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## Is otolith strontium a useful scalar of life cycles in estuarine fishes?

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### Abstract

The efficiency with which estuarine habitats produce fish is poorly understood due to the complexity of life cycles. Spatial dynamics of estuarine fishes comprise retentive and dispersive behaviors which occur on seasonal and ontogenetic scales. Salinity is an important scalar in the spatial dynamics of estuarine fishes, that may affect production and dispersal. In this paper, we review investigations that used otolith strontium (Sr) to chart estuarine movements of fishes. Based upon microprobe analysis of otolith Sr, variable patterns of estuarine ingress have been shown for bay anchovy *Anchoa mitchilli*, freshwater eel *Anguilla* spp., Japanese sea bass *Lateolabrax japonicus*, and Atlantic croaker *Micropogonias undulatus*. In anadromous fishes, striped bass *Morone saxatilis*, American shad *Alosa sapidissima*, and Arctic charr *Salvelinus alpinus*, otolith Sr has been used to record emigration of juveniles and adults from freshwater and oligohaline nurseries. These same species showed seasonal cycles in otolith Sr consistent with expectations on frequency of spawning migration. A critical yet seldom evaluated issue is the relative roles of salinity, temperature, ontogenetic stage, and physiological state on otolith Sr. In a review of the literature (1982–1997), we found that these effects were infrequently evaluated (10 of 27 species investigated). Rarer still were studies of the interaction of these effects on otolith Sr. Only a single study had calibrated a laboratory-based salinity vs. otolith Sr relationship using field data. Based upon values obtained through the literature review, we observed a positive relationship between otolith Sr and habitat salinities among freshwater, estuarine, and marine taxa. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Anadromy; Estuary; Life cycle; Migration; Otolith microchemistry; Strontium

### 1. Introduction

Estuaries serve as important and productive nurseries for many marine teleosts (Weinstein et al., 1980; Boesch and Turner, 1984; Ruiz et al., 1993). Despite an extensive literature supporting the role of estuaries

as critical fish habitat, the efficiency with which estuarine habitats produce fish remains poorly understood due to the complexity and variability of dispersal among habitats. Previous studies support the idea that salinity is a useful “yardstick” in delineating estuarine habitats. Estuarine-dependent species exhibit patterns of dispersal, retention, or physiological preferences which occur within specific salinity ranges, and salinity may act directly or indirectly in controlling distribution of these species (Bulgar et al.,

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1993; Lankford and Targett, 1994). Spatial behaviors may also be controlled by distribution of predators and suitable prey within estuaries, both of which are affected by salinity (Boesch, 1977; Weinstein et al., 1980; Currin et al., 1984; Lankford and Targett, 1994).

Recent advances in otolith microchemistry have provided researchers with a powerful means of tracking dispersal and retention throughout ontogeny. The approach yields both spatial and temporal information on fish dispersal and movement. First, spatial patterns of occurrence are inferred for important environmental scalars (typically salinity or temperature) through measurement of otolith microconstituents (Casselman, 1982). Secondly, precise measures are made within and among daily or seasonal (annular) increments of otoliths to construct a chronology of spatial occurrences which is related to fish age and ontogenetic stage (Radtke et al., 1988; Townsend et al., 1989). In this paper, microprobe analysis of otolith strontium (Sr) is evaluated as a scalar to measure estuarine habitat histories of individual larvae, juveniles, and adults.

Using estuarine-dependent species with various spatial life history tactics (Table 1), we show applications of otolith microprobe analysis for measuring (1) size- or age-specific ingress into estuarine nurseries, (2) ontogenetic patterns of coastal habitat use, (3) resident behaviors, and (4) spawning migrations. We then use a literature review (1982–1997) to address two questions: (1) Has the otolith Sr method been rigorously tested in past applications? (2) Among diverse taxa which occupy a range of salinity zones, do reported values support a positive relationship between otolith Sr and ambient salinity?

## 2. Methods

Samples were collected and analyzed in studies conducted by our laboratory over the past 5 years (Table 1). They represent five estuarine-dependent species each from different families, and each exhibiting unique spatial behaviors. Four species were studied from the Chesapeake Bay and Hudson River estuaries of North America. Japanese sea bass (*Lateolabrax japonicus*) were collected from Chikugo River, Japan.

Otoliths of test species were prepared for microanalysis as described by Secor and Piccoli (1996). X-

ray intensities for Sr and Ca elements were quantified using a JEOL JXA-840A wavelength dispersive electron microprobe with calcite and strontianite as standards. Analytical methods for measuring molar weights of Sr and Ca followed those of Secor (1992). Elemental chronologies consisted of series of point measurements of Sr and Ca concentrations taken across daily increments or annuli. Each measure sampled a point 5  $\mu\text{m}$  in diameter; points were spaced at 13–30  $\mu\text{m}$  increments, varying with desired resolution for each application. Otolith Sr:Ca measures were related to either fish age or otolith radius. By normalizing Sr to Ca in chronologies, small changes in analytical performance due to beam power density (accelerating voltage, beam current and angle) are diminished under the assumption that Ca and Sr respond similarly to these changes (Gunn et al., 1992). Also, because Sr substitutes for Ca ions in otoliths (Kalish, 1989; Farrell and Campana, 1996), it has become convention to express Sr as a fraction of Ca. However, it is noteworthy that calcium is relatively invariant within aragonitic otoliths (rarely varying more than 5%) and trends in otolith Sr:Ca ratios among taxa are driven by changes in Sr which can vary >10-fold (e.g. Otake et al., 1994; Thresher et al., 1994; Mugiya and Tanaka, 1995; Proctor et al., 1995).

