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Analysis of otolith $^{87}Sr/^{86}Sr$ to elucidate salinity histories of Nurseryfish *Kurtus gulliveri* (Perciformes:Kurtidae) in a tropical lowland river in northern Australia

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Abstract: The Nurseryfish *Kurtus gulliveri* is found in estuarine and freshwater reaches of tropical rivers in northern Australia and southern New Guinea. Nurseryfish have been recorded in salinities ranging from freshwater to seawater (salinity <0.5–36‰), but almost nothing is known of their movements. We conducted core-to-edge transect analyses of $^{87}Sr/^{86}Sr$ in the otoliths of 16 male and 14 female Nurseryfish collected from a tropical river in northern Australia to examine their movements across a freshwater–estuarine salinity gradient. Comparisons between water and otolith $^{87}Sr/^{86}Sr$ showed that most fish had $^{87}Sr/^{86}Sr$ values indicative of periods of saline (salinity > 4‰) residence during their early life history, usually followed by a distinct transition into brackish (0.5–4‰) or fresh water (<0.5‰) later in life. No differences were discernible between the salinity histories of male and female Nurseryfish. Analysis of the relationship between the otolith core-to-edge distance and fish mass indicated that most growth occurred in brackish water. We conclude that Nurseryfish are euryhaline rather than diadromous and that analysis of water and otolith $^{87}Sr/^{86}Sr$ is an effective method for assessing the movements of tropical riverine fishes and the potential importance of fish migration in driving foodweb subsidies.

Key words: otolith chemistry, strontium, euryhaline, diadromy, migration, estuary

The importance of landscape-scale energy, material, and organism transport in driving foodweb and ecosystem dynamics has become widely appreciated in recent years (e.g., Polis et al. 1997, Flecker et al. 2010). In tropical river systems, many fish species are euryhaline or diadromous and potentially act as important conduits for the flow of energy and materials between freshwater and estuarine/marine biomes (Winemiller and Jepsen 1998). However, at present, detailed information is lacking on the movements of most tropical fish species (Lucas and Baras 2001), and the extent to which migration across salinity gradients contributes to foodweb subsidies in tropical rivers remains largely unquantified.

A particularly useful method for studying the movements of fishes across salinity gradients is otolith chemistry analysis. Otoliths are crystalline structures formed by the gradual accretion of calcium carbonate—a process that continues throughout the life of the fish (Campana 1999). Dissolved ions in the surrounding water become incorporated in the otolith matrix as it accretes, and the chemical composition of the otoliths tends to be correlated with the chemistry of the ambient water (Macdonald and Crook 2010, Doubleday et al. 2013). The alkaline earth metals Sr and Ba have been used extensively to examine movement across salinity gradients because these metals substitute for Ca in the otolith matrix (Doubleday et al. 2014), and their concentrations and bioavailability vary strongly between fresh and sea water (e.g., Elsdon and Gillanders 2005, Crook et al. 2006). In recent times, Sr isotope ratios ($^{87}Sr/^{86}Sr$) have been used increasingly for this purpose (Kennedy et al. 2000, 2002, Walther et al. 2011, Huey et al. 2014). A major advantage of analyzing $^{87}Sr/^{86}Sr$ is that, unlike Sr:Ca and Ba:Ca, physiological regulation does not affect Sr isotope ratios in otoliths, and therefore, otolith and water $^{87}Sr/^{86}Sr$ can be matched di-

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rectly (Amakawa et al. 2012, Hughes et al. 2014, Schmidt et al. 2014). Furthermore, $^{87}Sr/^{86}Sr$ is essentially invariant in the marine environment (global value: 0.70916; McArthur and Howarth 2004), but it varies widely in fresh water because of variation in the underlying geology and local hydrology (Barnett-Johnson et al. 2008, Crook et al. 2013). This characteristic provides researchers with the capacity to calculate water $^{87}Sr/^{86}Sr$-mixing models across salinity gradients using marine and freshwater 'end-members' against which otolith $^{87}Sr/^{86}Sr$ can be directly compared to reconstruct ambient salinity throughout the life of a fish (see Walther and Limburg 2012).

The Nurseryfish, *Kurtus gulliveri* Castelnau, 1878, is a small-to-medium-sized fish (up to ~300 mm standard length [SL]) that occurs in estuaries and the freshwater reaches of tropical rivers in northern Australia and southern New Guinea (Berra 2003). The species exhibits an unusual form of parental care, and the male carries a mass of several hundred eggs on a supraoccipital hook (Weber 1910, 1913, de Beaufort 1914, Berra 2003, Berra et al. 2004). Males with egg masses and newly hatched larvae have been collected in freshwater reaches (Berra et al. 2004, 2007), whereas juveniles and adults have been recorded from fresh water to saline estuarine habitats (Berra et al. 2007, Pusey and Kennard, unpublished data, DAC, unpublished data). Extensive research has been done on Nurseryfish reproductive biology and early life history (Berra and Neira 2003, Berra and Aday 2004, Berra et al. 2007), anatomy and histology (Berra and Wedd 2001, Berra and Humphrey 2002, Carpenter et al. 2004, Berra et al. 2007), genetics (Ezaz et al. 2007, Sommer et al. 2011), disease (Humphrey and Berra 2006), age and growth (Berra and Aday 2004), and diet (Berra and Wedd 2001), but almost nothing is known of the species' movements. We addressed this knowledge gap by analyzing $^{87}Sr/^{86}Sr$ in the otoliths of Nurseryfish from a tropical river/estuary system in northern Australia to examine their movements and assess the potential significance of movement by Nurseryfish as a mechanism for transporting energy and nutrients across salinity gradients.

