PUBLISHED VERSION

Gillanders, Bronwyn
Otolith chemistry to determine movements of diadromous and freshwater fish

Aquatic Living Resources, 2005; 18:291-300

Copyright © EDP Sciences 2005

PERMISSIONS

www.edpsciences.org/alr

Authors can make their article, published by EDP Sciences, available on their personal site, their institution's web site and Open Archive Initiative sites, provided the source of the published article is cited and the ownership of the copyright clearly mentioned. These must be not for profit sites. Reprint and postprint may be used (with the publisher's PDF). Authors are requested to create a link to the publisher's internet service. The link must be accompanied by the following text "The original publication is available at www.edpsciences.org/alr".

22 December 2010

http://hdl.handle.net/2440/16524

Aquat. Living Resour. 18, 291–300 (2005)
© EDP Sciences, IFREMER, IRD 2005
DOI: 10.1051/alr:2005033
www.edpsciences.org/alr

Aquatic
Living
Resources

Otolith chemistry to determine movements of diadromous and freshwater fish

Bronwyn M. Gillanders[a]

Southern Seas Ecology Laboratories, School of Earth and Environmental Sciences, Darling Building DP 418, University of Adelaide, SA 5005, Australia

Received 11 February 2005; Accepted 31 May 2005

Abstract – Determining the timing or frequency of movement of fish and the relative importance of different habitats is difficult. Advances in otolith chemical techniques and interpretations (including elemental ratios and stable isotopes) suggest that this is a powerful method for determining movement of fish. To date, the majority of applications have involved marine fish, however, otolith chemistry has the potential to determine movements of diadromous and freshwater fish; I therefore review freshwater applications of otolith chemistry in this paper. Despite some limitations regarding strontium:calcium (Sr:Ca) ratios (e.g. Sr concentration of the water is not always measured, Sr:Ca ratios in freshwater can exceed marine waters, and mixed results for the relationship between otolith Sr and salinity), they have been widely used for a variety of applications involving diadromous species and more recently freshwater fish. In addition, barium:calcium (Ba:Ca) ratios have recently been used to determine movements of diadromous and estuarine species, as ambient ratios are possibly linked to environmental flows. Several studies have also investigated the use of multielemental otolith composition to discriminate between groups of fish collected from different lake or river systems, but a wider range of applications are possible. Several applications of Sr isotopes have also been investigated, most of which is focused on salmonids (e.g. distinguishing fish from different river systems, determining movement history of individual fish). Relatively few studies have investigated the use of other isotopes (e.g. oxygen, sulphur) for determining movements. Otolith elemental ratios and stable isotopes have great potential to determine movements of freshwater species, with possible applications likely to increase as analytical technology improves.

Key words: Otolith chemistry / Fish / Trace element / Sr isotopes / Sr:Ca / Freshwater / Diadromous / Flow / Review

Résumé – **Déterminer les déplacements des poissons diadromes et d'eau douce par la chimie de l'otolithe.** Déterminer le moment où la fréquence des déplacements des poissons et l'importance relative de différents habitats est difficile. Le progrès dans les techniques de la chimie de l'otolithe et les interprétations (rapports des éléments chimiques élémentaires et ceux des isotopes stables) suggèrent qu'il s'agit de méthodes performantes pour déterminer les déplacements des poissons. La majorité des applications a été développée chez les poissons marins ; cependant, la chimie de l'otolithe a la capacité potentielle de déterminer les mouvements des poissons diadromes et d'eau douce. Ainsi, j'ai donc fait la synthèse des applications de la chimie de l'otolithe en milieu dulçaquicole. Malgré quelques limites concernant les rapports strontium:calcium (Sr:Ca) (la concentration en Sr dans l'eau n'est pas toujours mesurée, les rapports Sr:Ca en eau douce peuvent excéder ceux en eau de mer, avec divers résultats pour les relations entre le Sr de l'otolithe et la salinité), ils ont été largement utilisés pour une grande variété d'applications relatives aux espèces diadromes, et plus récemment aux poissons d'eau douce. De plus, les rapports barium:calcium (Ba:Ca) ont été récemment utilisés pour déterminer les déplacements des espèces diadromes et estuariennes, en tant que rapports liés au débit et donc à l'environnement. Plusieurs études présentent l'utilisation de la composition chimique pluri-élémentaire de l'otolithe pour différencier des groupes de poissons capturés dans différents lacs ou bassins hydrographiques mais l'étendue des applications est plus large. Plusieurs applications des isotopes du Sr ont été étudiées ; la plupart porte sur les salmonidés (distinction des poissons de différents fleuves, détermination des déplacements au cours de la vie d'un poisson). Relativement peu d'études portent sur les autres isotopes (oxygène, sulfure) pour la détermination des déplacements. Les rapports des éléments chimiques et ceux de leurs isotopes stables ont un grand potentiel pour déterminer les déplacements des espèces d'eau douce, avec l'augmentation probable des possibilités d'applications conjointement avec l'amélioration des techniques analytiques.

---

[a] Corresponding author: `bronwyn.gillanders@adelaide.edu.au`

Article published by EDP Sciences and available at http://www.edpsciences.org/alr or http://dx.doi.org/10.1051/alr:2005033

1 Introduction

Ecology aims to determine the causes of the distribution and abundance of organisms. Two processes that potentially contribute to differences in distribution and abundance are movement and dispersal. Fundamental to the study of animal ecology is an understanding of movement patterns of animals, in both space and time (Pittman and McAlpine 2003). Such information is important in designing effective conservation and management strategies.

Diadromous fishes are important coastal and inland species, and comprise those species that move across salinity gradients as a routine part of their life history (McDowall 1988). Catadromous species spend most of their life in fresh water, but breed in saltwater, whereas anadromous species migrate from saltwater to freshwater to breed (see Table 1 for examples of diadromous species). In contrast, amphidromous species migrate from fresh water to the sea or vice versa, but the movement is not for the purpose of breeding (McDowall 1988) (Table 1). Many freshwater species also undergo some form of migration entirely within freshwater habitats (Reynolds 1983; Northcote 1997).

Although life histories of fish typically involve movement among spawning, growth, and refuge habitats, recent studies suggest that the life cycles of many species of fish have been over simplified and that considerable variability may exist within and among species and populations (Kennedy et al. 2002; Tzeng et al. 2002; Wells et al. 2003). For some species where diadromy was thought to be obligate, it may in fact be facultative (e.g. Pender and Griffin 1996; Tsukamoto et al. 1998; Katayama et al. 2000; Howland et al. 2001; Closs et al. 2003; Kotake et al. 2004). Paradigms of predictability and restricted movement of fish are likely to reflect the use of conventional tagging techniques for determining movement (Kennedy et al. 2002). Studies that show limited movement focus on the non-mobile part of the population that has been recaptured or on larger individuals (e.g. Gillanders et al. 2001). In addition, conventional tagging studies provide no data on the timing or frequency of movement and the relative importance of different habitats (Milton and Chenery 2003).

