Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*

Françoise Daverat[1],*, Karin E. Limburg[2], Isabel Thibault[3], Jen-Chieh Shiao[4], Julian J. Dodson[3], François Caron[6], Wann-Nian Tzeng[7], Yoshiyuki Iizuka[5], Håkan Wickström[8]

[1]Cemagref, 50 Avenue de Verdun, 33612 Cestas, France
[2]SUNY College of Environmental Science & Forestry, Syracuse, New York 13210, USA
[3]Département de Biologie, Université Laval, Ste-Foy, Québec G1K 7P4, Canada
[4]Institute of Cellular and Organismic Biology, and [5]Institute of Earth Sciences, Academia Sinica, 128, Section 2, Academia Road, Nankang, Taipei, Taiwan 115, ROC
[6]Ministère des Ressources Naturelles et de la Faune du Québec, 675, boul. René-Lévesque Est, Québec (Québec) G1R 5V7, Canada
[7]Institute of Fisheries Science, College of Life Science, National Taiwan University, Taipei, Taiwan 106, ROC
[8]Swedish Board of Fisheries, Institute of Freshwater Research, 178 93, Drottningholm, Sweden

ABSTRACT: Habitat use patterns of 3 species of temperate eels, *Anguilla anguilla*, *A. japonica* and *A. rostrata*, were investigated using otolith strontium:calcium ratio life history transects. Published and unpublished data from 6 sites (Canada, United States, Sweden, France, Taiwan and Japan) sampled across the geographical range of each eel species were compiled. Sr:Ca patterns indicated that the 3 species displayed similar patterns of habitat use. In all sites, patterns of habitat use consisted of either residency in one habitat (fresh, brackish, or marine) or movements between habitats. One movement pattern consisted of either a single change or 2 changes of habitat from fresh to brackish waters, or from brackish water to freshwater. Seasonal movements between fresh and brackish waters were observed for all 3 species. When only a single habitat switch event was detected, it occurred between 3 and 5 yr of age. Occurrence of eels with no freshwater experience was demonstrated, but such eels accounted for a smaller proportion of the overall sample than eels with some (even brief) freshwater experience. Contrary to the common convention that these are obligate catadromous species, we must now consider them as facultative catadromous, with far more flexibility in habitat use. The most variable parameter among study sites was the relative proportion, rather than the diversity, of lifetime spent in the various habitat use patterns. Eels found at higher latitudes exhibited a greater probability of remaining in the lower reaches of watersheds in brackish water. Diversity of habitat use appears to be a common strategy of temperate eel species, and, as a life history tactic, is under environmental control.

KEY WORDS: Habitat use · *Anguilla* spp · Otolith Sr:Ca

INTRODUCTION

Anguillid eel species display a remarkable similarity in their life history traits. Anguillidae all spawn in deep oceanic waters. Anguillid larvae, the leaf-like leptocephali, are advected by oceanic currents to continental shelves. The migration distance between spawning grounds and nursery areas varies with species, the European eel *Anguilla anguilla* undertaking the longest distance of migration (~6000 km). This species spawns in the Sargasso Sea and drifts with the Gulf Stream and North Atlantic Current to the continental

shelf of Europe and North Africa. The American eel *A. rostrata* also spawns in the Sargasso Sea and travels 2000 to 3000 km into North American waters while the Japanese eel *A. japonica* spawning area is located west of the Mariana Islands (NW Pacific) and its nursery grounds extend through continental waters of East Asia. Tropical species have shorter migrations (Marui et al. 2001). Leptocephalus larvae metamorphose into glass eels as they arrive at continental shelves (Bertin 1951, Tesch 2003). Glass eels become pigmented elvers as they penetrate estuaries, rivers and streams and complete their growth phase in a large choice of habitats (lagoons, estuaries, marshes, rivers, lakes and streams). The growth phase typically lasts from 3 to 15 yr and is followed by a second metamorphosis into silver eel, a pre-pubertal stage. Silver eels achieve their sexual maturation as they swim back to their spawning grounds (Van den Thillart et al. 2004).

Although the presence of yellow eels (juveniles) in brackish and marine waters has long been known, the dominating paradigm has been that eel growth phase was restricted to freshwater (Fontaine 1996). However, growing evidence from otolith microchemistry demonstrates the widespread occurrence of amphidromous and marine individuals that have experienced little or no freshwater (Tzeng et al. 1997, Tsukamoto et al. 1998, Limburg et al. 2003) and a high degree of flexibility in habitat use patterns.

Otolith growth patterns and chemical composition potentially provide detailed individual chronologies of habitat use that are of great value to ecological studies. Early studies on strontium incorporation into eel otoliths of *Anguilla japonica* showed that strontium:calcium (Sr:Ca) ratio levels correlated with the salinity of the water (Tzeng 1996, Kawakami et al. 1998). Strontium is taken up in proportion to ambient concentrations (Bath et al. 2000, Kraus & Secor 2004) and the effect of a shift in habitat on the Sr:Ca incorporation in the otolith of *A. anguilla* was demonstrated by Daverat et al. (2005). Measurements of Sr:Ca ratios across microstructural features in eel otoliths have been broadly used to infer life history periods spent in fresh, brackish, and marine environments (Bertin 1951, Tzeng et al. 1997, Tsukamoto et al. 1998, Tzeng et al. 2000, Limburg et al. 2003, Tesch 2003). These studies hypothesised the coexistence within eel *Anguilla* spp. populations of different life history tactics related to the choice of habitat (marine, brackish, freshwater) or a shift of habitat (Tsukamoto & Arai 2001, Jessop et al. 2002, Tzeng et al. 2002, Morrison et al. 2003, Kotake et al. 2004).