In the literature review, data were drawn from the primary literature from 1982 to 1997 (Table 2). We classified papers according to whether salinity, temperature, and/or physiological effects on otolith Sr were observed from individuals of known (measured) environmental histories or inferred from individuals with assumed environmental histories. Studies were distinguished by whether models were used to predict or fit otolith Sr responses to environmental scalars. Investigations reporting corroboration between laboratory- and field-derived models were identified. Normalized molar Sr:Ca ratios were obtained or calculated from Sr:Ca ratios reported in reviewed studies and compared to salinity. Mean values of Sr:Ca were used when reported, however, in several studies means were not explicitly given. In these cases, Sr:Ca values were approximated as the midpoint of the reported range. In some instances, salinity was not reported, and salinity levels were assumed based upon the known distribution of the population studied (e.g. offshore  $\sim 35$  ppt).

Table 1  
List of estuarine-dependent species examined by our laboratory for spatial tactics using otolith microanalysis of Sr<sup>a</sup>

| Species  | Spatial tactic   | Salinity vs. otolith Sr   | Collections or source for chronologies shown in figures   |
|--|--|---|---|
| American eel, <i>A. rostrata</i><br>(Anguillidae)          | Catadromous, glass eel ingress into estuary, juvenile retention in estuary                           | Tzeng (1996): positive relationship based upon lab-reared elver <i>A. japonica</i> ; Tzeng et al. (1997): freshwater criterion for <i>A. anguilla</i> | Hudson River (161 km from mouth), 1997; yellow eel, female, TL=55 cm (Fig. 1)   |
| American shad, <i>A. sapidissima</i><br>(Clupeidae)        | Anadromous, juvenile egress from estuary, spawning migrations  | Limburg (1995): threefold increase in Sr from freshwater young-of-year to marine adult  | Pamunkey River, Chesapeake Bay, 1995; adult female, TL=44 cm (Fig. 7)   |
| Bay anchovy, <i>A. mitchilli</i><br>(Engraulidae)          | Estuarine spawner, larval retention in estuary, larval ingress up-estuary                            | Positive relationship observed based upon field collections of juveniles by Kimura and Secor, (unpublished data)                                      | Chesapeake Bay, 1993; young-of-the-year, TL=4.5–5.0 cm (Fig. 3)   |
| Japanese sea bass, <i>L. japonicus</i><br>(Percichthyidae) | Coastal spawner, larval ingress into estuary, juvenile retention in estuary                          | Secor et al. (1998): lab- and field-based verification of positive logistic relationship  | Chikugo River, Ariake Sea, Kyushu, Japan, 1995; yearling, TL=21.0 cm (Fig. 2)   |
| Striped bass, <i>M. saxatilis</i><br>(Moronidae)           | Anadromous, juvenile egress from estuary, juvenile, adult, retention in estuary, spawning migrations | Secor et al. (1995b): lab and field based verification and prediction of salinity from otolith Sr.  | Hudson River and Chesapeake Bay, 1991–1994; adult males and females; Hudson River data published in Secor and Piccoli (1996) and Zlokovitz and Secor (1999) (Figs. 4–6) |

<sup>a</sup> The spawning tactic and those spatial tactics examined using otolith Sr are listed. Also presented are sources of evidence for a positive relationship between salinity and otolith Sr and information on biological attributes, collection site and year, and contributors to microprobe analyses (Secor and Piccoli, 1996; Secor et al., 1998; Zlokovitz and Secor, 1999).

Table 2  
Review of studies reporting the use of otolith strontium for teleost fishes<sup>a</sup>

