Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Ecological plasticity of the European eel *Anguilla anguilla* in a tidal Atlantic lake system in Ireland

Takaomi Arai[1], Aya Kotake[2], Chris Harrod[3,4], Michelle Morrissey[3] and T. Kieran McCarthy[3]

[1]Environmental and Life Sciences Programme, Faculty of Science, Universiti Brunei Darussalam, Jalan Tungku Link, Gadong, BE 1410, Brunei Darussalam; [2]Atmosphere and Ocean Research Institute, The University of Tokyo 5-1-5, Kashiwanoha, Kashiwa, Chiba 277-8564, Japan; [3]Department of Zoology, National University of Ireland, Galway, University Road, Galway, Ireland and [4]Instituto de Ciencias Naturales Alexander Von Humboldt, Universidad de Antofagasta, Avenida Angamos 601, Antofagasta, Chile

Original Article

Cite this article: Arai T, Kotake A, Harrod C, Morrissey M, McCarthy TK (2019). Ecological plasticity of the European eel *Anguilla anguilla* in a tidal Atlantic lake system in Ireland. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1189–1195. https://doi.org/10.1017/S0025315419000031

Received: 17 August 2018
Revised: 5 November 2018
Accepted: 3 January 2019
First published online: 7 February 2019

Key words:
Anguillid eel; habitat use; migration; otolith microchemistry; salinity gradient

Author for correspondence:
Takaomi Arai,
E-mail: takaomi.arai@ubd.edu.bn

Abstract

Recent studies have shown that anguillid eel populations in habitats spanning the marine–freshwater ecotone can display extreme plasticity in the range of catadromy expressed by individual fish. The apparent use of marine and freshwater habitats by the European eel *Anguilla anguilla* was examined by analysing the strontium (Sr) and calcium (Ca) concentrations in otoliths of eels collected from a tidal Atlantic lake system in Ireland. Variations of the Sr:Ca ratio in the otoliths indicated that a variety of environmental salinities had been experienced in the habitats that were occupied during the growth phase of these individuals in the tidal Atlantic lake system. The otolith microchemistry of these eels indicated that most of the eels had entered each salinity environment (freshwater (FW); brackish water (BW); marine-dominated water (MW) and full seawater (SW)) from fresh water to full seawater just after recruitment and had stayed in each environment until maturation without movement to other salinity environments. Only 2 of 93 (2%) eels had shifted their habitat once in their lives. This result suggests that each individual might have an environmental habitat preference, although each individual could move along a short (<2 km) salinity gradient.

Introduction

The European eel *Anguilla anguilla* is an important species both economically and ecologically. However, over the last two decades, sharp declines in indices of recruitment and escapement for several species of the temperate zone, including *A. anguilla* have led biologists to become increasingly concerned regarding their long-term conservation status (Dekker *et al.*, 2003). Many reasons for these eels' decline have been proposed, including overfishing of all life stages, habitat degradation, shifts in oceanic currents, barriers to migration (e.g. weirs, dams), accumulation of xenobiotic compounds and parasites (Casselman, 2003).

The life cycle of the European freshwater eel *A. anguilla* has five principal stages: the leptocephalus, glass eel, elver, yellow eel and silver eel stages (Bertin, 1956). The spawning area of *A. anguilla* is supposed to be in the Sargasso Sea (Schmidt, 1922, 1925). The larvae, leptocephali, drift on the Gulf Stream and are further transported by the North Atlantic Current across the Atlantic Ocean (Schmidt, 1922, 1925; Boëtius, 1985). The leptocephali presumably leave oceanic currents after metamorphosing into glass eels and then typically migrate upstream as elvers, 6–12 months after hatching (Arai *et al.*, 2000; Wang & Tzeng, 2000), to grow in the freshwater habitats of Europe and North Africa during the yellow eel stage. At ages that vary widely among individuals of both sexes, but especially among the larger older females, the yellow eels metamorphose into silver eels, which migrate downstream to the ocean to begin their journey to their spawning areas in the Sargasso Sea (Tesch, 2003).

Interest in eel biology has increased recently, not only due to conservation concerns, but also because several studies have shown that the catadromous life cycle of the eel is even more complicated than was previously considered. The migratory history of several species of anguillid eels has been studied using microchemical techniques that determine the ratios of strontium to calcium (Sr:Ca ratio) in their otoliths. Previous studies on the strontium incorporation into anguillid eel otoliths showed that the Sr:Ca level in their otoliths strongly correlated with the salinity of the water and was only slightly affected by other factors, such as water temperature, food and physiological factors (Tzeng, 1996; Lin *et al.*, 2007; Arai & Chino, 2017). Thus, the Sr:Ca ratios of otoliths could help to determine whether individual eels actually entered fresh water at the elver stage and remained in freshwater, estuarine or marine environments until the silver eel stage, or whether they move between different habitats with differing salinity regimes. Otolith microchemistry studies have revealed that certain yellow and silver eel stages of temperate and tropical anguillid eels never migrate into fresh water, but spend their entire life history in the ocean (Arai & Chino, 2012). Application of otolith Sr:Ca ratios to trace the migratory history of eels has also revealed intermediate otolith signatures between those of marine and freshwater residents for *A. anguilla*

(Arai *et al.*, 2006; Shiao *et al.*, 2006; Lin *et al.*, 2011), *A. japonica* (Tsukamoto & Arai, 2001; Arai *et al.*, 2003*a*, 2003*b*; Kotake *et al.*, 2003, 2005), *A. rostrata* (Lamson *et al.*, 2006), *A. australis* and *A. dieffenbachii* (Arai *et al.*, 2004), all of which appeared to reflect estuarine residence or showed clear evidence of switching between different salinity environments. It thus appears that a proportion of eels move frequently between different environments during their growth phase. Therefore, because individuals of several anguillid species have been found to remain in estuarine or marine habitats, it appears that anguillid eels do not all enter freshwater environments and that these species display more of a diverse migration in habitats (Tsukamoto & Arai, 2001; Arai & Chino, 2012).

