Abstract—Oceanic incidence and spawning frequency of Chesapeake Bay striped bass (*Morone saxatilis*) were estimated by using microchemical analysis of strontium in otoliths. Otoliths from 40 males and 82 females sampled from Maryland's portion of the Chesapeake Bay were analyzed for seasonal and age-specific patterns in strontium and calcium levels. The proportion of oceanic females increased from 50% to 75% between ages seven to 13; the proportion of oceanic males increased from 20% to ~50% between ages four to 13. Contrary to an earlier model of Chesapeake Bay striped bass migration, results indicated that a substantial number of males undertook oceanic migrations. Further, we observed no mass emigration of females from three to four years of age from the Chesapeake Bay. Seasonal patterns of estuarine habitat use were consistent with annual spawning runs by striped bass of mature age classes, but with noteworthy exceptions for newly mature females. Evidence of an early oceanic presence indicated that Chesapeake Bay yearlings move into coastal regions—a pattern observed also for Hudson River striped bass. Otolith microchemical analyses revealed two types of behaviors (estuarine and oceanic) that confirm migratory behaviors recently determined for other populations of striped bass and diadromous species (e.g., American eels [*Anguilla rostrata*] American shad [*Alosa sapidissima*] and white perch [*Morone Americana*]).

Oceanic migration rates of Upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis*

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As an estuarine-dependent species, striped bass (*Morone saxatilis*) demonstrate large plasticity in migration patterns (Secor and Piccoli, 1996). Striped bass in Chesapeake Bay are partial migrants; only a fraction of individuals will leave estuarine habitats for oceanic waters (Kohlenstein, 1981). Never the less, Chesapeake Bay striped bass are the major contributors to interjurisdictional ocean fisheries (Merriman, 1941; Wirgin et al., 1993). Rates of contributions by Chesapeake Bay striped bass to those fisheries are determined by lifetime patterns of habitat use, ontogenetic rates of egress from Chesapeake Bay, and regional rates of exploitation and natural mortality (Dorazio et al., 1994). Rates of oceanic residence have been shown to vary by sex and increase with age. Analyzing striped bass tagged in the Potomac River, Kohlenstein (1981) advanced the working hypothesis that young striped bass remain in or near the tributary in which they were spawned for two or three years. At this point a substantial proportion of immature females (ca. 50%) emigrate from the Bay, remaining in ocean waters until sexually mature (age 5–7 years). In contrast, males are mature by age 2 but remain in the Bay throughout their lives. This hypothesis remains untested, although substantial deviation from this proposed pattern is indicated by tagging studies and catch records.

From recaptured striped bass tagged on Chesapeake Bay spawning grounds, Dorazio et al. (1994) estimated that by 800 mm total length (TL), approximately half of the population (males and females combined) used ocean habitats. This length would correspond to an age of seven to 10 years (Secor et al., 1995b). Tagging studies comprise quasilongitudinal analyses, which could provide estimates of age-specific egress rates if tagged and recaptured fish are representative of the population. However, striped bass are moderately long lived and show migration behaviors that vary substantially with sex and age. Therefore, tagging studies often do not comprise sufficient spatial and temporal scales to provide the precise information needed to predict how Chesapeake Bay striped bass contribute to coastal fisheries.

Striped bass longevity exceeds 30 years (Merriman, 1941; Secor et al., 1995b). Life table analysis has indicated that maximum reproductive rate occurs relatively late in life (10–12 years) (Secor, 2002) and that accumulation of adult biomass (reproductive potential) represents an important "storage mechanism" (Warner and Chesson, 1995), improving the

odds of recruitment over the lifetime of a fish (Secor, 2000a, 2000b, in press). Life-table–based models (e.g., Goodyear, 1984) depend upon the assumption that annual spawning occurs, which remains unsubstantiated for this species. If spawning frequency declines with age, for instance, then generation time and age-at-maximum reproductive value will be substantially overestimated, which in turn will affect biological reference points (Marshall et al., 2003).

Electron probe micro-analysis (EPMA) of Sr has been developed as a method to reconstruct individual patterns of migration and habitat use by anadromous populations of striped bass (Secor, 1992). In estuarine environments, strontium is often a reliable tracer of salinity; higher marine concentrations (7 ppm) become diluted in estuarine environments by freshwater inputs when freshwater Sr:Ca end-members (where "end-members" are the source of a Sr:Ca ratio) are low (Ingram and Sloan, 1992). Kraus and Secor (2004a) surveyed available data and determined that 83% of estuaries have low freshwater end-members, indicating that the ratio of Sr to Ca should be positively (but not necessarily linearly) related to salinity in most estuaries.

In our study we applied EPMA to examine the fraction of Chesapeake Bay striped bass that migrate to ocean waters and the frequency at which females and males undertake spawning runs. We previously used this method to chart age- and sex-specific patterns of Hudson River striped bass (Secor and Piccoli, 1996; Zlokovitz and Secor, 1999; Secor et al., 2001). Expectations for ontogenetic rates of emigration (i.e., Kohlenstein, 1981) and annual spawning were tested. In addition, we sought evidence for contingent groups (subpopulation groups with similar lifetime migration patterns; Secor, 1999), which we observed previously in Hudson River striped bass.

Material and methods

Samples

Samples collected during spawning runs present the best opportunity to collect a representative sample of mixed age classes, sexes, and migratory behaviors. These samples comprise mostly those ages that have fully recruited to the mature population. We note in our study that this sample incompletely represents migratory behaviors for those females that have not yet become mature and are not participating in the year's spawning run. During the period 15 April–30 May 2000, we obtained samples of 247 male and 122 female striped bass from the upper Chesapeake Bay (N. of $39°00'$; $n=27$), mid-Bay (N. of $37°53W'$S. of $39°00'$; $n=76$); Choptank River ($n=199$), Patuxent River ($n=33$), and Potomac River ($n=28$). Capture methods were diverse and included the use of gill- and pound-nets (Maryland Department of Natural Resources monitoring), electro-shocking (National Marine Fisheries Service Northeast Center and University of Maryland scientific collections), and

charter boat angling. All fish were measured (fork length [FL] and weight [g]), sex and diet were determined, and otoliths and scales were collected. Fork lengths ranged from 685 to 1110 mm for females and from 320 to 1029 mm for males.

