	Female	6	80	4.8
SC-2	Santee-Cooper	Female	5	81	5.4
Juv-1	Patuxent River	Juvenile	0	—	—

Table 2

Effect of counting time on strontium and calcium counts. Accelerating voltage = 25 kV, probe current = 20 nA, sample size = $5\mu m^2$. Note that Sr and Ca show no decline with counting time which would indicate sample destruction.

Seconds counted	Counts/sec	
	Sr	Ca
0	585	16763
4	586	16678
8	576	16725
12	589	16869
16	586	16748
20	578	16847
24	570	16828
28	592	16850
32	603	16813

in microprobe analysis (Kalish 1991). Otolith sections were carbon-coated in a high-vacuum evaporator.

A sagitta from a juvenile striped bass sampled from the Patuxent River (Chesapeake Bay tributary) was similarly prepared and polished so that the core and all increments were sectioned (Secor et al. 1991). The juvenile's parentage, a 20 kg female that was assumed to be migratory based on its size (Kohlenstein 1981), was known because the juvenile was a marked hatchery fish released as a 9-day-old larva.

X-ray intensities for Sr and Ca elements were quantified using a JXA-840A JEOL wave-length dispersive electron microprobe (Central Facility for Microanalysis, Univ. Maryland, College Park MD 20742), with Calcite ($CaCO_3$) and Strontianite ($SrCO_3$) as standards. Striped bass otoliths were resilient to high-beam power densities compared with previous work on salmonid otoliths (Kalish 1990) and showed no diffusion of elements over a 32-sec counting period (Table 2). This permitted analysis of small

sample points ($5 \times 5\mu m$) at high accelerating voltage (25 kV) and probe current (20 nA). Background and peak counting times were each 20 sec for Sr, and 5 sec for Ca. Background counting times were equally divided below and above the peak position. The detection limit for Sr was 580 ppm. Precision was calculated at <1% for Ca counts and 8.2% for Sr counts (at Sr/Ca = 0.003) (1.96σ; Goldstein et al. 1981). The electron beam caused a physical disruption (a pit) at the section's surface which limited the proximity of adjacent points that could be accurately sampled. Initial analyses of Chesapeake sample otoliths at "step" distances of 8μm resulted in no Sr X-ray counts. This was probably due to physical disruptions among adjacent points because surface structure can cause artifacts in microprobe analysis (Kalish 1991). Analysis was therefore conducted at 13 and 20μm step sizes where positive counts occurred (Table 3). Transects (700–2600μm in length) across annuli in the otolith sections were selected. The electron microprobe sampled 60–130 points along these transects. Each point required ~70 sec of microprobe time. X-ray intensities were calculated using the ZAF procedure (Reed 1975), normalized to standards, and converted to elemental (atomic weight) ratios.

Due to their close proximity, individual points were not always visible in probed otolith sections. To relate Sr/Ca ratios to the

Table 3

Summary statistics for Sr/Ca ratios of Chesapeake Bay and Santee-Cooper samples. All ratio statistics have been multiplied by 1000 for presentation purposes. Age is given in parentheses below each sample. Step = distance between sampled points along transect.

Sample	Transect	Step (μm)	N	$\bar{x}$	SE	Mode	Median
MD-1	1	20	99	2.753	0.094	3.4	2.8
(21)	2	20	99	2.645	0.095	2.3	2.6
	3	13	60	3.713	0.124	4.7	4.0
	(age ≥ 7)						
MD-2	—	13	99	2.974	0.155	0	3.0
(8)							
MD-3	1	20	100	2.385	0.097	2.8	2.4
(9)	2	13	70	2.323	0.086	1.7	2.3
SC-1	—	20	130	0.937	0.061	0	0.9
(6)							
SC-2	—	13	99	0.241	0.054	0	0
(5)							

opaque zones of annuli checks, probed sections were viewed under a compound microscope and transect distances between annuli measured with an ocular scale. Because the distance between each microprobe measurement was known, distances between measurements can be converted to distances between annuli. Distances between annuli (annular increments) became narrow with increasing age (<50 μm) (Fig. 1), and points did not always sample directly on annuli. Therefore, it was necessary to assign an annulus to the closest sampled point. Points between annuli were assumed to sample age in linear proportion. For instance, if 10 points were sampled between annuli 5 and 6, then points would be assigned ages 5.0, 5.1, 5.2, . . . 6.0. A replicate scan was performed on two of the otolith samples. In the juvenile's otolith, not all daily increments were visible along the transect with scanning electron microscopy or light microscopy. Therefore, Sr/Ca ratios were related to standard length using an otolith/fish-length relation documented for the Potomac River population (Houde and Rutherford 1992).