The aim of this comparative study is first to explore the diversity of the different life histories of 3 species of temperate eels (*Anguilla anguilla*, *A. japonica* and *A. rostrata*) using variations in otolith Sr:Ca ratios. Sec-

ond, the influence of geographic location and species on the distributions of different eel life histories is investigated. Finally, we discuss the ecological meaning of the different nursery habitat use patterns as established strategies.

MATERIALS AND METHODS

The present work relies both on published (Tsukamoto & Arai, 2001, Tzeng et al. 2002, 2003, Limburg et al. 2003, Morrison et al. 2003, Daverat et al. 2005) and unpublished data from I. Thibault, J. J. Dodson, F. Caron, W. N. Tzeng, J. C. Shiao and Y. Iizuka. Data sets were chosen based on sample size, and sampling scale. Data sets dealing with eels which had probably been stocked or with impounded watercourses were discarded from this analysis in order to remove possible bias.

Main study sites. Most sites within the species' ranges (Fig. 1) are watersheds such as the Kaoping River (Taiwan), St. Jean River (Canada), East River (Canada), Hudson River (United States) and Gironde River (France) (Table 1).

Sample collection. Eels were collected by a variety of fishing methods including fixed traps on dams across rivers, electrofishing, fish wheels, eel pots, fyke nets, trawling, and lines as described in each project (Tsukamoto & Arai 2001, Jessop et al. 2002, Tzeng et al. 2002, Limburg et al. 2003, Morrison et al. 2003, Tzeng et al. 2003, Daverat et al. 2005).

Otolith preparation. For all studies, sagittal otoliths were extracted, cleaned to minimize chemical contamination, and embedded in resin. Otoliths were sectioned either on the sagittal plane or the frontal plane by fine polishing until the core was exposed. The surface of otoliths was smoothed with 1 and 0.5 μm diamond paste.

Otolith X-ray microprobe Sr:Ca analysis. Most samples were analysed using similar methodology with small variations as detailed in Tsukamoto & Arai (2001), Tzeng et al. (2002), Limburg et al. (2003), Morrison et al. (2003), and Daverat et al. (2005). A wavelength dispersive X-ray electron microprobe was used to obtain either maps of Sr and Ca X-ray intensity on the whole otolith surface, or a transect of measures along an axis from the core of the otolith to the edge (so-called 'life history transect').

Otolith microPIXE Sr:Ca analysis. Some Baltic Sea otoliths were analysed by proton-induced X-ray emission microanalysis (μPIXE), a method described in Limburg et al. (2003). A grid of 128 × 128 pixels was scanned to map out large areas of the otolith in order to obtain a picture (2-D map) of Sr:Ca ratios for the whole sample surface. The data sets were then normalised to counts per charge.
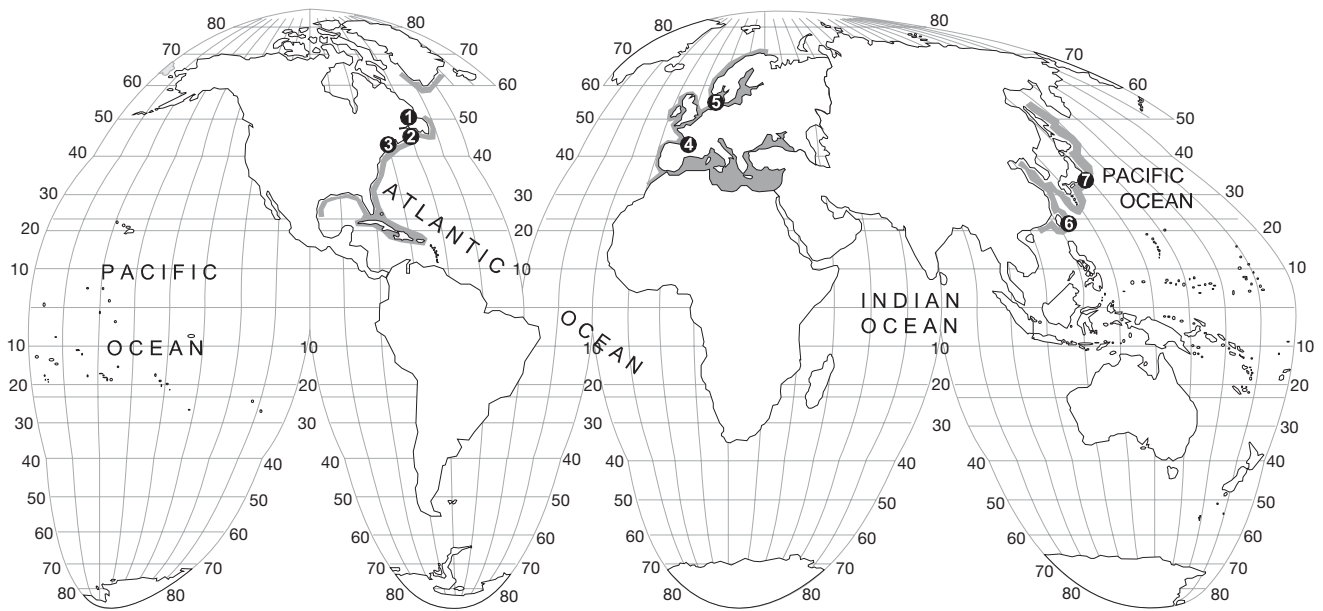
Fig. 1. *Anguilla anguilla, A. japonica* and *A. rostrata*. Main study sites showing the geographical range of each species: (1) Gaspé Peninsula, Quebec, Canada; (2) Nova Scotia, Canada; (3) Hudson River, United States; (4) Gironde River, France; (5) Baltic Sea exit, Sweden; (6) Kaoping River, Taiwan and (7) Japan