Otolith Sr:Ca measures

To conduct EPMA analyses, otoliths (sagittae) were extracted, soaked in 1% sodium hypochlorite solution, rinsed with deionized water, and embedded within a resin (Secor et al., 1992). Transverse sections, approximately 1 mm thick, were cut through the otolith cores with a metallurgical wafering saw. The sections were mounted on glass slides, polished on wetted 600-grain sandpaper, and polished again on a slurry of $0.3\text{-}\mu\text{m}$ alumina until their surfaces were free of pits and abrasions, which can cause artifacts in microprobe analysis (Kalish, 1990). Annuli were enumerated based upon standard criteria under optical microscopy (Secor et al., 1995b). Before analysis, otoliths were cleaned ultrasonically and carbon-coated in a high-vacuum evaporator.

X-ray intensities for Sr and Ca were quantified by using a JEOL 8900 electron probe microanalyzer (Center for Microscopy and Microanalysis, Univ. Maryland, College Park, MD). Calcite ($CaCO_3$) and strontianite ($SrCO_3$) were used as reference standards and the protocol was checked by using secondary standards containing both Ca and Sr. The details of this analysis can be found elsewhere (Secor and Piccoli, 1996). Detection limits for Sr were approximately 230 ppm (±2 standard errors). Four slides, each containing four otolith sections, were loaded into the specimen chamber of the microanalyzer. After initial calibration to Sr and Ca standards (at programmed settings and intervals), transect assignments were made for up to 16 otolith sections. Transects comprised a series of point measurements from young to old ages across the sectioned otolith. X-ray maps of otolith structure were collected by using wavelength spectrometers.

Sr was expressed as a ratio of Ca (Sr:Ca) because of expected competitive interactions between the isotopic species (Kraus and Secor, 2004a). Further Sr:Ca records were converted to salinity exposure profiles according to the model (Secor et al., 1995a):

$$\text{"Salinity inhabitance" } (sic) \text{ (psu)} = 40.3 \, (1+56.3 \, e^{\,-1523(\text{Sr:Ca})})^{-1}; \qquad r^2=0.94 \; ; n=54$$

where "salinity inhabitance" (*sic*) is the salinity level (practical salinity units, psu) in the otoliths for the period of time represented for each Sr:Ca datum.

Oceanic incidence of striped bass

For our analysis, a subsample of 122 fish (40 males and 82 females) was drawn from the upper Bay ($n=10$), mid-Bay ($n=46$), and Choptank River ($n=66$). Estimated salinity records for the last year of life (recent

habitat use) were determined from at least five point measurements taken across the last completely-formed annulus (i.e., the last full year of life prior to winter). Opaque zone formation on the otolith occurs just prior to the spawning season (Zlokovitz et al., 2003); therefore measurements were taken between the penultimate and most peripheral (recently formed) opaque zones. We selected the record of maximum salinity, because at least one point in this series can be influenced by the previous year's spawning run, Oceanic habitat use was defined as salinities >29, and individual fish were classified accordingly. Because of unequal sampling among ages, we analyzed four age classes by sex: 4–6, 7–9, 10–12, and 13–18 years of age. Two-way classification tables were constructed to evaluate differences between age classes and sexes in probability of recent oceanic residence.

Life history transects and spawning frequency

Life history transects of salinity exposure, a series of Sr:Ca ratios from the juvenile period to the end of life, were constructed from EPMA measurements from 30 female and 10 male striped bass. This subsample was drawn from the upper Bay ($n=2$), mid-Bay ($n=27$), and Choptank River ($n=11$). To weight seasonal data among ages, time series were selected so that four or five analyzed points were included for each annulus. Data were standardized (Z score= (*transect datum − transect mean*)/*transect standard deviation*) and plotted to examine variations about the transect mean (Sokol and Rohlf, 1981).

Time-series data represented by the life history transects were expected to show autocorrelation across seasonal points and ages. An appropriate method of data analysis that shows interdependence among repeated measures on the same individual is repeated measures multivariate analysis (RM-MANOVA) (Chambers and Miller, 1995). This analysis simultaneously fits several dependent variables to independent factors of interest (SAS, Statistical Analysis System, SAS Institute, Inc., Cary, NC) and evaluates the matrix equation,

$$S_t = \text{Sex}\beta + E,$$

where S_t = salinities at seasonal points; and
$\quad\quad t$ = relative distance between successive opaque zones.

For each fish, S_t is arrayed in n rows, *Sex* contains two treatment levels for each factor (male vs. female) arrayed in n rows, and E is the matrix of model residuals. Degrees of freedom in the analysis depend upon n, which represents the number of individual fish. To avoid the problem of interdependence of seasonal data for combined ages, separate MANOVAs were performed for each age class.

To conduct the RM-MANOVA, it was necessary to have equal numbers of seasonal points (S_t) for each age class. Therefore, narrow annuli that had fewer than three seasonal (interannual) points were omitted from analyses. This excluded analyses of some of the oldest age classes, which typically exhibit narrow annuli (Secor, 1992). For years sampled with more than four or five seasonal points, the extra points were omitted from our analysis. Selection of points to be included was based upon their proximity to the axial distances of the prescribed intervals (either [0, 0.25, 0.5, 0.75] or [0, 0.2, 0.4, 0.6, 0.8]). Individual probe points within transects were separated by 10 to 35 microns.

Results

Demographics

Ages among the sampled Maryland Chesapeake Bay striped bass ranged from three to 18 years and sizes ranged 320 to 1110 mm FL. Females were significantly older and larger than males (ANOVA; $P<0.01$) and grew at a faster rate. Males were more heavily represented by ages <10 years than females in age-frequency distributions, although fish with ages >15 years were observed for both sexes. Relatively strong year class contributions within the sample occurred for 1982, 1989, 1993, and 1996 and coincided with high young-of-the-year juvenile abundances observed in those years (Secor, 2000a).