| Species                          | Relationships to Sr    |                         |                       | Predictive lab-field |             |   | References  |
|----------------------------------|------------------------|-------------------------|-----------------------|----------------------|-------------|---|---|
|                                  | Vs. salinity           | Vs. temperature         | Vs. other             | Models               | Calibration | Comments  |   |
| <b>Anguilliformes</b>            |                        |                         |                       |                      |             |   |   |
| <i>Anguilla anguilla</i>         | Positive               | ND <sup>b</sup>         | ND                    | ND                   | ND          | Suggest salinity influences otolith Sr more than temperature or growth              | Tzeng et al., 1997  |
| <i>Anguilla japonicus</i>        | Positive (main factor) | Negative (minor factor) | ND                    | ND                   | ND          | Otolith Sr different between brackish and fresh water                               | Otake et al., 1994; Tzeng and Tsai, 1994; Tzeng, 1996                 |
| <i>Anguilla rostrata</i>         | Positive               | ND                      | ND                    | ND                   | ND          | Otolith Sr different between migrating eels from marine to freshwater               | Casselmann, 1982  |
| <b>Clupeiformes</b>              |                        |                         |                       |                      |             |   |   |
| <i>Alosa sapidissima</i>         | Positive               | ND                      | Diet effect           | ND                   | ND          | Threefold increase in Sr from freshwater juveniles to marine adults                 | Limburg, 1995   |
| <i>Clupea harengus</i>           | ND                     | Negative                | ND                    | Yes                  | ND          | Sr–temperature relationship used to reconstruct temperature history                 | Townsend et al., 1989, 1992; Radtke et al., 1990; Radtke et al., 1990 |
| <b>Cypriniformes</b>             |                        |                         |                       |                      |             |   |   |
| <i>Carassius auratus</i>         | Positive               | Mostly positive         | Hormonal effect       | Yes                  | ND          | Otolith Sr increased linearly with temperature from 16 to 24°C; decrease at 28°C    | Mugiya et al., 1991; Mugiya and Satoh, 1995; Mugiya and Tanaka, 1995  |
| <b>Salmoniformes</b>             |                        |                         |                       |                      |             |   |   |
| <i>Salvelinus alpinus</i>        | Positive               | ND                      | ND                    | ND                   | ND          | Large difference in otolith Sr between anadromous and non-anadromous adults         | Halden et al., 1995; Babaluk et al., 1997                             |
| <i>Oncorhynchus mykiss</i>       | Positive               | ND                      | ND                    | ND                   | ND          | Large difference in otolith Sr between anadromous and non-anadromous adults         | Kalish, 1990  |
| <i>Oncorhynchus nerka</i>        | Positive               | ND                      | ND                    | ND                   | ND          | Large differences in otolith Sr between anadromous and resident populations         | Rieman et al., 1994   |
| <b>Gadiformes</b>                |                        |                         |                       |                      |             |   |   |
| <i>Gadus morhua</i>              | ND                     | Negative                | ND                    | Yes                  | Yes         | Sr–temperature relationship used to hindcast distributions (calibration off by 3°C) | Radtke, 1984; Townsend et al., 1995                                   |
| <i>Macruronus novaezelandiae</i> | ND                     | ND                      | Age effects           | ND                   | ND          | Also suggested importance of reproductive anabolism on otolith Sr                   | Kalish, 1989  |
| <i>Pseudophysis barbatus</i>     | ND                     | Negative                | Physiological effects | Yes                  | ND          | Concluded temperature did not directly affect otolith Sr; physiological effect      | Kalish, 1991  |
| <b>Cyprinodontiformes</b>        |                        |                         |                       |                      |             |   |   |
| <i>Fundulus heteroclitus</i>     | ND                     | Inverse relationship    | ND                    | Yes                  | ND          | Sr–temperature relationship used to reconstruct temperature history                 | Radtke, 1989  |

Table 2 (Continued)

| Species                            | Relationships to Sr             |                                 |                    | Predictive lab-field |             |  | References  |
|------------------------------------|---------------------------------|---------------------------------|--------------------|----------------------|-------------|--|---|
|                                    | Vs. salinity                    | Vs. temperature                 | Vs. other          | Models               | Calibration | Comments   |   |
| <b>Perciformes</b>                 |                                 |                                 |                    |                      |             |  |   |
| <i>Arripis trutta</i>              | ND                              | Slight positive correlation     | Age/growth effects | ND                   | ND          | Also suggested importance of reproductive anabolism on otolith Sr                  | Kalish, 1989  |
| <i>Epinephelus guttatus</i>        | ND                              | No effect                       | Growth effect      | Yes                  | ND          | Concluded that temperature was not a significant factor affecting otolith Sr       | Sadovy and Severin, 1994                                  |
| <i>Girella elevata</i>             | ND                              | Equivocal temperature effect    | Age effect         | ND                   | ND          | Ambiguous results; suggested the need of validation studies prior to use           | Gallahar and Kingsford, 1992                              |
| <i>Haemulon plumieri</i>           | Highly variable                 | Negative                        | Growth effect      | Yes                  | ND          | Suggested otolith Sr was primarily a function of body growth and temperature       | Sadovy and Severin, 1992                                  |
| <i>Micropogonias undulatus</i>     | Positive                        | ND                              | ND                 | ND                   | ND          | Otolith Sr difference related to assumed migratory behavior                        | Fowler et al., 1995a,b;<br>Thorrold et al., 1997          |
| <i>Morone saxatilis</i>            | Positive (main factor)          | Minor effect                    | Growth effect      | Yes                  | Yes         | Sr-salinity relationship used to chart age- and sex-dependent movements            | Secor, 1992; Secor et al., 1995b; Secor and Piccoli, 1996 |
| <i>Oreochromis noluticus</i>       | Positive (main factor)          | ND                              | Diet effect        | ND                   | ND          | Sr in water was the primary source of otolith Sr; diet had minor effect            | Farrell and Campana, 1996                                 |
| <i>Pagrus major</i>                | ND                              | Positive                        | ND                 | ND                   | ND          | Differences in otolith Sr among three stations with different thermal gradients    | Arai et al., 1995   |
| <i>Pristipomoides filamentosus</i> | ND                              | Negative relationship suggested | ND                 | ND                   | ND          | Otolith Sr used to infer temperature history                                       | Radtke, 1987  |
| <i>Sciaenops ocellatus</i>         | No effect                       | Positive                        | Age/sex effect     | Yes                  | ND          | Three variables (Sr:K, Ca, Na) affected by temperature; no diet effect observed    | Hoff and Fuiman, 1993, 1995                               |
| <i>Stenogobius genivittatus</i>    | Negative relationship suggested | ND                              | ND                 | ND                   | ND          | Otolith Sr used to infer timing of migration from sea water to fresh water         | Radtke et al., 1988                                       |
| <i>Lentipes concolor</i>           | Positive                        | ND                              | ND                 | ND                   | ND          | Otolith Sr contrasted among amphidromous, marine, and freshwater species of gobies | Radtke and Kinzie, 1996                                   |
| <i>Thunnus thynnus</i>             | ND                              | Negative correlation suggested  | ND                 | ND                   | ND          | Otolith Sr used to infer temperature history                                       | Radtke and Morales-Nin, 1989                              |
| <b>Pleuronectiformes</b>           |                                 |                                 |                    |                      |             |  |   |
| <i>Microstomus pacificus</i>       | ND                              | ND                              | ND                 | ND                   | ND          | Surmised that otolith Sr patterns were related to temperature and age/growth       | Toole et al., 1993  |