Interpretation of measures of Sr:Ca ratios. The interpretation of Sr:Ca variations along the otolith radius in terms of habitat use pattern and movements between water masses was based on laboratory and field validations (Daverat et al. 2005). Frequency distributions of Sr:Ca values were compared for fish collected in freshwater, brackish and marine sites to verify that the gradient of Sr:Ca values was positively correlated with salinity gradient (Tzeng et al. 2002, Limburg et al. 2003, Morrison et al. 2003). Maps of Sr:Ca measures and line transects of Sr:Ca measures are interpreted as habitat use (freshwater, brackish water or marine

water) throughout life, as otoliths grow continually. Only the otolith Sr:Ca ratio measurements starting from the glass eel stage were interpreted.

Data analysis. Logistic regression was applied to the proportion of resident eels in the estuaries (number of residents divided by sample size). SAS software Ver. 8 (2000) was used to analyse the relationship between the proportion of residents in brackish water, and latitude as an explanatory variable. This technique is broadly used in ecology (Collett 1991, Oberdorff et al. 2001). The proportion of residents (presence/absence of residents) response curve describes the probability of residents being

Table 1. *Anguilla anguilla, A. japonica* and *A. rostrata*. Relevant characteristics of the major study sites

Ecosystem	Source	Species	Latitude (°N)	Water temperature range (°C)	Salinity range
Baltic exit, Sweden and Denmark	Limburg et al. (2003)	*A. anguilla*	55	2–18	0–25
Gironde River basin, France	Daverat & Tomás (2006)		44	7–24	0–35
Kaoping River basin, Taiwan	Tzeng et al. (2002)	*A. japonica*	22	18–30	0–32
Tone and Fukui river basins, Japan	Tsukamoto & Arai (2001)		30–37	6–23	0–29
Mikawa Bay (fed by 3 rivers), Japan	Tzeng et al. (2003)		34	8–28	25–33
Pearl River, China			23		0
Hudson River basin, United States	Morrison et al. (2003)	*A. rostrata*	42	0–27	0–24
East River, Canada	Jessop et al. (2002)		45	–1–17	0–32
St. Jean estuary, Canada	I. Thibault et al. (unpubl.)		48	–0.3–24	1–28
St. Jean River and Sirois Lake, Canada			48	0–24 (covered with ice in winter)	0

present as a function of an environmental variable (latitude). A Generalised Linear Model (GLM, McCullagh & Nelder 1989) with a binomial distribution and a logit link function was fitted to the proportion of brackish water residents. A level of $\alpha = 0.05$ was selected prior to conducting statistical testing.

RESULTS

Overall diversity of habitat use

Life history transects and their interpretation are illustrated for *Anguilla rostrata* (Fig. 2), *A. anguilla* (Fig. 3), and *A. japonica* (Fig. 4). Sr:Ca otolith values measured across site of capture, and species, remained in a narrow range of values. Freshwater Sr:Ca values varied from 1×10^{-3} for the Gironde estuary, France (*A. anguilla*, Fig. 3), and up to 3×10^{-3} for the Kaoping River, Taiwan (*A. japonica*, Fig. 4). Sr:Ca values ranged from 2×10^{-3} to 8×10^{-3} for estuaries whereas marine values were above 6×10^{-3}.

There is a considerable variety in patterns of habitat use, with more than 6 different patterns identified. The patterns consist of either residency in 1 habitat (fresh/brackish/marine) from glass eel through silver eel stages (or until collection), or what we term 'nomadic movements' between habitats (Table 2).