METHODS

Fish collection

Nurseryfish were collected from Marrakai Creek in the Northern Territory, Australia (site 11; Fig. 1, Table 1). Marrakai Creek is a tributary of the Adelaide River and is ~80 km upstream of the river mouth. Fish were collected using two 11-cm-mesh gill nets (2.5 m deep × 15 m long) set from 19 October to 18 November 2011 in water ranging in salinity from 0 to 7‰. The net was set during daylight hours of neap tide periods and was checked every 20 min for 2 to 3 h on each day. The net could safely and effectively be worked only for ~2 h before high tide to 30 min after high tide because of the strong tidal movement and the inability of the net to hold the bottom.

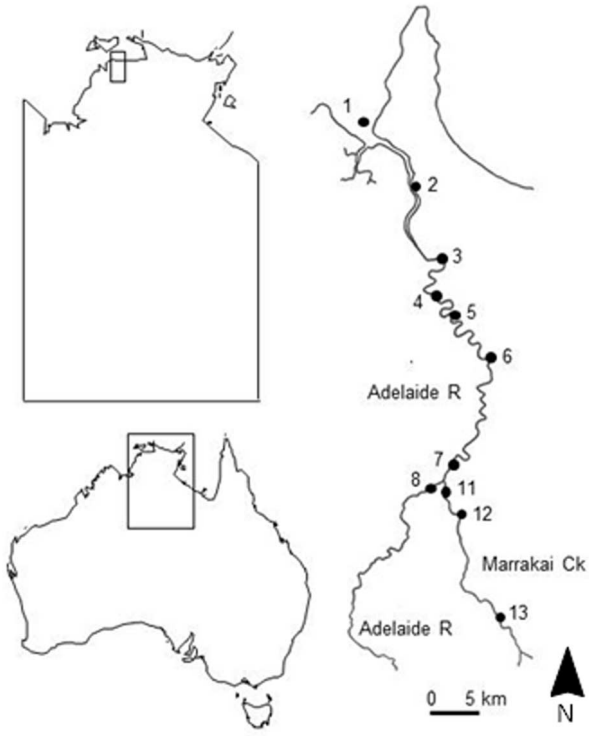

Figure 1. Map of the study area. Numbers refer to water collection sites (see Table 1). Sites 9 and 10 are off the map but were 65 km and 91 km upstream of site 8 on the Adelaide River.

Upon capture, fish were euthanized by overdose in Aqui-S® (100 mg/L; Aqui-S, Lower Hutt, New Zealand), measured (SL ± 1 mm), and weighed (nearest g), and their sex was assessed via examination for the presence of the sexually dimorphic supraoccipital hook. The sagittal otoliths were removed in the field and placed into labeled paper envelopes for storage prior to preparation for analysis.

Water collection and analysis

Water samples were collected in 125-mL acid-washed polyethylene bottles, refrigerated at 4°C, and transferred to the University of Melbourne. The salinity of each water sample was measured in the field using a Quanta® water-quality meter (Hydrolab Corp., Loveland, Colorado). This unit has a reported accuracy of ±1% and precision of 0.01‰. Small (20 mL) aliquots of each water sample were filtered through a 0.2-µm Acrodisc syringe-mounted filter (Pall Corporation, Port Washington, New York) into clean polystyrene beakers and dried overnight in a high-efficiency particulate air (HEPA)-filtered fume cupboard. Previous analyses have shown that filtering after transfer to the laboratory, rather than after sample collection in the field, has no influence on the $^{87}Sr/^{86}Sr$ ratio of the sub-0.2-µm fraction (Palmer and Edmond 1989, R. Maas [University of Melbourne], unpublished data). Sr was extracted using a single pass over 0.15 mL (4 × 12 mm) beds

Table 1. Details of 30 Nurseryfish collected from the lower reaches of Marrakai Creek and analyzed for otolith $^{87}Sr/^{86}Sr$. Age in years estimated as number of annual increments (Berra and Aday 2004). SL = standard length. Dates are formatted dd/mm/yyyy. * indicates length and mass data unavailable because a shark consumed part of the fish while in net.

Females					Males				
Code	Date	SL (mm)	Mass (g)	Age (y)	Code	Date	SL (mm)	Mass (g)	Age (y)
F1	20/10/2011	254	247	2	M1	20/10/2011	217	148	2
F2	18/11/2011	258	237	2	M2	20/10/2011	195	109	2
F3	18/11/2011	205	124	2	M3	20/10/2011	177	60	1
F4	18/11/2011	198	103	2	M4	20/10/2011	148	48	1
F5	18/11/2011	181	80	2	M5*	20/10/2011	–	–	1
F6	21/10/2011	269	335	2	M6	02/11/2011	224	149	2
F7	21/10/2011	279	315	3	M7	02/11/2011	223	135	2
F8	04/11/2011	259	263	3	M8	02/11/2011	195	103	2
F9	04/11/2011	205	120	2	M9	02/11/2011	185	82	2
F10	04/11/2011	139	35	1	M10	02/11/2011	154	49	1
F11	19/10/2011	266	301	3	M11	21/10/2011	198	118	2
F12	03/11/2011	151	47	1	M12	21/10/2011	195	98	1
F13	08/11/2011	245	228	2	M13	21/10/2011	195	105	2
F14	08/11/2011	227	178	2	M14	21/10/2011	140	40	1
					M15	21/10/2011	115	21	1
					M16	19/10/2011	225	172	2