<sup>a</sup> Predictive model indicates that the response of otolith Sr was measured to a range of known environmental conditions.

<sup>b</sup> ND=not determined.

### 3. Results and discussion

#### 3.1. Ingress

The rapid ingress into estuaries by *Anguilla rostrata* glass eels and elvers is well known. Ingress by European eels *A. anguilla* into estuaries coincided with a sudden depression of otolith Sr (Tzeng et al., 1997). Analysis of eels with known habitat histories from Swedish fjords allowed Tzeng et al. (1997) to verify that otolith Sr was positively related to known habitat salinities. We have observed similar results for American eel (Fig. 1a). American eel otoliths consistently exhibited two microstructural checks in the core

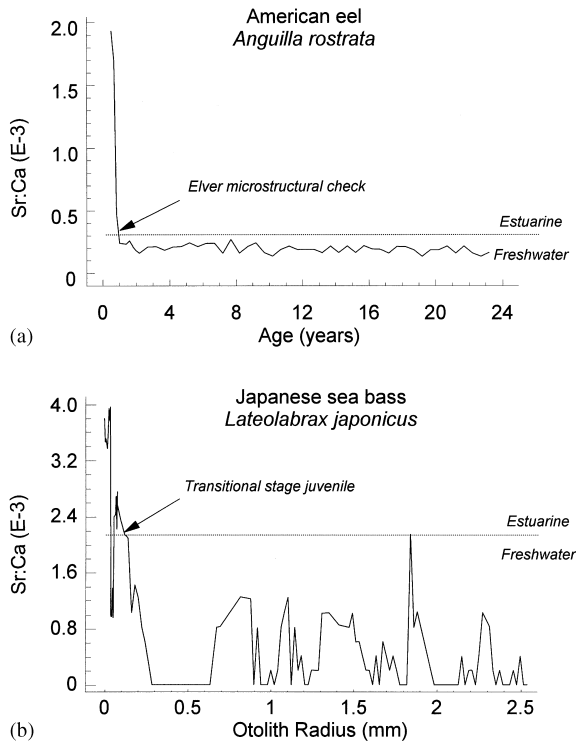


Fig. 1. Pattern of ingress into estuaries indicated by microprobe analysis of otolith Sr: (a) Otolith Sr chronology ( $n=1$ ) of a representative yellow eel (*A. rostrata*) collected in Hudson River, NY. Sr:Ca criterion for freshwater habitation is based upon Tzeng et al. (1997) study on *A. anguilla*; (b) Otolith Sr chronology ( $n=1$ ) of a representative Ariake Sea Japanese sea bass (*L. japonicus*) collected in Chikugo River, Kyushu, Japan. Sr:Ca criterion for freshwater habitation is based upon laboratory rearing studies (Secor et al., 1998).

region which are related to the two metamorphic events: leptocephalus–glass eel and glass eel–elver transformations (Lecomte-Finiger, 1992; Arai et al., 1997). Using these checks we inferred that otolith Sr level decreased rapidly during the glass eel stage. By early elver stage (prior to the first opaque zone), Sr leveled off at concentrations predicted for freshwater habitats (Tzeng et al., 1997). Presumably, the Sr chronology showed rapid ingress followed by persistence in a freshwater habitat. However, the initial decline of Sr after the first metamorphic check is believed to be unrelated to a habitat shift. Otake et al. (1994) suggested that rapid transformation of leptocephali composed of Sr-rich glycosaminoglycans, to glass eels caused a rapid decline in otolith Sr in Japanese eel *A. japonica*.

Similar to American and European eels, an early life history drop in Sr observed for Japanese sea bass *L. japonicus* was consistent with expected young-of-the-year ingress into a freshwater nursery and persistence in that habitat during the juvenile stage (Fig. 1b). Secor et al. (1998) observed a positive relationship between otolith Sr and salinity for this species. Radtke et al. (1988) and Radtke and Kinzie (1996), using otolith Sr, also demonstrated this type of spatial behavior — ingress to a freshwater nursery from coastal habitat — for two Hawaiian gobies.