Oceanic incidence of striped bass

Female fish, more often than male fish, were classified as having a recent period of oceanic residence based upon the analysis of the last fully formed annulus, but this difference was not significant (χ^2, $P>0.1$). For individual age classes with sample sizes >5, oceanic incidence ranged from 60% to 75% for females and from 17% to 50% for males (Table 1). There was an indication that the proportion of fish of both sexes with oceanic residence increased with age. Oceanic incidence was observed consistently for >50% of the females. For males, oceanic incidence was 8–32% less than for females within each age class. Error bars, based upon a binomial probability distribution, indicated a fairly well-estimated oceanic classification rate for the age class 10–12 years due to a relatively high sample size. For this age class, oceanic incidence was estimated at 59% and 50% for females and males, respectively. Conversely, use of oceanic habitat for males at ages <10 was poorly estimated because of low sampling size. Indeed, estimated ratios for this group could not be statistically resolved from zero. With increased size, oceanic incidence (sexes combined) tended to increase (Table 1), although there was a decline in the proportion of fish with evidence of oceanic residence from 65.8% for the size class 900–999 mm FL to 46.1% for the size class >1000 mm FL.

Life history transects

Life history transects showed considerable variability (Fig. 1). It is noteworthy that some males exhibited

some degree of oceanic incidence (fish identification [ID] number=98, 198, 260) throughout portions of their lives and many females exhibited a pattern of estuarine use (e.g., ID=197, 263, 271, 272, 280, 281). A single instance of freshwater residency was observed for a fairly long-lived female (ID=271; age=11 years; FL=875 mm). Mean lifetime salinity exposure differed significantly between males and females (Kruskal-Wallis ANOVA; *P*=0.01), with females exhibiting an average 10% higher use of high-salinity habitat during the mature portion (age>6) of their lives (Fig. 2).

The male sample, albeit small (*n*=10), did not exhibit age-dependent patterns in salinity exposure (Fig. 2). In part, high variance in older age classes (8–12) obscured any pattern of salinity exposure at ages <6 years. Females showed a strong and nearly linear trend of increased salinity exposure with age (Fig. 2). Modal salinity increased from a range of 20–25 to a range of 25–30 for ages 2 and 7, respectively. Interestingly, both males and females showed that a polyhaline (salinity>18) habitat was used during the period between age 1 and 2 years. Thus, yearlings may be preferentially using polyhaline regions, followed by a return of some individuals to lower salinity regions (because slightly depressed salinities were observed for ages 2 and 3 compared to age 1 yr in Fig. 2). We have observed a similar pattern in Hudson River striped bass (Zlokovitz et al., 2003). The ontogenetic trend of increased salinity exposure with age in females could be related to maturation (ages 6–8 years)—a pattern observed in two-thirds of female fish (Fig. 3). Males also showed a rise in salinity exposure with age, albeit less consistently (Fig. 4).

Spawning frequency

Life history transects for the sample of ten males and thirty females gave evidence of strong intra-annual patterns in the salinity levels of their habitat (Figs. 3 and 4). Intra-annual trends often showed nadirs at or near the opaque zone of the otolith, a pattern occurring in both males (e.g., ID=124, 196, 327) and females (e.g., ID=192, 297, 298). In some instances, seasonal cycles indicated either less than annual (Fig. 3: ID=320; Fig. 4: ID=298, 300) or greater than annual (Fig. 3: ID=99; Fig. 4: ID=295, 300) cycles in patterns of salinity exposure.

Significant seasonal effects on patterns of salinity exposure were observed for ages 6 and 8 and for pooled ages 6–11 (Table 2), indicating that across individuals there was a seasonal pattern in salinity exposure for

Table 1

Degree of oceanic incidence of Chesapeake Bay striped bass collected in 2000. Data is presented for age classes by sex, and for size-class pooled sexes (the latter to permit comparison with results of Dorazio et al., 1994). Lower (LCL) and upper (UCL) confidence limits are presented for oceanic incidence by age class.
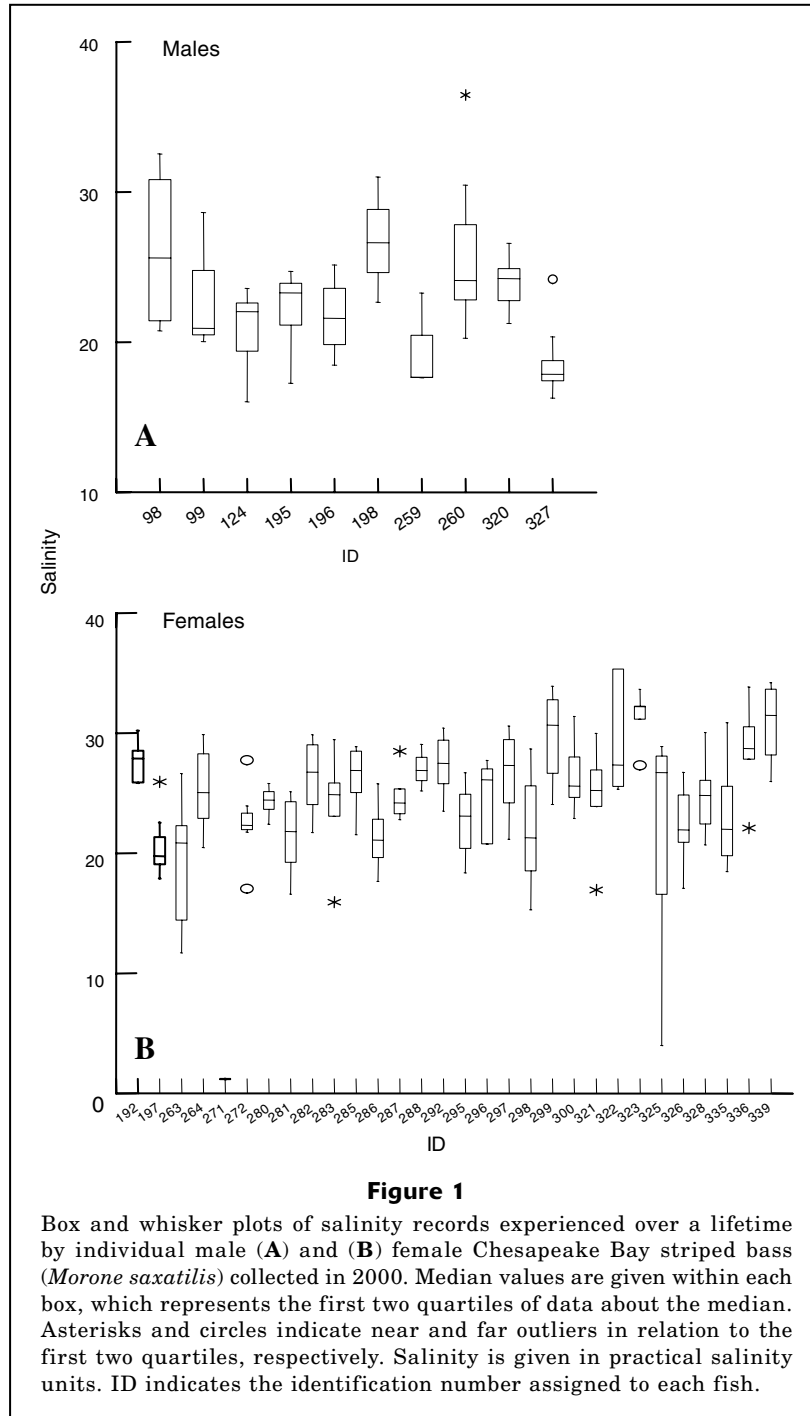
Age class (yr)	Oceanic incidence (%)	
	Males (*n;* LCL–UCL)	Females (*n;* LCL–UCL)
4–6	20.0 (5; 0–41.3)	—
7–9	25.0 (8; 0–50.2)	55.5 (18; 42.5–68.1)
10–12	50.0 (18; 37.4–62.5)	58.8 (51; 56.8–62.5)
13–18	44.4 (9; 34.0–77.4)	76.9 (13; 60.8–93.6)