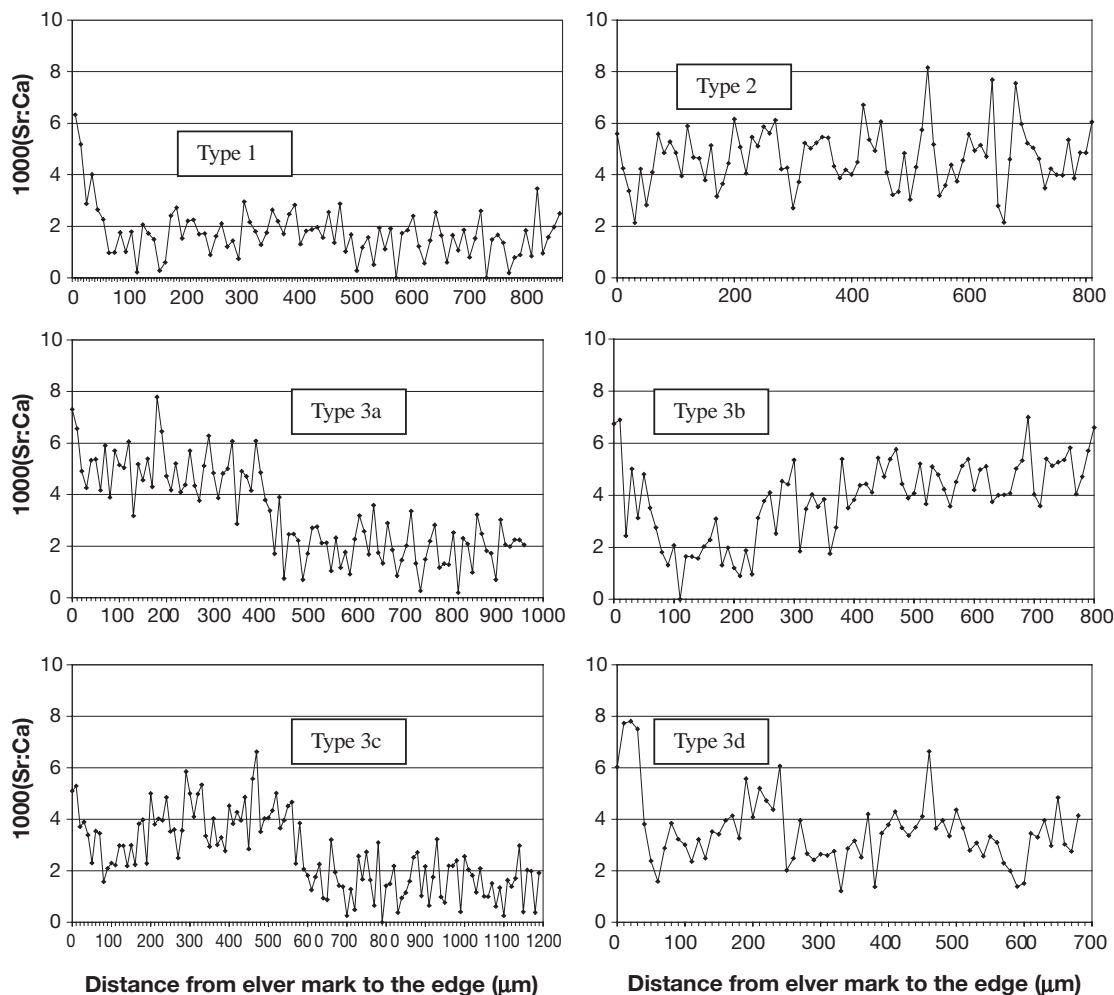The variability of movements is considerable, however, the general suite of movements may be sum-

Fig. 2. *Anguilla rostrata.* Sr:Ca ratio variations along transects from first annulus (elver check) to the otolith edge in American eels representative of the 6 main patterns of habitat use in the St. Jean River, St. Jean estuary and Sirois Lake, Gaspé Peninsula, Canada. Type 1: residence in freshwater; Type 2: residence in brackish habitat; Type 3: nomadic movements, 3a: residence in brackish environment more than 2 yr to freshwater, 3b: residence in freshwater, then movement to brackish habitat, 3c: freshwater residence, movement to estuary then movement to freshwater, 3d: other estuarine behavior with no defined pattern (I. Thibault et al. unpubl. data)

marised as follows: (1) residence in freshwater, followed by a move back to the estuary or the sea, (2) residence in brackish water, followed by residence in freshwater, (3) marine residence, with subsequent movement into brackish water (4) freshwater residence, movement to estuary/sea then movement to freshwater (2 changes of habitat), or (5) seasonal or irregular movements between marine and/or brackish and/or freshwater habitats. To a lesser extent, mixed modes of habitat use patterns were also found.

All patterns of habitat use were observed in the 3 species at nearly all the sites (Table 2). Note that Swedish eels reported in this study (Limburg et al. 2003) are unique in that they are already fingerling yellow eels by the time they recruit to freshwater,

with a part of their early life spent crossing the Baltic Sea. As such, their Sr:Ca pattern starts with a brackish or marine episode before recruitment to the estuary.

Schedules of habitat shift

The age at habitat shift has been estimated by several authors for eels displaying single habitat shifts. Comparisons (Table 3) showed that eels switched habitat within a narrow range of age classes. For most species and sites, habitat switches occurred before age class 5+ with most individuals switching at age class 3+ (Table 3).
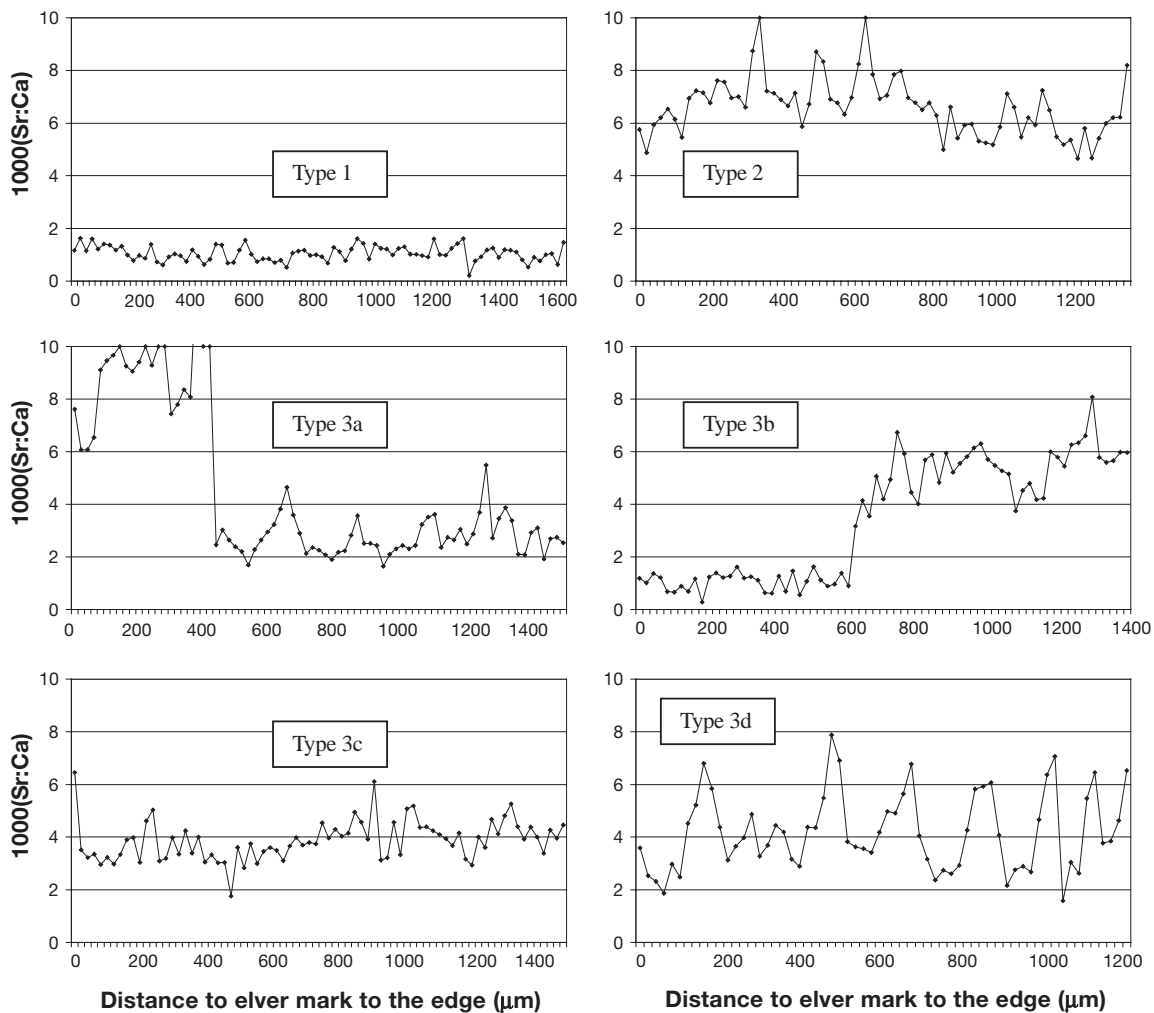

