Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish

Randy J. Brown and Kenneth P. Severin

Abstract: Water chemistry is thought to be the primary factor influencing fish otolith chemistry. Experimental results with freshwater and diadromous fish have been consistent with this paradigm, but with marine fish, they have often been ambiguous or contradictory. A review of water chemistry data indicated that Sr:Ca (mmol:mol) levels were higher in marine water than in most freshwater systems and that Sr:Ca variability was lower in marine water than in most freshwater systems. We therefore hypothesized that lifetime otolith Sr:Ca profiles of freshwater fish would exhibit low levels of Sr:Ca with moderate variability, of diadromous fish would exhibit highly variable Sr:Ca levels, and of marine fish would exhibit high levels of Sr:Ca with low variability. Otolith Sr:Ca profiles from 81 species of freshwater, diadromous, and marine fish revealed that freshwater fish had low levels of Sr:Ca and lower variability than expected relative to marine fish, diadromous fish had Sr:Ca levels and variability that were consistent with expectations, and marine fish had high maximum Sr:Ca levels, as expected, and high Sr:Ca variability, similar in magnitude to diadromous fish, which was not expected. These findings indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca variation for freshwater and diadromous fish but not for marine fish.

Résumé : On croit que la chimie de l’eau est le facteur principal qui influence la chimie des otolithes de poissons. Les études expérimentales utilisant des poissons d’eau douce ou des poissons diadromes s’accordent à ce paradigme, mais celles faites sur les poissons marins sont souvent ambiguës ou contradictoires. Un examen des données de chimie de l’eau indique que les valeurs de Sr:Ca (mmol:mol) sont plus élevées dans les eaux marines que dans la plupart des systèmes d’eau douce et que la variabilité de Sr:Ca est plus faible dans les eaux marines que dans la plupart des systèmes d’eau douce. Nous avons donc émis l’hypothèse selon laquelle les profils Sr:Ca des otolithes des poissons d’eau douce sur l’ensemble de leur vie présentent de faibles valeurs de Sr:Ca avec une variabilité modérée, ceux des poissons diadromes des valeurs de Sr:Ca très variables et ceux des poissons marins de fortes valeurs de Sr:Ca avec une faible variabilité. L’étude des profils de Sr:Ca de 81 espèces de poissons dulcicoles, diadromes et marins montre que les poissons d’eau douce ont de valeurs faibles de Sr:Ca et une variabilité plus faible qu’attendu par comparaison aux poissons marins, que les poissons diadromes ont des valeurs de Sr:Ca et une variabilité qui correspondent aux attentes et que les poissons marins ont des valeurs maximales fortes de Sr:Ca, tel qu’attendu, et une forte variabilité de Sr:Ca, de même importance que celle des poissons diadromes, ce qui n’était pas prévu. Ces observations indiquent que le Sr:Ca de l’eau est le facteur principal qui influence la variation de Sr:Ca chez les poissons dulcicoles et diadromes, mais pas chez les poissons marins.

[Traduit par la Rédaction]

Introduction

Fish populations around the world are being profoundly impacted by exploitation, development activities, and climate change (Hilborn et al. 2003). Understanding fish populations is essential to effective management and long-term preservation of these resources. The science of fish otolith chemistry is being used increasingly to improve our understanding of fish populations by identifying qualities such as essential habitats, migration patterns, and population structure (Campana 1999). Some applications of fish otolith chemistry are becoming almost routine, but there continues to be active research into environmental and physiological factors influencing the incorporation of trace elements into otoliths in the hopes of expanding our capabilities with the science.

The underlying paradigm of almost all otolith chemistry studies is that water chemistry is the primary factor influencing otolith chemistry. Strontium (Sr) has been the most important trace element investigated for several reasons: (*i*) its concentration (or molar ratio to calcium (Ca)) is rela-

Received 20 January 2009. Accepted 8 July 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 13 October 2009. J21005

Paper handled by Associate Editor Steven Campana.

R.J. Brown.[1] US Fish and Wildlife Service, 101 12th Avenue, Room 110, Fairbanks, AK 99701, USA.
K.P. Severin. Department of Geology and Geophysics, University of Alaska Fairbanks, Box 755780, Fairbanks, AK 99775-5780, USA.

[1] Corresponding author (e-mail: randy_j_brown@fws.gov).

Can. J. Fish. Aquat. Sci. **66**: 1790–1808 (2009) doi:10.1139/F09-112 Published by NRC Research Press

tively stable within but varies widely among aquatic habitats; (*ii*) it is metabolically inert and thought to move passively across membrane barriers separating water from blood and blood from endolymph; (*iii*) it has a 2^+ valence in solution and substitutes for Ca in precipitating otolith mineral; and (*iv*) it is found in relatively high concentrations in water and otoliths compared with other trace elements (Campana 1999; Secor and Rooker 2000). But, does this paradigm hold equally true for all teleost fish?

Experimental studies with juvenile diadromous fish have established unambiguous, positive correlations between the salinity of ambient water and the resulting otolith Sr concentration or molar ratio of Sr to Ca (Sr:Ca) (e.g., Secor et al. 1995; Farrell and Campana 1996; Zimmerman 2005). Field investigations with known life history, diadromous species, often using salinity as a proxy for Sr concentration or Sr:Ca in the water, have produced results consistent with experimental findings (e.g., Limburg 1995; Zimmerman and Reeves 2000; Arai et al. 2003). Practical applications of otolith Sr analyses with diadromous species have reportedly been successful in describing complex life history details and migration patterns for certain fish populations (e.g., Limburg et al. 2003; Yang et al. 2006; Brown et al. 2007).

Experimental studies with juvenile marine fish have not established consistent positive correlations between salinity treatment levels and otolith Sr concentration or Sr:Ca levels, or there have been significant interactive effects between salinity and environmental or physiological factors (e.g., Bath et al. 2000; Elsdon and Gillanders 2002; Martin et al. 2004). Field investigations of marine species with samples from known locations or life history qualities have produced more ambiguous results than for diadromous species. Many authors have suggested that temperature or physiological events such as spawning interact with water chemistry in complex ways to influence otolith chemistry for marine species (e.g., Campana et al. 1994; FitzGerald et al. 2004; Ashford et al. 2005). Practical applications of otolith Sr analyses with marine species are sometimes reported to be successful in describing life history details such as stock origins or geographic distribution for certain fish populations; however, they usually required the consideration of additional information including concentrations of multiple elements, isotopes, temperature data, and demographic information (e.g., Severin et al. 1995; Thorrold et al. 1998; Rooker et al. 2003). Although physiology is frequently identified as a factor influencing otolith chemistry of marine fish, it is rarely considered to be a factor for freshwater or diadromous fish.

Campana (1999) and Secor and Rooker (2000), in their reviews of the otolith chemistry literature, showed that average otolith Sr levels reported in the literature were greatest in marine, least in freshwater, and intermediate in diadromous fish. This pattern supports the general understanding that Sr levels and Sr:Ca are greater in marine water than in freshwater. Most marine teleost fish species maintain slightly greater fluid solute concentrations than freshwater fish, but both average close to one-third that of marine water (Black 1957). Fish are therefore hypotonic to marine water, where they must work to reduce solute uptake and retain water, and hypertonic to freshwater, where they must work to retain solutes and reduce water uptake. Diadromous species migrate between marine and fresh water and would experience a wider range of osmotic and Sr:Ca conditions than other life history categories. Though it is well established that Sr precipitation in otoliths is a competitive process among 2^+ valence ions in the endolymph (Campana 1999; Kraus and Secor 2004), the different osmotic conditions faced by fish in these different environments may affect the manner in which Sr ions become available to the endolymph.

Summaries of average water chemistry parameters indicate that freshwater systems (e.g., Livingston 1963; Martin and Meybeck 1979; Goldstein and Jacobsen 1987) are uniformly lower in Sr concentration and Sr:Ca molar ratios than marine systems (e.g., Culkin and Cox 1966). Early work by Odum (1957) and more recent work by Kraus and Secor (2004), however, indicate that freshwater Sr:Ca levels are variable among drainage systems and that a small percentage of rivers exhibit Sr:Ca levels greater than reported for marine water. We reviewed water chemistry data for freshwater and marine systems from online databases and from the formal literature to clarify the nature of Sr:Ca environments faced by fish living within these two habitats. We then modeled the estuarine Sr:Ca levels from a small number of river systems to illustrate this transitional environment. This review provides a more comprehensive understanding of Sr:Ca level and variability among habitats, as they relate to fish and otolith chemistry, than was previously available.

We tested patterns of otolith Sr:Ca in freshwater, diadromous, and marine categories of fish for consistency with the paradigm that water chemistry was the primary factor influencing otolith chemistry. Mature-sized, wild fish from these three life history categories were selected. Lifetime Sr:Ca profiles were created with core-to-margin transects to examine Sr:Ca level and variability for each fish. Unknown temperature and physiological effects were expected to influence Sr incorporation into otoliths of all three categories of fish and were considered to be common background factors. Based on our understanding of Sr:Ca differences between freshwater and marine environments, we hypothesized that freshwater fish would exhibit relatively low levels of otolith Sr:Ca with moderate variability, diadromous fish would exhibit high maximum Sr:Ca levels and high variability, reflecting the large range of Sr:Ca environments that they encounter, and marine fish would exhibit relatively high levels of otolith Sr:Ca with low variability.

Materials and methods

Water chemistry review

We reviewed water chemistry data from the United States Geological Survey (USGS 2007) database (n = 4138) and from the geochemistry literature (citations in Appendix A; n = 1861) to improve our understanding of the within-system variability and among-category differences of Sr and Ca in freshwater rivers and lakes, marine systems, and estuaries. Only the dissolved components of Sr and Ca were considered. They were standardized to $\mathrm{mg \cdot kg^{-1}}$, converted to molar concentrations, and presented as the molar ratios of Sr to Ca (Sr:Ca) reported in units of mmol Sr to mol Ca.

Strontium and Ca concentration data were found for 58 lake systems and 786 mainstem and tributary rivers from all continents except Antarctica. Data from closed-basin salt or alkaline lakes were not included in our analyses or figures because the extreme chemistry in these environments often precludes fish occupation and the outlier Sr:Ca values presented scaling problems in our figure. Marine water chemistry data consisted of 171 individual records from published accounts of voyages into most of the major oceans and seas of the world, low and high latitudes, from surface waters to depths of more than 5000 m, and from coral reefs in coastal areas to mid-ocean regions. Data from mid-ocean vents and black smokers were not included. In all, almost 6000 individual measurements of water Sr and Ca concentrations were compiled. Sr:Ca level and variability within and among freshwater and marine habitats were illustrated with a histogram.