FL size class (mm)	Oceanic incidence (%)	
	This study (*n*)	Dorazio et al. (1994)
300–599	20.0 (8)	<5.0
600–699	—	~8.0
700–799	42.9 (14)	~35.0
800–899	59.0 (44)	~80.0
900–999	65.8 (41)	~90.0
>1000	46.1 (13)	>95.0

mature age classes. The other analysis of five, rather than four, seasonal points of measurement in the otolith did not show strong evidence for seasonality, although pooled age classes 6–11 and 7–11 showed marginal significance at *P*=0.06. In the selection of individuals that contained five seasonal points, sample sizes were substantially reduced. This reduced sample size in turn would have resulted in less statistical sensitivity. Despite high variances among individuals for each seasonal measurement, there was a trend for a seasonal nadir in salinity exposure near the opaque zone on the otolith (seasonal interval=0) (Fig. 5). This trend was especially apparent in males, and in females >6 years.

There was a slight indication of sex-related differences in seasonality of salinity exposure. Significant between-sex differences occurred for S_0 at ages 8 and 11, and all mature age class groupings (Table 2). Significant differences occurred for $S_{0.25}$ at ages 8 and 9 and mature age groupings 7–11 and 8–11; and for $S_{0.5}$ at age 8 and all mature age groupings. Males were found at lower salinities at these seasonal points than were females (Fig. 5).

X-ray maps of Sr within otolith sections showed clear concentric patterns of alternating high and low regions of Sr in association with annuli (Fig. 6). X-ray maps confirmed the cyclical patterns observed in the life history transects (Figs. 3 and 4), but with greater apparent difference between peak and nadir levels of Sr. In one of the X-ray maps (Fig. 6, bottom panel), a high level of Sr occurred within the first annulus).

Figure 1

Box and whisker plots of salinity records experienced over a lifetime by individual male (**A**) and (**B**) female Chesapeake Bay striped bass (*Morone saxatilis*) collected in 2000. Median values are given within each box, which represents the first two quartiles of data about the median. Asterisks and circles indicate near and far outliers in relation to the first two quartiles, respectively. Salinity is given in practical salinity units. ID indicates the identification number assigned to each fish.

Discussion

Oceanic incidence of striped bass

Our analysis and that of Dorazio et al. (1994) does not support Kohlenstein's (1981) model of mass egress of female striped bass from Chesapeake Bay after ages two or three. Rather, our life history transects indicated a fairly gradual shift to use of ocean habitats—a shift associated with maturation at ages five to eight (Table 1; Fig. 2). For mature age classes, evidence of oceanic residence was observed for 50–75% of the female sample. Also, in contrast to previous expectations, otolith microanalysis indicated that a large fraction of males leave Chesapeake Bay, albeit at rates <50%.

Mirroring the results of Dorazio et al.'s (1994) tagging experiment, our results showed a trend of increasing oceanic residence with fish size, but found
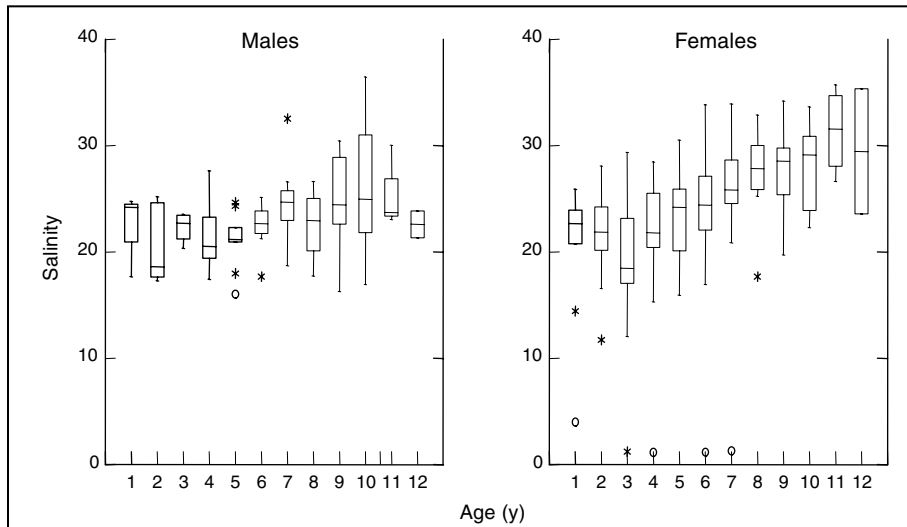
Figure 2