of EICHROM™ Sr resin (50–100 μm; Eichrom, Chicago, Illinois). Matrix elements were washed off the resin with 2 M and 7 M HNO_3, followed by elution of clean Sr in 0.05 M HNO_3 (Pin et al. 1994). The total blank, including syringe-filtering, was ≤0.1 ng. Based on the signals obtained in the inductively coupled plasma mass spectrometer (ICP-MS), ≥400 ng of Sr were present in each sample split, implying sample-to-blank ratios ≥ 4000. Therefore, blank corrections were unnecessary. Sr isotope analyses were carried out on a Nu Plasma multicollector ICP-MS (Nu Instruments, Wrexham, UK) interfaced with an ARIDUS desolvating system (CETAC, Omaha, Nebraska; see Maas et al. 2005). Mass bias was corrected by normalizing to $^{87}Sr/^{86}Sr = 8.37521$, and results are reported relative to a value of 0.710230 for the SRM987 Sr isotope standard.

Internal precision (2 SE) based on at least thirty 10-s integrations ranged from ±0.000011 to 0.000031. Reproducibility (2 SD) was approximately ±0.000040. Three analyses of modern sea water produced an average $^{87}Sr/^{86}Sr$ of 0.709162 ± 0.000016 (2 SD), virtually identical to the accepted marine ratio of 0.709160, adjusted to SRM987 = 0.710230 (McArthur and Howarth 2004). Mixing models of $^{87}Sr/^{86}Sr$ were calculated over the salinity gradient for the Adelaide River and Marrakai Creek with the least saline freshwater sample and a marine (salinity = 36.0‰) sample collected from the Adelaide River mouth on 11 August 2010 as end-members.

Otolith preparation and Sr isotope analysis. Otoliths from 14 female and 16 male Nurseryfish were embedded in 2-part epoxy resin (EpoFix®, Struers, Ballerup, Denmark) and transversely sectioned to a thickness of ~300 μm through the primordium with a slow-speed saw. The sections were polished with lapping film (9 μm), rinsed with deionized water, air dried, and mounted on glass slides with epoxy resin. All fish were aged by counting annual increments under a dissecting microscope according to the methods of Berra and Aday (2004). Laser ablation–ICP-MS (LA-ICPMS) was used to measure Sr isotope ratios ($^{87}Sr/^{86}Sr$) in the otoliths. The experimental system consisted of a Nu Plasma multicollector ICP-MS, coupled to a HelEx laser ablation system (Laurin Technic, Canberra, Australia, and the Australian National University) constructed around a Compex 110 excimer laser (Lambda Physik, Gottingen, Germany) operating at 193 nm.

Otolith mounts were placed in the sample cell, and the ablation path for each sample was digitally plotted using GeoStar software (version 6.14; Resonetics, Nashua, New Hampshire) and a 400× objective coupled to a video-imaging system. Ablation transects were run from the otolith core to the proximal edge. A 55-μm laser spot was used, and the laser was operated at 80 mJ, pulsed at 10 Hz, and scanned at 5 μm/s. Ablation was done under pure He to minimize redeposition of ablated material, and the sample was then rapidly entrained in the Ar carrier gas flow. Corrections for Kr and ^{87}Rb interferences were made fol-

lowing Woodhead et al. (2005), and mass bias was corrected by reference to an $^{86}Sr/^{88}Sr$ ratio of 0.1194. Iolite (version 2.13; Paton et al. 2011) that operates within IGOR Pro (version 6.2.2.2; WaveMetrics, Lake Oswego, Oregon) was used to process data offline, with data corrected for potential Ca argide/dimer interferences. A modern marine carbonate standard composed of mollusk shells ($^{87}Sr/^{86}Sr$ value = 0.70916 according to long-term laboratory measurements, identical to the accepted modern seawater value of 0.709160; McArthur and Howarth 2004) was analyzed after every 10 otolith samples to allow calculation of external precision. Mean (±1 SD) values of $^{87}Sr/^{86}Sr$ values in the modern marine carbonate standard (n = 24) run throughout the analyses were 0.70917 ± 0.00013, with external precision (expressed as ±2 SE) calculated as ±0.00005. Mean within-run precision, measured as ±2 SE, was ±0.00004. Following chemical analysis, the core-to-edge distance of each transect was measured under a dissecting microscope with image analysis software (ImagePro®; Media Cybernetics, Rockville, Maryland).

Analysis of individual salinity histories

The $^{87}Sr/^{86}Sr$ transect data for each fish were examined in relation to the water-mixing models to assess their lifetime salinity histories. A lack of variation in water $^{87}Sr/^{86}Sr$ at salinities >~4‰ limited the inference that could be drawn regarding otolith material accreted in ambient water of salinity 4–36‰ (see below). Therefore, for consistent interpretation of the otolith chemistry data in relation to the water-mixing models, we defined saline water as salinity 4–36‰, brackish water as 0.5–4‰, and freshwater as salinity <0.5‰. The relationship between otolith core-to-edge distance (i.e., transect length in mm) and fish mass (g) was examined with least-squares regression to estimate the amount of growth under each salinity category. To ensure that smaller size classes were represented and the model intercept was biologically relevant—thus reducing the potential for model bias (see Campana 1990)—the regression analysis included 13 additional Nurseryfish (53–147 mm SL) collected as part of a separate study from the South Alligator River ~110 km to the east of the Adelaide River.