Figure 1

Back-scatter electron micrograph of otolith from striped bass *Morone saxatilis* Sample MD-1. Twenty-one annuli are clearly visible along the sulcus (s) and sulcal ridge. Transects 1 and 2 were performed at 20 μm step size; Transect 3 began at the 7th annular check and 13 μm step size. The probed transect previous to Transect 3 was performed at 8 μm step size and resulted in no positive Sr counts. Note that individual probed points are visible in a series of physical disruptions (pits) for Transects 1 and 2.

Results

Mean Sr/Ca ratios in Chesapeake striped bass were three to four times greater than Santee-Cooper striped bass (Table 3; Figs. 2,3). This trend is consistent with a salinity influence on the ratio, because Santee-Cooper striped bass are confined to freshwater and both Santee-Cooper females were sexually mature. Although substantial variation occurred in Sr/Ca between South Carolina samples, both samples were near the electron microprobe's detection limit of Sr/Ca (Sr/Ca = 0.0008). Instrumental precision decreases markedly as the detection limit is approached, which may produce spurious variation. Peaks and nadirs in the Sr/Ca ratios were apparent in Chesapeake striped bass, and in fish >age-4, these patterns generally showed an annual cycle (Fig. 2). This is most apparent for sample MD-1. Because low Sr/Ca ratios can be associated with
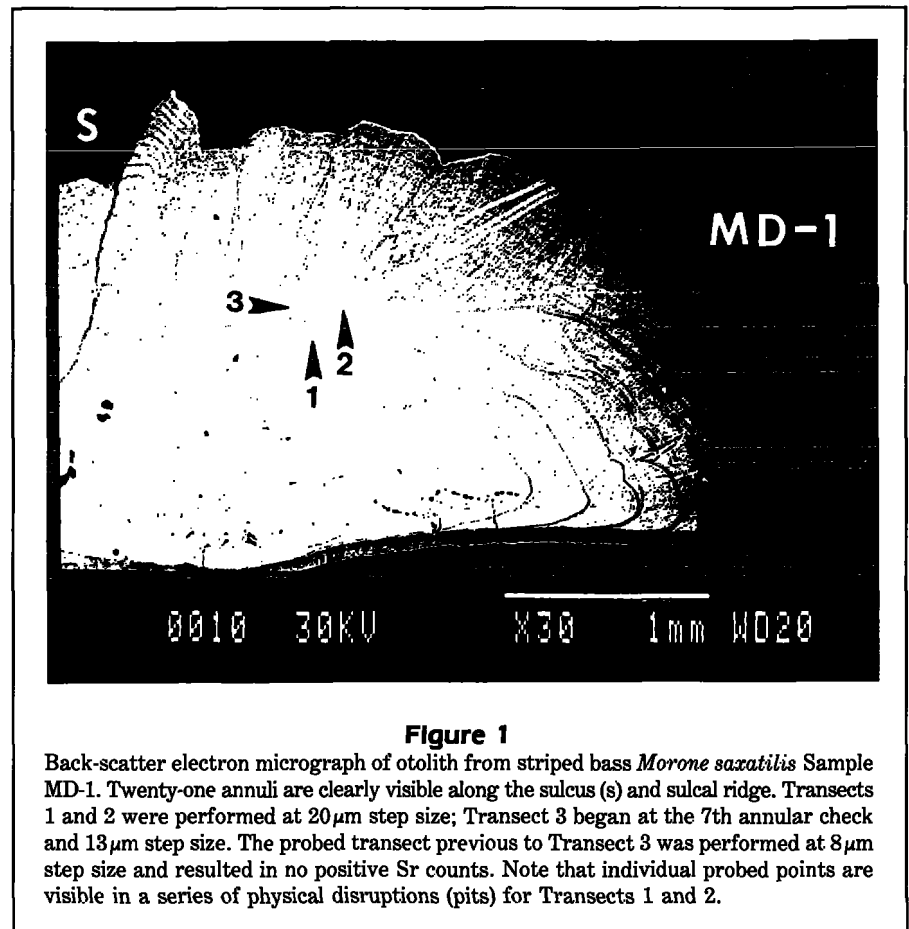
freshwater excursions, results indicate yearly migration for this large female.