Box whisker plots of age-specific salinities experienced by Chesapeake Bay striped bass (*Morone saxatilis*) collected in 2000. Salinity data for each fish include quarterly seasonal salinity records. Median values are given within each box, which represents the first two quartiles of data about the median. Asterisks and circles indicate near and far outliers in relation to the first two quartiles, respectively. Salinity is given in practical salinity units. ID indicates the identification number assigned to each fish.
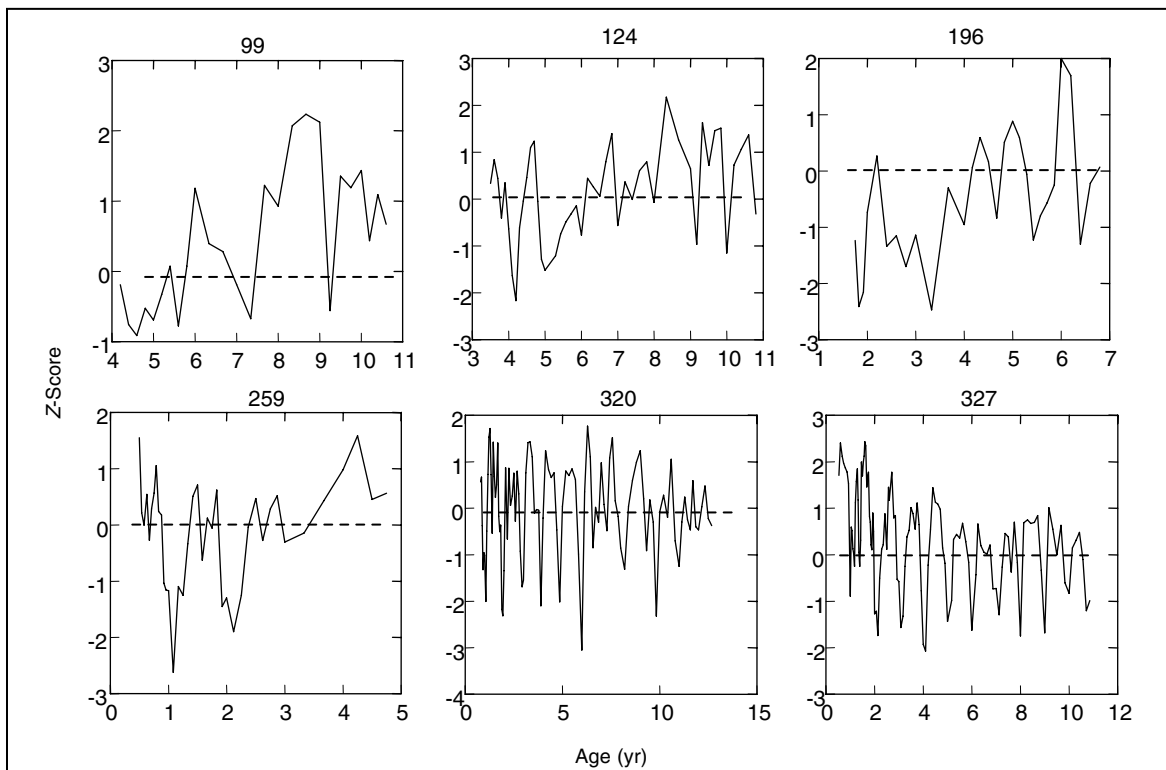

Figure 3

Standardized life history transects for male Chesapeake Bay striped bass (*Morone saxatilis*) collected in 2000. ID, an identification number assigned to each fish, is presented above each panel. Z-score indicates standardized salinity records for each fish where Z=(record−mean)/standard deviation. Dashed line demarcates the mean.