The regression relationship was then used to convert the $^{87}Sr/^{86}Sr$ transect distance (mm) into an estimate of the % of total mass assimilated in each salinity category for each individual fish. To demonstrate, if the first 0.5 mm of a 1.5-mm $^{87}Sr/^{86}Sr$ transect corresponded to a salinity range of 4–36‰, the mass assimilated within that salinity range would have been calculated as 7.2 g using the regression equation $y = 54.133x^{2.92}$ (see Results). If the remaining 1.0 mm of the $^{87}Sr/^{86}Sr$ transect corresponded to a salinity range of 0.5–4‰, the total mass of the fish would have been calculated as 176.8 g using the regression equation, and the mass assimilated in the 0.5–4‰ salinity range estimated as 169.6 g by subtracting 7.2 g (i.e., the mass assimilated at salinity 4–36‰). The % mass assimilated in each salinity category would then be calculated by dividing the mass for each salinity category by the total modeled mass and multiplying by 100.

RESULTS

Water chemistry

The marine sample (salinity = 36.0‰, $^{87}Sr/^{86}Sr$ = 0.709147) collected at the mouth of the Adelaide River estuary corresponded closely to the modern seawater value of 0.70916 reported by McArthur and Howarth (2004) (Table 2, Fig. 2A). Samples collected from the upper freshwater reaches of the Adelaide River and Marrakai Creek above the tidal influence (sites 9, 10, 13; Fig. 1) had relatively high $^{87}Sr/^{86}Sr$ (range: 0.734457–0.777853), reflecting the radiogenic geology of the region (McCulloch et al. 2005). The water-mixing models showed little variation in $^{87}Sr/^{86}Sr$ at salinities of 4–36‰, followed by a very steep increase in $^{87}Sr/^{86}Sr$ at salinities <~4‰ (Fig. 2A, B). The modeled $^{87}Sr/^{86}Sr$ values corresponded closely to empirical samples of intermediate salinity, indicating that the assumption of conservative mixing of Sr inherent in the mixing models was valid (Walther and Limburg 2012).

Otolith chemistry and individual salinity histories

No clearly discernible differences in the $^{87}Sr/^{86}Sr$ otolith transects were found between male and female Nurseryfish (Figs 3, 4). Eleven of the 16 males (69%) and 12 of the 14 females (86%) had $^{87}Sr/^{86}Sr$ values indicative of residence in saline water (>4‰) at the otolith core, whereas 4 of 16 males (25%; M6, M10, M13, M15) and 2 of 14 females (14%; F6, F11) had $^{87}Sr/^{86}Sr$ values indicative of brackish conditions at the otolith core. Only 1 male (M4; Fig. 4) had otolith core $^{87}Sr/^{86}Sr$ values indicative of freshwater residence. The otolith core values do not necessarily correspond with the actual salinity at the time of spawning or hatching because a 55-μm laser spot integrates at least several days of growth, and movement across salinity gradients could have occurred over that time scale. Limitations in temporal resolution are inherent in this type of analysis and need to be considered when interpreting the results.

Despite individual variation in $^{87}Sr/^{86}Sr$ values at the otolith core, all fish had $^{87}Sr/^{86}Sr$ values indicative of residence in water of salinity >4‰ at some stage during the early life history (i.e., within the first 0.6 mm of the transect, corresponding to <95 mm SL; Figs 3, 4, 5A). Following residence in saline water during the early life history, all 30 fish analyzed showed evidence of a transition into brackish or fresh water later in life, but this evidence was more pronounced in some fish (e.g., F1, M12) than others

Table 2. Locations, sampling dates, and results of chemical analysis of water collected from the Adelaide River and Marrakai Creek. Internal precision (2 SE) ranged from 0.000011 to 0.000031 across all samples. Numbers of sites correspond to numbers in Fig. 1. Fish were collected from site 11.

Site	Latitude/longitude	Date(s)	Salinity (‰)	Sr (ppm)	$^{87}Sr/^{86}Sr$
1. Adelaide River	12°13.370′S, 131°13.711′E	11 August 2010	36.0	2.4	0.709147
2. Adelaide River	12°16.959′S, 131°17.013′E	11 August 2010	35.8	3.6	0.709180
3. Adelaide River	12°22.756′S, 131°19.271′E	11 August 2010	32.6	2.5	0.709197
4. Adelaide River	12°25.758′S, 131°19.069′E	11 August 2010	25.6	2.3	0.709206
5. Adelaide River	12°27.560′S, 131°20.230′E	11 August 2010	19.7	2.0	0.709309
6. Adelaide River	12°30.440′S, 131°23.405′E	11 August 2010	7.7	1.1	0.709557
7. Adelaide River	12°39.426′S, 131°20.276′E	11 August 2010	0.60	0.16	0.713225
		6 November 2012	3.98	0.84	0.711093
		27 February 2013	0.09	0.023	0.723447
8. Adelaide River	12°41.123′S, 131°18.431′E	11 August 2010	0.42	0.12	0.714901
		6 November 2012	3.80	0.81	0.711195
		27 February 2013	0.08	0.021	0.725071
		27 February 2013	0.17	0.04	0.719699
9. Adelaide River	13°14.405′S, 131°06.478′E	3 October 2012	0.12	0.013	0.739946
		14 June 2013	0.13	0.018	0.740887
10. Adelaide River	13°28.997′S, 131°05.846′E	3 October 2012	0.01	0.004	0.736280
		14 June 2013	0.04	0.004	0.734457
*11. Marrakai Creek	12°40.861′S, 131°20.131′E	11 August 2010	0.48	0.13	0.714450
		4 November 2011	1.05	0.363	0.712385
		6 November 2012	3.09	0.67	0.711657
12. Marrakai Creek	12°42.793′S, 131°20.420′E	11 August 2010	0.36	0.11	0.716543
		6 November 2012	2.53	0.57	0.713619
13. Marrakai Creek	12°49.715′S, 131°22.118′E	24 July 2013	0.04	0.002	0.777853