Bay anchovy *Anchoa mitchilli*, which spawn within estuaries, showed patterns of otolith Sr which implied variable rates of larval ingress (up-estuary dispersal) (Fig. 2). Otolith Sr chronologies indicated that juveniles collected at up-estuary oligohaline sites originated from down-estuary regions, whereas those anchovy collected at down-estuary sites showed less evidence of upstream dispersal. Preliminary results relating salinity to Sr levels in recently formed regions of bay anchovy otoliths supported a positive relationship between otolith Sr and habitat salinity. This trend can be observed in Fig. 2, where the Sr:Ca ratio of the last sampled points in chronologies are inversely correlated to the salinity of the site of capture. In recent research by Thorrold et al. (1997), gradual rates of ingress by Atlantic croaker *Micropogonias undulatus* larvae and juveniles were indicated by laser-ablation analysis of otolith Sr.

Applications of the microprobe analysis of otolith Sr have demonstrated variable rates of ingress among estuarine-dependent species. Eels, Ariake Sea Japa-

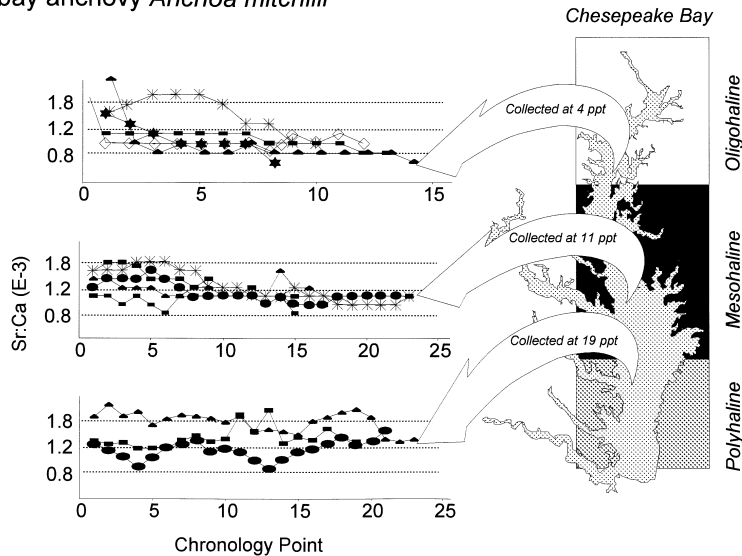
bay anchovy *Anchoa mitchilli*

Fig. 2. Otolith Sr chronologies for juvenile bay anchovy (*A. mitchilli*) collected in Chesapeake Bay, USA. Samples collected from oligohaline ( $n=5$ ), mesohaline ( $n=5$ ), and polyhaline ( $n=3$ ) sites. Collection sites of sampled juveniles shown on map of Chesapeake Bay. Chronology point is used as a proxy for age or length during the larval and early juvenile stages.

nese sea bass, and Hawaiian goby showed rapid rates of ingress followed by juvenile periods of residency. Bay anchovy and Atlantic croaker showed more gradual and variable rates of ingress. Further refinement and application of otolith microanalysis to problems of ingress could demonstrate relationships between metamorphosis, competency, and habitat transitions, and examine the role of physical forces to successful arrival into estuarine nurseries.

### 3.1.1. Egress and coastal dependency

Size-dependent, down-estuary movements are common in juveniles of estuarine fishes (Herke, 1971; Yakupzack et al., 1977). Size-dependent emigration may represent a trade-off between increased predation risk and increased forage opportunities (Werner et al., 1983), both of which are positively related to salinity (Weinstein and Brooks, 1983; Currin et al., 1984). Limburg (1995, 1998) has used otolith Sr to measure varying rates of coastal egress by young-of-the-year juvenile anadromous herrings (*Alosa* spp.). Interestingly, Limburg demonstrated that a small number of “anomalous” juveniles re-invade freshwater environments following their initial coastal egression.

Examination of otolith Sr for Hudson River and Chesapeake Bay striped bass *Morone saxatilis* showed variable patterns of size- and age-specific coastal dependency (Fig. 3). Hudson River population males and females showed similar rates of increased coastal habitat use with age but Chesapeake Bay males tended to reside in the Bay throughout their lives (Secor and Piccoli, 1996). Despite these general trends, individual salinity chronologies showed a range of behaviors (Fig. 4). In some instances, striped bass emigrated to coastal habitats early in life and re-invaded freshwater-oligohaline estuarine habitats as adults. Babaluk et al. (1997) observed patterns of Sr in Arctic charr *Salvelinus alpinus* consistent with coastal egress following the first several years of life.