Figure 4

Standardized life history transects for female Chesapeake Bay striped bass (*Morone saxatilis*) collected in 2000. ID, an identification number assigned to each fish, is presented above each panel. *Z*-score indicates standardized salinity records for each fish where *Z*=(record–mean)/standard deviation. Dashed line demarcates the mean.
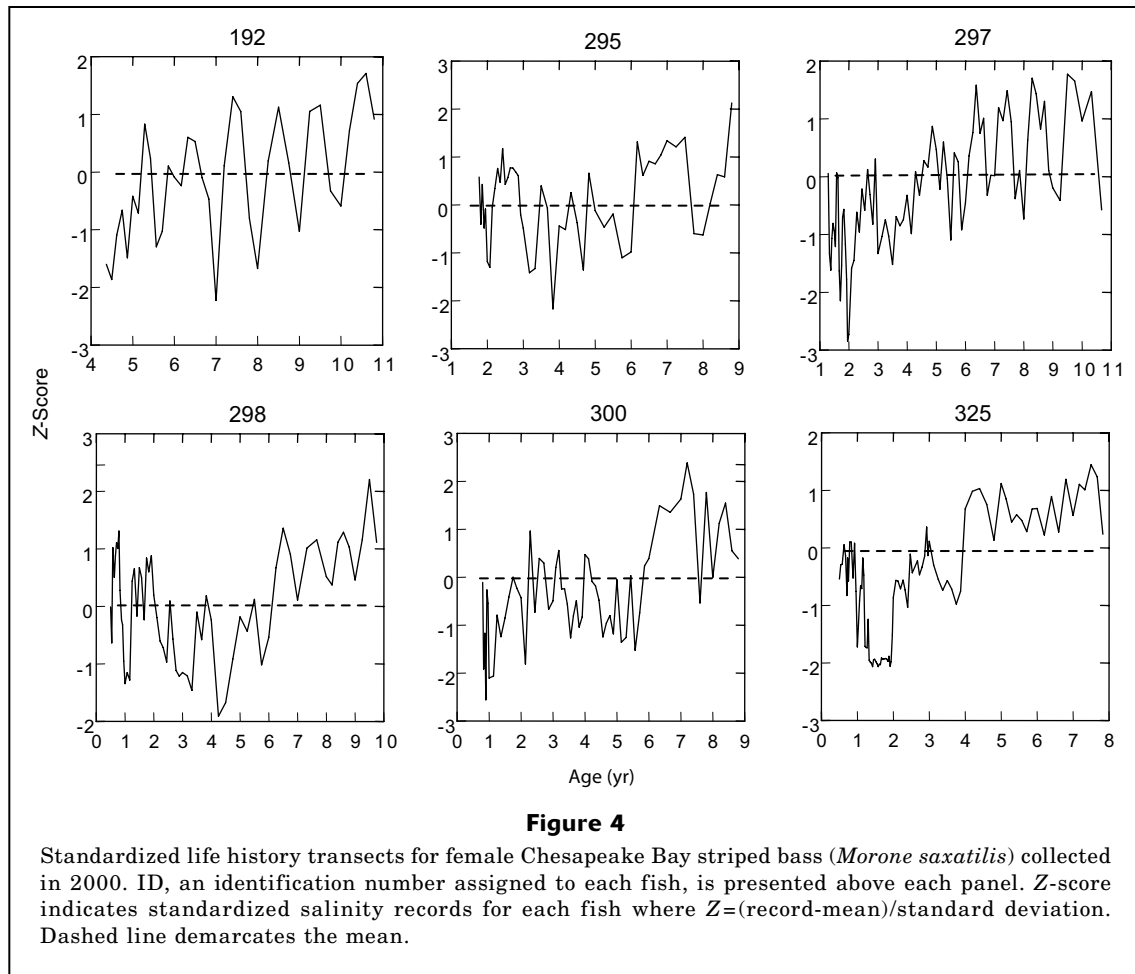
two important differences. First, we did not observe >90% oceanic incidence at >900 mm TL (877 mm FL) (Table 1). Rather, a substantial fraction of striped bass remained resident in Chesapeake Bay throughout their lives regardless of age or size. At ages >12 years, 25% of the female sample was estimated to have be resident in Chesapeake Bay. As an extreme example, one individual female resided in freshwater during its entire 11-yr lifespan. Secondly, early rates of oceanic migrations at sizes <700 mm TL (<685 mm FL) were substantially higher than rates indicated in the Dorazio et al. (1994) model, which predicted <5% of individuals migrate to ocean waters. Several factors may have contributed to the different results. Dorazio et al. (1994) predicted the degree to which Chesapeake Bay striped bass migrate to coastal regions north of Cape May New Jersey. Thus, their recapture sample represents only a subset of possible coastal fish. This bias would tend to underestimate oceanic residence; yet the Dorazio et al. (1994) estimates tend to be higher for larger mature striped bass. Recapture and reporting rates probably varied between coastal and Chesapeake regions because of more restrictive fishing regulations in Chesapeake Bay that contributed to an overestimate of migrant fish to northern ocean habitats.

In comparing our results to those of past tagging studies, we must also carefully consider limitations to the otolith microchemistry approach. We have sought to overcome some of the past hurdles regarding low sample size and resolution, yet these remain principal concerns. Despite large improvements in microprobe technology, otolith microchemistry remains a very expensive and time-consuming procedure to evaluate population-specific patterns in fish migration. Sample sizes, while larger than in many past projects, remain modest. Also, ages and sizes were not uniformly distributed in the populations sampled because of strong year classes, and this lack of uniform distribution would curtail generalizations across size and age classes. This strong year class phenomenon is common in striped bass, and it is likely that migration patterns in Chesapeake Bay striped bass typically will be influenced by dominant year classes (Merriman, 1941).

A central assumption in using strontium as a tracer of salinity levels is that the ratio of strontium to calcium (Sr:Ca) in the otolith can accurately distinguish between oceanic (salinity >29) and estuarine (salinity <30) habitat use. First, the designation, between oceanic and estuarine water is somewhat arbitrary, particularly considering that the mouth of Chesapeake

Table 2

Repeated measures MANOVAs for effects of sex on seasonal salinities experienced by Chesapeake Bay striped bass (*Morone saxatilis*). S_t= salinity at seasonal point t, where t = relative distances between successive opaque zones in otoliths. "Season" is defined by two intervals on the otolith as a proportion of otolith increment width. Univariate F tests (P-values reported) for contrasts between males and females are given for each seasonal point. Differences among seasonal salinities ("Seasonality") within each age were evaluated with a Wilk's statistic (Chambers and Miller, 1995). The interaction between season and sex tested whether sex affected patterns of seasonality in salinity levels in otoliths. NS=not significant.

| Age (yr) | n | Contrast between males and females | | | | Seasonality | Season × Sex |
		S_0	$S_{0.25}$	$S_{0.5}$	$S_{0.75}$		
1	11	NS	NS	NS	NS	NS	NS
2	19	NS	NS	NS	NS	NS	NS
3	21	NS	NS	NS	NS	NS	NS
4	29	NS	NS	NS	NS	NS	NS
5	33	0.09	NS	NS	NS	NS	NS
6	35	NS	NS	NS	NS	**0.02**	**0.04**
7	32	NS	NS	NS	NS	NS	NS
8	22	**0.02**	**0.01**	**0.04**	NS	**0.04**	NS
9	22	NS	**0.03**	NS	NS	NS	NS
10	20	NS	NS	NS	NS	NS	NS
11	7	**0.04**	NS	0.07	NS	0.07	NS
6–11	138	**0.04**	NS	**0.02**	NS	**0.04**	NS
7–11	103	**0.04**	**0.01**	**0.03**	NS	0.09	NS
8–11	71	**0.03**	**0.002**	**0.01**	NS	NS	NS