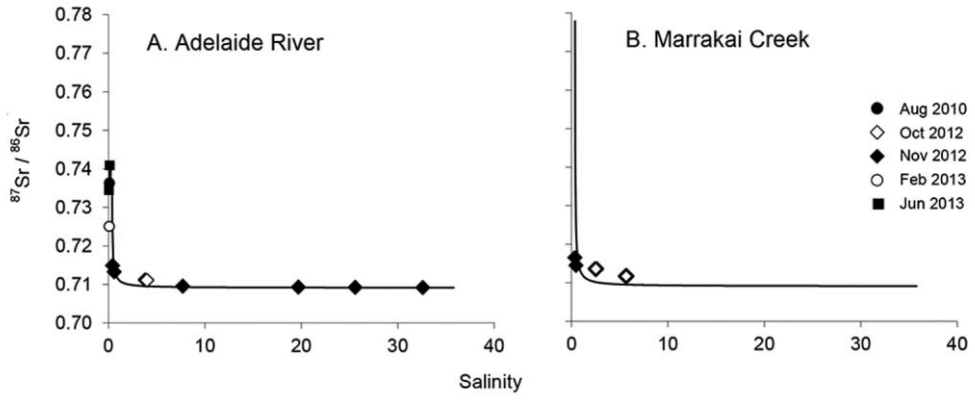

Figure 2. Mixing models (lines) of water $^{87}Sr/^{86}Sr$ across salinity gradient in the Adelaide River (A) and Marrakai Creek (B). The marine end-member sample used to calculate both models was collected from Adelaide River site 1 on 11 August 2010 (salinity = 36.0‰, $^{87}Sr/^{86}Sr$ = 0.709147). Freshwater end-member samples were collected from Adelaide River site 10 on 3 October 2012 (salinity = 0.01‰, $^{87}Sr/^{86}Sr$ = 0.736280) and from Marrakai Creek site 13 on 29 July 2013 (salinity = 0.04‰, $^{87}Sr/^{86}Sr$ = 0.777853). Symbols represent empirical samples collected from intermediate salinities.