Lack of agreement among replicate transects (Fig. 2) probably was due to the manner in which ages were assigned, spatial resolution, and within-sample variability. Probed points of replicate transects could not be directly "lined up" with respect to annuli. This offset occasionally resulted in the interpretation that an annuli was associated with a peak in one transect and a nadir in the other transect (e.g., annuli 15, 18, and 19 in Transect 1 vs. these annuli in Transect 2 for MD-1; Fig. 2). Transects 1 and 2 for Sample MD-1 (20 μm step size) sampled few points between successive annuli at older ages, and the accuracy with which points could be assigned to annuli was less (Fig. 4). Transect 3 for MD-1 (13 μm step size) clearly shows increased resolution of the ratio across annular increments. Similarly, Transect 2 (13 μm) for MD-3 revealed several more peaks and nadirs after the 5th annulus than did Transect 1 (20 μm). The overall Sr/Ca ratio was significantly different between Transects 1 and 2 for MD-3 (Table 4, t 3.06, $p <$ 0.01). Replicate transects in MD-1, where step size
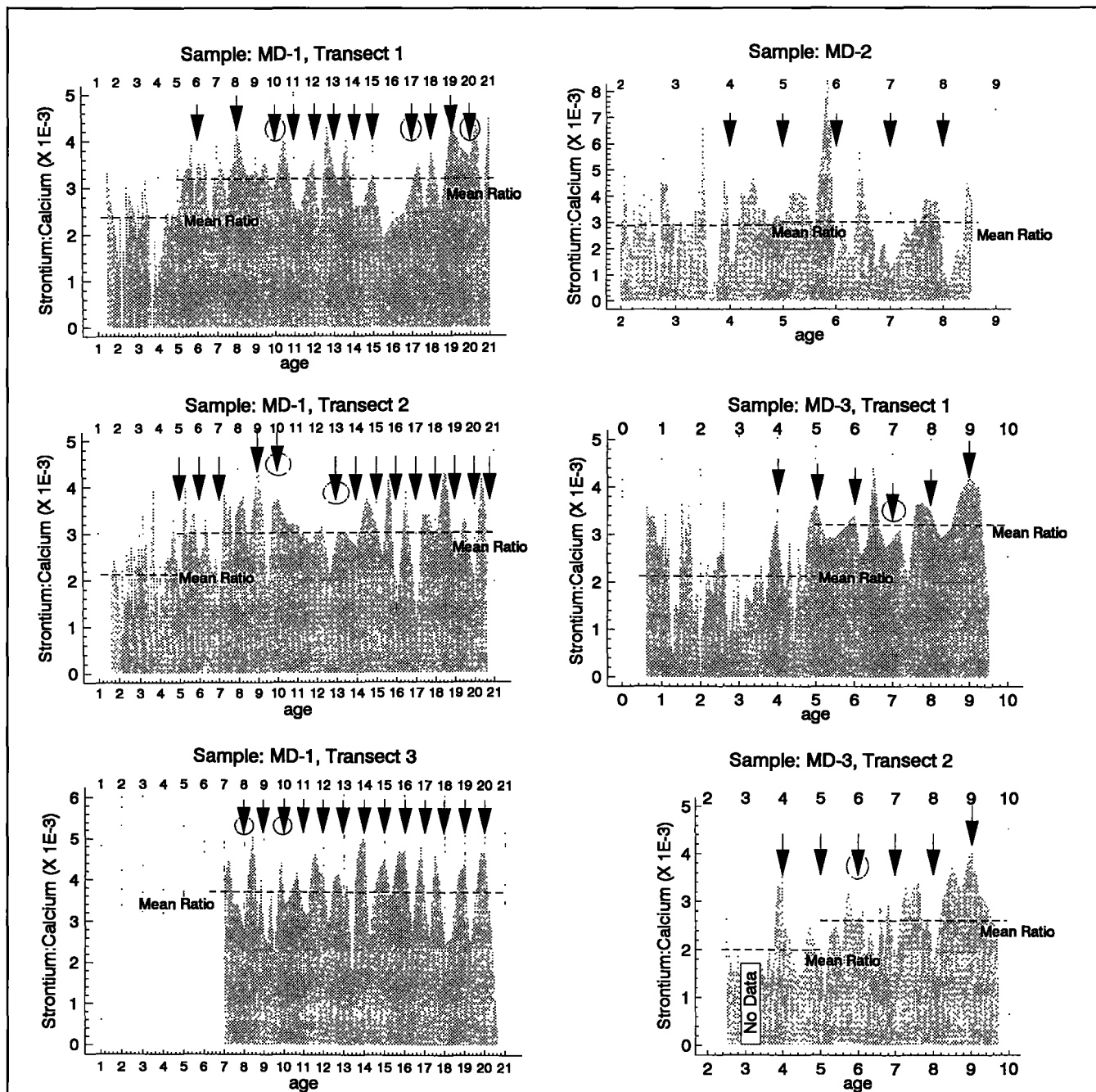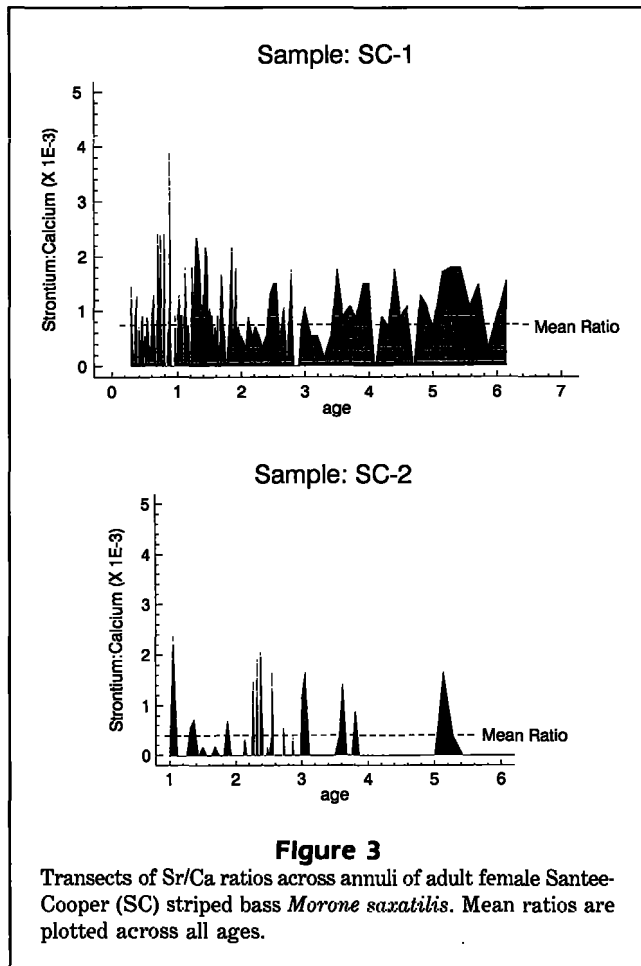
Figure 2