The best evidence for movement of fish is observing recognizable or tagged fish shifting from one place to another; however, such data are difficult to obtain for multiple life history stages. Alternative methods for determining origins and movements of fish are therefore required. One of the most rapidly growing fields of fisheries science is the use of elements in calcified structures, such as ear-bones (otoliths), to answer ecological questions related to movement. Two features of otoliths make them particularly amenable for recording aspects of the environment in which the fish have lived. First, the acellular and metabolically inert structure of otoliths ensures that any chemicals accreted onto the growing surface are permanently retained (Campana 1999). Second, the otolith continually grows (from prior to hatching to time of death) ensuring that the entire life of the fish is recorded (Campana 1999). Otoliths therefore record an accurate chronology of exposure to environmental conditions, including salinity, temperature, and composition of ambient water. Information on environmental conditions that the fish has lived in can then be coupled with the age (either annual or daily) of the fish to provide unprecedented information on the timing and frequency of movement, as well as the relative importance of different habitats.

Analysis of strontium concentrations has been widely used for tracing salinity history and reconstructing past environmental histories of fish. Other elements and isotopes within otoliths are also influenced by environmental variables and may be useful to answer ecological questions similar to strontium. The objective of this paper is to investigate the use of otolith chemistry to determine movements of diadromous and freshwater fish across salinity or other chemical gradients in freshwater-estuarine systems. Although otolith chemistry has been widely used in marine applications (see for example Gillanders 2005), it has only recently been applied to freshwater systems, therefore the focus will be on freshwater and diadromous fish. Specifically, I will review past research using (1) Sr:Ca ratios, (2) other elemental ratios, (3) multielement signatures, (4) Sr isotopes, and (5) other isotopes (e.g. O, C, and S) to determine population structure, natal, juvenile and adult habitats, as well as movement throughout the entire life history.

2 Material and methods

A literature search was used to investigate studies using otolith chemistry to determine movements of diadromous and freshwater fish and whether any studies had attempted to link otolith chemistry to changes in freshwater flow. For this, I searched Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts) for the period 1971 to September 2004 using a combination of keywords: (1) otolith and (2) movement, migration, flow, or chemistry. From these searches and my personal library, relevant publications that dealt with otolith chemistry and either diadromous or freshwater fish were examined. I do not purport to have examined all of the many studies that report changes in Sr:Ca ratios of otoliths of diadromous species, but rather have provided examples of the types of studies conducted.

3 Results and discussion

3.1 Sr:Ca ratios

Otolith Sr has been widely used to determine past environmental histories of fish (Kalish 1990; Limburg 1995; Kimura et al. 2000; Secor and Rooker 2000; Rooker et al. 2004); in particular, it is widely assumed that there is a positive relationship between otolith Sr and ambient salinity (see review: Secor and Rooker 2000). Thus, differences in otolith Sr have been widely used to infer movement between freshwater and marine waters (e.g. Limburg 1995, 1998; Secor et al. 1995; Tzeng et al. 1997), because concentrations of ambient Sr can be up to 8 times higher in marine waters than freshwater. Thus, parts of the otolith formed when the fish was in marine waters typically exhibit higher Sr:Ca ratios than layers deposited when the fish was resident in fresh waters (Fig. 1). Secor and Rooker's (2000) review of the literature (between 1982 and 1997) found a positive relationship between otolith Sr and salinity for a diverse range of species from different environmental conditions. However, many of the studies did not

Table 1. Examples of catadromous, anadromous and amphidromous species from within Australia. # Australian populations are sustained by annual stocking and no part of the natural life cycle is spent at sea (Allen et al. 2002); * introduced species; τ marginally catadromous; α maybe catadromous; β amphidromy uncertain. Further information on the taxonomic and world-wide geographic distribution of diadromy can be found in McDowall (1988).

Type of diadromy	Family	Species	Common name
Anadromous	Geotriidae	*Geotria australis*	Pouched lamprey
	Mordaciidae	*Mordacia mordax*	Short-headed lamprey
	Salmonidae	*Oncorhynchus mykiss*	Rainbow trout*
	Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon*
	Salmonidae	*Salmo salar*	Atlantic salmon#*
	Salmonidae	*Salmo trutta*	Brown trout*
	Retropinnidae	*Retropinna tasmanica*	Tasmanian smelt
	Galaxiidae	*Lovettia sealii*	Tasmanian whitebait
Catadromous	Anguillidae	*Anguilla australis*	Short-finned eel
	Anguillidae	*Anguilla reinhardtii*	Marbled eel
	Galaxiidae	*Galaxias maculatus*	Common jollytail τ
	Clupeidae	*Potamalosa richmondia*	Freshwater herringα
	Centropomidae	*Lates calcarifer*	Barramundi
	Percichthyidae	*Macquaria novemaculeata*	Australian bass τ
	Mugilidae	*Mugil cephalus*	Sea mullet
	Bovichtidae	*Pseudaphritis urvillii*	Congoli, tupong τ
Amphidromy	Galaxiidae	*Galaxias brevipinnis*	Climbing galaxias
	Galaxiidae	*Galaxias cleaveri*	Tasmanian mudfish
	Galaxiidae	*Galaxias truttaceus*	Trout minnow
	Gobiidae	*Pseudogobius olorum*	Swan River goby
	Eleotridae	*Gobiomorphus australis*	Striped gudgeon β
	Eleotridae	*Gobiomorphus coxii*	Cox's gudgeon β

measure Sr concentration of ambient water and therefore it is not clear whether such a relationship would exist after factoring out the effects of ambient water. It would, however, seem plausible that the effect of ambient Sr outweighs that of salinity in influencing otolith chemistry given the inconsistent experimental results observed for the relationship between salinity and otolith Sr (see below) and the strong positive associations found between ambient Sr and otolith Sr (Bath et al. 2000; Milton and Chenery 2001; Elsdon and Gillanders 2003). To interpret otolith Sr:Ca data it would be beneficial to know the concentration of the water (see also Martin et al. 2004).

Many studies assume that ambient environmental concentrations of Sr vary between fresh water and sea water because it is widely accepted that Sr is higher in sea water than fresh water. However, a recent study suggested that the range of Sr values in fresh waters was extensive, with some values exceeding those in marine waters (see Fig. 2 in Kraus and Secor 2004). If the ambient Sr:Ca is the primary determinant of otolith Sr:Ca, then for fish reared in fresh water with ambient Sr:Ca values greater than marine values (i.e. greater than 9 mmol Sr mol^{-1} Ca) the otolith Sr:Ca may exceed that of fish reared in seawater (Kraus and Secor 2004). I am not aware of similar data for other freshwater systems, but it would be valuable to investigate these. By comparison, in oceanic waters ambient Sr and Sr:Ca varies by only 2–3% globally (de Villiers 1999).

Although Secor and Rooker (2000) found an overall positive relationship between otolith Sr and salinity when many studies were combined, individual studies have found mixed results including no relationship (e.g. Fowler et al. 1995; Hoff and Fuiman 1995; Chesney et al. 1998; Elsdon and Gillanders 2002; Rooker et al. 2004), a negative relationship (e.g. Radtke et al. 1988; Elsdon and Gillanders 2002) and a positive relationship (e.g. Tzeng 1996; Kawakami et al. 1998). In addition, an interaction between salinity and temperature has also been found, such that the response between otolith Sr and salinity depended on the temperature (Secor et al. 1995; Elsdon and Gillanders 2002).