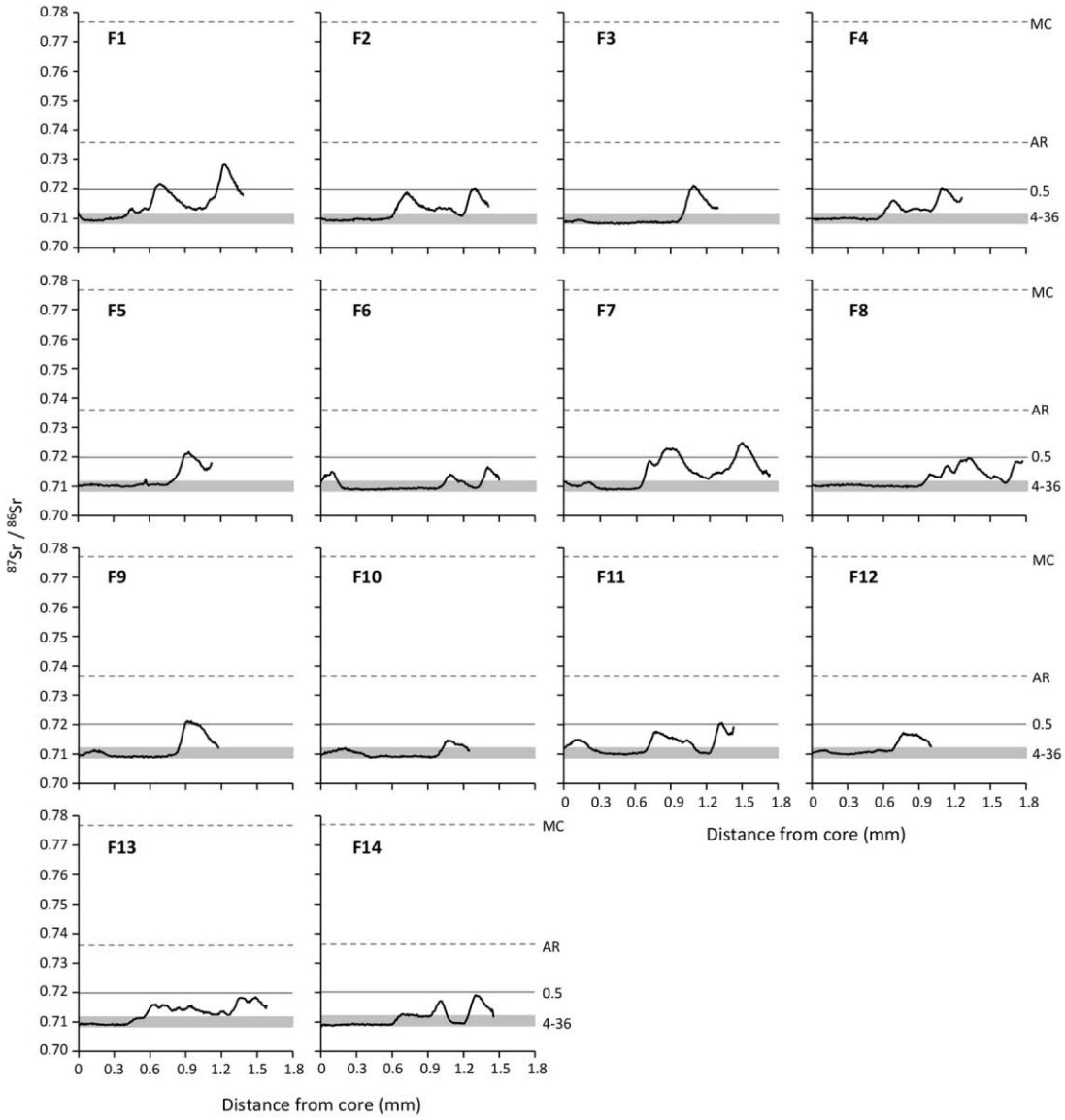

Figure 3. Core-to-edge otolith $^{87}Sr/^{86}Sr$ transects for female Nurseryfish. The shaded area shows the range of modeled water $^{87}Sr/^{86}Sr$ values for Marrakai Creek at salinities 4–36‰, and the unbroken line represents salinity = 0.5‰. The broken lines AR and MC show the least saline freshwater end-members used in the $^{87}Sr/^{86}Sr$ water-mixing models for the Adelaide River and Marrakai Creek, respectively.

(e.g., F10, M14) (Figs 3, 4). Most fish subsequently showed evidence of periodic residence in saline habitats for short periods after the initial transition (Figs 3, 4). None of the fish had $^{87}Sr/^{86}Sr$ values that reached the freshwater end-member values of the upper reaches of Marrakai Creek or the Adelaide River (sites 10, 13; Table 2; Figs 3, 4), suggesting that the movements of Nurseryfish were limited to brackish and saline water in the estuary and the lower freshwater reaches of the catchment.

A strong linear relationship existed between otolith core-to-edge distance and SL (r^2 = 0.8567; Fig. 5A). The intercept of the regression equation (5.65 mm) corresponded closely with the observed size-at-hatch for Nurseryfish (5 mm; Berra and Neira 2003), indicating that it had biological relevance and that core-to-edge distance was a reliable predictor of fish size (Campana 1990). The relationship between otolith core-to-edge distance and mass also was strong (r^2 = 0.8995; Fig. 5B), with mass increasing as a power function (exponent = 2.92) of core-to-edge distance. This result reflects an isometric relationship between body length and mass (see Weatherley and Gill 1987, Crook and Gillanders 2013). Some heterogeneity of variance was apparent in both regression models, and examination of residuals showed that variance tended to increase with length and mass. This variation may affect the sensitivity of the model used to back-calculate mass from core-to-edge distance, but the above observations (concordance between intercept and size-at-hatch, power function