Coastal lagoons are increasingly recognized as being in need of fundamental research in addition to the considerable number of applied studies that focus on specific local environmental or natural resource issues (Kennish & Paerl, 2010). Lagoons are located at the interface between land and sea, and it has been estimated that they comprise ~13% of the world's coastal areas (Kjerve, 1990). Lagoons typically provide breeding areas for birds, fishes and crustaceans that can often be used to support local fisheries and ecologically sustainable tourism activities (Kennish & Paerl, 2010). However, despite being of great importance in terms of biodiversity, fisheries and recreational activities, coastal lagoons are threatened throughout the world by a series of anthropogenic impacts (Berkes & Seixas, 2005; Kennish & Paerl, 2010). The threats to lagoon ecosystems and to habitats with which they are linked in terms of hydrodynamics or ecology vary according to region and intensity of human activity (Berkes & Seixas, 2005; Kennish & Paerl, 2010). The European eel is a typical fish in lagoon systems in Ireland (Moriarty, 1996). Investigations into this eel's ecology and local migratory behaviour in lagoon ecosystems could provide new perspectives that might underpin lagoon conservation plans and provide new information on the population ecology of the declining European eel.

In this paper, we seek to contribute to a better understanding of the ecology of coastal lagoon populations of eels in north-western Europe. Specifically, we present results of a study of eel migrations in a complex coastal lagoon system and adjacent marine habitats in Ireland through the otolith microchemistry (Sr:Ca ratios). We provide new information on habitat utilization patterns and local movements of European eel and we discuss the life-history plasticity of eels (Arai & Chino, 2012) that enables them to effectively exploit habitats across a wide salinity spectrum.

Materials and methods

Study site

We sampled eels along a short (~2 km) marine–freshwater salinity gradient in four basins of Lough (lake) Ahalia in County Galway, western Ireland (53°23′N 9°34′W, Figure 1). Lough Ahalia is an Atlantic coastal lake that consists of a series of basins forming the lower section of the River Screebe catchment. The system flows into the Atlantic Ocean via a single exit in Camus Bay. The lowest basin (surface area ~25 ha, mean depth = 1.6 m) receives twice daily saline intrusions on flood tides. The saline influence continues, but intensity weakens in the central basin (surface area ~60 ha, mean depth = 2.5 m), which receives saline input on spring tides (i.e. fortnightly). The upper basin (surface area ~40 ha, mean depth = 1.7 m) is entirely freshwater with a single significant inflow from the Screebe River, which drains the upper part of the catchment. The scale and intensity of the saline influence on the lower and central sections varies with the tidal cycle (e.g. spring to neap) and the strength and direction of the wind. The Screebe system supports a recreational fishery for migratory salmon (*Salmo salar*) and brown trout (*S. trutta*). This system was chosen for the study because it displays a very marked salinity gradient (0.5–34‰) over a relatively short linear distance (~2 km) and importantly, the eel stock is unexploited.

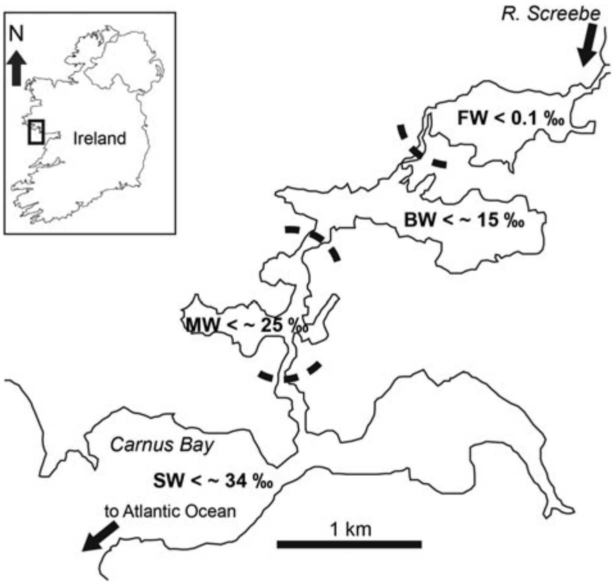

Fig. 1. Lough Ahalia, showing location in Ireland and the four distinct salinity zones referred to in this study: fresh water (FW; 12 eels), brackish water (BW; 24 eels), marine dominated (MW; 36 eels) and full seawater (SW; 21 eels) collected from four distinct salinity zones.

Salinity

To characterize typical salinity values within the four basins of Lough Ahalia, we collected bimonthly (September 2003–June 2004) salinity data from a series of locations over a 200-m grid (N = 30). Salinity values were recorded every 50 cm throughout the water column using a Hydrolab 4a Datasonde (Hydrolab Inc., USA). Significant variation between salinity values was recorded within each basin so using 90th percentile benthic salinity, we classified them into four distinct salinity zones: freshwater (FW: <0.1‰); brackish water (BW: ~15‰); marine-dominated water (MW: ~25‰) and full seawater (SW: ~34). As eels are typically benthic species, we consider benthic salinities to be most representative of their habitats.