Despite the potential difficulties of reconstructing environmental histories of fish using otolith Sr:Ca researchers have used this methodology in a wide range of applications, especially for diadromous fish (Table 2). Besides inferring fish movement, including timing, between fresh water and sea water, otolith Sr:Ca ratios can determine the contribution of diadromous versus non-diadromous recruitment to coastal populations (e.g. giant kokopu, *Galaxias argenteus,* David et al. 2004). Profiles of Sr:Ca ratios were determined from the edge through the core of transverse sections of otoliths, using micro-PIXE (particle induced X-ray emission). Relatively low and constant Sr:Ca ratios were suggestive of recruitment from a freshwater environment, whereas high Sr:Ca ratios at the core of the otolith suggested recruitment from a marine environment (Fig. 1) (David et al. 2004). Although a relatively small number of fish were examined from each site (n = 1–10 fish/site), the majority of fish had recruited to either freshwater or estuarine environments, suggesting that non-diadromous recruitment was important, even where there was direct access to the sea (David et al. 2004). Diadromous recruitment may, however, be important in maintaining populations across large spatial scales (e.g. colonizing new streams).

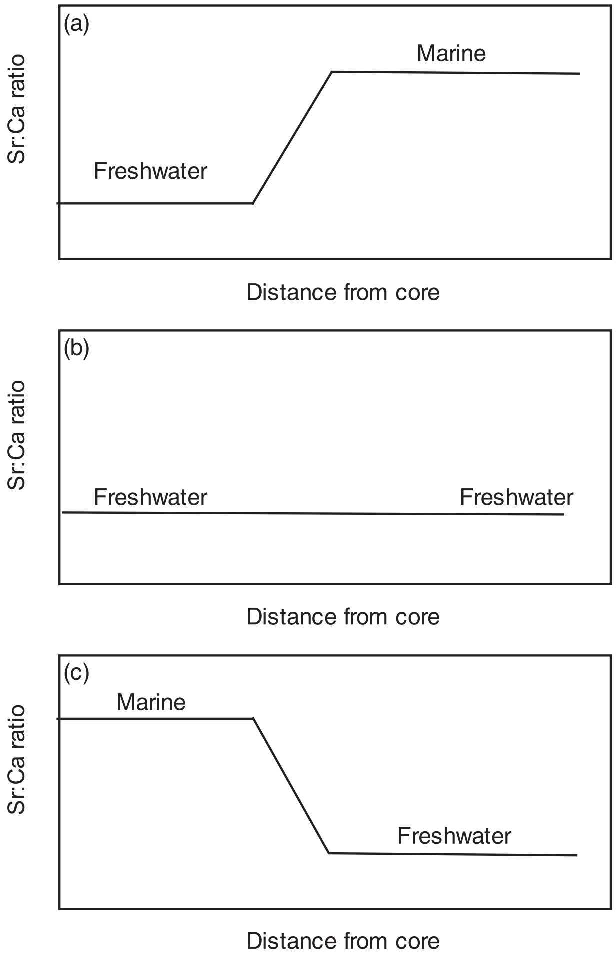

Fig. 1. Hypothetical diagrams showing Sr:Ca ratios in fish otoliths from the core to the edge of the otolith. (a) Fish moving from freshwater to marine waters, (b) fish remaining in fresh water and (c) fish moving from marine to fresh waters.

Many studies have investigated diadromous migratory patterns using Sr:Ca ratios (e.g. Kotake et al. 2004). Anguillid eels, in particular, are one group in which many studies have shown that catadromy is facultative rather than obligate (Tsukamoto et al. 1998; Tsukamoto and Arai 2001; Jessop et al. 2002; Kotake et al. 2004). One study suggested that bays may provide better feeding and growth conditions than freshwater habitats, although a latitudinal cline may also be found (Kotake et al. 2004). Thus, if feeding and growth conditions are better in bays than freshwater habitats, few fish may be catadromous, whereas if conditions are better in fresh water, then larger numbers may be catadromous.

By combining Sr:Ca ratios with fish age, additional information can be obtained. For example, Chang et al. (2004) found that habitat use changed with the age of mullet (*Mugil cephalus*), such that 26.7% and 10.5% of age 1^+ and 2^+ mullet respectively inhabited fresh water and that no fish 3^+ or older inhabited fresh water. In contrast, the number of mullet that migrated offshore from freshwater and estuarine areas increased with age (Chang et al. 2004). Based on temporal changes in otolith Sr:Ca ratios of individual fish, two types of migratory history were identified (Type 1: fish migrating between estuary and offshore waters, but rarely entering fresh waters; Type 2: fish migrating between fresh waters and offshore waters). Growth of fish, however, was not affected by migratory type (Chang et al. 2004).

In a novel application, natural chemical markers (Sr:Ca ratios) in otoliths were used to identify the probable source and date of introduction of exotic lake trout (*Salvelinus namaycush*) into Yellowstone Lake, Wyoming, USA (Munro et al. 2005). This application was possible because the water and otolith chemistry of trout differed among the three large lakes. Resident lake trout reared in different lakes showed little variation along the otolith growth axis, whereas suspected transplants showed a large and rapid increase in otolith Sr:Ca, which indicated a marked shift in water chemistry beyond any natural variation. Timing of the abrupt otolith Sr:Ca shift suggested that trout were introduced in the late 1980s, although more recent introductions had occurred. This is one of the few published studies to use Sr:Ca ratios in a solely freshwater application.

3.2 Other elements

Most studies on fish otoliths have focused on using Sr:Ca ratios as a proxy for salinity. However, other elements, such as Ba:Ca, may also be useful indicators of salinity, but have been largely unexplored. Relationships between riverine input to marine waters and trace elements in corals have recently been examined (e.g. Alibert et al. 2003). Peaks in Ba:Ca ratios of inshore corals were strongly correlated with flood events, which carried fresh water to the site (see Fig. 5 in Alibert et al. 2003). In low salinity areas (0–5 ppt), Ba is desorbed from fine-grained suspended particles and is then advected with riverine plumes to offshore areas where it behaves as an essentially conservative tracer (McCulloch et al. 2003). Ba:Ca ratios of corals have therefore been used to record sediment flux to coastal waters and were correlated with maximum river flow (McCulloch et al. 2003).

In otoliths, ambient Ba:Ca concentrations positively influence Ba:Ca concentrations of fish otoliths (Bath et al. 2000; Elsdon and Gillanders 2003; Wells et al. 2003) and scales (Wells et al. 2000, 2003). Partition coefficients (which are useful for comparing elemental discrimination) indicated that ambient Ba:Ca levels had a greater effect on otolith chemistry than either salinity or temperature (see Fig. 1 in Elsdon and Gillanders 2004). Ba concentrations are high in freshwater estuaries, largely because these estuaries receive inputs of sediment from land runoff and Ba is closely bound to sediments (Li and Chan 1979) and bioavailability of Ba is higher in freshwater than saltwater (Turner et al. 1981). Since barium exhibits estuarine release, with peak Ba concentrations depending on salinity, hydrodynamics and transport of riverine suspended particulate matter (SPM), a relationship often exists between Ba in the water and salinity (Coffey et al. 1997). After the Ba maxima, a negative linear relationship is found between Ba in the water and salinity (see figures in Coffey et al. 1997). The Ba maxima occurs at different salinities in different estuaries depending on discharge volume which is related to time of year, therefore, seasonal differences within an estuary are also found (Coffey et al. 1997). Salinity-Ba relationships may

Table 2. Applications of Sr and Sr:Ca in freshwater and diadromous fish. There may be some overlap among applications, although slightly different questions are addressed.