The variability of Sr:Ca within individual river systems was examined and graphically compared with the marine system using box plots. Sr:Ca data from 20 rivers were examined. Ten large river drainages from several continents for which Sr:Ca data were available from many mainstem and tributary sites were selected to illustrate the Sr:Ca variability within a drainage. Ten large North American rivers for which Sr:Ca data were available for multiple years and seasons from lower-drainage, mainstem sampling sites were selected to illustrate the Sr:Ca variability within a limited reach of a drainage over a long period of time. All 171 marine Sr:Ca observations were included.

Three rivers with median Sr:Ca levels less than marine water and one river with a median Sr:Ca level greater than marine water were selected to illustrate the relationship between Sr:Ca and salinity in estuary waters. The selected rivers included the Indigirka (Sr:Ca = 2.32) and the Indus (Sr:Ca = 3.58), which had relatively low levels of dissolved solutes, and the Mississippi (Sr:Ca = 2.01) and St. Johns (Sr:Ca = 13.83), which had relatively high levels of dissolved solutes. Concentrations of Sr and Ca were modeled across an estuarine salinity gradient from 0 to 35 practical salinity units (psu) with a progressive series of complementary mixing fractions of fresh and salt water using the following equation:

$$c_{\mathrm{a}i} = [(c_{\mathrm{f}i}) \cdot (1 - p)] + [(c_{\mathrm{m}i}) \cdot (p)]$$

where $c_{\mathrm{a}i}$ is the concentration (mg:kg) of element i in ambient estuarine water, $c_{\mathrm{f}i}$ is the concentration of element i in freshwater, $c_{\mathrm{m}i}$ is the concentration of element i in marine water, i represents dissolved Sr or Ca, and ambient salinity is $p{\cdot}35$, where p ranges from 0 to 1. Freshwater Sr and Ca concentrations used in this model were median values for the selected rivers. Average marine water Sr and Ca concentrations from our literature sources were 7.64 (standard deviation (SD) = 0.53) and 405.87 (SD = 27.49) mg·kg^{-1}, respectively, and the mean Sr:Ca level was 8.61 mmol:mol. The variable "p" ranged from 0 to 1 and reflected ambient salinity as a proportion of marine salinity, which was modeled at 35 psu. End-member concentrations of Sr and Ca were used to model Sr:Ca (mmol:mol) values and were plotted against salinity.

Fish otolith selection, preparation, and analysis

Otoliths from 28 freshwater, 21 diadromous, and 32 marine fish species were examined in this study (Appendix B). Taxonomy and nomenclature in this paper are consistent with Fishbase (2008). Mature-sized, wild-caught fish were used in all cases. They were collected from locations and in circumstances ensuring they had lived only in freshwater, in both freshwater and marine water, or only in marine water, respectively. One sample per species was included in among-habitat analyses. Within-species variability was explored with additional analyses of 20 individuals each from freshwater drum (*Aplodinotus grunniens*), a freshwater species, Bering cisco (*Coregonus laurettae*), a diadromous species, and sablefish (*Anoplopoma fimbria*), a marine species.

One otolith from each fish was thin-sectioned through the core and mounted on a glass slide. Most were sectioned in the transverse plane, but some unusually shaped otoliths were sectioned in other planes. Each section was 200–300 µm thick, and growth increments from the core region to the margin were visible with transmitted light. They were polished on a lapidary wheel with 1 µm diamond abrasive and coated with a conductive layer of carbon in preparation for microprobe analyses.

A wavelength-dispersive electron microprobe (microprobe) was used for chemical analyses of otoliths. The technology functions by directing a focused beam of electrons to points on a sample surface. Atoms within the material are ionized by the electron beam and emit X-rays unique to each element. Spectrometers are tuned to count the X-rays from elements of interest. The electron beam used here was 5 µm in diameter and was operated at an accelerating voltage of 15 kilo-electron volts and a nominal current of 20 nanoamperes. According to Gunn et al. (1992), the electron beam penetrates less than 3 µm into otolith material. Strontium and Ca X-rays were counted for 25 s at each point along a core-to-margin transect (core precipitated early in life, margin precipitated late in life) for each otolith. Center-to-center distance between points was 8 µm. Element-specific X-ray counts at each point are proportional to the concentration of the element in the sampled material (Reed 1997; Goldstein et al. 2003). Strontianite and calcite standards were used with established quantitative procedures to develop conversion factors between X-ray count data and elemental concentration estimates in units of mg·kg^{-1}, as detailed by Brown et al. (2007). Elemental concentrations of Sr and Ca were converted to molar concentrations using the following equivalencies:

$$\left(\frac{\mathrm{Sr}_{\mathrm{moles}}}{\mathrm{kg}}\right) = \left(\frac{\mathrm{Sr}_{\mathrm{mg}}}{\mathrm{kg}}\right)\left(\frac{1_{\mathrm{mole}}}{87.620_{\mathrm{g}}}\right)\left(\frac{1_{\mathrm{g}}}{1000_{\mathrm{mg}}}\right)$$

and

$$\left(\frac{\mathrm{Ca}_{\mathrm{moles}}}{\mathrm{kg}}\right) = \left(\frac{\mathrm{Ca}_{\mathrm{mg}}}{\mathrm{kg}}\right)\left(\frac{1_{\mathrm{mole}}}{40.078_{\mathrm{g}}}\right)\left(\frac{1_{\mathrm{g}}}{1000_{\mathrm{mg}}}\right)$$

Calcium is found in much greater concentration than Sr in fish otoliths and behaves as a constant in the ratio of Sr:Ca (Campana 1999; Secor and Rooker 2000). Variability in otolith Sr:Ca is, therefore, due almost exclusively to variation in Sr concentration. Consistent with this understanding, we observed a relatively constant Ca concentration among samples at approximately 389 000 mg·kg^{-1}, with a standard error (SE) of approximately 0.23%, or about 900 mg·kg^{-1}. Strontium concentration varied widely, ranging from just over our detection limit of approximately 330 mg·kg^{-1} to more than 17 000 mg·kg^{-1}. The SEs of the Sr concentration estimates were proportionally greater near detection limits than at higher concentrations, resulting in approximately 150 mg·kg^{-1} near detection limits and 300 mg·kg^{-1} at the greatest concentrations (Fig. 1).

Three measures of otolith Sr and Sr:Ca variability were analyzed: (*i*) an index of the coefficient of variation (CV) of Sr X-ray count data, which is a function of each data point in a profile relative to the mean value; (*ii*) the range of Sr:Ca, which is a function of only two data points within each profile; and (*iii*) an index of the total variation of each profile, which was an additive function of the Sr:Ca differences between each sequential pair of data points (see Riesz et al. 1990, p. 10, eq. 3). Raw X-ray count data (without the background removed) from homogeneous material are Poisson-distributed, with a mean equal to the variance (Goldstein et al. 2003). An index of the CV of Sr X-ray count data (CVI) was calculated as

$$\mathrm{CVI} = \left(\frac{s}{\bar{X}}\right) \cdot \left(\frac{\sqrt{\bar{X}}}{\bar{X}}\right)^{-1} = \left(\frac{s}{\sqrt{\bar{X}}}\right)$$

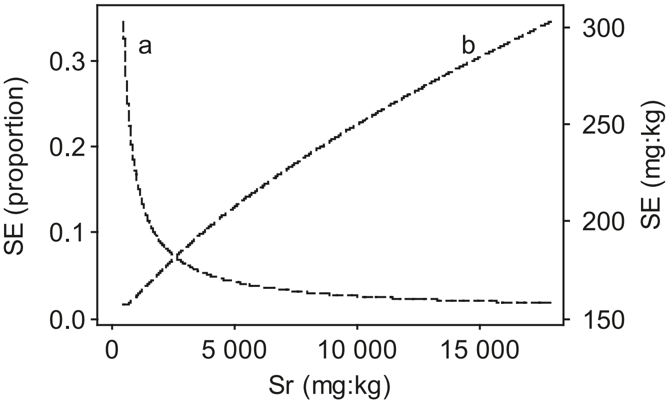
where $\left(\frac{s}{\bar{X}}\right)$ was the actual CV and $\left(\frac{\sqrt{\bar{X}}}{\bar{X}}\right)$ was the CV expected from homogeneous material. If an otolith were homogeneous for Sr, the CVI would equal approximately one, and if Sr concentration varied widely across an otolith, the CVI would be much larger than one. The Sr:Ca range statistic was simply the difference between the greatest and lowest values in each profile. The total variation of Sr:Ca (T_v) across each profile was calculated as

$$T_\mathrm{v} = \sum_{2}^{n} |(x_k) - (x_{k-1})|$$

where n is the number of sample points in the profile, x is the Sr:Ca value, and $k = 2, 3, \ldots, n$. Standardized residuals from the least-squares linear regression of all T_v were used as the index statistics to account for the wide variation in n among profiles. One-way analysis of variance (ANOVA) procedures were used to test null hypotheses that mean values of CVI, range Sr:Ca, and the index of total variation from the six sample groups of fish were equal versus the alternative hypothesis that at least one group was different. Prior to analysis, the CVI and range Sr:Ca statistics were $\log_{10}$-transformed (log(statistic + 1)) to normalize distributions and equalize variances among categories. Tukey's honestly significant difference (HSD) method of multiple comparisons was conducted a posteriori with a family error rate of 0.05 to determine the relative positions of the groups.

Two measures of otolith Sr:Ca level were analyzed: median and maximum Sr:Ca, which are single-point data values within each profile. Median Sr:Ca was selected rather than mean Sr:Ca because the median value better represents the bulk of data in skewed distributions and is very similar to the mean in normally distributed data. One-way ANOVA procedures were used to test null hypotheses that mean values of log-transformed median and maximum Sr:Ca data from the six sample groups of fish were equal versus the alternative hypotheses that at least one group was different. Following significant results, a posteriori analyses using Tukey's HSD method of multiple comparisons with a family error rate of 0.05 were conducted to determine the relative positions of the groups.

Fig. 1. Standard error (SE) variation across a wide range of otolith Sr concentration estimates expressed in (*a*) proportion of the estimate and (*b*) units of mg:kg.