Transects of Sr/Ca ratios across annuli increments of Maryland striped bass *Morone saxatilis*. Mean ratios are plotted for ages <5 and ages ≥5 for each sample. See Table 3 for step sizes. Arrows indicate presumed freshwater excursions. Circled arrows indicate nadirs in ratios which were consistent with an annual cycle but did not coincide with annuli.

was 20 μm for both transects, did not significantly differ.

Despite the differences among transects, the overall trend in Chesapeake fish was a nadir in Sr/Ca ratio at or shortly after annuli that coincided with spring

spawning runs (Merriman 1941, Robinson 1960). This trend occurred only in fish >4 years old. There was a significant increase in the overall Sr/Ca ratio in fish >5 years for two of three Chesapeake fish (Table 4).

Sample: SC-1

Sample: SC-2

Figure 3

Transects of Sr/Ca ratios across annuli of adult female Santee-Cooper (SC) striped bass *Morone saxatilis*. Mean ratios are plotted across all ages.

Strontium was not detected in the Patuxent River juvenile striped bass otolith until it reached ~8 mm SL (Fig. 5). Because larvae less than this size tend to utilize freshwater nurseries (Houde and Rutherford 1992), this further verified that freshwater residence results in low levels of otolith Sr.

Discussion

Annulus formation

Rate and season of annulus formation in striped bass otoliths are critical to interpretation of the results on annual and seasonal changes in otolith microchemistry. Heidinger and Clodfelter (1987) validated the hypothesis of yearly annulus formation for young (<5 years old) striped bass. However, no directed research has documented the time of annulus formation in striped bass otoliths or scales despite their widespread use in fisheries (e.g., Beamish and McFarlane 1983). Several investigators have made the observation that annuli are not observed until spawning season in scales (Merriman 1941, Robinson 1960) and otoliths (M. White, S.C. Wildl. Mar. Resour., Bonneau SC 29431, pers. commun.). Based on these limited observations and the general trend of spring annulus formation in other North American temperate fishes, it was assumed that annular check formation occurred during or just prior to the spawning season (February–April).

Figure 4

Number of sampled points between annuli checks at two step sizes. Contours for a hypothetical 50 μm annular increment are plotted at 13 and 20 μm step sizes.

Salinity effect on otolith microchemistry

Because Chesapeake samples had substantially higher Sr/Ca ratios than South Carolina samples, there appears to be a salinity effect on the ratio. This conclusion is further substantiated by the juvenile otolith that was examined and showed nondetectable Sr/Ca ratio during the early-larval period, a time when Chesapeake tributary larvae generally occur above the salt-wedge (Uphoff 1989, Houde and Rutherford 1992). Patterns in otolith Sr/Ca in adults were consistent with expected seasonal changes in ambient salinity. The range of ratios found for Chesapeake striped bass was similar to those found by Kalish (1989) for 12 marine species (Sr/Ca 0.0018
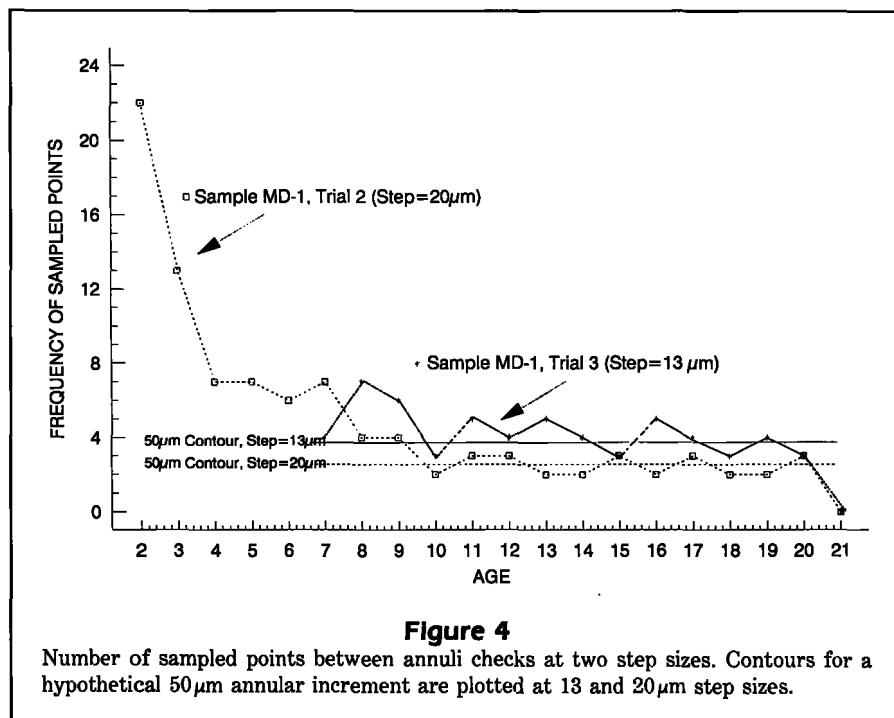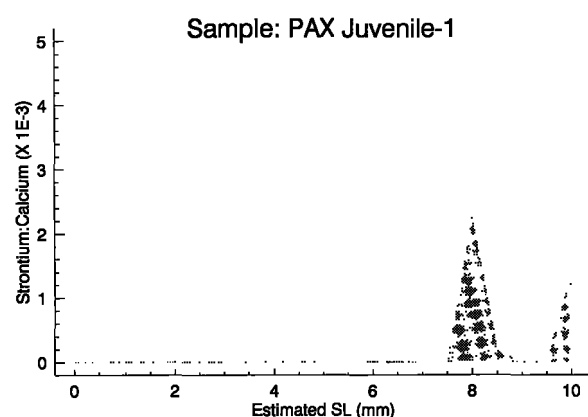
Table 4

Comparison of ratios between probed points <5 or ≥5 years. Significant differences ($p<0.001$) are shown by an asterisk.