| Age | n | Contrast between males and females | | | | | Seasonality | Season × Sex |
		S_0	$S_{0.2}$	$S_{0.4}$	$S_{0.6}$	$S_{0.8}$		
5	31	0.09	NS	NS	NS	NS	NS	NS
6	31	NS	NS	NS	**0.03**	NS	NS	NS
7	22	NS	**0.003**	NS	NS	NS	NS	NS
8	19	**0.02**	0.07	**0.02**	NS	NS	NS	NS
9	13	NS	**0.01**	**0.02**	NS	NS	NS	NS
10	11	NS	NS	**0.02**	NS	NS	NS	NS
11	5	NS	NS	NS	NS	NS	NS	NS
6–11	101	**0.001**	0.007	**0.001**	**0.01**	**0.05**	0.06	NS
7–11	70	**0.001**	**0.001**	**0.001**	NS	NS	0.06	NS
8–11	48	**0.005**	**0.01**	**0.001**	0.08	NS	NS	NS

Bay averages about 25–30 psu during summer and fall months. Still, it was necessary to have a designation for assessing habitat use, and the above designations may have resulted in a liberal estimate of oceanic residence. A second issue is the resolution of the relationship of otolith Sr-Ca ratio to salinity. Resolution level estimated by experimental work of Secor et al. (1995a) was a salinity of 6 psu, which would support the contention that estimates presented here are fairly precise if error is unbiased. Still, the relationship between otolith Sr:Ca and salinity was logistic and very rapid changes in Sr:Ca were predicted to occur with small changes in salinity at salinities between 25 and 35 psu. These rapid changes at high salinities could indicate higher unexplained variability at salinities >24 psu.

Finally, our samples were unequally weighted across subpopulations of striped bass. For instance, no lower Chesapeake Bay subpopulations (those spawning in the James, York, and Rappahannock systems) were represented in our sample). Recent tagging studies have either focused more narrowly on the Potomac River (Kohlenstein, 1981) or have drawn a larger and more representative sample from the Maryland section of Chesapeake Bay (Dorazio et al., 1994). Studies on Virginia subpopulations of striped bass have historically shown low rates of oceanic residence (<5%; Vladykov and Wallace, 1952; Massman and Pacheco, 1961). Kohlenstein (1981) effectively argued that these and other early tagging studies (i.e., Mansueti, 1961) were not appropriately stratified to provide evidence of an increased likelihood of oceanic residence by larger size fish.

In sum, we believe that our otolith microchemistry results indicate higher rates of early oceanic residency in females and overall higher rates of oceanic migrations by males than were observed in previous tag-

Figure 5

Seasonal patterns in salinity exposure as recorded in the otoliths of Chesapeake Bay striped bass (*Morone saxatilis*) collected in 2000. Mean salinities and standard errors are shown for age classes <7 and >6 years. Seasonal interval indicates the relative distances from the opaque zones in the otolith, which are formed in early spring. Intervals represent the seasons as a proportion of annual otolith increment width.

ging studies (Kohlenstein, 1981; Dorazio et al., 1994). Further, increasing trends in oceanic habitat use with age observed in our study are consistent with the two previous tagging studies. The increased incidence of males in ocean environments shown in our study and previous ones could reflect a true increased likelihood of emigration, perhaps driven by increased striped bass density, or by poorer habitat conditions in Chesapeake Bay. This view would be consistent with the near historically high abundances of Chesapeake Bay striped bass and the increased incidence of summertime hypoxia in Chesapeake Bay during the past two decades (Hagy et al., 2004). However, error due to the otolith microchemistry approach in classifying fish to oceanic or estuarine habitat use must be acknowledged and caution should precede application of the estimates of oceanic residence provided in this study.

Spawning frequency

In general, otolith microchemical analyses gave evidence for the view that most mature striped bass undertake annual spawning runs. For females, immature age classes did not show significant seasonality in changes in salinity, but many mature age classes did. Further, cycles in salinity were largely defined by a nadir that

occurs during early spring as evidenced by changes in the chemistry of the opaque zone of the otolith. Thus, evidence of the use of low-salinity habitat was recorded near the opaque zone, consistent with the view of an annual up-estuary migration to low-salinity spawning habitats. Where such nadirs were not observed in the otolith microchemistry, two interpretations are plausible: 1) no spawning migration occurred, or 2) the otolith microchemistry method had insufficient resolution to allow us to detect the spawning migration. The resolution issue relates to two problems. First, the spacing of the microprobe assays could have been such that a spawning run event was missed. Second, spawning-run striped bass occur in low-salinity regions for short periods during which they are not growing and thus incorporating Sr material into their otoliths. In this instance, there would be an insufficient signal for otolith microanalysis of Sr to detect. Despite these likely sources of error, we were still able to detect a dominant annular cycle in otolith Sr for mature age classes of males and females. Therefore, we believe that the otolith microchemistry analysis supports annual spawning for the majority of mature Chesapeake Bay striped bass.