Application	Example
Related to diadromy	
The contribution of diadromous versus non-diadromous recruitment to populations	Rieman et al. 1994; Arai et al. 2003b; David et al. 2004
When individual fish moved between marine and freshwater environments during their life history	Radtke et al. 1988; Howland et al. 2001
Sr-salinity relationship used to determine age- and sex-dependent movements	Secor 1992; Secor et al. 1995; Secor and Piccoli 1996; Chang et al. 2004
Otolith Sr contrasted among different life history (amphidromous, marine, freshwater) types within a family	Radtke and Kinzie 1996
Reconstruct migratory history of past environments inhabited by fish (e.g. freshwater, estuarine and marine) or examine variation in migratory history	Kafemann et al. 2000; Secor and Rooker 2000; Tsukamoto and Arai 2001; Jessop et al. 2002; Arai et al. 2003a; Kotake et al. 2003; Shiao et al. 2003; Tzeng et al. 2003; Zlokovitz et al. 2003; Chang et al. 2003
Discriminate progeny of anadromous and freshwater resident females	Kalish 1990; Rieman et al. 1994; Volk et al. 2000
Clarify use of freshwater habitat	Chang et al. 2004
Not necessarily linked to diadromy	
Identify source and timing of introduction of an exotic species	Munro et al. 2005
Timing and duration of metamorphosis	Otake et al. 1994; Arai et al. 1999
Stock or population discrimination	Babaluk et al. 2002

also be estuarine dependent as Guay and Falkner (1998) found several negative correlations. Studies of the environmental history of fish could take advantage of the natural distribution of Ba in the water. The freshwater occupancy of fish, for example, could be determined including timing of movements between freshwater and marine waters and amount of time spent in each habitat (see below).

Black bream (*Acanthopagrus butcheri*) caught in fresh water had approximately double the otolith Ba:Ca of those from saltwater estuaries, therefore, fish with otolith Ba:Ca concentrations $\leq 5\ \mu\text{mol mol}^{-1}$ were classified as resident to saltwater, and those with $\geq 6\ \mu\text{mol mol}^{-1}$ resident to fresh water (Elsdon and Gillanders 2005). The amount of time that fish spent in fresh water ranged between 0% (Port Adelaide, SA) and 95% (Ewens Ponds, SA) with individual fish moving between freshwater and marine waters up to 6 times (Elsdon and Gillanders 2005). In addition, multiple types of migratory behaviour occurred in fish collected from the same estuary, suggesting far more complex behaviours than previously known. In a similar study, barramundi (*Lates calcarifer*) stocked into weirs also showed a complex pattern of Ba:Ca throughout the life of the fish (Mike Cappo, Australian Institute of Marine Science, Townsville, Australia, personal communication). Because movement was limited, changes in Ba:Ca were thought to correspond to dam overflow and suburban storm-water runoff, but Ba may also have been mobilized from sediment resuspension resulting from sand mining (Cappo, personal communication). Thus, Ba:Ca ratios of territorial fish or fish showing limited movement may be used to indicate freshwater flow within a river system.

Pender and Griffin (1996) found that Ba (and Sr) in scales could be reliably used to differentiate barramundi reared in freshwater and saltwater, because these elements were related to environmental histories. Their analyses indicated three groups of fish (marine, mixed, and freshwater), and that some fish did not occupy fresh water. This application used whole scales which represented a life-time integrated signature, and was therefore not able to determine the timing or frequency of movements.

Milton et al. (2000) investigated whether heavy metals (e.g. Cu, Pb, Zn) in fish otoliths of barramundi could be used to infer movement into waters that were contaminated by heavy metals. Their results suggested that Cu was not a good indicator of a fish's exposure to heavy metals since Cu concentration in the otoliths did not rise during freshwater residency. Freshwater concentrations of elements appear reasonably similar to seawater, with the exception of the common marine salts and therefore a range of other elements may be useful (see Fig. 5 in Campana 1999).

3.3 Multielement signatures

Several studies have investigated the use of multielemental composition to distinguish groups of fish collected in lakes (Bronte et al. 1996; Brazner et al. 2004), or from different river systems (e.g. Thorrold et al. 1998; Morris et al. 2003; Wells et al. 2003), with most studies of this type conducted on fish that spend at least part of their life cycle within marine waters. The elements analysed in the freshwater studies largely depend on the instrumentation used. For example, studies utilizing

ICP-MS instruments generally analyse Mg, Mn, Sr, and Ba, although K, and Pb have also been analysed. In contrast, particle induced X-ray emission (PIXE) studies have also analysed Fe and Br in addition to some of the other elements. Many marine applications of multielemental composition have been published (e.g. Gillanders and Kingsford 1996; Campana et al. 2000; Thorrold et al. 2001; Gillanders 2002), and it is only a matter of time before similar applications are utilized in freshwater systems (e.g. determining the contribution of different river systems to adult populations, and estimates of life history diversity within and among streams).

3.4 Sr isotopes

Another approach for evaluating origins and migration of fish is the use of Sr isotopes in otoliths. The ^{87}Sr/^{86}Sr ratio of seawater has essentially remained the same for the past 400 000 years (0.70918) and is similar across the world's oceans, whereas the Sr isotopic composition of river water reflects the ^{87}Sr/^{86}Sr ratio of the rocks in the catchment area (average for major rivers emptying into San Francisco Bay 0.7065) (Ingram and Sloan 1992). If there are differences in geology of the catchment then natural geographic differences in Sr isotopes of river waters would be expected. Since the otolith ^{87}Sr/^{86}Sr ratio is primarily determined by ambient water chemistry, otoliths from fish collected from river systems with different geology should differ (Kennedy et al. 1997, 2000; Ingram and Weber 1999). Isotope ratios are not influenced by temperature and salinity or biological factors (e.g. growth, maturation) therefore they are likely to be more useful as an environmental tracer (Kennedy et al. 2000).

Strontium isotopes have been used to distinguish juvenile salmon from different tributaries of the Connecticut River (Vermont, USA) (Kennedy et al. 1997, 2000), and the Sacramento-San Joaquin system (California, USA) (Ingram and Weber 1999). The overall objective of these studies was to determine the rearing stream from which adult salmon originated, based on the freshwater signature. Prior to achieving such an objective, it was necessary to demonstrate that different populations of juvenile salmon could be distinguished (Table 3). Following this, the ocean-derived Sr signature in returning salmon was separated from the freshwater signature since there was limited spatial and temporal variability in the marine δ^{87}Sr. The freshwater signature of adult fish was then used to estimate the contribution of different tributaries to production of adult salmon (and smolts). Further work is underway in Central Valley rivers (California, USA) to determine the contribution of salmon from these rivers and hatcheries to the fishery (Rachel Barnett-Johnson and others, University of California Santa Cruz, California, USA, unpublished data).