Sample	Transect	Age <5 −	Age <5 SD	Age <5 N	Age ≥5 −	Age ≥5 SD	Age ≥5 N	t
MD-1	1	2.17	0.89	44	3.22	0.68	55	6.62*
	2	2.16	0.89	44	3.03	0.64	55	5.09*
MD-2	—	2.96	1.50	65	3.01	1.66	34	0.15
MD-3	1	2.15	0.93	78	3.20	0.67	22	4.95*
	2	2.01	0.62	35	2.61	0.70	35	3.78*

Figure 5

Transect of Sr/Ca ratios for the early-larval period from a juvenile striped bass *Morone saxatilis* sampled from the Patuxent River, 1991. Transect distance was converted to standard length using regression of standard length on otolith length for Potomac River striped bass larvae (Houde et al. 1992). Transect points were converted to larval lengths assuming a linear growth rate and constant otolith length:fish length relationship.

−0.0062) and 1 freshwater species (Sr/Ca 0.0005–0.0010).

Radtke (1984) and others (Townsend et al. 1989, Radtke et al. 1990) have shown an inverse relationship between temperature and otolith Sr/Ca ratio. If there were such an inverse relationship in adult striped bass otoliths, then ratios would increase during fall and winter and decrease during spring and summer, a pattern which would to some degree parallel the pattern seen for anadromous striped bass.

Kalish (1989, 1991) in recent directed research found no temperature relationship for otolith Sr/Ca ratio, and suggested that seasonal changes in fish physiology can cause incidental correlation between temperature and Sr/Ca ratios. Based on evidence for seasonal, growth,

and age effects on Sr/Ca ratios, he postulated that during certain periods of active metabolism, Ca-binding proteins are more abundant in the serum which results in a higher relative fraction of free Sr available for deposition onto the otolith. If Sr/Ca ratios in the otolith are controlled by physiological processes alone, then a different pattern of Sr/Ca ratios would be expected compared with those observed for striped bass, i.e., Sr/Ca ratios would tend to rise in late-winter and early-spring during vitellogenesis but might also be high during periods of active growth. However, physiological effects such as sexual maturation and stress could explain both the increase in Sr/Ca ratio after the 5th annulus in Samples MD-1 and MD-3, and seasonal (subannular) patterns which varied among samples (e.g., the major peak which proceeded the 6th annulus in Sample MD-2; Fig. 2).

Although results exist for few species, the magnitude of the salinity effect found in this and other studies (Casselman 1982, Kalish 1989 and 1990) may be greater than differences expected due to physiological condition (Kalish 1989, 1991) and temperature alone (Radtke 1984, Townsend et al. 1989, Radtke et al. 1990). Similar to my findings, Kalish (1989, 1991) reported a three- to four-fold difference in Sr/Ca ratio between groups of young rainbow trout exposed to either freshwater or saltwater. Casselman (1982) reported a three-fold difference in Sr/Ca ratio between the marine and freshwater life-history phases of American eel. In laboratory-rearing studies on larval herring *Clupea harengus*, temperature effects resulted in no more than a two-fold difference in Sr/Ca ratios (Townsend et al. 1989, Radtke et al. 1990), although a complementary field study conducted by Townsend et al. (1989) showed that temperatures of 1–12°C had a four-fold effect on Sr/Ca ratio. Physiological condition has been associated with an approximate two-fold effect on Sr/Ca ratio in juvenile Australian salmon *Arripis trutta* (Kalish 1989).

A three-fold difference in Sr/Ca ratio in otoliths is consistent with the probable influence of ambient concentrations of Sr and Ca, since the Sr/Ca ratio is at least four times greater in saltwater than in freshwater (Casselman 1982, Radtke et al. 1988, Kalish 1989 and 1990). Further, Berg (1968) has shown substantially less physiological discrimination against Sr than Ca in scale formation, and Kalish (1989) shows excellent correspondence between otolith microchemistry and the chemical composition of endolymph that bathes the otolith. Therefore, ambient levels of Sr could be reflected in the otolith's microchemistry (Mugiya and Takahashi 1985, Kalish 1989) dependent upon the degree of physiological discrimination against Sr.

