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:

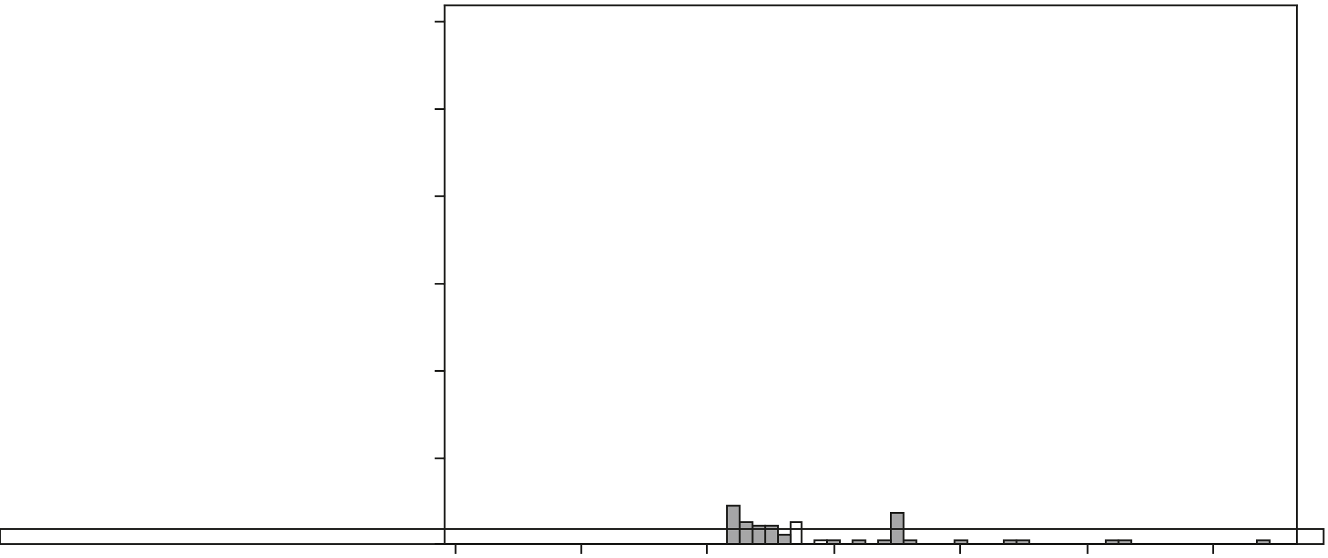
$$c_{ai} = [(c_{fi}) \times (1 - p)] + [(c_{mi}) \times (p)]$$

where c_a is the concentration (mg:kg) of element i in ambient estuarine water, c_f is the concentration of element i in freshwater, c_m is the concentration of element i in marine water, i represents dissolved Sr or Ca, and ambient salinity is $p \times 35$, 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) $mg \cdot kg^{-1}$, 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 tium 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: ( ) 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



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

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

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

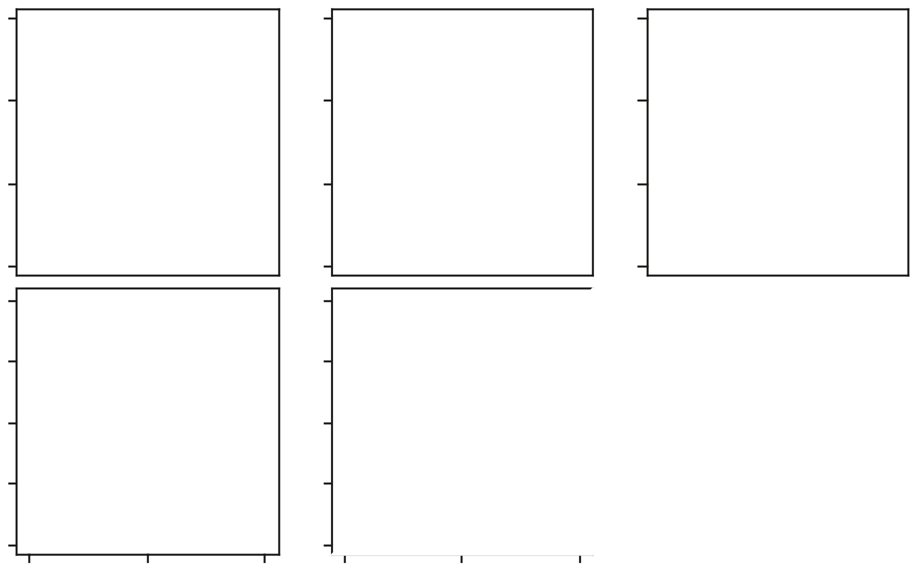
Mixing curves modeled across the estuarine salinity gradients from the four selected rivers revealed a high rate of Sr:Ca change at low salinity levels that declined exponentially as salinity increased (Fig. 4). Surge and Lohmann (2002) derived this same pattern empirically across three estuaries in Florida, and Zimmerman (2005) measured it in his experimental Sr:Ca habitats as well. Rivers with lower