Fish collection

European eels were sampled between September 2003 and November 2004 using unbaited summer fyke nets (Poole, 1990) at sites along the salinity gradient in four basins of Lough Ahalia (Figure 1). In FW, BW, MW and SW basins, eels were collected on 19 August 2004, 17 September 2003 and 19 August 2004, 13 May 2004, 7–9 October 2004 and 19 November 2004 and 15 October 2004, respectively. Fyke nets are selective for eels of total length (TL) >300 mm (McCarthy *et al.*, 1999). A total of 93 specimens (FW = 12, BW = 24, MW = 36, SW = 21) were used in this study. Fish sampling was in accordance with a guide for animal experimentation at National University of Ireland (NUI) and fish-handling approval was granted by the animal experiment committee of NUI.

After measurement of TL (to 1 mm), body weight (to 1 g) and eye diameter (to 0.01 mm), the sex of each eel >300 mm long was determined by visual observation of the gonads according to Tesch (2003), i.e. eels having thin regularly lobed organs were males, while individuals having more broad and folded curtain-like gonads were females. An eye index appears to be one of the best indicators of the onset of reproductive maturation in silver

Table 1. Biological characteristics of *Anguilla anguilla* specimens used for otolith microchemistry analyses

					Total length (mm)		Body weight (g)	
Salinity zone	Sampling date	Stage	Sex	Number of eels	Range	Mean ± SD	Range	Mean ± SD
FW	19 August 2004	Y	M	4	313–419	363±45.6	86–111	80.8±23.6
		Y	F	8	359–552	430±60.7	77–316	141±77.1
BW	17 September 2003	Y	M	7	278–436	370±64.3	36–146	88.3±42.8
	19 August 2004	Y	F	17	381–698	481±100	91–217	208±153
MW	13 May 2004	Y	M	1	379		105	
		Y	F	8	338–527	456±65.6	71–278	168±76.4
		Y	U	3	329–340	336±6.1	54–85	68.1±15.9
	7–9 October 2004	S	M	16	298–434	354±32.4	46–128	77.9±21.2
	19 November 2004	S	F	8	359–919	540±193	97–1836	466±600
SW	15 October 2004	Y	M	3	290–355	315±34.8	39–78	54.3±20.8
		Y	F	18	360–755	537±119	78–896	346±222

FW, fresh water; BW, brackish water; MW, marine-dominated water; SW, seawater.
Y, yellow eel; S, silver eel.
M, male; F, female; U, undifferentiated.

eels of this species (Pankhurst, 1982). We classified eels with an eye index less than 6.5 as sexually immature adults (yellow eel) and those over 6.5 as sexually mature adults (silver eels). The eye index was calculated according to Pankhurst (1982) as follows:

$$\text{Eye index} = \{[(A + B)/4]^2 \times \pi/\text{TL}\} \times 100$$

where A is the horizontal eye diameter (mm) and B is the vertical eye diameter (mm).

Based on the result and the Pankhurst criteria (Pankhurst, 1982), there were in total 69 yellow (all FW, BW and SW eels and 12 MW eels) and 24 MW silver eels (Table 1). We analysed the migratory histories for yellow and silver eels separately in MW eels.

Otolith preparation and microchemical analysis

Sagittal otoliths were extracted from each fish, embedded in epoxy resin (Struers, Epofix) and mounted on glass slides. Otoliths were ground and polished as described by Arai *et al.* (2006), cleaned in an ultrasonic bath, and rinsed with deionized water prior to being examined.

For electron microprobe analyses, all otoliths (93 specimens) were platinum (Pt)-palladium (Pd) coated by a high vacuum evaporator. Otoliths were used for 'life-history transect' analysis of Sr and Ca concentrations, which were measured along the longest axis of each otolith from the core to the edge using a wavelength dispersive X-ray electron microprobe (JEOL JXA-8900R) as described in Arai *et al.* (2006). Wollastonite ($CaSiO_3$) and Tausonite ($SrTiO_3$) were used as standards. The accelerating voltage and beam current were 15 kV and 1.2×10^{-8} A, respectively. The electron beam was focused on a point 10 μm in diameter, with measurements spaced at 10 μm intervals.

Trace elemental signatures in the edge of otoliths accumulate in the final part of the fish's life before natural death or capture and have been used to trace migrations (Arkhipkin *et al.*, 2009; Schuchert *et al.*, 2010). Sr:Ca ratios of otolith edges were examined for all specimens.

Statistical analyses

Differences among data for comparisons of biological characteristics such as TL and body weight of four salinity basins (FW, BW, MW and SW) in yellow and silver eels, the average Sr:Ca ratios outside of the elver mark and the average Sr:Ca ratios in otolith edges for FW, BW, MW and SW yellow eels and MW silver eels, were tested by a Kruskal–Wallis test. Differences between data for comparison of the average Sr:Ca ratios outside of the elver mark between the two types for MW silver eels were analysed using the Mann–Whitney U-test (Sokal & Rohlf, 1995).

Results

Biological characteristics

The TL of *Anguilla anguilla* collected from four salinity zones ranged from 278–919 mm (Table 1). The TL of the yellow eels ranged from 278–436 mm (358 ± 53.8 mm; mean ± SD) and 338–755 mm (489 ± 107 mm) for males and females, respectively. For silver eels, TL ranged from 298–434 mm (354 ± 32.4 mm) and 359–919 mm (540 ± 193 mm) for males and females, respectively. There were significant differences in total length between FW and SW and between MW and SW in yellow eels for females (Kruskal–Wallis test, df = 23, $P < 0.05$–0.01). However, no significant differences occurred in total lengths between other salinity zones (14 combinations) in yellow and silver eels for females and males (Kruskal–Wallis test, df = 2 to 32, $P > 0.05$).