Otolith microchemistry and migratory history

The otolith microchemistry method offers great potential to address questions related to time of maturation and frequency of spawning. A distinct positive shift in Sr/Ca ratio at 5 years in samples MD-1 and MD-3 could be indicative of maturation or onset of coastal migration. Current estimates of age-at-maturation for Chesapeake population females indicate that <30% of females are mature by age 5 years (Maryland DNR 1991). Kohlenstein (1981) showed through a tagging study that the majority of female striped bass migrate by 5 years. Lack of a shift in MD-2 might indicate that this individual was a male or had a different migration history.

All Maryland striped bass samples showed annual peaks and valleys in Sr/Ca ratios. Based on a salinity effect, it can be inferred that valleys represent excursions into strontium-poor freshwater habitats. Assuming that large, mature adults venture into freshwater or low-salinity habitats to spawn, then spawning frequency can be estimated.

Precision error and spatial resolution of the electron microprobe analysis is critical in the proposed application of charting individual migratory histories. Precision errors were indicated by differences in Sr/Ca patterns and overall level between transects of the same sample (e.g., MD-3). Changing spatial resolution between measurements of 20 and 13 μm permitted greater resolution of seasonal (subannular) patterns. A more complete series of measures along a transect is taken at lower step sizes because gaps between measured points become narrower. This effect could explain variation in mean Sr/Ca levels among transects for the same sample. Alternatively, lack of agreement between transects could indicate machine precision limits in detecting Sr/Ca levels.

A decline in otolith growth rate with age also caused a decrease in spatial resolution (Fig. 4). At a 13 μm step size, four or five measurements were taken per annular increment in fish >7 years. Therefore, each measurement can correspond to several months of the fish's life. This would explain why nadirs in Sr/Ca ratio rarely approached zero after the 5th annulus. Tagging studies indicate that adult striped bass can migrate between freshwater and coastal habitats within a month (Mansueti 1961, Chapoton and Sykes 1961, Waldman et al. 1990). Peaks and nadirs observed in otolith Sr/Ca ratio may therefore represent temporally-averaged values. Laboratory verification studies are planned to gauge the spatial sensitivity of otolith microchemistry to resolve changes in ambient salinity.

Other life-history applications

An ingenious application of the Sr/Ca method to early-life-history consequences of anadromy was made by Kalish (1990). He was able to detect Sr in the core of salmonid otoliths (the earliest deposited material). Under the rationale that maternally-derived protein influenced offspring otolith microchemistry, it was possible to segregate offspring on the basis of whether they originated from eggs spawned by anadromous (high Sr/Ca) or nonanadromous (low Sr/Ca) females. In my study, a single striped bass juvenile of known anadromous parentage had no detectable Sr in the otolith core. In contrast to salmonid embryos and larvae, striped bass obtain relatively small amounts of maternal protein and lipids, and the period of endogenous feeding is considerably shorter. Also, the chorion of striped bass eggs is highly permeable; therefore, ambient concentrations of Sr could have a greater influence on otolith microchemistry.

Substantial variation in Sr/Ca ratio occurred for young adult (≤5 years old) Chesapeake fish. In all samples, values ranged below detection limits. Presumably these values represent excursions unrelated to spawning by young fish into freshwater systems. Freshwater and slightly saline environments in the upper reaches of Chesapeake Bay tributaries may serve as foraging grounds. Future research could analyze the duration and seasonality of freshwater habitation by fishes that reside in the Chesapeake Bay.

Further verification studies are needed to establish whether estuarine and marine phases can be distinguished using Sr/Ca ratios. Ratios tended to continuously increase following nadirs, and this pattern could indicate exposure to waters of increasing salinity. A verification study could be carried out by probing the last deposited otolith material (the edge) for Sr/Ca and relating that ratio to the salinity in which the striped bass was sampled in the field or through laboratory rearing studies (Kalish 1989, Townsend et al. 1989, Radtke et al. 1990). A key comparison will be that between samples from estuarine habitats (salinity 5–20 ppt) and marine habitats (≥32 ppt). Should differences be detectable between these groups, then it will be possible to infer detailed patterns of anadromy and related life-history traits.

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