Fig. 3. *Anguilla anguilla.* Sr:Ca ratio variations along transects from first annulus (elver check or glass eel mark) to the otolith edge in European eels representative of 6 different patterns of habitat use in the Gironde Watershed, SW France. Type 1: residence in freshwater; Type 2: residence in coastal environment; Type 3: residence in the estuary; Type 3a–d: nomadic movements; 3a: residence in marine compartment, movement to the estuary; 3b: Residence in freshwater, movement to the estuary; 3d: Seasonal movements between the lower and upper part of the estuary (Daverat et al. 2005)
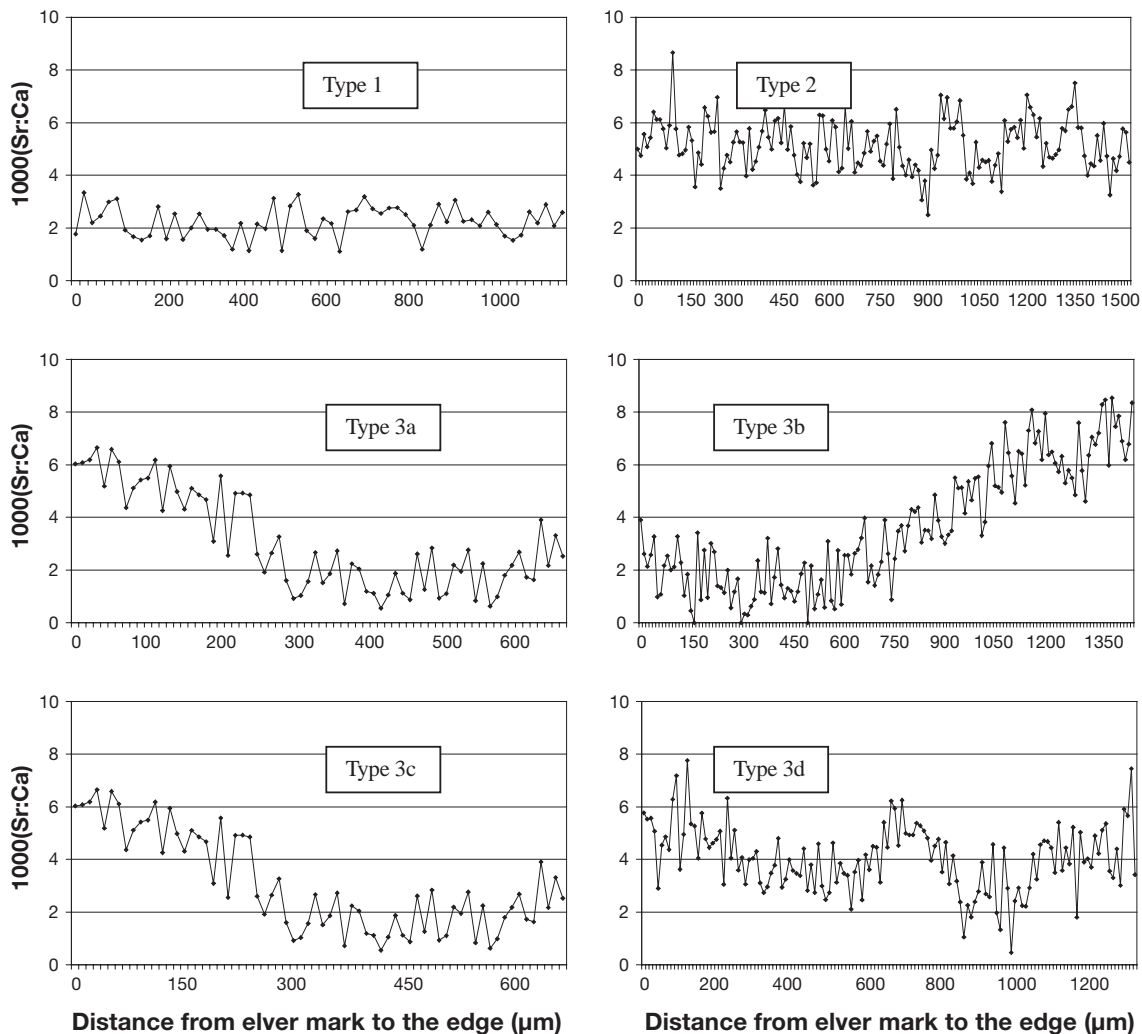
Fig. 4. *Anguilla japonica.* Sr:Ca ratio variations along transects of Japanese eel otoliths from the first annulus (from glass eel stage) to the otolith edge representative of the main habitat use patterns and collected in the middle and lower reaches of the Kaoping River, SW Taiwan. Type 1: residence in freshwater; Type 2: residence in seawater; Type 3: nomadic movements; 3a: residence in the estuary, movement to freshwater; 3b: residence in freshwater, movement to the estuary; 3c: freshwater residence, movement to estuary then movement to freshwater; 3d: other estuarine behavior with no defined pattern (Tzeng et al. 2002)