The body weight of *A. anguilla* collected from the four salinity zones ranged from 36–1836 g (Table 1). The body weight of the yellow eels ranged from 36–146 g (81 ± 34.4 g; mean ± SD) for males and from 71–896 g (240 ± 195 g) for females. For silver eels, the body weight ranged from 46–128 g (78 ± 21.2 g) for males and from 97–1836 g (540 ± 193 g) for females. There were significant differences in body weight between FW and SW and between MW and SW in yellow eels for females (Kruskal–Wallis test, df = 22, $P < 0.05$–0.005), but no significant differences occurred in total length between other salinity zones (14 combinations) in yellow and silver eels for females and males (Kruskal–Wallis test, df = 2 to 28, $P > 0.05$).

Otolith microchemistry

The Sr:Ca ratios in the transects along the radius of each otolith showed the same common feature of a high ratio near the centre of the otolith; outside the otolith core, however, there were

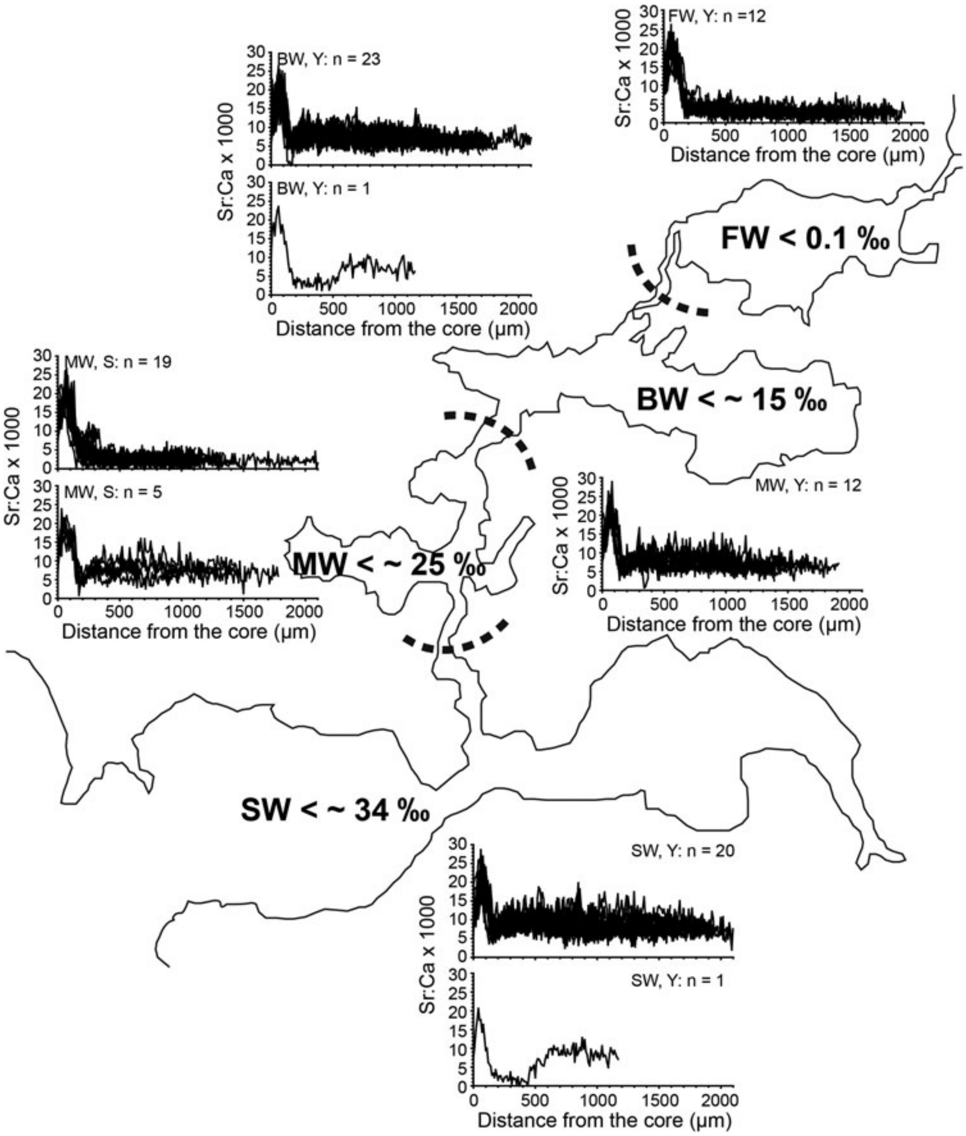

Fig. 2. Sr:Ca profiles measured along line transects from the core (0 μm) to the edge of the otolith for all the *A. anguilla* specimens collected in the four zones of Lough Ahalia. Y: yellow eel, S: silver eel. FW: freshwater, BW: brackish water, MW: marine dominated, SW: full seawater. The line history transects showed a single movement from one low salinity habitat to a high salinity habitat, were separated (one from a BW yellow eel, the other from an SW yellow eel). In MW, the line history transects were separated as three categories, constantly low values (19 silver eels) and relatively high values of all (12) yellow and 5 silver eels.

generally three different patterns (Figure 2). All otolith specimens had a central core region with high Sr:Ca ratio with a maximum of more than 25×10^{-3} (Figure 2) surrounded by an elver mark corresponding to the period of their leptocephalus and early glass eel stages in the ocean that could be observed with a light microscope. The radius of the elver mark in *Anguilla anguilla* ranged from 110–210 μm.