The movement history of individual fish can be constructed using Sr isotopes. Two different approaches have been used, namely (1) using a micromill to drill small amounts of otolith material ($<25\ \mu$g) and analyzing Sr isotopes using a thermal ionization mass spectrometer (TIMS) (Kennedy et al. 2002), and (2) analyzing Sr isotopes in a transverse section of the otolith using a laser ablation multi-collector inductively coupled plasma mass spectrometer (LA-MC-ICPMS) (Milton and Chenery 2003). Kennedy et al. (2002) were able to characterize the Sr isotopic signatures in four major stages in the life cycle of Atlantic salmon (*Salmo salar*), including prefeeding hatchery development, rearing stream growth, smolt out-migration, and ocean residence (see Fig. 2 in Kennedy et al. 2002). Analysis of an adult salmon that lived exclusively at the hatchery showed little variation in ^{87}Sr/^{86}Sr ratio, whereas significant variation in ^{87}Sr/^{86}Sr ratio was found in returning adult salmon (Table 3) (Kennedy et al. 2002). Milton and Chenery (2003) analysed the Sr isotope ratio for the entire life history of 13 fish collected from 4 sites; fish ranged in age from 190 to 667 days. The age at which fish migrated to the sea from a remote population varied from 2 to 5 months, with most fish spending about 3 months in the sea before migrating back to the upper river. In contrast, fish collected from the lower estuary and from the sea spent most of their life in marine waters. Tagging studies are unable to provide the level of information obtained using Sr isotopes, since tagging data provides no information on the timing or frequency of movements. Sr isotopes may, however, only detect movements at low salinities. For example, salinities greater than 5‰ were difficult to distinguish in one study (Milton and Chenery 2003), whereas another found Sr isotopes were particularly sensitive for salinities up to 25‰ (Ingram and Sloan 1992); sensitivity may be dependent on geology. The Sr isotope mixing curve will determine the salinities for which Sr isotopes will provide useful information (see Fig. 3 in Ingram and Sloan 1992; and Fig. 6 in Milton and Chenery 2003), and may need to be determined for each system.

Since Sr isotopic signatures depend on the bedrock geology, it should be possible to predict from geological maps whether sites are likely to show sufficient geochemical variation (Kennedy et al. 2000). Rocks containing calcium carbonate, such as limestones and evaporites, which are easily eroded, have high Sr concentrations (up to 1000 ppm) and low ^{87}Sr/^{86}Sr ratios (Palmer and Edmond 1992). By comparison, silicate rocks (e.g. schist), which are more resistant to weathering, have lower Sr contents and higher ^{87}Sr/^{86}Sr ratios (Palmer and Edmond 1992). In addition, rocks with higher Rb:Sr ratios will also have higher ^{87}Sr/^{86}Sr ratios, since ^{87}Sr is produced through radioactive decay of ^{87}Rb (Kennedy et al. 2000). Thus, older rocks tend to have higher ^{87}Sr/^{86}Sr ratios and younger rocks tend to have lower ^{87}Sr/^{86}Sr ratios; these differences may alter isotope signatures between regions. Kennedy et al. (2000) found that Sr isotopic values of 29 sampling locations in the Connecticut River (USA) were consistent with geological predictions. In the Murray Darling River system (MDRS) dramatically different ranges of ^{87}Sr/^{86}Sr were found in suspended particulate matter between the Murray and Darling River systems, due to differences in the composition and ages of rocks in their catchment (Douglas et al. 1995). Carbonates are of limited extent in the MDRS and there is minor basaltic material within some catchments (e.g. McIntyre River), but not others (e.g. Ovens River) (Douglas et al. 1995); these rocks would contribute to low ^{87}Sr/^{86}Sr. In contrast, granitic and metasedimentary rocks of the Murray River system may contribute to high ^{87}Sr/^{86}Sr ratios (Douglas et al. 1995). Thus, the variability in geology of an area will determine the spatial limitations of using Sr isotopes as geochemical markers (Kennedy et al. 2000).

Table 3. Studies using Sr isotopes to investigate ecological questions related to freshwater and estuarine fish.

Species	Objective	Method	Results	Reference
Atlantic salmon *Salmo salar*	Determine whether juveniles from different rearing sites can be differentiated	Collected fish & water from 10 salmon stocking sites in two major watersheds of Connecticut River (USA); analysed ^{87}Sr/^{86}Sr ratio	Using δ^{87}Sr values in salmon vertebrae & water fish from 10 rearing sites were separated into 8 distinct groups	Kennedy et al. 1997
Atlantic salmon *Salmo salar*	Determine whether populations of juveniles can be distinguished	Sampled juvenile salmon vertebrae & otoliths, & water from 29 study sites in two major watersheds of Connecticut River (USA) across 4 years (1995-1998); analysed ^{87}Sr/^{86}Sr ratio using TIMS	Sr isotopes distinguished all 8 regions in one basin & 7 of the 10 regions in the other basin; Sr isotopes in water are stable across seasons and years	Kennedy et al. 2000
Atlantic salmon *Salmo salar*	Reconstruct the environmental history of individuals	Measured age-specific ^{87}Sr/^{86}Sr ratios in otoliths of 4 adult fish which were captured as they returned to spawn in the Connecticut River (USA); otolith subsamples drilled using micromill and Sr isotopes measured using TIMS	Found little variability in ^{87}Sr/^{86}Sr ratio for adult fish that lived in hatchery, but significant variability in ^{87}Sr/^{86}Sr ratio for returning adult salmon	Kennedy et al. 2002
Chinook salmon *Oncorhynchus* tshawytscha	Determine the degree of variation in the ^{87}Sr/^{86}Sr composition of otoliths from known locations	Sampled juvenile fish otoliths reared at or near 5 hatchery sites in the Sacramento-San Joaquin system (USA); analysed ^{87}Sr/^{86}Sr ratio using TIMS	All 5 sites significantly different	Ingram and Weber 1999
Hilsa *Tenualosa ilisha*	Determine whether transects of Sr isotope ratios can be used to infer movement between rivers and the sea for different stages of the life history	Otoliths of fish collected from coastal, estuarine & freshwater reaches of major rivers in Bangladesh; transverse sections of otoliths analysed by LA-MC-ICPMS	Fish born in all main rivers in Bangladesh, all fish moved widely and entered marine waters by 1 year of age; most fish returned to freshwater after sexual maturity, but not necessarily to natal region	Milton and Chenery 2003
Common galaxiid *Galaxias maculatus*	Investigate Sr-isotopic variations on the scale of 10 µm	Ground otolith analysed by LA MC-ICPMS using slit approx. 147 × 3 µm in size slowly traversed across the otolith	Clear shift in ^{87}Sr/^{86}Sr ratio between core (identical to modern seawater value) and edge (period of growth in freshwater environment) of otolith	Woodhead et al. 2005
Arctic char *Salvelinus alpinus*	Investigate whether differences in life history were recorded in the Sr isotopic signature	LA MC-ICPMS on polished surface of otolith	Marked change in ^{87}Sr/^{86}Sr composition across otolith, but possibly fractionation problems	Waight et al. 2002

Thermal ionization mass spectrometer (TIMS).

Sr isotope ratios hold great promise for providing an accurate environmental history that each fish has experienced. The approach will have limited application for marine fishes or fishes living in the lower estuary, since Sr isotope ratios are stable in marine waters. The greatest application will be for species that move across strong salinity gradients (e.g. diadromous species) or between rivers with vastly different geology (Milton and Chenery 2003). Coupled with age estimates, and the use of micromilling or laser ablation enabling fine spatial resolution along the otolith growth axis (see for example Woodhead et al. 2005), Sr isotopes will provide increasing detail about movement of individuals between bodies of water.