Otolith chemistry studies of diadromous species identify ontogenetic trends in Sr or Sr:Ca to infer migrations between freshwater and marine water (e.g., Brenkman et al. 2007; Brown and Severin 2007). Based strictly on our understanding of Sr:Ca variability in water, freshwater and marine categories of fish were not expected to have distinct or predictable ontogenetic Sr:Ca trends. Instead, it was hypothesized that their Sr:Ca levels would exhibit relatively low variation around a mean value due to annual temperature patterns, physiological effects, and small within-habitat water chemistry fluctuations. Despite these expectations, ontogenetic trends in marine fish otolith chemistry have been detected previously and were thought to be the result of physiological factors rather than water chemistry variation (Brophy et al. 2004; Morales-Nin et al. 2005; Miller 2007). To characterize ontogenetic trends in otolith Sr:Ca, we used the slope parameter from the least-squares linear regression of Sr:Ca for each profile as an indicator. We tested the null hypothesis that mean slope parameters for all six groups of fish were equal with a one-way ANOVA. Upon significant results, a posteriori analysis using Tukey's HSD method of multiple comparisons with a family error rate of 0.05 were conducted to determine the relative positions of the groups.

Characteristic otolith Sr and Sr:Ca variability, Sr:Ca levels, and ontogenetic trends in Sr:Ca among freshwater, diadromous, and marine fish species were illustrated based on a principal components analysis (Jolliffe 1986). Analytical factors from each fish included log-transformed CVI, range, median, and maximum Sr:Ca data, and the total variation index and slope factors. The eigenvalues and eigenvectors for the principal components were tabulated, and the essential variation among life history groups and representative species was illustrated with an ordination plot of the first two principal components.

Graphs of otolith Sr:Ca variation across core-to-margin transects, lifetime Sr:Ca profiles, illustrate ontogenetic trends and have been widely used to describe migrations be-

Fig. 2. Histogram (not stacked) illustrating Sr:Ca (mmol:mol) variability in marine (darkly shaded bars; n = 171), river (lightly shaded bars; n = 786), and lake (open bars; n = 58) habitats.

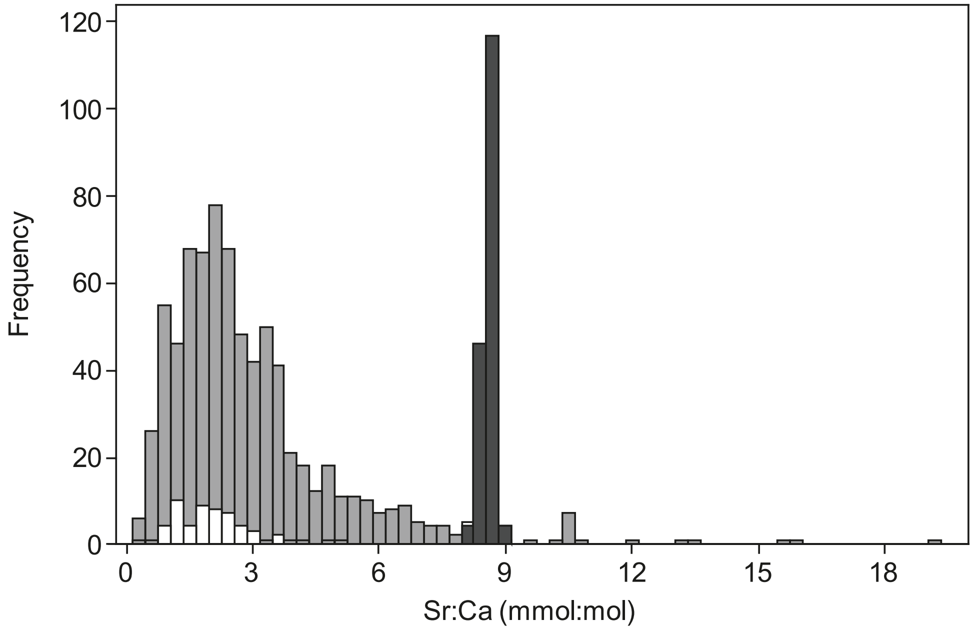
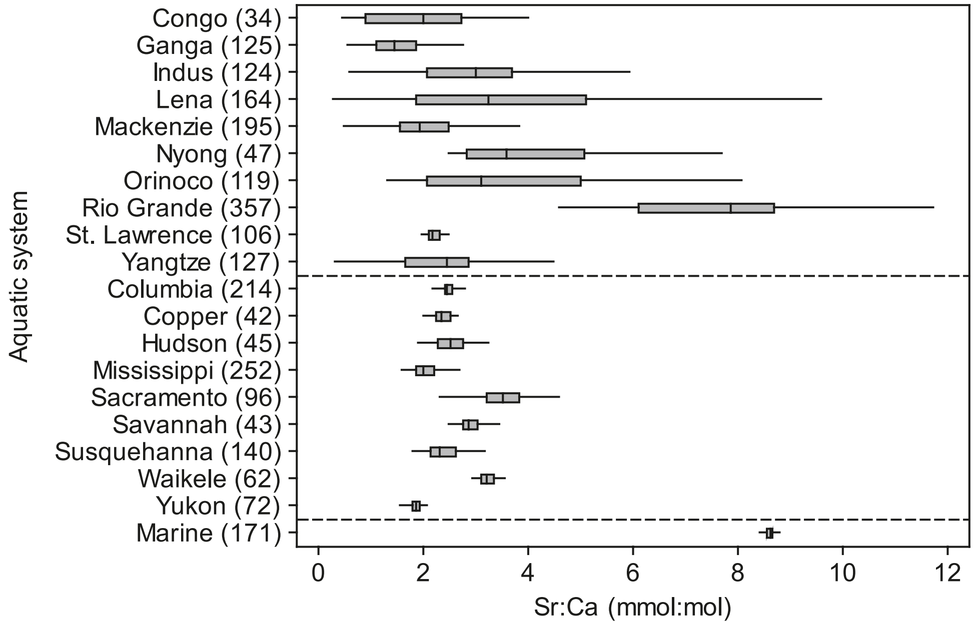


Fig. 3. Sr:Ca variability within 10 large river drainages (upper section), 10 lower mainstem reaches (middle section), and the marine environment (lower section). Sample sizes for each river and for the marine system are indicated in parentheses. All box plots in this paper include median line, interquartile range box, and whiskers that encompass more than 95% of data points. No outliers are shown.



tween freshwater and marine environments (e.g., Tzeng 1996; Howland et al. 2001; Brenkman et al. 2007). General trends in otolith Sr:Ca common to each category were illustrated with a representative selection of species. Several species were represented in both freshwater and diadromous categories, and the Sr:Ca profiles of some of these pairs are presented to illustrate category-specific patterns. Several families were represented by multiple species, and Sr:Ca profiles of some of these family groups are presented to illustrate common patterns. Several additional unique or unusual otolith Sr:Ca profiles are presented and discussed. Because the total number of sample points varied widely among otolith core-to-margin transects, profiles were created with Sr:Ca values plotted against the proportion of the core-to-margin transect for each point.

The partition coefficient for Sr was calculated as

$$D_{\mathrm{Sr}} = \left(\frac{\mathrm{Sr}}{\mathrm{Ca}}\,\mathrm{otolith}\right) \cdot \left(\frac{\mathrm{Sr}}{\mathrm{Ca}}\,\mathrm{water}\right)^{-1}$$

When used in otolith chemistry studies, it is an indicator of the osmoregulatory resistance that an element encounters

Fig. 4. Modeled estuary mixing curves of Sr:Ca versus salinity (psu) for (*a*) Indigirka, (*b*) Indus, (*c*) Mississippi, and (*d*) St. Johns rivers.

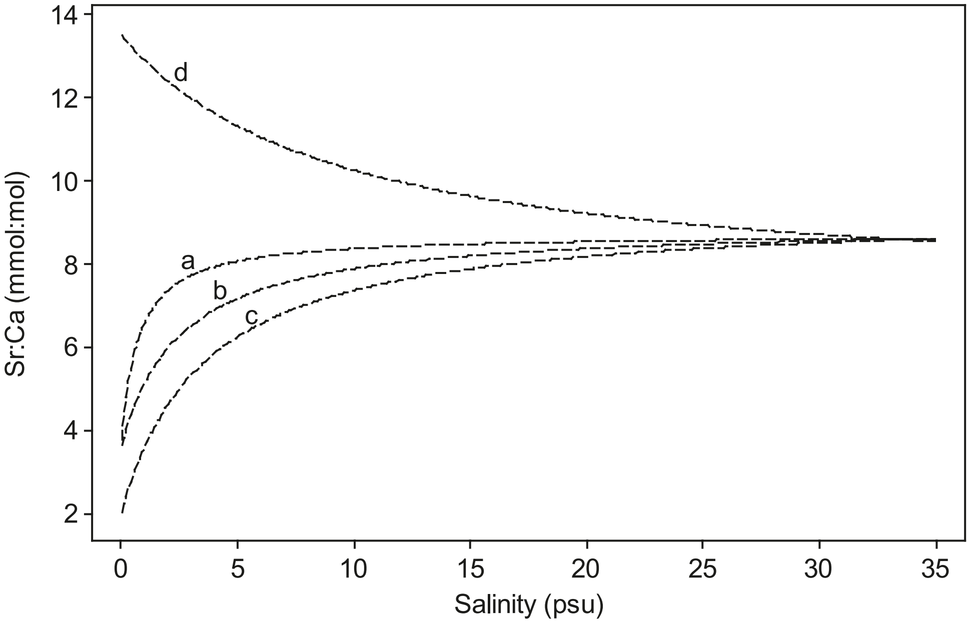
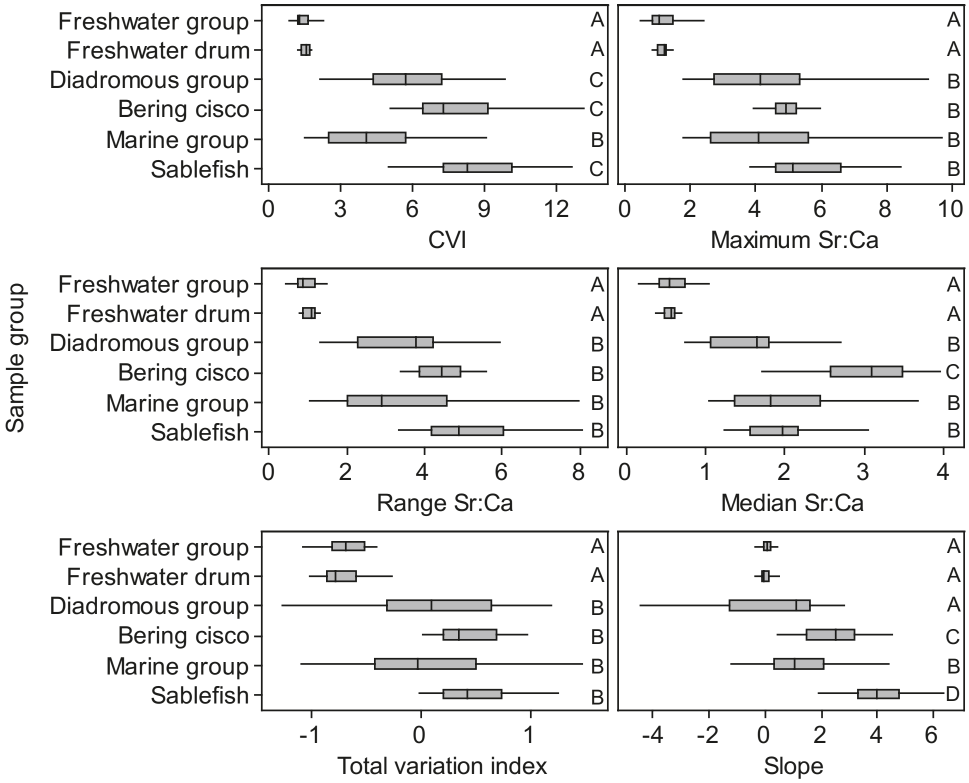