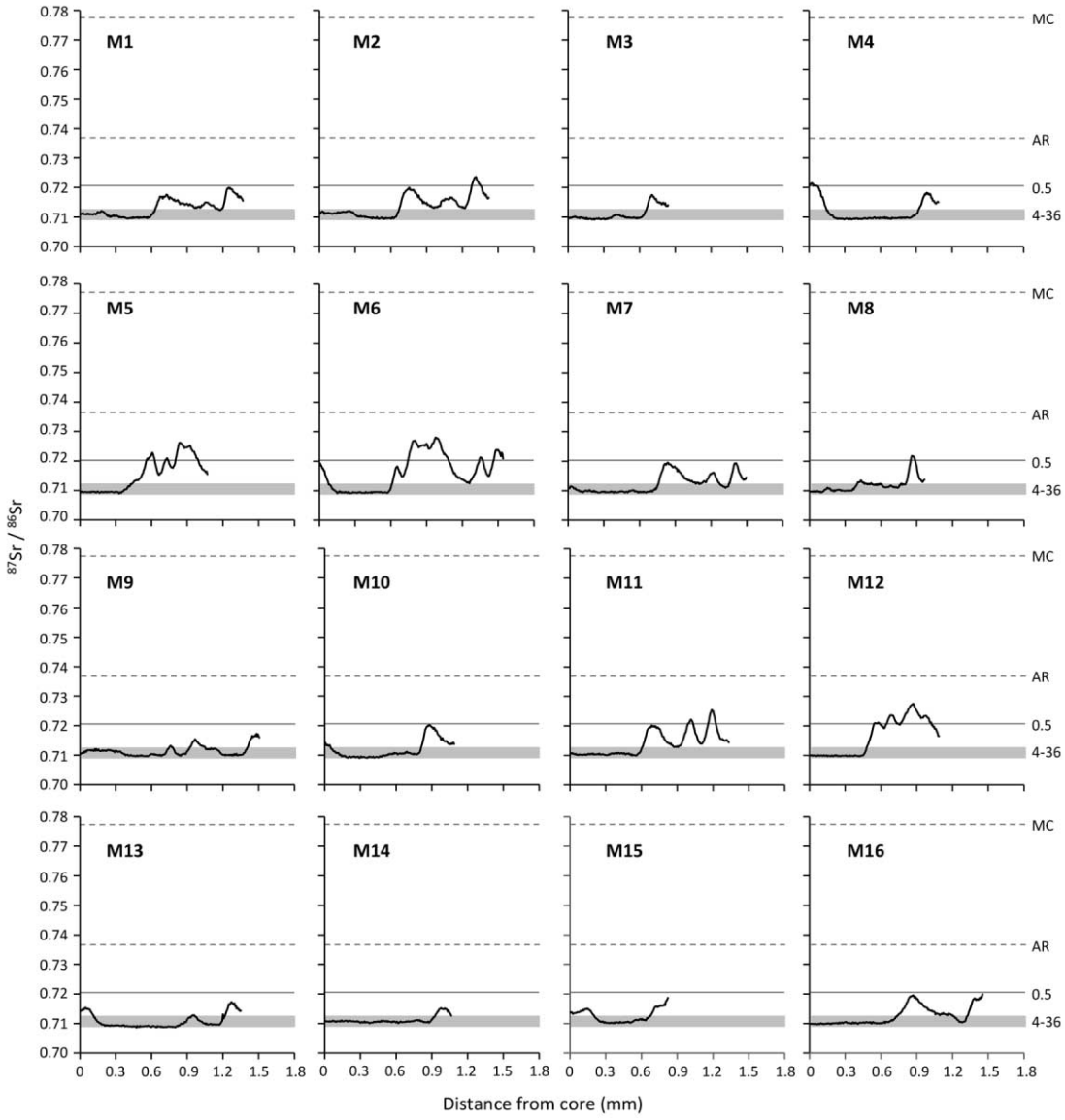

Figure 4. Core-to-edge otolith $^{87}Sr/^{86}Sr$ transects for male Nurseryfish. The shaded area shows the range of modeled water $^{87}Sr/^{86}Sr$ values for Marrakai Creek at salinities 4–36‰, and the unbroken line represents salinity = 0.5‰. The broken lines AR and MC show the least saline freshwater end-members used in the $^{87}Sr/^{86}Sr$ water-mixing models for the Adelaide River and Marrakai Creek, respectively.

reflecting isometry) and the strength of the mass:core-to-edge relationship suggest that any bias in the back-calculated estimates is unlikely to be significant in the context of the aims of our study, and thus, the results presented are robust. The estimates of mass assimilated under different salinity ranges suggested that most growth occurred while fish were resident in brackish water (mean 66%), followed by saline (25%) and fresh (8%) water (Table 3).

DISCUSSION

Our results provide the first detailed information regarding the salinity histories and movements of Nurseryfish and demonstrate the applicability of this technique for elucidating the migratory patterns of tropical riverine fishes. Despite considerable variation in the $^{87}Sr/^{86}Sr$ transects among individual fish, most fish spent at least part of their early life histories in relatively saline water (salinity >4‰) before transitioning to brackish (0.5–4‰) or fresh (<0.5‰) water where they then spent most of their adult lives.

A potential explanation for the observed patterns of $^{87}Sr/^{86}Sr$ variation is that they reflect variation in ambient water chemistry caused by seasonal, hydrologic, or tidal fluctuations in $^{87}Sr/^{86}Sr$, rather than active movement by fish across salinity gradients. Repeated sampling of water $^{87}Sr/^{86}Sr$ in Marrakai Creek provided little evidence of strong temporal variation within sampling sites. However,

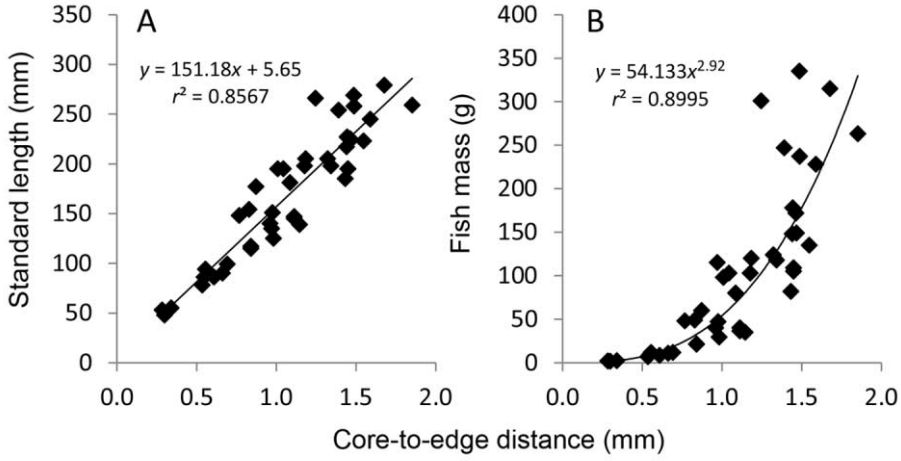

Figure 5. Relationship between fish standard length (A) and mass (B) and otolith core-to-edge distance along the transect axis used to analyze $^{87}Sr/^{86}Sr$.

some temporal variation in $^{87}Sr/^{86}Sr$ was apparent at sites 7 and 8 in the Adelaide River, with lower values during periods of low freshwater flow in August 2010 and November 2012 than during high flows in February 2013 (Table 2). We have observed a similar pattern (wet season: 0.729–0.731, dry season: 0.719–0.720) in the Daly River 130 km to the west of our study area (DAC, unpublished data). Temporal variation in water $^{87}Sr/^{86}Sr$ in the study region appears to be driven by a predominance of surface runoff containing weathered aluminosilicates during the wet season vs higher groundwater inflows influenced by limestone and secondary carbonates in the dry season (Hagedorn et al. 2011, Walther et al. 2011). Given the immense seasonal variation in rainfall and evaporation rates in the wet–dry tropics of Northern Australia (Warfe et al. 2011), seasonal variation in $^{87}Sr/^{86}Sr$ is likely to be common in many rivers and estuaries in this region and may be a contributing factor to the observed variation in the otolith $^{87}Sr/^{86}Sr$ transects of the analyzed Nurseryfish.

Table 3. Estimated growth (% fish mass) while resident in each salinity category based on analysis of the relationship between the otolith core-to-edge distance and fish mass. Freshwater = salinity <0.5‰, brackish = salinity 0.5–4‰, saline = 4–36‰. SD = standard deviation.