Variations in proportions of habitat use patterns

Freshwater habitats

In rivers, the majority of sampled eels were freshwater residents, with the exception of *Anguilla rostrata* in the St. Jean River and Sirois Lake (Quebec) (Table 4). The proportion of freshwater resident eels typically increased with the distance to the sea: *A. rostrata* freshwater residents in the Hudson River sampled 190 km upstream from the river's mouth accounted for 100% of the sample. The same proportion of freshwater residents (100%) was observed for *A. japonica* in the Pearl River and *A. anguilla* in the Garonne River, in both cases 200 km upstream from the river mouths. Meanwhile, in the St. Jean River and Sirois Lake, the proportion of eels that were residents in freshwater (23 and 44% respectively) was lower than the proportion of eels (77 and 56%) that undertook movements between habitats of different salinity.

Estuaries and coastal sites

A considerable fraction of the eels collected in estuaries and coastal sites had experienced freshwater at some point, and in most cases this freshwater episode occurred early in life (Fig. 5). The proportion of fish

Table 2. *Anguilla anguilla*, *A. japonica* and *A. rostrata.* Diversity of habitat use patterns by species and by site, occurrence in the sample (+), or number of individuals

Habitat use patterns	*A. anguilla*		*A. japonica*		*A. rostrata*		
	SW France[a]	Sweden[b]	Taiwan[c]	Japan[d]	E Canada[e]	NE USA[f]	NE Canada[g]
Residence in freshwater							
River	83	–	6	6	18	14	36
Estuary	24	–	8	2	0	0	11
Sea	0	0	–	6	–	–	–
Lake	–	–	–	–	16	–	–
Residence in brackish water							
River	2	–	0	+	32	0	0
Estuary	80	–	3	+	29	10	2
Sea	8	9	–	+	–	–	–
Lake	–	–	–	–	0	–	–
Residence in marine water							
River	0	–	0	0	0	0	0
Estuary	0	–	0	1	0	0	0
Sea	26	3	–	11	–	–	–
Lake	–	–	–	–	0	–	–
Nomadic movements							
River	0	–	0	+	28	0	6
Estuary	69	–	+	+	19	19	65
Sea	9	63	–	+	0	–	–
Lake	–	–	–	–	20	–	–

[a]Daverat & Tomás (2006); [b]Limburg et al. (2003); [c]Tzeng et al. (2002); [d]Tsukamoto & Arai (2001); [e]Thibault et al. (unpubl. data); [f]Morrison et al. (2003); [g]Jessop et al. (2002)

Table 3. *Anguilla* spp. Age at habitat change for eels switching habitat once

Life history	Year of shift	Source
Residence in brackish site, then shift to freshwater habitat	<6+	I. Thibault et al. (unpubl. data)
Residence in freshwater, then shift to brackish water	<6+	
Residence in freshwater, then shift to brackish water	<5+	Tzeng et al. (2002)
2 yr in fresh water, 1 yr in brackish and then residence in freshwater	3+	
Residence in freshwater, then shift to brackish water	<5+	Daverat & Tomás (2006)
Residence in freshwater, then shift to brackish water	<5+	Morrison et al. (2005)

sampled in the estuary that experienced freshwater at least once accounted for 95% in the Kaoping estuary, 50% in the Gironde estuary, 65% in the Hudson River estuary, 40% in the St. Jean estuary, and 17% in the Baltic Sea sample. Residency in estuaries and coastal sites is a less common life history trait than nomadic movements between water masses of different salinity sometimes including freshwater habitats. The proportion of fish that switched habitat at least once varied from 41% for *Anguilla anguilla* in the Gironde estuary to 81% for *A. japonica* in the Koaping estuary. Meanwhile, the proportion of marine and brackish residents in brackish sites varied from 5% for *A. japonica* in the Koaping estuary to 60% for *A. rostrata* in the St. Jean estuary. Considering the silver eel fraction as shown in 2 studies either on *A. anguilla* (Limburg et al. 2003) or