3.5 Other isotopes

Oxygen and carbon isotopes have also been used to determine the migratory behaviour of fish, although this application has mostly been applied to species other than freshwater fishes (but see Nelson et al. 1989; Northcote et al. 1992). Typically, depleted values of δ^{13}C and δ^{18}O have been found in the headwaters and enriched values in the coastal seawater, with δ^{18}O values of fish otoliths following those of their rearing waters (Peterson and Fry 1987; Northcote et al. 1992). The δ^{13}C values of fish otoliths also followed those of the rearing waters, but were offset by approximately 5–9‰. Fish that had more positive values of δ^{18}O than their capture locations were assumed to have migrated from coastal seawaters. Where there was a disparity between otolith and capture water δ^{18}O values, it was assumed that these fish were not long-term residents at their capture site (Northcote et al. 1992). The δ^{18}O of surface waters changes in response to the freshwater budget, namely evaporation, precipitation and runoff, as well as advection (Rohling and Bigg 1998). Thus, δ^{18}O values will be enriched by evaporation and depleted by freshwater input. In addition, the isotopic composition of river waters also covers a wide range of values reflecting precipitation over the entire catchment area, as well as contributions from melt-water (e.g. from glaciers and snow) (Rohling and Bigg 1998). Significant variation in δ^{18}O values in coastal waters are therefore likely. Temporal variation is also possible, unlike for Sr isotopes. If actual salinities are to be calculated then the effect of temperature will need to be removed (e.g. see Hendy et al. 2002 for an example using corals).

Sulphur isotopes may also show a strong marine-freshwater gradient (Limburg 1998). Few studies have utilized sulphur isotopes (^{34}S / ^{32}S) of otoliths to determine movements and life history parameters (but see Weber et al. 2002), although several have investigated sulphur isotopes of fish tissue (e.g. muscle) (e.g. Hesslein et al. 1991). Weber et al. (2002) found that hatchery raised and naturally spawned juvenile Chinook salmon (*Oncorhynchus tshawytscha*) varied in δ^{34}S in both muscle and otoliths by 13‰. These differences reflected dietary differences, because hatchery fish were raised on commercial feeds that consisted of 80–90% protein from marine sources, whereas wild salmon had a freshwater diet (Weber et al. 2002). This method could be useful for identifying hatchery fish, but only where the hatchery feed has a marine-based isotopic signal, significant growth and feeding has occurred in the hatchery which outweighs the bedrock geology and signature of the wild population (Weber et al. 2002). Similar applications to Sr isotopes could then be utilized.

4 Conclusion

Although a large number of studies of otolith chemistry have been made on diadromous species, there are relatively few published studies on solely freshwater species. The majority of the research has focused on Sr:Ca ratios with fewer studies utilizing other individual elements (e.g. Ba, Cu) or multielemental composition. For species where movement is minimal or in enclosed systems, Ba:Ca ratios of otoliths may provide information on freshwater flows to the system. Ba:Ca ratios may provide similar information to that of Sr:Ca ratios, although distinguishing between movement and freshwater input will be necessary. Sr isotopes have largely been used on salmonids but show great promise for reconstructing the timing of movements in other freshwater and diadromous species. Relatively few studies have investigated the use of other isotopes for determining movements. There is great scope for using elemental ratios and stable isotopes for determining movements of freshwater species. The possible applications are likely to increase as analytical technology improves.

Acknowledgements. Financial support was provided by an ARC QEII fellowship. The manuscript benefited from discussions with Mike Cappo, Travis Elsdon, and Andrew Munro. Constructive comments on a previous draft were provided by Travis Elsdon, Andrew Munro and two anonymous referees.

References

Alibert C., Kinsley L., Fallon S.J., McCulloch M.T., Berkelmans R., McAllister F., 2003, Source of trace element variability in Great Barrier Reef corals affected by the Burdekin flood plumes. Geochim. Cosmochim. Acta 67, 231-246.

Allen G.R., Midgley S.H., Allen M., 2002, Field guide to freshwater fishes of Australia. Western Australian Museum, Perth.

Arai T., Goto A., Miyazaki N., 2003a, Use of otolith microchemistry to estimate the migratory history of the threespine stickleback, *Gasterosteus aculeatus*. J. Mar. Biol. Assoc. UK 83, 223-230.

Arai T., Hayano H., Asami H., Miyazaki N., 2003b, Coexistence of anadromous and lacustrine life histories of the shirauo, *Salangichthys microdon*. Fish. Oceanogr. 12, 134-139.

Arai T., Limbong D., Otake T., Tsukamoto K., 1999, Metamorphosis and inshore migration of tropical eels *Anguilla* spp. in the Indo-Pacific. Mar. Ecol. Prog. Ser. 182, 283-293.

Babaluk J. A., Campbell J. L., Evans C. L., Halden N. M., Mejia S. R., Nejedly Z., Reist J.D., Teesdale W. J., 2002, Micro-PIXE analysis of strontium in Arctic char, *Salvelinus alpinus*, otoliths from Quttinirpaaq National Park, Nunavut, Canada. Nuclear Instruments Methods Physics Res. B: Beam Interactions with Materials and Atoms 189, 190-195.

Bath G.E., Thorrold S.R., Jones C.M., Campana S.E., McLaren J.W., Lam J.W.H., 2000, Strontium and barium uptake in aragonitic otoliths of marine fish. Geochim. Cosmochim. Acta 64, 1705-1714.

Brazner J.C., Campana S.E., Tanner D.K., 2004, Habitat fingerprints for Lake Superior coastal wetlands derived from elemental analysis of yellow perch otoliths. Trans. Am. Fish. Soc. 133, 692-704.

Bronte C.R., Hesselberg R.J., Shoesmith J.A., Hoff M.H., 1996, Discrimination among spawning concentrations of Lake Superior lake herring based on trace element profiles in sagittae. Trans. Am. Fish. Soc. 125, 852-859.

Campana S.E., 1999, Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. Mar. Ecol. Prog. Ser. 188, 263-297.

Campana S.E., Chouinard G.A., Hanson J.M., Frechet A., Brattey J., 2000, Otolith elemental fingerprints as biological tracers of fish stocks. Fish. Res. 46, 343-357.

Chang C.W., Iizuka Y., Tzeng W.N., 2004, Migratory environmental history of the grey mullet *Mugil cephalus* as revealed by otolith Sr:Ca ratios. Mar. Ecol. Prog. Ser. 269, 277-288.

Chesney E.J., McKee B.M., Blanchard T., Chan L.-H., 1998, Chemistry of otoliths from juvenile menhaden *Brevoortia patronus*: Evaluating strontium, strontium:calcium and strontium isotope ratios as environmental indicators. Mar. Ecol. Prog. Ser. 171, 261-273.

Closs G.P., Smith M., Barry B., Markwitz A., 2003, Non-diadromous recruitment in coastal populations of common bully (*Gobiomorphus cotidianus*). N.Z. J. Mar. Freshw. Res. 37, 301-313.

Coffey M., Dehairs F., Collette O., Luther G., Church T., Jickells T., 1997, The behaviour of dissolved barium in estuaries. Est. Coast. Shelf Sci. 45, 113-121.

David B., Chadderton L., Closs G., Barry B., Markwitz A., 2004, Evidence of flexible recruitment strategies in coastal populations of giant kokopu (*Galaxias argenteus*), pp. 23, Department of Conservation, Wellington.

de Villiers S., 1999, Seawater strontium and Sr/Ca variability in the Atlantic and Pacific oceans. Earth Planet. Sci. Lett. 171, 623-634.