In *Anguilla anguilla*, the change in Sr:Ca values outside the elver mark was generally divided into three types corresponding to the elver, yellow and/or silver stages (Figure 2): (1) constantly low values generally ranging from $\sim 1.93–3.99 \times 10^{-3}$ (all FW yellow eels and 19 MW silver eels); (2) relatively high values generally ranging from $\sim 6.22–9.48 \times 10^{-3}$ with no apparent movement into fresh water (23 BW yellow eels, all MW yellow eels, 5 MW silver eels and 20 SW yellow eels); and (3) values that showed a single movement at ~500 μm from one low salinity habitat ($1.90–3.30 \times 10^{-3}$) to a high salinity habitat ($7.48–8.22 \times 10^{-3}$) (two specimens; one from a BW yellow eel, the other from an SW yellow eel).

The average Sr:Ca ratios (± SD) outside of the elver mark for FW, BW, MW and SW yellow eels and MW silver eels were $3.34 \pm 0.33 \times 10^{-3}$, $7.25 \pm 0.76 \times 10^{-3}$, $7.50 \pm 0.54 \times 10^{-3}$, $8.33 \pm 0.82 \times 10^{-3}$ and $3.93 \pm 2.04 \times 10^{-3}$, respectively. There were significant differences in the average Sr:Ca ratios between eight combinations for FW, BW, MW and SW yellow eels and MW silver eels (Kruskal–Wallis test, df = 18 to 40, $P < 0.0005–0.0001$; Table 2); however, no significant differences were found for those of two combinations (Kruskal–Wallis test, df = 24 to 29, $P > 0.05$; Table 2). Interestingly, a significant difference was also found in the average Sr:Ca ratios between the two types (constantly low values (2.94 ± 0.60, N = 19) and relatively high values were found (7.52 ± 0.91, N = 5)) for MW silver eels (Mann–Whitney *U*-test, df = 4, $P < 0.0005$) (Figure 2).

The average Sr:Ca ratios (± SD) in otolith edges for FW, BW, MW and SW yellow eels and MW silver eels were $3.18 \pm 0.80 \times 10^{-3}$, $6.67 \pm 1.58 \times 10^{-3}$, $7.43 \pm 2.32 \times 10^{-3}$, $8.15 \pm 1.92 \times 10^{-3}$ and $3.74 \pm 2.18 \times 10^{-3}$, respectively. There were significant differences in the average Sr:Ca ratios between seven combinations for FW, BW, MW and SW yellow eels and MW silver eels (Kruskal–Wallis test, df = 13–41, $P < 0.01–0.0001$; Table 3); however, no significant differences were found for those of three combinations (Kruskal–Wallis test, df = 16 to 30, $P > 0.05$; Table 3).

Table 2. Statistical results (*P* value) of the average otolith Sr:Ca ratios outside of the elver mark between each habitat in yellow and silver eels

	FW yellow eels	BW yellow eels	MW yellow eels	MW silver eels	SW yellow eels
FW yellow eels	1	<0.0001	<0.0001	0.193	<0.0001
BW yellow eels		1	0.267	<0.0001	<0.0001
MW yellow eels			1	<0.0001	0.0016
MW silver eels				1	<0.0001
SW yellow eels					1

FW: fresh water; BW: brackish water; MW; marine dominated; SW: seawater.

Table 3. Statistical results (*P* value) of Sr:Ca ratios in otolith edges between each habitat in yellow and silver eels

	FW yellow eels	BW yellow eels	MW yellow eels	MW silver eels	SW yellow eels
FW yellow eels	1	<0.0001	<0.0001	0.288	<0.0001
BW yellow eels		1	0.323	<0.0001	0.0080
MW yellow eels			1	0.00017	0.372
MW silver eels				1	<0.0001
SW yellow eels					1

FW, fresh water; BW, brackish water; MW; marine dominated; SW, seawater.

Discussion

The variation of otolith Sr:Ca ratios indicated that *Anguilla anguilla* experienced a variety of environmental salinities in a tidal Atlantic lake system of Ireland. The otolith microchemistry of these eels indicated that 91 of 93 (98%) eels had entered each salinity environment basin relatively quickly after recruitment and had stayed in each environment basin until maturation without movement to another salinity environment. Only 2 of 93 (2%) eels had shifted their habitat once in their lives (Figure 2). The result suggests that each individual might have an environmental habitat preference, although each individual could move along a short (<2 km) salinity gradient. The apparent habitat use and movement patterns in this study support the findings of previous research on other temperate eels that appear typically to have notably localized home ranges but do very occasionally move to different areas. For example, studies on *A. rostrata* have determined that their yellow eels have a restricted home range and that they return to their initial habitat after foraging outside their territory (Bozeman *et al.*, 1985; Ford & Mercer, 1986; Oliveira, 1997) or return to their home range after being artificially displaced (Parker, 1995). Similarly, studies of New Zealand eels concluded that the large eels have restricted home ranges and typically only move short distances within these streams (Burnet, 1969; Chisnall & Hicks, 1993; Jellyman & Sykes, 2003).