Fig. 5. Box plots illustrating characteristic patterns of otolith Sr and Sr:Ca variability, levels, and ontogenetic trends among freshwater, diadromous, and marine fish as indicated with CVI, Sr:Ca range, the total variation index, maximum and median Sr:Ca data, and slope coefficients. Lettering on the right of each panel indicates results of Tukey's multiple comparisons procedures. Sample groups that are similar are indicated with the same letter and those that are significantly different are indicated with different letters.

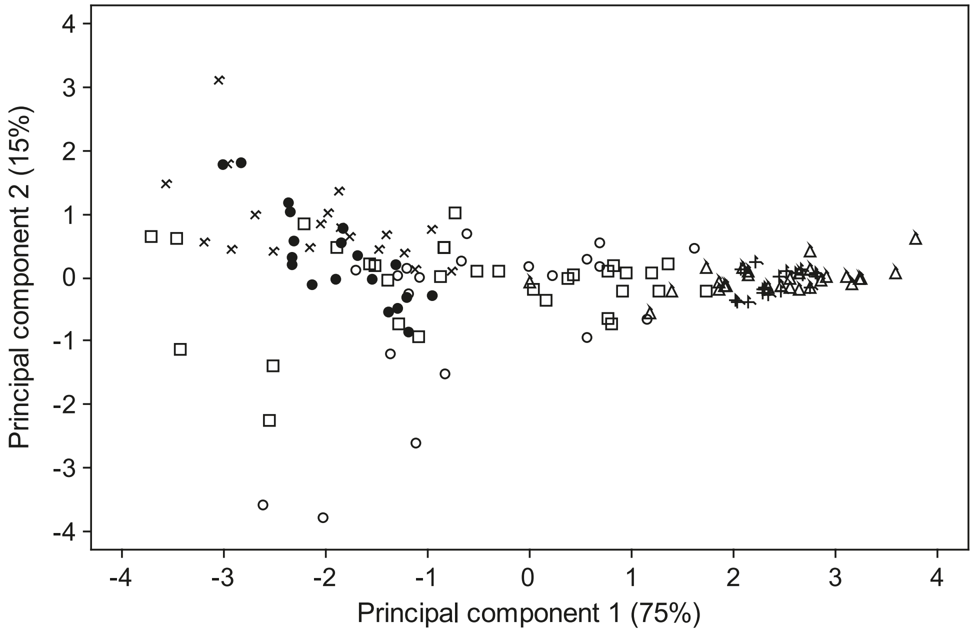


when moving from the water, through the blood, into the endolymph, and eventually to a precipitation site on the otolith. Values near one indicate little resistance relative to Ca, and values approaching zero indicate high resistance (Campana 1999). Water Sr:Ca levels experienced by freshwater and diadromous species in this study were not known with enough confidence to calculate D_{Sr} values. Marine fish, however, were considered to have experienced a relatively constant Sr:Ca environment of approximately 8.61 mmol:mol throughout life. A D_{Sr} profile was therefore prepared for each marine fish, including the sablefish group. Lifetime variability of D_{Sr} values for the marine species were illu-

Table 1. Eigen analysis of the correlation matrix and loading table for the first five principal components of log-transformed CVI, range, median, and maximum Sr:Ca data, and the total variation index and slope coefficient factors from the otoliths of freshwater, diadromous, and marine fish species.

Variable	PC1	PC2	PC3	PC4	PC5
Eigenvalue	4.47	0.92	0.34	0.23	0.05
Proportion	0.75	0.15	0.06	0.04	0.01
Cumulative proportion	0.75	0.90	0.95	0.99	1.00
CVI	–0.46	0.03	0.23	–0.38	0.74
Range Sr:Ca	–0.46	–0.05	0.13	–0.36	–0.29
Total variation index	–0.36	–0.57	0.35	0.65	0.03
Median Sr:Ca	–0.41	0.08	–0.84	0.29	0.18
Maximum Sr:Ca	–0.46	–0.08	–0.08	–0.25	–0.57
Slope	–0.27	0.81	0.32	0.39	–0.10

Fig. 6. Ordination diagram of the first two components from a principal components analysis of log-transformed CVI, range, median, and maximum Sr:Ca data, and the total variation index and slope coefficient factors from the otoliths of six groups of fish; freshwater species (△), freshwater drum (+), diadromous species (○), Bering cisco (●), marine species (□), and sablefish (×). Approximately 90% of the variability among groups was encompassed by these two principal components. One outlier from the diadromous group was located outside of the scales presented at $X = –5.90$, $Y = –6.42$.



strated with box plots and discussed. Maximum otolith Sr:Ca levels of marine species were thought to reflect their minimum osmoregulatory resistance to Sr while experiencing marine Sr:Ca levels. Distributions of maximum D_{Sr} values for marine species and for the sablefish group were illustrated with a box plot.

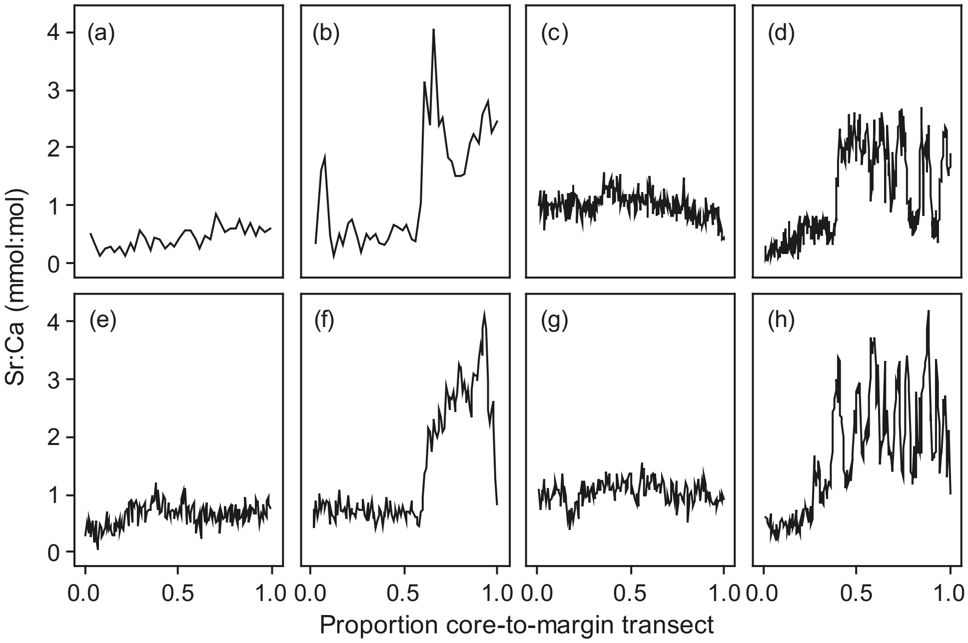
Results

Water chemistry

River and lake environments varied across a wider range of Sr:Ca than did marine environments (Fig. 2). Median river (2.39) and lake (1.92) Sr:Ca levels were much lower than the marine level (8.61). Sr:Ca levels ranged from 0.27 to 19.18 in rivers, 0.20 to 5.02 in lakes, and 8.17 to 8.87 in marine water. Less than 3% of the 786 rivers reviewed here, and none of the lakes, had median Sr:Ca levels that exceeded minimum marine levels. Sr:Ca variability within entire drainages was clearly greater than in limited reaches of drainages (Fig. 3), and marine waters were comparatively invariable.

Mixing curves modeled across the estuarine salinity gradients from the four selected rivers revealed a high rate of Sr:Ca change at low salinity levels that declined exponentially as salinity increased (Fig. 4). Surge and Lohmann (2002) derived this same pattern empirically across three estuaries in Florida, and Zimmerman (2005) measured it in his experimental Sr:Ca habitats as well. Rivers with lower dissolved-solute concentrations (Indigirka and Indus rivers) approached marine Sr:Ca levels more precipitously than those with higher dissolved-solute concentrations (Mississippi and St. Johns rivers). The mixing curve for the St.

Fig. 7. Sr:Ca profiles of four pairs of freshwater (first and third columns) and anadromous (second and fourth columns) conspecifics including (*a* and *b*) threespine stickleback (*Gasterosteus aculeatus*), (*c* and *d*) striped bass (*Morone saxatilis*), (*e* and *f*) kokanee and sockeye salmon (*Oncorhynchus nerka*), and (*g* and *h*) humpback whitefish (*Coregonus pidschian*).



Johns River, one of the rare rivers with Sr:Ca levels greater than marine levels, declined to the marine Sr:Ca level, whereas the other rivers rose to the marine level. These data indicate that diadromous fish moving through an estuary would experience greater Sr:Ca change between salinities 0 and 10, when they are hypertonic to the environment, than between salinities 10 and 35, as they become hypotonic to the environment.