Douglas G.B., Gray C.M., Hart B.T., Beckett R., 1995, A strontium isotopic investigation of the origin of suspended particulate matter (SPM) in the Murray-Darling River system, Australia. Geochim. Cosmochim. Acta 59, 3799-3815.

Elsdon T.E., Gillanders B.M., 2002, Interactive effects of temperature and salinity on otolith chemistry: Challenges for determining environmental histories of fish. Can. J. Fish. Aquat. Sci. 59, 1796-1808.

Elsdon T.E., Gillanders B.M., 2003, Relationship between water and otolith elemental concentrations in juvenile black bream *Acanthopagrus butcheri*. Mar. Ecol. Prog. Ser. 260, 263-272.

Elsdon T.E., Gillanders B.M., 2004, Fish otolith chemistry influenced by exposure to multiple environmental variables. J. Exp. Mar. Biol. Ecol. 313, 269-284.

Elsdon T.E., Gillanders B.M., 2005, Alternative life-history patterns of estuarine fish: Barium in otoliths elucidates freshwater residency. Can. J. Fish. Aquat. Sci. 62, 1143-4452.

Fowler A.J., Campana S.E., Jones C.M., Thorrold S.R., 1995, Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. Can. J. Fish. Aquat. Sci. 52, 1421-1430.

Gillanders B.M., 2002, Connectivity between juvenile and adult fish populations: Do adults remain near their recruitment estuaries? Mar. Ecol. Prog. Ser. 240, 215-223.

Gillanders B.M., Kingsford M.J., 1996, Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. Mar. Ecol. Prog. Ser. 141, 13-20.

Gillanders B.M., Ferrell D.J., Andrew N.L., 2001, Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): How useful are data from a cooperative tagging programme? Mar. Freshw. Res. 52, 179-192.

Gillanders B.M., 2005, Using elemental chemistry of fish otoliths to determine Connectivity between estuarine and coastal habitats. Est. Coast. Shelf Sci. 64, 47-57.

Guay C.K., Falkner K.K., 1998, A survey of dissolved barium in the estuaries of major Arctic rivers and adjacent seas. Cont. Shelf Res. 18, 859-882.

Hendy E.J., Gagan M.K., Alibert C.A., McCulloch M.T., Lough J.M., Isdale P.J., 2002, Abrupt decrease in tropical Pacific sea surface salinity at end of little ice age. Science 295, 1511-1514.

Hesslein R.H., Capel M.J., Fox D.E., Hallard K.A., 1991, Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the Lower Mackenzie River basin, Canada. Can. J. Fish. Aquat. Sci. 48, 2258-2265.

Hoff G.R., Fuiman L.A., 1995, Environmentally induced variation in elemental composition of red drum (*Sciaenops ocellatus*) otoliths. Bull. Mar. Sci. 56, 578-591.

Howland K.L., Tonn W.M., Babaluk J.A., Tallman R.F., 2001, Identification of freshwater and anadromous inconnu in the Mackenzie River system by analysis of otolith strontium. Trans. Am. Fish. Soc. 130, 725-741.

Ingram B.L., Sloan D., 1992, Strontium isotopic composition of estuarine sediments as paleosalinity-paleoclimate indicator. Science 255, 68-72.

Ingram B.L., Weber P.K., 1999, Salmon origin in California's Sacramento-San Joaquin river system as determined by otolith strontium isotopic composition. Geology 27, 851-854.

Jessop B.M., Shiao J.-C., Jizuka Y., Tzeng W.N., 2002, Migratory behaviour and habitat use by American eels *Anguilla rostrata* as revealed by otolith microchemistry. Mar. Ecol. Prog. Ser. 233, 217-229.

Kafemann R., Adlerstein S., Neukamm R., 2000, Variation in otolith strontium and calcium ratios as an indicator of life-history strategies of freshwater fish species within a brackish water system. Fish. Res. 46, 313-325.

Kalish J.M., 1990, Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. 88, 657-666.

Katayama S., Radtke R.L., Omori M., Shafer D.J., 2000, Coexistence of anadromous and resident life history styles of pond smelt, *Hypomesus nipponensis*, in Lake Ogawara, Japan, as determined by analyses of otolith structure and strontium: calcium ratios. Environ. Biol. Fish. 58, 195-201.

Kawakami Y., Mochioka N., Morishita K., Tajima T., Nakagawa H., Toh H., Nakazono A., 1998, Factors influencing otolith strontium/calcium ratios in *Anguilla japonica* elvers. Environ. Biol. Fish. 52, 299-303.

Kennedy B.P., Blum J.D., Folt C.L., Nislow K.H., 2000, Using natural strontium isotopic signatures as fish markers: Methodology and application. Can. J. Fish. Aquat. Sci. 57, 2280-2292.

Kennedy B.P., Folt C.L., Blum J.D., Chamberlain C.P., 1997, Natural isotope markers in salmon. Nature 387, 766-767.

Kennedy B.P., Klaue A., Blum J.D., Folt C.L., Nislow K.H., 2002, Reconstructing the lives of fish using Sr isotopes in otoliths. Can. J. Fish. Aquat. Sci. 59, 925-929.

Kimura R., Secor D.H., Houde E.D., Piccoli P.M., 2000, Up-estuary dispersal of young-of-the-year bay anchovy *Anchoa mitchilli* in the Chesapeake Bay: Inferences from microprobe analysis of strontium in otoliths. Mar. Ecol. Prog. Ser. 208, 217-227.

Kotake A., Arai T., Ohji M., Yamane S., Miyazaki N., Tsukamoto K., 2004, Application of otolith microchemistry to estimate the migratory history of Japanese eel *Anguilla japonica* on the Sanriku coast of Japan. J. Appl. Ichthyol. 20, 150-153.

Kotake A., Arai T., Ozawa T., Nojima S., Miller M.J., Tsukamoto K., 2003, Variation in migratory history of Japanese eels, *Anguilla japonica*, collected in coastal waters of the Amakusa Islands, Japan, inferred from otolith Sr/Ca ratios. Mar. Biol. 142, 849-854.

Kraus R.T., Secor D.H., 2004, Incorporation of strontium into otoliths of an estuarine fish. J. Exp. Mar. Biol. Ecol. 302, 85-106.

Li Y.-H., Chan L.-H., 1979, Desorption of Ba and ^{226}Ra from riverborne sediments in the Hudson estuary. Earth Planet. Sci. Lett. 43, 343-350.

Limburg K.E., 1995, Otolith strontium traces environmental history of subyearling American shad *Alosa sapidissima*. Mar. Ecol. Prog. Ser. 119, 25-35.

Limburg K.E., 1998, Anomalous migrations of anadromous herrings revealed with natural chemical tracers. Can. J. Fish. Aquat. Sci. 55, 431-437.

Martin G.B., Thorrold S.R., Jones C.M., 2004, Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). Can. J. Fish. Aquat. Sci. 61, 34-42.

McCulloch M., Fallon S., Wyndham T., Hendy E., Lough J., Barnes D., 2003, Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421, 727-730.

McDowall R.M., 1988, Diadromy in fishes. Migrations between freshwater and marine environments. Timber Press, Portland, Oregon.

Milton D.A., Chenery S.P., 2001, Sources and uptake of trace metals in otoliths of juvenile barramundi (*Lates calcarifer*). J. Exp. Mar. Biol. Ecol. 264, 47-65.