Harrod *et al.* (2005) showed that the somatic composition of eels differed along the salinity gradient in Lough Ahalia, which is the same study site as this study. The lipid-treated C:N data showed differences in body composition, with BW eels having lower mean lipid-treated C:N than eels from FW or MW. These differences were due to a small but significant reduction in mean carbon content in BW fish. The greatest contrast between BW eels and eels from other salinity zones was dietary, with BW eels feeding at a lower trophic level. Harrod *et al.* (2005) suggested that their diet may include an increased proportion of macroinvertebrates relative to eels from the other salinity zones, and the most abundant littoral macroinvertebrate taxa in the BW zone are isopods (e.g. *Sphaeroma* spp.) and amphipods (*Gammarus* spp.). These taxa have low mean carbon content relative to values typically recorded from other benthic invertebrates (Salonen *et al.*, 1976; Penczak, 1985; Frost *et al.*, 2003) or fishes, both from Lough Ahalia, or other systems (Penczak, 1985; Tanner *et al.*, 2000). The reduced muscle carbon content in BW eels relative to FW or MW fish may be related to differences in diet. Therefore, the diverse salinity habitat uses found in this study might also be related to the feeding preference of each eel because we found significant differences in their somatic growth (TL and body weight) between FW and SW and between MW and SW in yellow eels for females. There was some evidence that in Lough Ahalia, faster growth was associated with increased salinity (Harrod *et al.*, 2005). Similar patterns of enhanced growth in brackish water have been observed in *A. anguilla* (Fernandez-Delgado *et al.*, 1989) and other species of *Anguilla*, e.g. *A. rostrata* (Lamson *et al.*, 2006) and *A. japonica* (Tzeng *et al.*, 2003). Tzeng *et al.* (2003) have suggested that the energetic costs of osmoregulation are minimized in eels in salinities closest to that of their body fluids (10.5–14), and they propose that this may contribute to the better growth seen in marine and brackish eels. However, marine and estuarine productivity tend to be higher than that in adjacent fresh waters at higher latitudes (Gross, 1987; Gross *et al.*, 1988) and mixohaline eels may simply have access to greater food resources.

Two distinct groups of Sr:Ca ratios were found in MW silver eels (Figure 3). Such distribution was not found in other salinity environments. The lower Sr:Ca ratio value individuals (19 eels) might just migrate from the freshwater upstream for downstream migration as silver eels for spawning in the Atlantic Ocean. In contrast, the higher Sr:Ca ratio value individuals (5 eels) might reside in the MW environment as with MW yellow eel individuals or might come from the SW environment.

Otolith Sr:Ca ratios from the otolith edge provide information on the environment experienced by the fish prior to capture (Arkhipkin *et al.*, 2009; Schuchert *et al.*, 2010). The criteria ratios of FW, BW, MW and SW in Lough Ahalia were 3.18×10^{-3}, 6.67×10^{-3}, 7.43×10^{-3} and 8.15×10^{-3}. However, the criterion ratios of fresh water varied among study sites ranging from $0.72–5.29 \times 10^{-3}$ (Arai *et al.*, 2006; Shiao *et al.*, 2006; Tabouret *et al.*, 2010). It is apparent that the otolith Sr:Ca ratios of *Anguilla anguilla* living in fresh water can vary substantially between regions. Furthermore, the criterion ratios of seawater

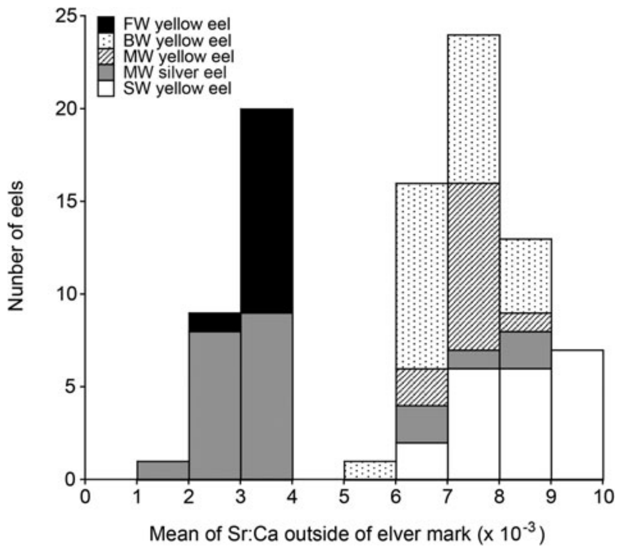

Fig. 3. Distribution of the mean Sr:Ca ratio values outside the elver mark in each otolith of the specimens used in the present study.

also varied among study sites ranging from >4.9–6.0 × 10^{-3} (Arai *et al.*, 2006; Tabouret *et al.*, 2010). This may be due to region-specific spatial and temporal variation in Sr:Ca concentrations in the water (Kraus & Secor, 2004; Munro *et al.*, 2005), different equipment used for measurement of otolith Sr:Ca ratios or the effect of water temperatures (Campana, 1999; Elsdon & Gillanders, 2002; Martin *et al.*, 2004).

Gross (1987) proposed that diadromy occurs when the gain in fitness from using a second habitat minus the migration costs of moving between habitats exceeds the fitness from staying in only one habitat. When glass eels migrate from offshore seawater to upstream fresh water for habitat and feeding, they have to overcome the osmotic pressure of a saline environment. If they stayed in the estuary habitat, their osmoregulatory cost would be lower than that in either fresh water or seawater. Estuaries function as a nursery and feeding grounds for the juveniles of many fish species (Lenanton, 1982). Many commercially important fish can be present because estuaries provide suitable food resources, as well as shelter, absence of turbulence, and reduced predation (Blaber *et al.*, 1985). These conditions may confine the eel to estuarine waters; hence, estuary-dependent eels are predominant in the European eel *Anguilla anguilla* (Arai *et al.*, 2006; Shiao *et al.*, 2006), Japanese eel *A. japonica* (Tsukamoto & Arai, 2001; Arai *et al.*, 2003*a*, 2003*b*; Kotake *et al.*, 2003, 2005), American eel *A. rostrata* (Lamson *et al.*, 2006) and New Zealand eels *A. australis* and *A. dieffenbachii* (Arai *et al.*, 2004). For *A. anguilla* in Ireland, the ecological implications for habitat use are similar to those in other regions. These eels migrate flexibly among freshwater, brackish water and seawater environments.