Fish otoliths

Statistics

Initial ANOVA tests of all three otolith Sr and Sr:Ca variability statistics, the two otolith Sr:Ca level statistics, and the ontogenetic trend statistic among the six groups of fish were all highly significant ($P < 0.001$ in all tests). Subsequent contrasts between groups were significant at the family error level of $\alpha = 0.05$. All measures of variability and level indicated that freshwater species exhibited significantly less otolith Sr and Sr:Ca variability and significantly lower levels of otolith Sr:Ca than diadromous or marine species (Fig. 5). The freshwater species and freshwater drum groups exhibited similar measures of otolith Sr and Sr:Ca variability and otolith Sr:Ca level. Freshwater species groups exhibited no particular ontogenetic trend, as indicated by the slope statistic. The freshwater species and freshwater drum groups had similar mean slopes to the diadromous species group, which included several catadromous species, but had significantly lower mean slopes than the Bering cisco, marine species, and sablefish groups.

Diadromous and marine species groups exhibited general similarity in measures of Sr and Sr:Ca variability and Sr:Ca level, and although they differed significantly in mean slopes, all exhibited substantial variability in ontogenetic trends compared with the freshwater species groups (Fig. 5). All four diadromous and marine species groups had statistically similar range Sr:Ca and total variation index measures of Sr:Ca variation, and maximum measures of Sr:Ca levels. The marine species group had a significantly lower CVI statistic than other diadromous or marine species groups, which were similar. The Bering cisco group had a significantly higher median Sr:Ca statistic than other diadromous or marine species groups, which were similar. Mean slopes of Bering cisco, marine species, and sablefish groups were all positive and significantly greater than freshwater species groups.

Principal components analysis

The principal components analysis was effective at consolidating 90% of the essential variability of the six comparative measures that we examined into the first two principal components (Table 1). The ordination plot of the first two principal components illustrated the domains of, or area occupied by, each group relative to the others (Fig. 6). The freshwater species and freshwater drum groups shared a common domain in a relatively discrete region of the plot. The Bering cisco and sablefish groups shared a common regional domain that substantially intersected with the domains of diadromous and marine species groups, but not with the domains of the freshwater species groups. The diadromous and marine species groups occupied the largest regional domains in the plot, intersecting with each other over a substantial region, and with all other groups, except freshwater drum, to some extent. Consistent with the statistical results of our six measures of Sr and Sr:Ca variability, level, and ontogenetic trends, the principal components analysis illustrated that the Sr:Ca profiles of the freshwater species groups were distinctly different than those of the diadromous and marine species groups, which were more similar than they were different.

Sr:Ca profiles

Sr:Ca profiles of pairs of freshwater and anadromous conspecifics revealed a visually distinctive pattern of Sr:Ca variation between categories. All four of the Sr:Ca profiles from the freshwater category had relatively low Sr:Ca levels and low variation (Fig. 7, first and third columns). This contrasted with the Sr:Ca profiles of their anadromous conspecifics that had low Sr:Ca levels initially, reflecting their natal origins in fresh water, followed by significantly elevated Sr:Ca levels later, reflecting their subsequent migrations to marine environments (Fig. 7, second and fourth columns). The Sr:Ca spike in the core region of the anadromous threespine stickleback (*Gasterosteus aculeatus*; Fig. 7*b*) is thought to be an indicator of an anadromous mother, a phenomenon documented for other anadromous species (Kalish 1990; Volk, et al. 2000; Zimmerman and Reeves 2000). The oscillating pattern of Sr:Ca peaks and nadirs in the profiles of the anadromous striped bass (*Morone saxatilis*; Fig. 7*d*) and humpback whitefish (*Coregonus pidschian*; Fig. 7*h*) indicated repeated migrations between marine and freshwater environments as discussed by Secor and Piccoli (2007) for striped bass.

Family groups of species exhibited similar ontogenetic patterns of Sr:Ca variability, level, and distribution, at least within life history categories. Rockfish species (Sebastidae; Fig. 8, top row), exhibited consistently low Sr:Ca levels compared with many other marine species as reflected by maximum Sr:Ca levels of approximately 3 mmol:mol or less. Flatfish species (Pleuronectidae; Fig. 8, second row), exhibited greater variation than rockfish with distinct ontogenetic trends in their Sr:Ca profiles towards higher values later in life. The maximum Sr:Ca level within the flatfish samples was approximately 4 mmol:mol in Pacific halibut (*Hippoglossus stenolepis*; Fig. 8*f*). Sculpin species (Cottidae; Fig. 8, third row) included one freshwater and two marine representatives. The freshwater species, slimy sculpin (*Cottus cognatus*; Fig. 8*g*), exhibited a consistently low level of Sr:Ca with no ontogenetic trend. By contrast, the marine sculpins' Sr:Ca profiles ranged from low levels early in life to relatively high levels later in life that reached a maximum of approximately 8 mmol:mol in a fourhorn sculpin (*Triglopsis quadricornis*; Fig. 8*i*). Similar to the sculpins, cod species (Gadidae; Fig. 8, bottom row) included one freshwater and two marine representatives. Burbot (*Lota lota*) are classified in the family Gadidae by the American Fisheries Society (2004) but in the family Lotidae in Fishbase (2008). We placed burbot with Gadidae species in this figure to highlight the contrast between the patterns of otolith Sr:Ca exhibited by closely related freshwater and marine species. Burbot exhibited a relatively constant low level Sr:Ca profile with no ontogenetic trend (Fig. 8*j*). The marine cod species ranged from very low levels early in life to relatively high levels later in life that reached a maximum of approximately 9.7 mmol:mol in a Pacific cod (*Gadus macrocephalus*; Fig. 8*l*). These data suggest that closely related species within a life history category exhibit similar patterns of otolith Sr:Ca variability, level, and distribution.

The St. Johns River in northern Florida has an extraordinarily high level of Sr:Ca, with a median value of 13.83 mmol:mol (USGS 2007). Several Clupeidae species spawn in the St. Johns River, including anadromous blueback herring (*Alosa aestivalis*) and hickory shad (*A. mediocris*) (Harris et al. 2007). Otolith Sr:Ca profiles of blueback herring and hickory shad from the St. Johns River are presented in contrast to the profile of an anadromous American shad (*A. sapidissima*) from the Hudson River, which has a median Sr:Ca level of 2.49 mmol:mol (USGS 2007). The ontogenetic patterns of Sr:Ca for the American shad (Fig. 9*a*) is consistent with that observed in other anadromous species (see Fig. 7), with low levels in the otolith core region reflecting the chemistry of the freshwater natal environment followed by a distinct rise in Sr:Ca levels reflecting migration to sea. The blueback herring (Fig. 9*b*) and the hickory shad (Fig. 9*c*) from the St. Johns River exhibited Sr:Ca patterns more typical of catadromous species (see Fig. 10), with high levels in their core regions reflecting the unusually high Sr:Ca environment of their natal river followed by a drop in otolith Sr:Ca when they migrated to sea. These data support Kraus and Secor's (2004) contention that water Sr:Ca molar ratios are more predictive than salinity of otolith Sr:Ca levels.

Sr:Ca data from the otolith of a black crappie (*Pomoxis nigromaculatus*) exhibited the greatest variability and the highest levels of all freshwater species examined. It was an outlier in the principal components analysis (Fig. 6, the triangle located close to the 0, 0 position), grouping more with the diadromous and marine species groups than with the freshwater species group. The Sr:Ca profile of the black crappie (Fig. 9*e*) is presented in contrast with the profiles of an Alaska blackfish (*Dallia pectoralis*; Fig. 9*d*), exhibiting a typical freshwater fish profile, and an Arctic cisco (*Coregonus autumnalis*; Fig. 9*f*), exhibiting a typical anadromous fish profile. The oscillating pattern of Sr:Ca variation in the profile of the black crappie is clearly more similar in form and magnitude to that from anadromous species than from freshwater species. The black crappie used in this study was captured in Echo Canyon Reservoir in the state of Colorado, USA. The reservoir goes through a dramatic annual cycle of high water after the annual snowmelt, followed by a progressive decline in water level through the rest of the year. Although the Sr and Ca chemistry of Echo Canyon Reservoir is not known, it is thought that the variation in annual water level results in dramatic cycles of diluted and concentrated dissolved solutes, which in turn are reflected in the otolith Sr:Ca profiles of the fish living there.

High ontogenetic variation and maximum levels of otolith Sr:Ca were observed in the Sr:Ca profiles for some diadromous and marine species. The highest otolith Sr:Ca value recorded among the species in this study, 21.80 mmol:mol, was from an anadromous broad whitefish (*Coregonus nasus*; Fig. 10*c*) from Northwest Alaska. Quantitative analyses of this otolith showed that the maximum concentration of elemental Sr was approximately 17 900 mg:kg (95% CI = 17 300 – 18 500 mg:kg). The core region had a uniformly low level of Sr:Ca, consistent with the freshwater natal environment of the species, followed by a region of dramatic peaks and nadirs, consistent with multiple migrations between environments. The fish apparently returned to freshwater to stay at some point later in life, based on a drop in Sr:Ca back towards natal levels. The Sr:Ca profiles of two catadromous species, Atlantic tarpon (*Megalops atlanticus*;

Fig. 8. Sr:Ca profiles of three species within each of four families. Sebastidae species (top row) include (*a*) rougheye rockfish (*Sebastes aleutianus*), (*b*) yelloweye rockfish (*S. ruberrimus*), and (*c*) quillback rockfish (*S. maliger*). Pleuronectidae species (second row) include (*d*) Bering flounder (*Hippoglossoides robustus*), (*e*) Arctic flounder (*Liopsetta glacialis*), and (*f*) Pacific halibut (*Hippoglossus stenolepis*). Cottidae species (third row) include (*g*) slimy sculpin (*Cottus cognatus*), (*h*) Arctic staghorn sculpin (*Gymnocanthus tricuspis*), and (*i*) fourhorn sculpin (*Triglopsis quadricornis*). Gadidae species (fourth row) include (*j*) burbot (*Lota lota*; see discussion in text on family classification of burbot), (*k*) saffron cod (*Eleginus gracilis*), and (*l*) Pacific cod (*Gadus macrocephalus*). Note that the *Y* scale is consistent within family groups, but different among them.