### 3.1.2. Residency

Despite the presumed anadromous behaviors of Chesapeake Bay and Hudson River striped bass, we have observed that some striped bass live their lives in freshwater-oligohaline habitats (Fig. 4) (Secor and Piccoli, 1996). These chronologies showed the same range in otolith Sr as those shown for a freshwater population of striped bass (Secor, 1992). Babaluk et al.

striped bass *Morone saxatilis*

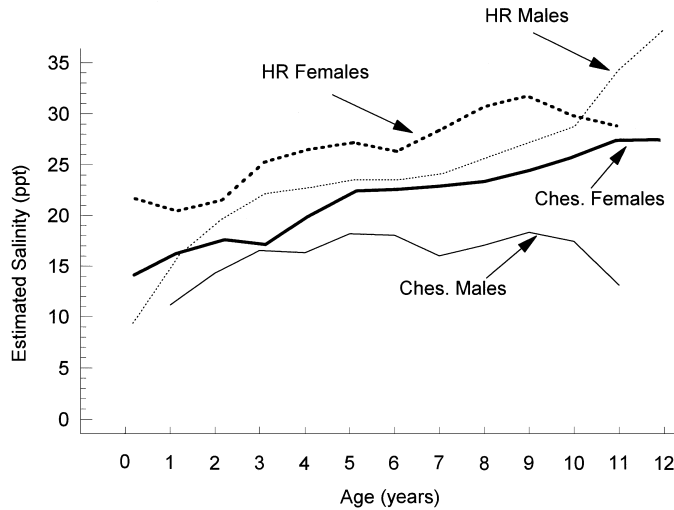


Fig. 3. Mean age-specific habitat salinities for striped bass (*M. saxatilis*) from the Hudson River, NY ( $n=25$  males, 25 females) and Chesapeake Bay, MD ( $n=21$  males, 34 females). Salinity chronologies based upon laboratory and field studies on the relationship of ambient salinity and otolith Sr:Ca (Secor et al., 1995b). Analyses from Secor and Piccoli (1996).

(1997) demonstrated clear differences in Sr levels in otoliths of resident and anadromous ecotypes of Arctic charr. American eel captured in freshwater reaches of the Hudson River exhibited Sr chronologies consistent

with freshwater residency during the yellow-eel stage (Fig. 1a). This chronology is similar to those constructed by Tzeng et al. (1997) for European eel captured at freshwater sites.

striped bass *Morone saxatilis*

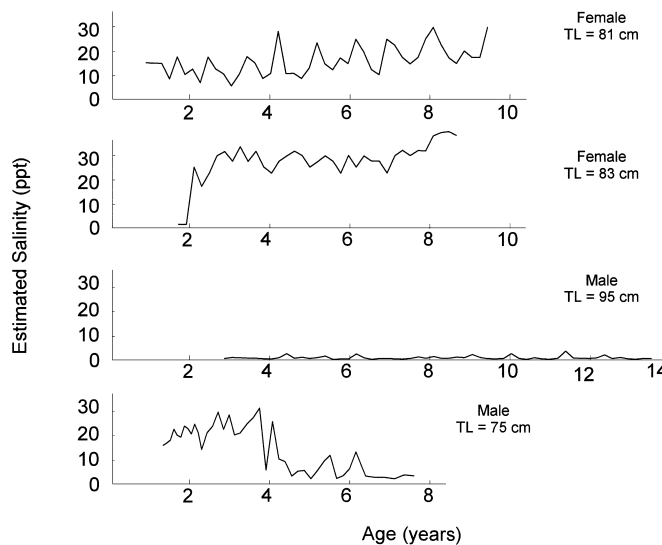


Fig. 4. Salinity chronologies for four Hudson River, NY striped bass (*M. saxatilis*) captured on the spawning grounds, Spring 1991. Salinity chronologies were based upon laboratory and field studies on the relationship of ambient salinity and otolith Sr:Ca (Secor et al., 1995b). Total length (TL) and sex is given for each chronology.



### 3.2. Spawning migrations

Salinity chronologies of adult striped bass often exhibited annual cycles which were suggestive of spawning migrations (Fig. 5a). Secor and Piccoli (1996) observed annual troughs in salinity chronologies for regions of the otoliths formed just after the opaque zone. The opaque zone forms in early spring just prior to spawning (Secor et al., 1995c). However, the trough rarely reached freshwater salinities, where striped bass spawn. Because otoliths probably do not grow substantially during spawning runs, freshwater spawning events may be under-represented by electron microprobe analysis of otolith Sr (Secor and Piccoli, 1996). A chronology of otolith Sr for a female American shad showed cycles which were also suggestive of spawning runs (Fig. 5b). The largest trough

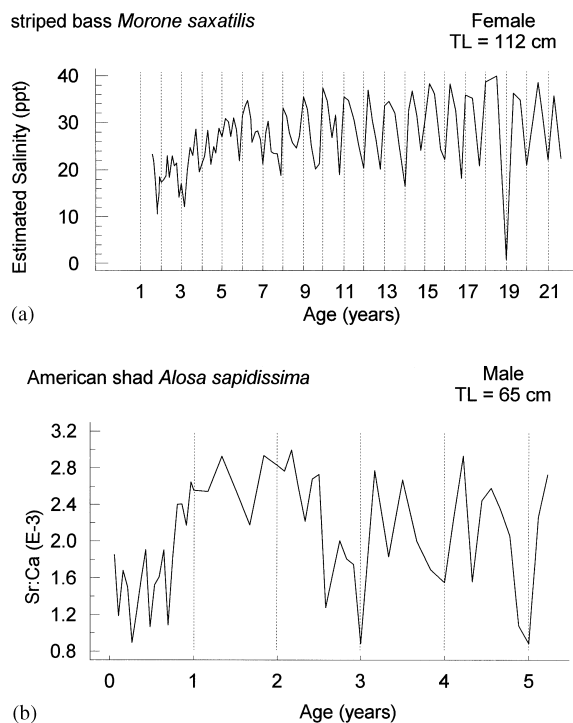


Fig. 5. Annual cycles in otolith Sr suggestive of anadromous spawning runs: (a) Otolith salinity chronology for female Chesapeake Bay, MD striped bass (*M. saxatilis*). Salinity chronology based upon laboratory and field studies on the relationship of ambient salinity and otolith Sr:Ca (Secor et al., 1995b); (b) Otolith Sr chronology for American shad (*A. sapidissima*) ( $n=1$ ) collected in the Chesapeake Bay, VA.