Author ORCID. Takaomi Arai, 0000-0001-9440-7933

Financial support. This work was supported in part by Universiti Brunei Darussalam under the Competitive Research Grant Scheme (Vot No. UBD/OVACRI/CRGWG(003)).

References

Arai T and Chino N (2012) Diverse migration strategy between freshwater and seawater habitats in the freshwater eels genus *Anguilla*. *Journal of Fish Biology* **81**, 442–455.

Arai T and Chino N (2017) Influence of water salinity on the strontium:calcium ratios in otoliths of the giant mottled eel, *Anguilla marmorata*. *Environmental Biology of Fishes* **100**, 281–286.

Arai T, Otake T and Tsukamoto K (2000) Timing of metamorphosis and larval segregation of the Atlantic eels, *Anguilla rostrata* and *A. anguilla*, as revealed by otolith microstructure and microchemistry. *Marine Biology* **137**, 39–45.

Arai T, Kotake A, Ohji M, Miller MJ, Tsukamoto K and Miyazaki N (2003*a*) Occurrence of sea eels of *Anguilla japonica* along the Sanriku Coast of Japan. *Ichthyological Research* **50**, 78–81.

Arai T, Kotake A, Ohji M, Miyazaki N and Tsukamoto K (2003*b*) Migratory history and habitat use of Japanese eel *Anguilla japonica* in the Sanriku Coast of Japan. *Fisheries Science* **69**, 813–818.

Arai T, Kotake A, Lokman PM, Miller MJ and Tsukamoto K (2004) Evidence of different habitat use by New Zealand freshwater eels, *Anguilla australis* and *A. dieffenbachii*, as revealed by otolith microchemistry. *Marine Ecology Progress Series* **266**, 213–225.

Arai T, Kotake A and McCarthy TK (2006) Habitat use by the European eel *Anguilla anguilla* in Irish waters. *Estuarine Coastal and Shelf Science* **67**, 569–578.

Arkhipkin AI, Schuchert PC and Danyushevsky L (2009) Otolith chemistry reveals fine population structure and close affinity to the Pacific and Atlantic oceanic spawning grounds in the migratory southern blue whiting (*Micromesistius australis australis*). *Fisheries Research* **96**, 188–194.

Berkes F and Seixas CS (2005) Building resilience in lagoon social-ecological systems: a local-level perspective. *Ecosystems* **8**, 967–974.

Bertin L (1956) *Eels – A Biological Study*. London: Cleaver-Hume Press.

Blaber SJM, Young JW and Dunning MC (1985) Community structure and zoogeographic affinities of the coastal fishes of Dampier region of northwestern Australia. *Australian Journal of Marine and Freshwater Research* **36**, 247–266.

Boëtius J (1985) Greenland eels. *Anguilla rostrata* Lesueur. *Dana* **4**, 41–48.

Bozeman EK, Helfman GS and Richardson T (1985) Population size and home range of American eels in a Georgia tidal creek. *Transaction of American Fisheries Society* **114**, 821–825.

Burnet AMR (1969) The growth of New Zealand freshwater eels in three Canterbury streams. *New Zealand Journal of Marine and Freshwater Research* **3**, 376–384.

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* **188**, 263–297.

Casselman JM (2003) Dynamics of resources of the American eel, *Anguilla rostrata*: declining abundance in the 1990s. In Aida K, Tsukamoto K and Yamauchi K (eds), *Eel Biology*. Tokyo: Springer-Verlag, pp. 255–274.

Chisnall BL and Hicks BJ (1993) Age and growth of longfinned eels (*Anguilla dieffenbachii*) in pastoral and forested streams in the Waikato River basin, and in two hydroelectric lakes in the North Island. *New Zealand Journal of Marine and Freshwater Research* **27**, 317–332.

Dekker W, Casselman JM, Cairns DK, Tsukamoto K, Jellyman D and Lickers H (2003) Worldwide decline of eel resources necessitates immediate action: Québec Declaration of Concern. *Fisheries* **28**, 28–30.

Elsdon TS and Gillanders BM (2002) Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. *Canadian Journal of Fisheries and Aquatic Science* **59**, 1796–1808.

Fernandez-Delgado C, Hernando JA, Herrera M and Bellido M (1989) Age and growth of yellow eels, *Anguilla anguilla*, in the estuary of the Guadalquiver River (south-west Spain). *Journal of Fish Biology* **34**, 561–570.

Ford TE and Mercer E (1986) Density, size distribution and home range of American eels, *Anguilla rostrata*, in a Massachusetts salt marsh. *Environmental Biology of Fishes* **17**, 309–314.

Frost PC, Tank SE, Turner MA and Elser JJ (2003) Elemental composition of littoral invertebrates from oligotrophic and eutrophic Canadian lakes. *Journal of the North American Benthological Society* **22**, 51–62.

Gross MR (1987) The evolution of diadromy fishes. *American Fisheries Society Symposium* **1**, 14–25.

Gross MR, Coleman RM and McDowall RM (1988) Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291–1293.

Harrod C, Grey J, McCarthy TK and Morrissey M (2005) Stable isotope analyses provide new insights into ecological plasticity in a mixohaline population of European eel. *Oecologia* **144**, 673–683.

Jellyman DJ and Sykes JRE (2003) Diel and seasonal movements of radio-tagged freshwater eels, *Anguilla* spp., in two New Zealand streams. *Environmental Biology of Fishes* **66**, 143–154.