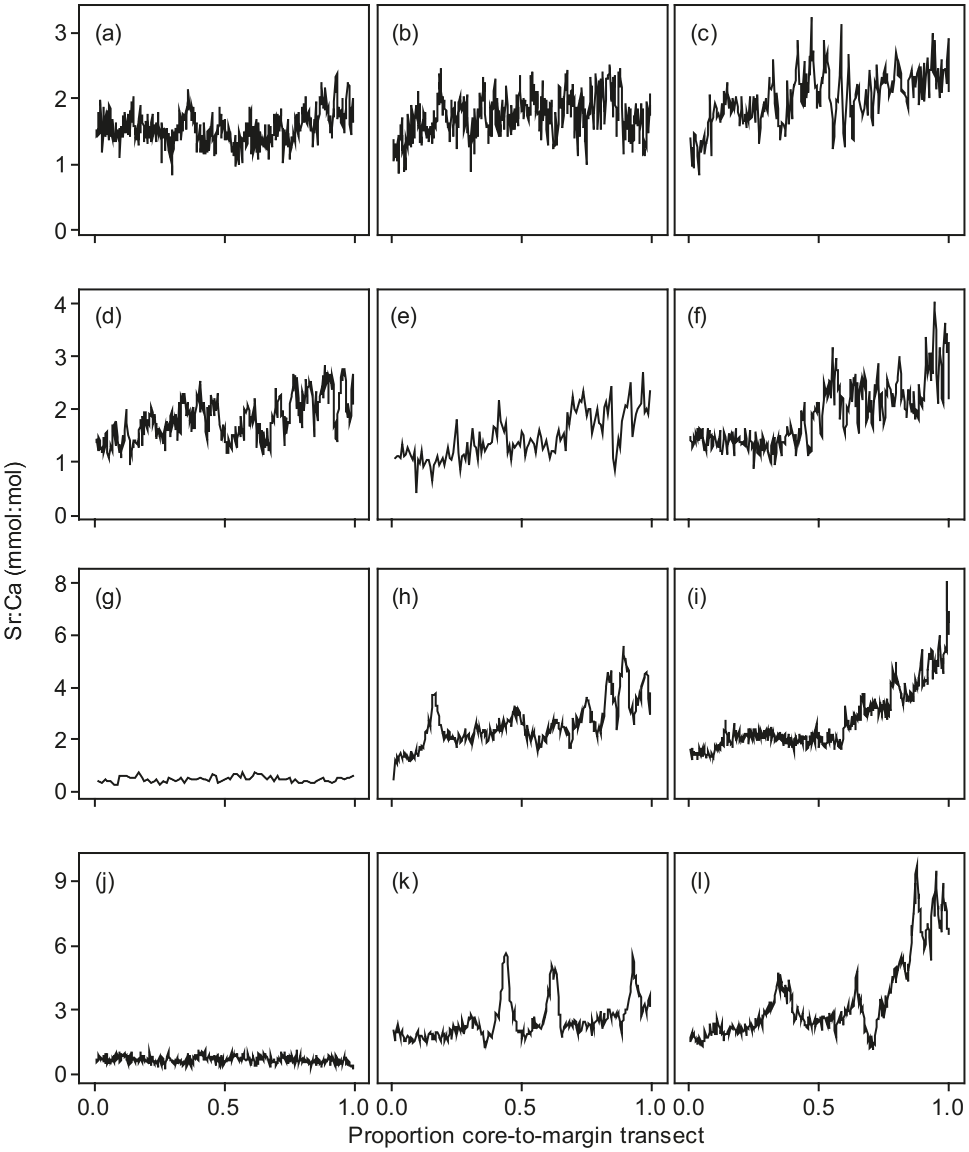


Fig. 10*a*) and European eel (*Anguilla anguilla*; Fig. 10*b*), revealed high levels of Sr:Ca in the core regions of their otoliths, consistent with their marine origins, followed by precipitous declines in Sr:Ca to low levels, consistent with their migrations into freshwater environments. Atlantic tarpon are not obligated to migrate into freshwater environments, but the sample in this study was collected from Lake Nicaragua, a large freshwater lake located approximately 190 km by river from the sea.

The highest otolith Sr:Ca value recorded among marine species in this study, 13.93 mmol:mol, was from the core region of a stout eelblenny (*Anisarchus medius*; Fig. 10*f*) collected during an offshore, benthic-sampling expedition in the Chukchi Sea. Quantitative analyses of this otolith showed that the maximum concentration of elemental Sr was approximately 11 500 mg:kg (95% CI = 11 000 – 12 000 mg:kg). The Sr:Ca profile of a sablefish (Fig. 10*d*) exhibited an ontogenetic pattern similar to that observed in anadromous species such as the humpback whitefish (Fig. 7*h*) presented earlier, with low Sr:Ca levels in the core region, followed by an oscillating series of peaks and nadirs through the rest of its life. The Sr:Ca profile of an Antarctic toothfish (*Dissostichus mawsoni*; Fig. 10*e*) exhibited an ontogenetic trend and maximum level of otolith Sr:Ca similar to those of the fourhorn sculpin (Fig. 8*i*) and Pacific cod (Fig. 8*l*) presented earlier. They all had low levels of Sr:Ca in the core regions followed by progressive increases in Sr:Ca that attained maximum levels in excess of 8 mmol:mol late in life.

Fig. 9. Sr:Ca profiles of six anadromous and freshwater species that illustrate some unusual effects of extraordinary freshwater environments on otolith chemistry. The first row highlights three anadromous Clupeidae species: (*a*) American shad (*Alosa sapidissima*) came from the Hudson River, which has a median Sr:Ca level of 2.49 mmol:mol; (*b*) blueback herring (*A. aestivalis*) and (*c*) hickory shad (*A. mediocris*) originated in the St. Johns River in Florida, which has an unusually high median Sr:Ca level of 13.83 mmol:mol. The second row includes Sr:Ca profiles of (*d*) Alaska blackfish (*Dallia pectoralis*), a typical freshwater species, (*e*) black crappie (*Pomoxis nigromaculatus*), a freshwater species captured in an impoundment that experiences widely fluctuating water level cycles each year, and (*f*) Arctic cisco (*Coregonus autumnalis*), a typical diadromous fish.

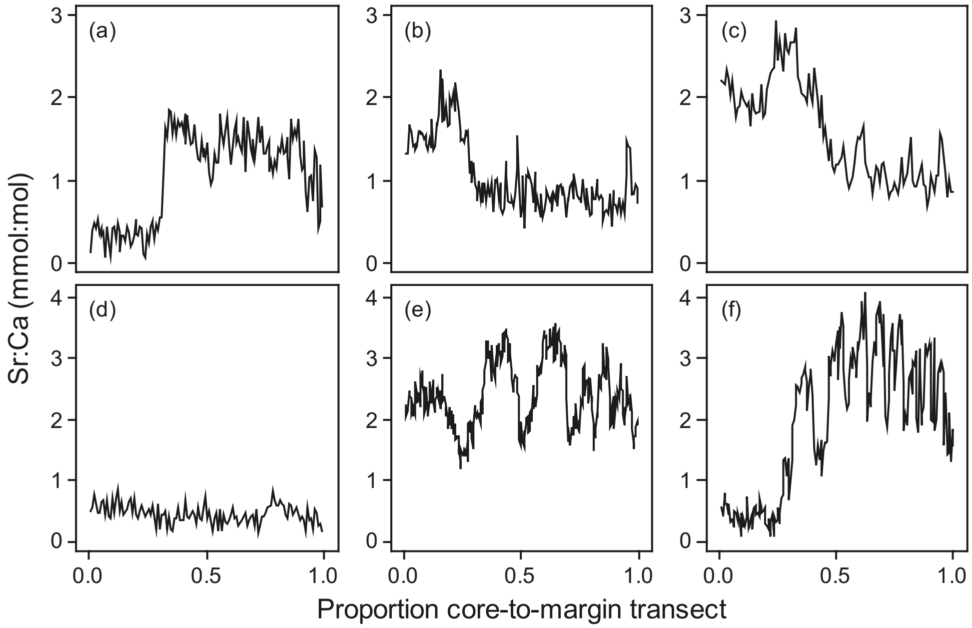


Fig. 10. Sr:Ca profiles of diadromous (top row) and marine (bottom row) species with unusually high Sr:Ca variation and high maximum Sr:Ca levels. Note that the *Y* scale is unique for each profile. (*a*) Atlantic tarpon (*Megalops atlanticus*) and (*b*) European eel (*Anguilla anguilla*) are catadromous and (*c*) broad whitefish (*Coregonus nasus*), which had the highest maximum Sr:Ca value of any fish examined (21.80 mmol:mol), is anadromous. The Sr:Ca profile of the sablefish had the appearance of a typical anadromous species such as the humpback whitefish, with relatively low Sr:Ca levels in the core followed by a series of oscillating peaks and nadirs across the rest of the profile. (*e*) Antarctic toothfish (*Dissostichus mawsoni*) exhibited a progressive ontogenetic trend towards very high Sr:Ca levels that peaked at over 9 mmol:mol. (*f*) Stout eelblenny (*Anisarchus medius*) had extraordinarily high Sr:Ca levels in the core region of its otolith (almost 14 mmol:mol).