Table 4. *Anguilla anguilla*, *A. japonica* and *A. rostrata.* Reference and composition of freshwater habitat samples

| Species	Location	Distance from river mouth (km)	Sample size	Freshwater residents (%)	Source
A. anguilla	Garonne River, France	200	23	100	Daverat & Tomás (2006)
	Dordogne River, France	80	40	95	
A. japonica	Kaoping River, Taiwan	40	6	100	Tzeng et al. (2002)
	Pearl River, China	200	74	100	Tzeng et al. (2003)
	Fukui River, Japan	–	2	100	Tsukkamoto & Arai (2001)
	Tone River, Japan	–	5	80	
A. rostrata	Hudson River, United States	190	14	100	Morrison et al. (2003)
	St. Jean River, Canada	4.5	78	23	I. Thibault et al. (unpubl. data)
	Sirois Lake, Canada	80	36	44	
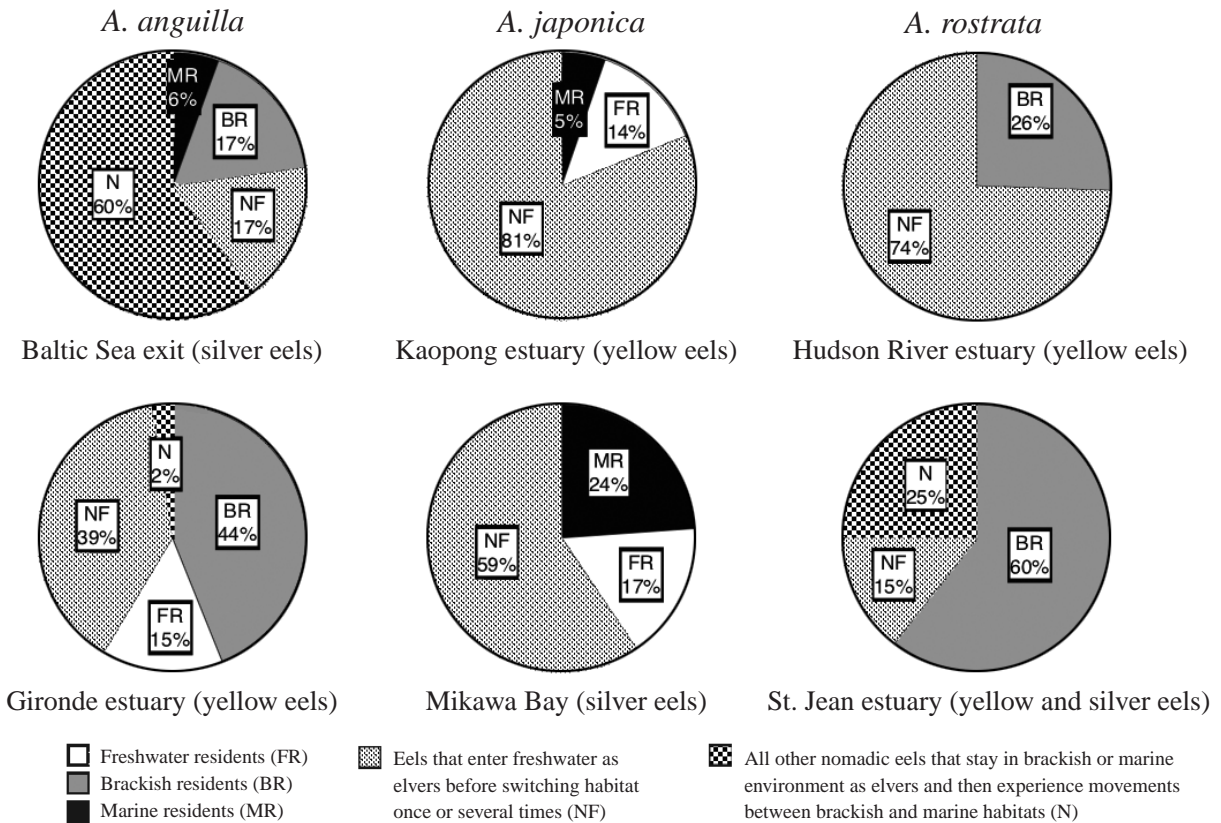
Fig. 5. *Anguilla anguilla*, *A. japonica* and *A. rostrata.* Proportions of habitat use patterns in brackish and marine sites
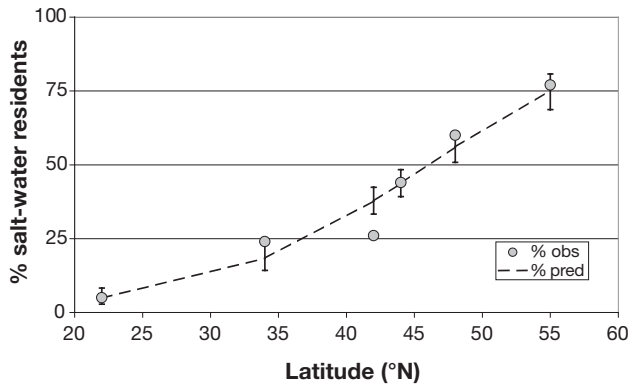

Fig. 6. *Anguilla anguilla*, *A. japonica* and *A. rostrata.* Relation between percentage of salt water residents and latitude in the different estuaries presented in this study (% observed [obs]), and associated break-point regression fit (model % predicted [pred]; error bars: ±SD, R^2 = 0.3)

on *A. japonica* (Tzeng et al. 2003), the samples were mainly composed of 'nomadic' eels. Eels found at higher latitudes exhibited a greater probability of remaining in the lower reaches of watersheds in brackish water (Fig. 6, logit model; p < 0.0001, R^2 = 0.3)