in otolith Sr occurred at 3 years and may represent first spawning since American shad typically mature at 3–5 years of age. Another deep trough occurred at the fifth annulus. The shallow trough at the fourth annulus may indicate a spawning migration which was incompletely sampled due to spacing among probed points. Alternately, the level of the trough was similar to sub-annual troughs in depth, which could indicate that this individual did not spawn during its fourth year of life. Cyclical patterns in otolith Sr, indicative of spawning runs have also been observed for Arctic charr (Halden et al., 1995; Babaluk et al., 1997).

The otolith microanalysis method could resolve reproductive schedules in anadromous fishes, if there is sufficient otolith growth during spawning runs to represent ingress and egress to and from spawning grounds. Technological developments which increase the spatial resolution of probe measurements of otolith Sr across annular zones will advance this application. As an example, the spatial resolution of measurements of Sr by micro-PIXE (proton-induced X-ray emission) is an order of magnitude higher than the electron microprobe. Its application on Arctic charr (Halden et al., 1995) provided a more compelling pattern of annual cycles than we have observed for other anadromous fishes using the electron microprobe.

### 3.3. Literature review

Salinity, temperature, and physiological effects were reported in 13, 15, and 11 of the reviewed studies, respectively. Physiological influences on otolith Sr included diet, endocrine status, age, size, ontogenetic stage, stress, and growth. Studies on laboratory or field-collected fish with known environmental histories occurred for 10 of the 27 species studied. Only three studies attempted to construct predictive models of salinity or temperature from otolith Sr. For Atlantic herring *Clupea harengus* and Atlantic cod *Gadus morhua*, laboratory-based models substantially over-estimated (by 3–6°C) temperature levels predicted from field-based models (Townsend et al., 1989, 1995). Townsend et al. (1989) suggested that the cause of the discrepancy for Atlantic herring was stress experienced by laboratory-reared individuals, resulting in elevated otolith Sr levels. For striped bass, Secor et al. (1995b) compared slopes of salinity vs. otolith Sr:Ca ratio relationships

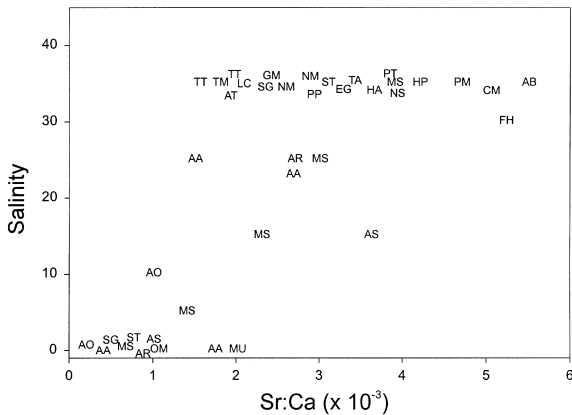


Fig. 6. Meta-analysis of relationship between otolith Sr:Ca ratios and ambient salinity for 27 species of estuarine and marine fishes. Species codes: AA: *A. anguilla*, AB: *A. butcheri* (1), AO: *A. oxyrinchus* (4), AR: *A. rostrata*, AS: *A. sapidissima*, AT: *A. trutta*, CM: *C. myriaster* (3), EG: *E. guttatus*, FH: *F. heteroclitus*, GM: *G. morhua*, HP: *H. papillosus* (1), HA: *H. atlanticus* (1), *L. campechanus* (4), MU: *M. undulatus*, MS: *M. saxatilis*, NM: *N. macropterus*, NS: *N. scoraenoides*, OM: *O. mykiss*, PM: *P. major*, PP: *P. filamentosus*, PT: *P. tetricus*, ST: *S. trutta*, SG: *S. genivittatus*, TA: *T. atun*, TM: *T. maccoyii*, TT: *T. thynnus* (4), TD: *T. declivis*. Numbers in parentheses denote references of species not previously given: 1: Kalish, 1989, 2: present study, 3: Otake et al., 1997, 4: Zdanowicz, unpublished data.

and found good agreement between field and laboratory-based predictions.

The relative contributions of salinity and temperature to variance in otolith Sr were reported in four studies. In goldfish *Carassius auratus*, Mugiya and Tanaka (1995) observed that otolith Sr:Ca was ca. fivefold more responsive to ambient Sr:Ca concentrations (i.e. salinity) than temperature. In Atlantic croaker, Fowler et al. (1995a,b) observed a positive effect of temperature on otolith Sr, but no significant effect of salinity on otolith Sr. However, salinity (26 and 35 ppt) and temperature (20 and 25°C) ranges were relatively limited in that study. Secor et al. (1995b) observed a dominant influence of salinity over temperature on Sr:Ca ratios of striped bass otoliths. Temperature and its interaction term with salinity accounted for only 7% of the total variation in Sr:Ca; salinity accounted for 86% of variation in otolith Sr:Ca.