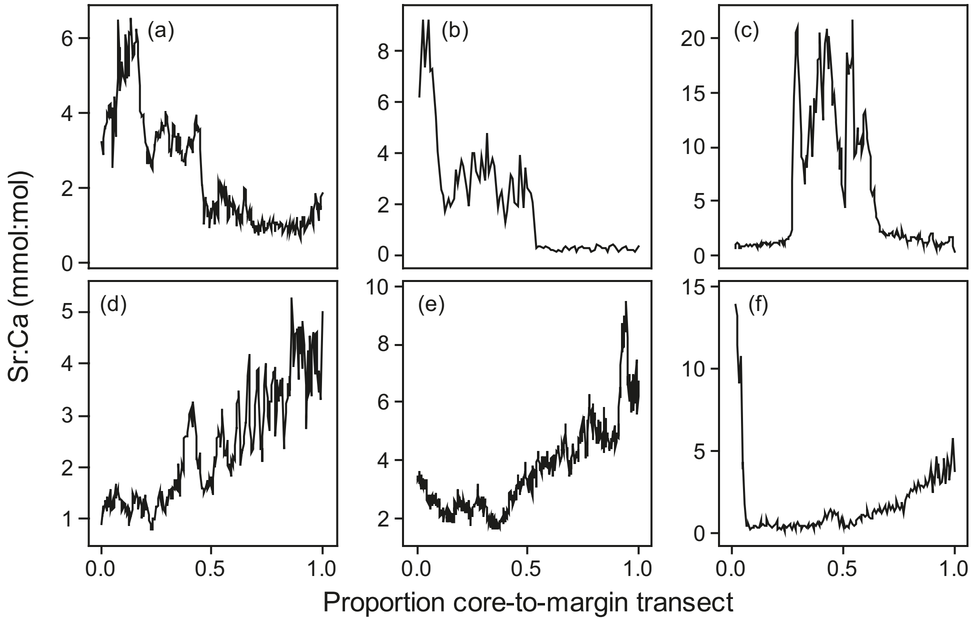
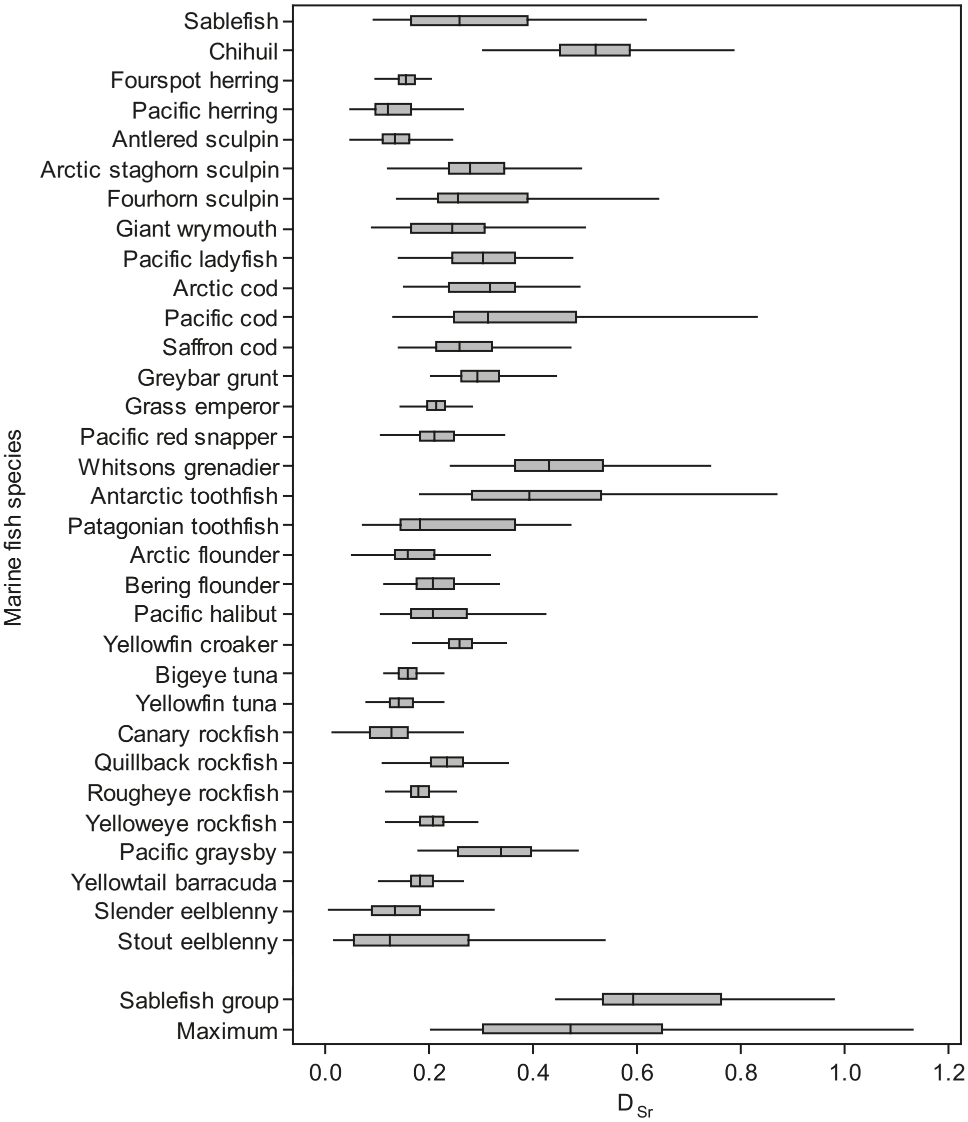


Fig. 11. Box plots illustrating the variability of D_{Sr} in marine fish (ordered as in Appendix B). The distribution of maximum D_{Sr} for the sablefish and marine species groups are displayed in the lower two box plots. Note that no outliers are presented with these box plots for clarity due to scaling issues. As a result, the maximum D_{Sr} box plot extends beyond the upper range of those for individual fish.



D_{Sr}

Substantial variability of D_{Sr} values was evident within individual otoliths of marine species, as well as among species (Fig. 11). Maximum D_{Sr} for marine species ranged from 0.20 for the fourspot herring (*Herklotsichthys quadrimaculatus*) to 1.62 for the stout eelblenny. Maximum D_{Sr} for the sablefish species group ranged from 0.44 to 0.98, well within the range for the marine species group. The average level of the statistic was 0.54 for the marine species group and 0.66 for the sablefish group. Otolith Sr:Ca levels greater than 8.61 in marine species produce D_{Sr} greater than 1, indicating that Sr concentration is being enhanced in the endolymph relative to marine Sr:Ca levels or that Ca movement into the endolymph is being specifically restricted. Three marine species had maximum Sr:Ca levels greater than 8.61. Only two, the stout eelblenny and the Pacific cod, had sufficiently high maximum Sr:Ca levels that the difference could not be attributed to error in the measurements of otolith Sr and Ca concentrations.

Discussion

The paradigm that water chemistry is the primary factor influencing otolith chemistry appears to apply reasonably well to freshwater and diadromous species and less well to marine species, at least for Sr:Ca. Freshwater species had the lowest otolith Sr:Ca levels of the three life history groups, which was expected. They exhibited significantly less lifetime otolith Sr:Ca variation than diadromous or marine species, even though marine species were expected to exhibit the least variability. Marine species exhibited nearly the same otolith Sr:Ca variability as diadromous species, which was unexpected given the relative homogeneity of Sr:Ca in marine environments and the high variability of environmental Sr:Ca experienced by diadromous fish. Diadromous and marine species groups exhibited similar median and maximum levels of otolith Sr:Ca. Diadromous fish were expected to have lower median levels than marine fish, which these data did not support, and similar maximum levels, which these data did support. All measures of otolith

Sr:Ca variability and level between freshwater and diadromous species were consistent with expectations. Inconsistencies with expected otolith Sr:Ca variability between marine and freshwater species and marine and diadromous species, as discussed above, suggest that factors other than water chemistry influence Sr:Ca variation in otoliths of marine species, a concept previously considered by Secor and Rooker (2000).

Controlled laboratory experiments testing the effects of water chemistry and other environmental factors on otolith chemistry have used juvenile fish almost exclusively with the explicit or implied assumption that their findings applied to the species through life. The reasons for using juvenile fish are obvious, particularly for long-lived species: large numbers of small individuals can be reared in various treatments and the material that precipitates during treatment can easily be identified and sampled (e.g., Zimmerman 2005). A shortcoming of using juveniles to identify factors influencing lifetime patterns of trace element incorporation in otoliths, analogous to extending a regression line beyond the data range, became apparent when ontogenetic trends in otolith chemistry were reported for older fish living in the relatively homogeneous marine environment (e.g., Brophy et al. 2004; Morales-Nin et al. 2005). We identified positive ontogenetic trends in otolith Sr:Ca from most of the marine species examined in this study. Extreme otolith Sr:Ca differences between core and margin regions of marine species exceeded 6 mmol:mol, which is comparable with extreme differences for diadromous species. This magnitude of variation can be explained based on water chemistry for diadromous species but not for marine species.

Based on his work on seasonal variation in blood and endolymph chemistry of a marine fish, Kalish (1991) argued that physiology was a major factor influencing otolith chemistry. He proposed that the concentration of dissolved proteins in the blood affected the availability of dissolved cations, including Sr, to the endolymph because of the tendency of the cations to bind with proteins. A higher concentration of proteins in the blood resulted in less dissolved cations being available to the endolymph and the precipitating otolith. He presented data indicating that the concentration of dissolved proteins in the blood was related to physiological stages associated with life history events such as feeding periods and gonad development. Although these events were correlated with temperature, Kalish (1991) argued that temperature influenced physiology, which in turn affected the availability of Sr to the otoliths, rather than affecting the kinetic energy of dissolved ions, which is considered to be a primary mechanism for temperature effects of abiotic precipitation of aragonite (Kinsman and Holland 1969).

Kinsman and Holland (1969) showed that the coprecipitation of Sr in abiotic aragonite was in equilibrium with ambient water chemistry in a temperature-dependent manner. Increasing temperature increased the kinetic energy of ions in solution. The incorporation of ions into the precipitating mineral created a microzone concentration gradient that was repopulated through diffusion at a rate described by the distribution coefficient, which was influenced by temperature. They estimated a D_{Sr} of 1.12 for abiotic aragonite precipitated at 25 °C and determined that there was a negative correlation with temperature. Assuming similar equilibrium dynamics for biogenic aragonite, the D_{Sr} of coral aragonite was used to estimate historical ocean surface water temperatures (Smith et al. 1979; Beck et al. 1992; de Villiers et al. 1994). More recent work suggested that algal symbionts with some coral species were responsible for as much as 65% of the observed variation in Sr:Ca, complicating what appeared to be a simple calculation of previous water temperature from the chemistry of coral aragonite (Cohen et al. 2002). Similar efforts to correlate temperature and otolith Sr:Ca in fish have produced ambiguous results overall, indicating significant physiological controls on otolith chemistry that appear to vary considerably by species and perhaps through ontogeny (i.e., Sadovy and Severin 1994; Martin et al. 2004; Rooker et al. 2004).