DISCUSSION

Diversity and relative proportions of habitat use

Regardless of species or site, *Anguilla anguilla*, *A. japonica* and *A. rostrata* displayed a wide repertoire of habitat use patterns, with up to 6 main types identified for each site as well as a number of less common, intermediate patterns. Moreover, the main patterns of habitat use were the same for the 3 species collected in different sites, with either residence in freshwater/brackish/marine habitat or 'nomadic movement' among habitats. In addition, the patterns of movements found for the 'nomadic eels' were also very consistent. Either a single shift of habitat following a downstream or an upstream movement, or seasonal movements, were found in most of the cases described in our comparisons. Regularity in life history was also observed for eels undertaking a single habitat shift, with the change occurring around age 3+ for the 3 species. This suggests that an individual eel's ability to change habitat is related to a favourable window for movement, probably driven by size rather than age. The influence of hormones

on individual migration ability deserves investigation, as growing evidence suggests that glass eels' first habitat selection is partly controlled by thyroid hormones (Edeline et al. 2004). In addition, freshwater habitats might not be very attractive for 3+ yellow eels as most of our freshwater samples, with the exception of Sirois Lake, do not have 'nomads' that migrate from the estuary to the river. Differences in productivity between freshwater and brackish (estuarine) habitats, and the resulting lower growth of eels in temperate freshwater sites (Helfman et al. 1984, Helfman et al. 1987, Fernandez-Delgado et al. 1989, Lobon-Cervia et al. 1995, Morrison & Secor 2003), might explain this phenomenon. The similarity of habitat use patterns in *A. rostrata*, *A. anguilla*, and *A. japonica* strongly suggests that plasticity in temperate eels is a common life history trait across anguillid species and sites. This observation is also supported by studies on southern temperate eels, such as *A. dieffenbachii* and *A. australis* (Arai et al. 2004).

What seems more variable than the diversity of habitat use patterns is their relative proportion among the different species and geographic regions. For example, in the St. Jean estuary (48° N), 60% of the eels sampled in the estuary remained in the estuary compared to 35% estuarine residency in the Hudson River estuary (42° N). A predominance of brackish dwelling eels was observed in the Baltic Sea (55 to 60° N) while only 44% of eels were residents in the Gironde estuary (44° N). In the same manner, in the Koaping River (22° N), only 5% of eels were marine residents compared to 24% in Mikawa Bay, Japan (34° N). Hence, at the northernmost edge of the species' range, eels tend to be confined in brackish water, as shown by (Arai et al. 2003, Kotake et al. 2004). Natural and artificial obstacles present on the watercourse also constrain habitat use patterns, as in an impounded watercourse in Canada, where *Anguilla rostrata* displayed only 3 different behaviours (Cairns et al. 2004). This evidence of geographical variability suggests that habitat use pattern expression is determined by environmental conditions.

Strategies of nursery and feeding habitat use

Regardless of habitat use patterns, all eels share similar marine migrations both from and to their spawning grounds, and display varying levels of catadromy. We emphasize that the plasticity of habitat use patterns at the individual level is a process by which eels occupy their nursery and feeding grounds. Within these areas, the plasticity in habitat use patterns is a strategy that allows eels to colonise a wide variety of ecosystems at the scale of the species' geographical ranges. Unlike other fish species, the niche of eels appears not to be specialised during their growing phase. In accordance with the higher prevalence of anadromy in higher latitudes among salmonids (Gross et al. 1988), eels tend to preferentially occupy brackish and marine habitats at the northern extremes of their distributional ranges for feeding.

Diadromy of eels and colonisation processes

Although individual authors have reported on the wide variety of habitat uses by individual species, this interspecies comparison demonstrates the breadth of the behavioural repertoire at the genus level, a new insight into eel ecology. It now appears that the genus *Anguilla* is facultatively (rather than obligate) catadromous, and also, that many individuals captured in estuaries are marine amphidromous (Gross 1988). The combined data sets show a greater proportion of eels that entered freshwater even for a short period of their life span than of eels classified as marine or brackish habitat residents.

Although catadromy is not obligatory, it nevertheless remains a major life history trait for anguillid eels. Compared to marine ecosystems, freshwater stream/river habitats are generally less risky in terms of predation (Jonsson & Jonsson 1993), and also carry a lower density of eels than brackish sites, as a result of population diffusion processes (Ibbotson et al. 2002). These features permit the survival of a larger diversity of phenotypes and genotypes than in brackish sites characterised by high densities and mortality rates.

The evolution of the high degree of habitat use plasticity documented in this review suggests a remarkable 'bet-hedging' strategy for anguillids as a group. Whether such plasticity represents an ancestral state that is retained among anguillids would require investigation of habitat use patterns of tropical species, hypothesised as ancestral within anguillids. Studies of *Anguilla marmorata* (Resh et al. 1999) and of *A. bicolor bicolor* and *A. bicolor pacifica* (J.-C. Shiao pers. comm.) demonstrated that these tropical eel species can use both freshwater, estuarine and marine habitats.

In conclusion, we have shown that 3 species of anguillid eels display remarkable flexibility in habitat use. These can be classified into several 'eco-types,' whose frequencies appear to vary at least with latitude. More studies of this sort, in more regions, would further elaborate the patterns we have seen.

Strategic sampling along latitudinal, productivity, or other gradients would allow testing of alternate hypotheses concerning what it is that structures local populations into the different eco-types. Diadromy in eels is more complex than a simple separation into catadromous and non-catadromous individuals. The variants we show, which include marine amphidromy, might be more appropriate to qualify eel life cycles.

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