Factors other than salinity and temperature have been shown to affect Sr deposition rates including growth, developmental or reproductive stage, genet-

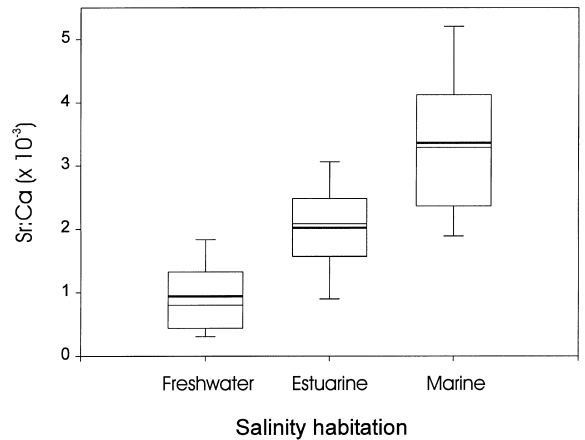


Fig. 7. Salinity-regime estimates of the Sr:Ca ratio for estuarine and marine teleosts. Number of species used to estimate mean Sr:Ca ratios differed among ecosystems: freshwater (0–5 ppt)=10 spp., estuarine (5–25 ppt)=11 spp., and marine (>25 ppt)=20 spp. Sr:Ca ratios of several species collected from estuarine ecosystems for which salinity data were not reported are included in the analysis: *C. regalis*, *L. xanthurus*, *M. undulatus*, *P. saxatilis*, and *P. americanus* (Zdanowicz, unpublished data). Interquartile range (25th and 75th percentile) is shown by extent of boxes, with normal and boldface horizontal lines within boxes representing median (50th percentile) and mean, respectively. Error bars depict 10th and 90th percentile.

ics, and diet (Kalish, 1989; Sadovy and Severin, 1992; Limburg, 1995; Secor et al., 1995b; Farrell and Campana, 1996). These biological influences have not been systematically contrasted to salinity and temperature effects on otolith Sr.

Mean Sr:Ca ratios reported in the literature ranged from 0.3 to  $5.2 \times 10^{-3}$ , and although highly variable among species, ambient salinity was positively related to the Sr:Ca ratios of taxa surveyed ( $r=0.71$ ) (Fig. 6). There was a significant difference (ANOVA,  $p<0.01$ ) in Sr:Ca ratios among taxa collected from three different salinity regimes: freshwater (0–5 ppt)  $0.9 \times 10^{-3}$ , estuarine (5–25 ppt)  $2.3 \times 10^{-3}$ , and marine (>25 ppt)  $3.4 \times 10^{-3}$  (Fig. 7). A large range in otolith Sr:Ca values for marine fish indicates that factors other than salinity are important in determining variations in Sr:Ca levels for this group. Relatively few intermediate salinity level (estuarine) fish have been investigated so the form of the relationship between salinity and Sr:Ca among taxa remains uncertain. However, we found it remarkable that a positive relationship emerged between salinity and Sr:Ca, despite the

diverse taxa and range of methodology contained in the data set.

#### 4. Summary

The influence of spatial behaviors on the population dynamics of estuarine fishes remains poorly understood, particularly due to empirical limitations of current methods (catch analysis, tagging, hydroacoustics). While these methods provide a means of detecting spatial behaviors, data obtained are typically “averaged” at the population level and are thus too coarse to provide a scale of detection which can explicitly link spatial and demographic dynamics. Microprobe analysis of otolith Sr and estimation of individual salinity chronologies can demonstrate a diversity of spatial life history tactics in estuaries. Individual habitat history is collapsed into a single vector, salinity, which should facilitate quantitative analysis on the role of spatial dynamics on recruitment, production, exploitation, and susceptibility to pollution. The assumption that salinity is a useful yardstick delineating estuarine habitats is critical to the technique, but existing literature supports this premise. Comprehensive applications of otolith microanalysis, such as those we have reported for striped bass (Secor and Piccoli, 1996; Zlokovitz and Secor, 1999), require deliberate consideration of the relationship between ambient salinity and otolith Sr.

While the use of otolith microchemistry for reconstructing environmental histories of marine fishes is well recognized and reported, the fundamental question, whether fish otoliths can function as “faithful environmental chronometers?” (Secor et al., 1995a), remains largely untested. Existing information on the relationship between otolith Sr and salinity across species suggests that otolith Sr is a useful scalar of estuarine habitat use. Despite the fact that our empirical review was based on a diverse range of species from contrasting environmental conditions (i.e. variable temperature and representing a range of ontogenetic stages and physical states), a positive relationship between otolith Sr and salinity emerged. Nevertheless, levels of otolith Sr among taxa were highly variable within the same salinity regime and thus the promise of this technique for detecting fine-scale patterns of dispersal or retention within an

estuary remains in question. Since factors other than salinity influence the uptake of otolith Sr (e.g. genetics, physiology, temperature), rigorous empirical testing of these factors along with salinity need to be examined before we can properly evaluate whether otolith Sr can precisely and accurately hindcast spatial histories of estuarine fishes.

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