Salinity category	Mean	SD	Minimum	Maximum
Total (n = 30)				
Freshwater	8.32	15.00	0	64.28
Brackish	66.14	17.30	27.56	96.83
Saline	25.53	18.74	2.81	62.52
Female (n = 14)				
Freshwater	5.74	10.02	0	31.50
Brackish	70.06	15.49	46.26	96.83
Saline	24.51	16.03	2.81	53.33
Male (n = 16)				
Freshwater	10.58	18.34	0	64.28
Brackish	62.99	19.05	27.56	90.82
Saline	26.43	21.32	3.94	62.52

Nonetheless, several lines of evidence suggest that active movement across salinity gradients is undertaken by Nurseryfish. First, if fish were sedentary and variation in ambient water chemistry at the collection site were driving the observed variation in $^{87}Sr/^{86}Sr$, one would expect very similar $^{87}Sr/^{86}Sr$ transects among individuals of the same age class (Walther et al. 2011). Instead, individual variation was high among fish of the same age class. Furthermore, the fish analyzed comprised 3 age classes, but the extended period of characteristically low $^{87}Sr/^{86}Sr$ values (salinity >4‰) consistently occurred in the region of the otolith representing the early life history (<95 mm SL). If variation in water chemistry at the sampling location alone had driven the patterns of $^{87}Sr/^{86}Sr$, the extended period of low $^{87}Sr/^{86}Sr$ should have occurred at different life-history stages for fish of different ages (Walther et al. 2011). Thus, our results suggest that most Nurseryfish collected from Marrakai Creek spent at least part of their early life history in water of salinity >4‰ in the estuary before transitioning upstream to brackish or fresh water, where they then remained for most of their adult lives. However, our analyses were restricted to fish sampled from a single location, and our results do not provide information on whether such movement patterns are representative of the species in other parts of its distribution.

Arising from these observations is the issue of whether Nurseryfish should be considered diadromous. According to McDowall (1997), diadromous migrations: 1) are regu-

lar, physiologically mediated movements between fresh water and the sea; 2) occur at predictable times and at characteristic life-history phases in each species; 3) involve most members of a species' populations and usually are obligatory; and 4) necessarily involve 2 reciprocal migrations, one from fresh water to the sea, and the other in the opposite direction. Our finding of movement between fresh and saline water during the early life history in most individuals suggests that Nurseryfish partially fulfill these criteria. Other fishes that undertake migrations between fresh water and the estuarine reaches of river systems have commonly been classified as marginally diadromous (e.g., Inanga *Galaxias maculatus*, McDowall 1988; Australian Bass *Macquaria novemaculeata*, Jerry and Baverstock 1998; Mullet *Liza macrolepis*, Chang and Iizuka 2012).

However, other aspects of our findings do not support classification of the movements of Nurseryfish as diadromous migrations. Considerable individual variation existed both in the near-core $^{87}Sr/^{86}Sr$ values (representing the larval and early juvenile phases) and in the timing of the transition to freshwater/brackish habitats, results suggesting that the timing of movement is neither predictable nor characteristic of a specific life-history stage at the individual level. Furthermore, following transition, most fish appeared to reside primarily in brackish rather than fresh water during most of the adult phase and, thus, do not satisfy the criteria for diadromy. These observations are concordant with previous surveys of larval, juvenile, and adult Nurseryfish across a wide range of salinities (Berra and Neira 2003, Sommer et al. 2011, DW, unpublished data, DAC, unpublished data). Based on these observations, we suggest that Nurseryfish should be considered a euryhaline, rather than diadromous, species.

Our finding that most Nurseryfish spent most of their adult lives at salinities <4‰ demonstrates that the vast majority of tissue was assimilated while the fish were living in fresh or brackish water. Nonetheless, some energy and nutrients assimilated in more saline regions of the estuary are likely to have been transported by Nurseryfish to brackish and freshwater regions because most fish undertook a transition to less saline water during the early phases of the life history. In comparison to diadromous species with more uniform and predictable migration patterns (e.g., Pacific Salmon *Oncorhynchus* spp., Naiman et al. 2002; Australian Grayling *Prototroctes maraena*, Berra 1982, Crook et al. 2006), quantifying the energy and nutrients transported across ecotones via Nurseryfish movement would be a challenging task because of the complexity and variability of movement patterns exhibited. For instance, it would be necessary to sample fish from a range of locations to ensure that any spatial variation in movement patterns was accounted for. The rates of mortality at different life-history stages and salinities would have to be quantified to identify the locations in which assimilated tissue is ultimately incorporated into the local food web (Flecker et al. 2010). Nevertheless, we think that our approach to estimating growth under variable salinity regimes using otolith $^{87}Sr/^{86}Sr$ transect analysis combined with otolith back-calculation has considerable potential for developing quantitative estimates of foodweb subsidies resulting from the migration of euryhaline and diadromous fishes.

As the number of studies using newly available technologies grows, and the quality and quantity of information pertaining to fish migration increases, it is becoming increasingly clear that fishes exhibit a wide range of often highly flexible migration strategies (Koehn and Crook 2013). Even archetypal examples of diadromous life-history modes, such as catadromy in the anguillid eels, have recently been shown to be facultative and highly plastic. Many eels never enter fresh water and, thus, cannot be considered diadromous, let alone catadromous (see Tsukamoto et al. 1998, Arai and Chino 2012). The movement patterns of Nurseryfish revealed in our study provide yet another example of a fish species that exhibits high levels of individual variability and cannot be easily pigeon-holed into the classical definitions of migratory modes. Nonetheless, such species are likely to play important roles in the transport of energy and nutrients within and between aquatic biomes.

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