Alternatively, spawning in striped bass may occur less than once a year. Less than an annual spawning, once thought to be specific to relatively few taxa (e.g.,
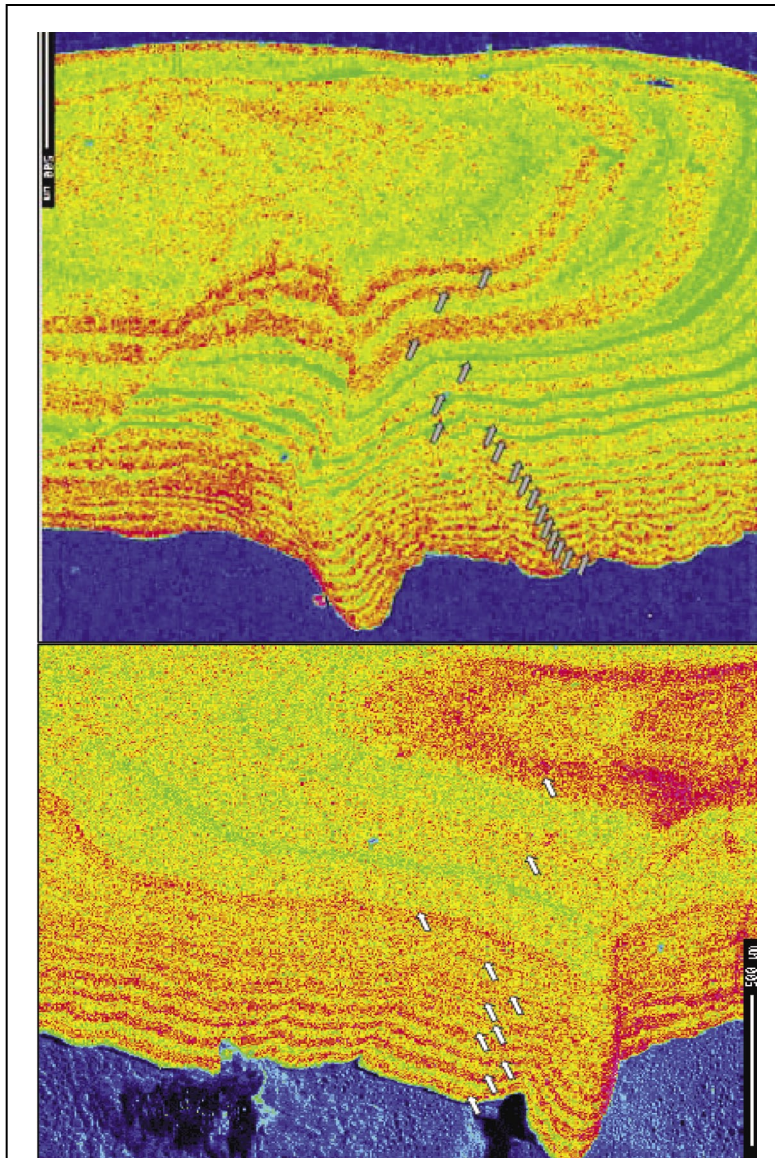
Figure 6

X-ray composition maps of srontium (Sr) seen in otolith for two female striped bass (*Morone saxatilis*) (17 and 11 years old) collected in Chesapeake Bay in 2000. Arrows demarcate annuli. The "warmer" colors (red, orange) represent regions with higher Sr concentrations whereas the "cooler" colors (yellow, green) represent regions with lower Sr concentrations. Composition maps show the coincidence of strontium banding patterns with banding patterns of annuli, indicative of annual anadromous migrations from high to low salinity waters.

sturgeons; Gross et al., 2002) could in fact be common in some longer-lived species (Rideout et al., 2005). For instance, data-archiving electronic tags inserted on Atlantic bluefin tuna (*Thunnus thynnus*) have definitively shown that many adults are found outside spawning habitats for an entire annual spawning season (Block et al., 2005). Further evidence is provided by the reproductive behavior of Atlantic cod (*Gadus morhua*;

Jørgensen et al., 2006), a species that does not always spawn each year because of density dependence or other environmental limits on its ability to provision gonads. Interestingly, evidence for this can be observed in two female life history transects in our study of striped bass (Fig. 4: ID=295, 300), where no nadir was observed at age seven following a clear nadir at age six (female striped bass typically mature between five and seven

years of age). We also should expect that, for similar energetic reasons, not every female, which undertakes a springtime up-estuary migration, will actually spawn. Some mature females in a spawning run will not spawn; rather, they will reabsorb final-stage oocytes (first author, personal observ.). Therefore, accurate measurement of spawning frequency depends on both the probability of successful spawning in the field and the frequency of up-estuary migratory runs.

X-ray maps confirmed an annual cycling in otolith strontium, but also showed cycles during the immature period of females, contrary to patterns observed from life history transects. Further, X-ray mapping and life history transects indicated that many yearlings move into oceanic regions—a pattern observed for Hudson River striped bass (Zlokovitz et al., 2003) but not yet described for Chesapeake Bay striped bass. The possibility that young-of-the-year or yearling striped bass are present in ocean environments deserves additional research in the Chesapeake Bay and elsewhere.

Contingent migration behavior

In past research on Hudson River striped bass, we observed modalities in lifetime migration behaviors (Secor et al., 2001); groups of individuals that share similar migration behaviors with some, but not all, members of their population are termed "contingents" (Hjort, 1914[1]; Gilbert 1917[2]; Secor, 1999). In particular, one contingent comprising a small fraction of the Hudson River springtime sample was resident to freshwater and oligohaline regions and was heavily contaminated by polychlorinated biphenyls—an apparent consequence of this lifetime migration behavior (Zlokovitz and Secor, 1996; Ashley et al., 2000). A similar contingent migration behavior has been reported for the Steweiacke River population of striped bass in Nova Scotia (Morris et al., 2003). In contrast, only a single Chesapeake Bay striped bass (of 40 analyzed) exhibited freshwater resident behavior. Small sample sizes could indicate considerable error in estimates of the frequency of this behavior among populations if these estimates are based on research to date, but the fact that three distinct populations exhibited this behavior in our study indicates that contingent migration structuring is common to Chesepeake Bay striped bass.

Contingent migration structure has been observed across diverse taxa, such as American eels (*Anguilla rostrata*), American shad (*Alosa sapidissima*), white perch (*Morone americana*), bluefish (*Pomatomus salta-*

trix), and Atlantic bluefin tuna (Secor, 1999, in press; Fromentin and Powers, 2005). Here, a nursery or foraging habitat associated with one contingent migration behavior may make a small contribution in a given year, but over a decade may contribute significantly to spawning stock biomass. Thus, over generation-long time scales, we should expect that minority lifetime migration behaviors can contribute significantly to sustained recruitment. Further research is needed to determine the proximate cause of contingent structure, but based upon research on the sympatric white perch, we advance the hypothesis that Chesapeake Bay striped bass contingent migration structuring results from divergent early growth rates and dispersal behaviors associated with early growth (Kraus and Secor, 2004b).

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