Kennish MJ and Paerl HW (2010) *Coastal Lagoons: Critical Habitats of Environmental Change*. Boca Raton, FL: CRC Press.

Kjerve B (ed.) (1990) Coastal lagoons. In *Coastal Lagoon Processes*, Elsevier Oceanographic Series 60. Amsterdam: Elsevier, pp. 1–8.

Kotake A, Arai T, Ozawa T, Nojima S, Miller MJ and 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. *Marine Biology* **142**, 849–854.

Kotake A, Okamura A, Yamada Y, Utoh T, Arai T, Miller MJ, Oka HP and Tsukamoto K (2005) Seasonal variation in migratory history of the Japanese eel, *Anguilla japonica*, in Mikawa Bay, Japan. *Marine Ecology Progress Series* **293**, 213–221.

Kraus RT and Secor DH (2004) Incorporation of strontium into otoliths of an estuarine fish. *Journal of Experimental Marine Biology and Ecology* **302**, 85–106.

Lamson H, Shiao JC, Iizuka Y, Tzeng WN and Cairns DK (2006) Movement patterns of American eels (*Anguilla rostrata*) between salt- and freshwater in a coastal watershed, based on otolith microchemistry. *Marine Biology* **149**, 1567–1576.

Lenanton TCJ (1982) Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Australian Journal of Marine and Freshwater Research* **33**, 881–900.

Lin SH, Chang CW, Iizuka Y and Tzeng WN (2007) Salinities, not diets, affect strontium/calcium ratios in otoliths of *Anguilla japonica. Journal of Experimental Marine Biology and Ecology* **34**, 254–263.

Lin YJ, Yalçin-Özdilek S, Iizuka Y, Gümüş A and Tzeng WN (2011) Migratory life history of European eel *Anguilla anguilla* from freshwater regions of the River Asi, southern Turkey and their high otolith Sr:Ca ratios. *Journal of Fish Biology* **78**, 860–868.

Martin GB, Thorrold SR and Jones CM (2004) Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). *Canadian Journal of Fisheries and Aquatic Science* **61**, 34–42.

McCarthy TK, Cullen P and O'Connor W (1999) The biology and management of River Shannon eel populations. *Fishery Bulletin* (*Dublin*) **17**, 9–20.

Moriarty C (1996) The European eel fishery in 1993 and 1994. *Fishery Bulletin* (*Dublin*) **14**, 1–52.

Munro AR, McMahon TE and Ruzycki JR (2005) Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. *Canadian Journal of Fisheries and Aquatic Science* **62**, 79–87.

Oliveira K (1997) Movement and growth rates of yellow phase American eels in the Annaquatucket River, Rhode Island. *Transactions of American Fisheries Society* **126**, 638–646.

Pankhurst NW (1982) Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). *Journal of Fish Biology* **21**, 127–140.

Parker SJ (1995) Homing ability and home-range of yellow-phase American eels in a tidally dominated estuary. *Journal of the Marine Biological Association of the United Kingdom* **75**, 127–140.

Penczak T (1985) Phosphorus, nitrogen and carbon cycling by fish populations in two small lowland rivers in Poland. *Hydrobiologia* **120**, 159–165.

Poole WR (1990) Summer fyke nets as a method of eel capture in a salmonid fishery. *Aquaculture and Fisheries Management* **21**, 259–262.

Salonen K, Sarvala J, Hakala I and Viljanen ML (1976) The relation of energy and organic carbon in aquatic invertebrates. *Limnology and Oceanography* **21**, 724–730.

Schmidt J (1922) The breeding places of the eel. *Philosophical Transactions of Royal Society of London B* **211**, 179–208.

Schmidt J (1925) The breeding places of the eel. *Smithsonian Institute Annual Report* **1924**, 279–316.

Schuchert PC, Arkhipkin AI and Koenig AE (2010) Traveling around Cape Horn: otolith chemistry reveals a mixed stock of *Patagonian hoki* with separate Atlantic and Pacific spawning grounds. *Fisheries Research* **102**, 80–86.

Shiao JC, Ložys L, Iizuka Y and Tzeng WN (2006) Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. *Journal of Fish Biology* **69**, 749–769.

Sokal RR and Rohlf FJ (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd Edn. New York, NY: WH Freeman.

Tabouret H, Bareille G, Claverie F, Pécheyran C, Prouzet P and Donard OFX (2010) Simultaneous use of strontium:calcium and barium: calcium ratios in otoliths as markers of habitat: application to the European eel (*Anguilla anguilla*) in the Adour basin, South West France. *Marine Environmental Research* **70**, 35–45.

Tanner DK, Brazner JC and Brady VJ (2000) Factors influencing carbon, nitrogen, and phosphorus content of fish from a Lake Superior coastal wetland. *Canadian Journal of Fisheries and Aquatic Science* **57**, 1243–1251.

Tesch FW (2003) *The Eel*, 5th Edn. Oxford: Blackwell Publishing.

Tsukamoto K and Arai T (2001) Facultative catadromy of the eel, *Anguilla japonica*, between freshwater and seawater habitats. *Marine Ecology Progress Series* **220**, 265–276.

Tzeng WN (1996) Effects of salinity and ontogenetic movements on strontium:calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica* Temminck and Schlegel. *Journal of Experimental Marine Biology and Ecology* **199**, 111–122.

Tzeng WN, Iizuka Y, Shiao JC, Yamada Y and Oka HP (2003) Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*). *Aquaculture* **216**, 77–86.

Wang CH and Tzeng WN (2000) The timing of metamorphosis and growth rates of American and European eel leptocephali: a mechanism of larval segregative migration. *Fisheries Research* **46**, 191–205.