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.

Sr:Ca profiles

Sr:Ca profiles of pairs of freshwater and anadromous conspecifics revealed a visually distinctive pattern of Sr:Ca var-

Fig. 10*a*) and European eel (*A*[illegible] *a a*[illegible] *a*; 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 environ-



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 (*e ı c ı . ad ac a-ı*) 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

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

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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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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	*Cat t cat t*	European eel	*A a a a*	Sablefish	*A a b a*
Black crappie	*P ac at*	Barramundi	*ate ca ca e*	Chihuil	*Ba e a a e*
Green sunfish	*e c a e*	American shad	*A a a d a*	Fourspot herring	*e t c t ad ac at*
Smallmouth bass	*c te d e*	Blueback herring	*A a ae t a*	Pacific herring	*C ea a a*
Prickly sculpin	*C tt a e*	Hickory shad	*A a ed c*	Antlered sculpin	*E d ce a*
Slimy sculpin	*C tt c at*	Atlantic tarpon	*e a at a t c*	Arctic staghorn sculpin	*ca t t c*
Lake chub	*C e be*	Ninespine stickleback	*t t*	Fourhorn sculpin	*ad c*
Northern pike	*E c*	Threespine stickleback	*a te te ac eat*	Giant wrymouth	*C taca t de a te*
Burbot	*ta ta*	Striped bass	*e a at*	Pacific ladyfish	*E a*
Threespine stickleback	*a te te ac eat*	Rainbow smelt	*O e da*	Arctic cod	*B e ad a da*
Channel catfish	*cta ctat*	Arctic cisco	*C e a t a*	Pacific cod	*ad ac ce a*
Striped bass	*e a at*	Bering cisco	*C e a ettae*	Saffron cod	*E e ac*
Yellow perch	*e ca a e ce*	Broad whitefish	*C a*	Greybar grunt	*ae e a c at*
Trout-perch	*P e c c a c*	Chinook salmon	*O c c t a t c a*	Grass emperor	*et at ca d*
Arctic char	*Sa e a*	Coho salmon	*O c c tc*	Pacific red snapper	*t a e*
Arctic grayling	*a a ct c*	Dolly Varden	*Sa e a a*	Whitson's grenadier	*ac t*
Broad whitefish	*C e a*	Humpback whitefish	*C e d c a*	Antarctic toothfish	*D t c a*
Dolly Varden	*Sa e a a*	Inconnu	*Ste d e c c t*	Patagonian toothfish	*D t c e e de*
Humpback whitefish	*C e d c a*	Least cisco	*C e a d e a*	Arctic flounder	*etta ac a*
Inconnu	*Ste d e c c t*	Sockeye salmon	*O c c e a*	Bering flounder	*de b t*
Kokanee	*O c c e a*	Steelhead	*O c c*	Pacific halibut	*te e*
Lake trout	*Sa e a a c*			Yellowfin croaker	*b a cad*
Lake whitefish	*C e c ea*			Bigeye tuna	*be*
Least cisco	*C e a d e a*			Yellowfin tuna	*a baca e*
Rainbow trout	*O c c*			Canary rockfish	*Seba te e*
Round whitefish	*P c d ace*			Quillback rockfish	*Seba te a e*
Freshwater drum	*A d t e*			Rougheye rockfish	*Seba te a e t a*
Alaska blackfish	*Da a ect a*			Yelloweye rockfish	*Seba te be*
				Pacific graysby	*Ce a a a e*
				Yellowtail barracuda	*S ae a a ca da*
				Slender eelblenny	*e ab c*
				Stout eelblenny	*A a c ed*