Campana (1999) discussed temperature, major life history transitions, somatic growth rate, and the rate of crystal formation as factors other than water chemistry that may influence otolith Sr:Ca variation in a homogenous environment such as the sea. Somatic growth rate is positively correlated with overall protein synthesis in fish. Campana (1999) proposed that high rates of system-wide protein synthesis extended to endolymph proteins, which are thought to dictate otolith growth. High growth rates are thought to reduce Sr incorporation into otoliths, whereas low growth rates are thought to enhance Sr incorporation (e.g., Sadovy and Severin 1994). Somatic growth rate may be influenced by temperature or life history events such as metamorphosis or spawning or simply through ontogeny as a long-lived fish approaches maximum size. Although temperature variation and physiological events may be responsible for the high otolith Sr:Ca variability observed in many of the marine species examined here, freshwater species that experience similar lifetime temperature variation and physiological events do not exhibit similarly high otolith Sr:Ca variation. It is clear that the factors affecting Sr incorporation into fish otoliths differ fundamentally in effect or magnitude for the three life history categories of fish.

Data presented here demonstrate that there is no unified theory of Sr incorporation in fish otoliths that can be applied to all fish everywhere. Factors influencing Sr incorporation into fish otoliths are different in either effect or magnitude for different species, families, and life history categories. The positive correlation of water Sr:Ca on otolith Sr:Ca for diadromous fish moving between freshwater and marine environments appears to be universal, although the magnitude of the effect may vary by species (Secor and Rooker 2000; Zimmerman 2005) or family. Our water chemistry review indicated that the marine Sr:Ca environment was more homogeneous than either freshwater or brackish environments. Therefore, factors influencing otolith Sr:Ca variation in marine species are more likely to be physiological in nature, as discussed by Kalish (1991), Campana (1999), and Secor and Rooker (2000), rather than the result of exposure to heterogenous environments. Physiological factors do not appear to influence otolith Sr:Ca variation in freshwater species or the influence may be so minor that it is not recognized. Physiological factors may have an influence on otolith Sr:Ca variation in diadromous species when they are in the sea and hypotonic to the environment like marine species. If so, it is not identified because we almost always interpret otolith Sr:Ca variation in diadromous species as an indication of migration between freshwater, estuarine, and marine environments (Howland et al. 2001; Arai et al. 2003; Yang et al. 2006). Despite this possibility, most scientists are comfortable interpreting the migration histories of freshwater and diadromous species based on their Sr:Ca profiles. The distinct patterns observed in the Sr:Ca profiles of marine species are chemical records of life history events that we are not yet able to interpret with confidence. Carefully designed field or long-term experimental studies may be required to identify major factors responsible for otolith Sr:Ca variation in marine species, which would allow interpretation of the life history stories they contain.

Acknowledgements

This investigation would not have been possible without the contributions of otolith samples from the collections of many different fisheries scientists and other interested individuals. They include J. Adams (US Fish and Wildlife Service (USFWS)), J. Akaran (USFWS), J. Baker (US Geological Survey (USGS)), N. Bickford (University of Alaska Fairbanks), B. Carter (USFWS), F. DeCicco (Alaska Department of Fish and Game (ADFG)), N. de Graff (Cannic-a-nick Environmental Sciences, Canada), P. Horn (National Institute of Water and Atmospheric Research (NIWAR), New Zealand), K. Howland (Fisheries and Oceans Canada), K. Limburg (State University of New York), S. Maclean (Alaska Department of Natural Resources), P. Martinez (Colorado Division of Wildlife), R. McBride (Florida Fish and Wildlife Conservation Commission), A. McDougall (Northern Fisheries Center, Australia), M. Millard (USFWS), J. Miller (Mequon, Wisconsin), J. Moreland (Seward Sealife Center, Alaska), R. Morris (Colorado Division of Wildlife), K. Munk (ADFG), K. Niemela (USFWS), T. Otis (ADFG), T. Reinert (Georgia Cooperative Fish and Wildlife Research Unit), C. Sutton (NIWAR, New Zealand), F. Von Hippel (University of Alaska Anchorage), J. Wexler (Inter-American Tropical Tuna Commission, California), and C. Zimmerman (USGS). Water chemistry data that were not presented in Alexander et al. (2001) were graciously provided by J. Alexander. Constructive reviews of two earlier drafts helped to focus, refine, and improve this manuscript. We greatly appreciate these material, data, and conceptual contributions.

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Appendix A

Table A1. Literature sources of water chemistry data, habitat types, and geographic regions examined.

Citation	Habitat	Geographic region
Alexander et al. 2001	River	Australia
Andersson et al. 1994	River	Europe
Blum et al. 1994	River	North America
Cameron et al. 1995	River	North America
Culkin and Cox 1966	Marine	Oceans worldwide
Dalai et al. 2003	River	Asia
Dessert et al. 2001	River	Asia
de Villiers 1999	Marine	Atlantic and Pacific oceans
de Villiers et al. 1994	Marine	Atlantic and Pacific oceans
Edmond et al. 1995	River	South America
Edmond et al. 1996	River	South America
Fabricand et al. 1967	Marine	Atlantic Ocean
Faure et al. 1967	Marine, river, and lake	North America and Atlantic Ocean
Gaillardet et al. 1997	River	South America
Gislason et al. 1996	River	Iceland
Goldstein and Jacobsen 1987	River and lake	Worldwide
Han and Liu 2004	River	Asia
Huh and Edmond 1999	River	Asia
Huh et al. 1998a	River	Asia
Huh et al. 1998b	River	Asia
Karim and Veizer 2000	River	Asia
Katz et al. 1977	River	Middle East
Krishnaswami et al. 1992	River	Asia
Livingston 1963	River and lake	North America and Europe
Martin and Meybeck 1979	River	Worldwide
Millot et al. 2003	River	North America
Moon et al. 2007	River	Asia
Negrel et al. 1993	River	Africa
Odum 1957	River and lake	North America and Pacific Islands
Pande et al. 1994	River and lake	Asia
Petelet et al. 1998	River	Europe
Qin et al. 2006	River	Asia
Reeder et al. 1972	River and lake	North America
Trivedi et al. 1995	River	Asia
USGS 2007	River	North America
Viers et al. 2000	River	Africa
Wadleigh et al. 1985	River	North America
Wu et al. 2005	River and lake	Asia
Xu and Liu 2007	River	Asia
Yang et al. 1996	River and lake	North America

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Appendix B

Table B1 follows.

Table B1. Freshwater, diadromous, and marine fish species examined in this study ordered by family and common name.

Freshwater		Diadromous		Marine	
Common name	Species	Common name	Species	Common name	Species
Longnose sucker	*Catostomus catostomus*	European eel	*Anguilla anguilla*	Sablefish	*Anoplopoma fimbria*
Black crappie	*Pomoxis nigromaculatus*	Barramundi	*Lates calcarifer*	Chihuil	*Bagre panamensis*
Green sunfish	*Lepomis cyanellus*	American shad	*Alosa sapidissima*	Fourspot herring	*Herklotsichthys quadrimaculatus*
Smallmouth bass	*Micropterus dolomieu*	Blueback herring	*Alosa aestivalis*	Pacific herring	*Clupea pallasii*
Prickly sculpin	*Cottus asper*	Hickory shad	*Alosa mediocris*	Antlered sculpin	*Enophrys diceraus*
Slimy sculpin	*Cottus cognatus*	Atlantic tarpon	*Megalops atlanticus*	Arctic staghorn sculpin	*Gymnocanthus tricuspis*
Lake chub	*Couesius plumbeus*	Ninespine stickleback	*Pungitius pungitius*	Fourhorn sculpin	*Triglopsis quadricornis*
Northern pike	*Esox lucius*	Threespine stickleback	*Gasterosteus aculeatus*	Giant wrymouth	*Cryptacanthodes giganteus*
Burbot	*Lota lota*	Striped bass	*Morone saxatilis*	Pacific ladyfish	*Elops affinis*
Threespine stickleback	*Gasterosteus aculeatus*	Rainbow smelt	*Osmerus mordax*	Arctic cod	*Boreogadus saida*
Channel catfish	*Ictalurus punctatus*	Arctic cisco	*Coregonus autumnalis*	Pacific cod	*Gadus macrocephalus*
Striped bass	*Morone saxatilis*	Bering cisco	*Coregonus laurettae*	Saffron cod	*Eleginus gracilis*
Yellow perch	*Perca flavescens*	Broad whitefish	*Corgonus nasus*	Greybar grunt	*Haemulon sexfasciatum*
Trout-perch	*Percopsis omiscomaycus*	Chinook salmon	*Oncorhynchus tshawytscha*	Grass emperor	*Lethrinus laticaudis*
Arctic char	*Salvelinus alpinus*	Coho salmon	*Oncorhynchus kisutch*	Pacific red snapper	*Lutjanus peru*
Arctic grayling	*Thymallus arcticus*	Dolly Varden	*Salvelinus malma*	Whitson’s grenadier	*Macrourus whitsoni*
Broad whitefish	*Coregonus nasus*	Humpback whitefish	*Coregonus pidschian*	Antarctic toothfish	*Dissostichus mawsoni*
Dolly Varden	*Salvelinus malma*	Inconnu	*Stenodus leucichthys*	Patagonian toothfish	*Dissostichus eleginoides*
Humpback whitefish	*Coregonus pidschian*	Least cisco	*Coregonus sardinella*	Arctic flounder	*Liopsetta glacialis*
Inconnu	*Stenodus leucichthys*	Sockeye salmon	*Oncorhynchus nerka*	Bering flounder	*Hippoglossoides robustus*
Kokanee	*Oncorhynchus nerka*	Steelhead	*Oncorhynchus mykiss*	Pacific halibut	*Hippoglossus stenolepis*
Lake trout	*Salvelinus namaycush*			Yellowfin croaker	*Umbrina roncador*
Lake whitefish	*Coregonus clupeaformis*			Bigeye tuna	*Thunnus obesus*
Least cisco	*Coregonus sardinella*			Yellowfin tuna	*Thunnus albacares*
Rainbow trout	*Oncorhynchus mykiss*			Canary rockfish	*Sebastes pinniger*
Round whitefish	*Prosopium cylindraceum*			Quillback rockfish	*Sebastes maliger*
Freshwater drum	*Aplodinotus grunniens*			Rougheye rockfish	*Sebastes aleutianus*
Alaska blackfish	*Dallia pectoralis*			Yelloweye rockfish	*Sebastes ruberrimus*
				Pacific graysby	*Cephalopholis panamensis*
				Yellowtail barracuda	*Sphyraena flavicauda*
				Slender eelblenny	*Lumpenus fabricii*
				Stout eelblenny	*Anisarchus medius*