Milton D.A., Chenery S.R., 2003, Movement patterns of the tropical shad hilsa (*Tenualosa ilisha*) inferred from transects of ^{87}Sr/^{86}Sr isotope ratios in their otoliths. Can. J. Fish. Aquat. Sci. 60, 1376-1385.

Milton D.A., Tenakanai C.D., Chenery S.R., 2000, Can the movements of barramundi in the Fly river region, Papua New Guinea be traced in their otoliths? Estuar. Coast. Shelf Sci. 50, 855-868.

Morris J.A., Rulifson R.A., Toburen L.H., 2003, Life history strategies of striped bass, *Morone saxatilis*, populations inferred from otolith microchemistry. Fish. Res. 62, 53-63.

Munro A.R., McMahon T.E., Ruzycki J.R., 2005, Natural chemical markers identify source and date of introduction of an exotic species: Lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Can. J. Fish. Aquat. Sci. 62, 79-87.

Nelson C.S., Northcote T.G., Hendy C.H., 1989, Potential use of oxygen and carbon isotopic composition of otoliths to identify migratory and non-migratory stocks of the New Zealand common smelt: A pilot study. N.Z. J. Mar. Freshw. Res. 23, 337-344.

Northcote T.G., 1997, Potamodromy in Salmonidae - living and moving in the fast lane. N. Am. J. Fish. Manage. 17, 1029-1045.

Northcote T.G., Hendy C.H., Nelson C.S., Boubee J.A.T., 1992, Tests for migratory history of the New Zealand common smelt (*Retropinna retropinna* (Richardson)) using otolith isotopic composition. Ecol. Freshw. Fish 1, 61-72.

Otake T., Ishii T., Nakahara M., Nakamura R., 1994, Drastic changes in otolith strontium/calcium ratios in leptocephali and glass eels of Japanese eel *Anguilla japonica*. Mar. Ecol. Prog. Ser. 112, 189-193.

Palmer M.R., Edmond J.M., 1992, Controls over the strontium isotope composition of river water. Geochim. Cosmochim. Acta 56, 2099-2111.

Pender P.J., Griffin R.K., 1996, Habitat history of barramundi *Lates calcarifer* in a North Australian river system based on barium and strontium levels in scales. Trans. Am. Fish. Soc. 125, 679-689.

Peterson B.J., Fry B., 1987, Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18, 293-320.

Pittman S.J., McAlpine C.A., 2003, Movements of marine fish and decapod crustaceans: Process, theory and application. Adv. Mar. Biol. 44, 205-294.

Radtke R.L., Kinzie R.A., 1996, Evidence of a marine larval stage in endemic Hawaiian stream gobies from isolated high-elevation locations. Trans. Am. Fish. Soc. 125, 613-621.

Radtke R.L., Kinzie R.A., Folsom S.D., 1988, Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fish. 23, 205-213.

Reynolds L.F., 1983, Migration patterns of five fish species in the Murray-Darling river system. Aust. J. Mar. Freshw. Res. 34, 857-871.

Rieman B.E., Myers D.L., Nielson R.L., 1994, Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. Can. J. Fish. Aquat. Sci. 51, 68-77.

Rohling E.J., Bigg G.R., 1998, Paleosalinity and delta-O-18 - a critical assessment. J. Geophys. Res. 103, 1307-1318.

Rooker J.R., Kraus R.T., Secor D.H., 2004, Dispersive behaviors of black drum and red drum: Is otolith Sr:Ca a reliable indicator of salinity history? Estuaries 27, 334-341.

Secor D.H., 1992, Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. Fish. Bull. 90, 798-806.

Secor D.H., Henderson-Arzapalo A., Piccoli P.M., 1995, Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? J. Exp. Mar. Biol. Ecol. 192, 15-33.

Secor D.H., Piccoli P.M., 1996, Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19, 778-793.

Secor D.H., Rooker J.R., 2000, Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fish. Res. 46, 359-371.

Shiao J.C., Iizuka Y., Chang C.W., Tzeng W.N., 2003, Disparities in habitat use and migratory behavior between tropical eel *Anguilla marmorata* and temperate eel *A. japonica* in four Taiwanese rivers. Mar. Ecol. Prog. Ser. 261, 233-242.

Thorrold S.R., Jones C.M., Campana S.E., McLaren J.W., Lam J.W.H., 1998, Trace element signatures in otoliths record natal river of juvenile American shad (*Alosa sapidissima*). Limnol. Oceanogr. 43, 1826-1835.

Thorrold S.R., Latkoczy C., Swart P.K., Jones C.M., 2001, Natal homing in a marine fish metapopulation. Science 291, 297-299.

Tsukamoto K., Arai T., 2001, Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. Mar. Ecol. Prog. Ser. 220, 265-276.

Tsukamoto K., Nakai I., Tesch W.-V., 1998, Do all freshwater eels migrate? Nature 396, 635-636.

Turner D.R., Whitfield M., Dickson A.G., 1981, The equilibrium speciation of dissolved components in freshwater and seawater at 25 °C and 1 atm pressure. Geochim. Cosmochim. Acta 45, 855-881.

Tzeng W.-N., 1996, Effects of salinity and ontogenetic movements on strontium:calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica* Temminck and Schlegel. J. Exp. Mar. Biol. Ecol. 199, 111-122.

Tzeng W.N., Iizuka Y., Shiao J.C., Yamada Y., Oka H.P., 2003, Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*). Aquaculture 216, 77-86.

Tzeng W.N., Severin K.P., Wickstrom H., 1997, Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Mar. Ecol. Prog. Ser. 149, 73-81.

Tzeng W.N., Shiao J.C., Iizuka Y., 2002, Use of otolith Sr:Ca ratios to study the riverine migratory behaviors of Japanese eel *Anguilla japonica*. Mar. Ecol. Prog. Ser. 245, 213-221.

Volk E.C., Blakley A., Schroder S.L., Kuehner S.M., 2000, Otolith chemistry reflects migratory characteristics of Pacific salmonids: Using otolith core chemistry to distinguish maternal associations with sea and freshwaters. Fish. Res. 46, 251-266.

Waight T., Backer J., Peate D., 2002, Sr isotope ratio measurements by double-focusing MC-ICPMS: techniques, observations and pitfalls. Int. J. Mass Spectrom. 221, 229-244.

Weber P.K., Hutcheon I.D., McKeegan K.D., Ingram B.L., 2002, Otolith sulfur isotope method to reconstruct salmon (*Oncorhynchus tshawytscha*) life history. Can. J. Fish. Aquat. Sci. 59, 587-591.

Wells B.K., Bath G.E., Thorrold S.R., Jones C.M., 2000, Incorporation of strontium, cadmium, and barium in juvenile spot (*Leiostomus xanthurus*) scales reflects water chemistry. Can. J. Fish. Aquat. Sci. 57, 2122-2129.

Wells B.K., Rieman B.E., Clayton J.L., Horan D.L., Jones C.M., 2003, Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: The potential application of hard-part chemistry to describe movements in freshwater. Trans. Am. Fish. Soc. 132, 409-424.

Woodhead J., Swearer S., Hergta J., Maasa R., 2005, In situ Sr-isotope analysis of carbonates by LA-MC-ICP-MS: Interference corrections, high spatial resolution and an example from otolith studies. J. Analyt. Atomic Spectrometr. 20, 22-27.

Zlokovitz E.R., Secor D.H., Piccoli P.M., 2003, Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish. Res. 63, 245-259.