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Migration Behavior and Habitat Use by Juvenile Japanese Eels *Anguilla japonica* in Continental Waters' as Indicated by Mark-Recapture Experiments and Otolith Microchemistry

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Shih-Huan Lin, Yoshiyuki Iizuka, and Wann-Nian Tzeng (2012) Migration behavior and habitat use by juvenile Japanese eels *Anguilla japonica* in continental waters' as indicated by mark-recapture experiments and otolith microchemistry. *Zoological Studies* **51**(4): 442-452. The migratory behavior of Japanese eels *Anguilla japonica* in continental waters was examined by a mark-recapture experiment with 3263 wild and marked culture-originating yellow eels. The experiment was conducted in Dapong Bay and the Kaoping River estuary in southwestern Taiwan over a 4-yr period in 2003-2006. The migratory environmental history of the marked and wild eels was reconstructed by examining temporal changes in otolith strontium (Sr)/calcium (Ca) ratios by an electron probe micro-analysis (EPMA). Otolith Sr/Ca ratios of recaptured eels indicated that juvenile yellow eels preferred a brackish environment similar to the wild population. Otolith Sr/Ca ratios revealed that estuarine contingents were higher in both the river (75.5%) and bay (60%) than were freshwater contingents (river, 22%; bay, 25%) and seawater contingents (river, 2.5%; bay, 15%). The recapture rate of marked eels sharply decreased with increasing distance from the release site, and the maximum dispersal distance of eels was < 2 km, indicating that the eels may exhibit territorial behavior after recruitment to the river. The recapture rate also sharply decreased with time, indicating that heavy harvesting of eels occurred in a short time after release. The specific habitat use and limited home range suggest that eels could easily be subjected to overfishing, which should be considered when planning conservation and fisheries management policies.
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Key words: *Anguilla japonica*, Habitat use, Migratory behavior, Otolith Sr/Ca ratios, Mark-recapture.

The Japanese eel *Anguilla japonica* is a catadromous fish, widely distributed from Taiwan in the south, through China, Korea, and Japan in the north (Tesch 1977). It spawns west of the Mariana Is. in the Pacific Ocean (Tsukamoto 1992 2006). After hatching, eel larvae, leptocephali, are transported by the North Equatorial and Kuroshio Currents from the spawning ground and metamorphose to glass eels on the continental shelves of northeastern Asian countries. Migration from the spawning ground to the estuaries takes approximately 4-6 mo (Cheng and Tzeng 1996). Glass eels become pigmented elvers in estuaries, which then grow into yellow eels in rivers. At maturation, yellow eels become silver and migrate downstream to spawn and die (Tesch 1977). The Japanese eel is an economically important aquaculture species in Taiwan, and elvers are over-exploited during their upstream migration in estuaries (Tzeng 1984 1985). The population of Japanese eel has decreased to approximately 10%-20% of the level in 1980 as have the European eel

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A. anguilla and American eel *A. rostrata* (Dekker 2003). The reason for the population decline of these 3 temperate eel species is not clear, but might be due to such factors as overfishing, pollution, climate change, habitat degradation, the unavailability of (freshwater) habitats due to dams, parasite infection, etc. (Haro et al. 2000, Feunteun 2002, Robinet and Feunteun 2002, Dekker 2004). Compared to European and American eels, studies of the Japanese eel during its continental life stage are very limited. Thus, a better understanding of its habitat use and migratory behavior in the continental life stage is important for making conservation and fishery management policies for the recovery of eel populations.

Otoliths of teleost fishes grow by rhythmic deposition of aragonite crystals within a protein matrix with daily and annual schedules which permit the determination of a fish's age (Degens et al. 1969, Pannella 1971, Tzeng et al. 1994). Elements deposited in otolith increments reflect those in the ambient water; for example, strontium (Sr)/calcium (Ca) ratios in otoliths of eels are approximately 4.8-times higher in seawater than in fresh water (Tzeng 1996, Campana 1999, Lin et al. 2007), which permits a reconstruction of fish migratory behavior between freshwater and marine environments (Tzeng et al. 1997 2002, Tsukamoto and Arai 2001, Cairns et al. 2004, Daverat et al. 2006, Jessop et al. 2008). Studies of otolith Sr/Ca ratios found that Japanese, European, and American eels are facultatively migratory species, in that habitat use in the juvenile stage is plastic, and some yellow eels may skip the freshwater life phase and complete their life cycle in a saline-water environment (Tzeng et al. 1997 2002, Tsukamoto and Arai 2001, Daverat et al. 2006, Jessop et al. 2008). However, the time resolution of elemental signatures in otoliths is unable to reveal short-term information, such as daily movements and small-scale dispersals of eels and subsequently their territorial behavior.

In this study, we used mark-recapture methods to investigate short-term and small-scale movements and dispersal of Japanese eels, to test their home range behavior in continental waters'. We also examined otolith Sr/Ca ratios to identify the types of facultative migration of the recaptured and wild Japanese eels to understand their habitat use. This information is crucial for conservation and management of this eel during its continental life stage.

MATERIALS AND METHODS

Environmental characteristics of the study sites

Mark-recapture experiments with Japanese eels were conducted in Dapong Bay and in the Kaoping River estuary in southwestern Taiwan in Sept. and Oct. 2003 and 2005, and Aug. 2006 (Fig. 1). Dapong Bay is a semi-closed coastal lagoon with a shallow outlet connected to the sea and 2 small freshwater outlets through which agriculture irrigation water is discharged. Freshwater input into the bay is very small except following heavy rainfall. The salinity of the bay body is about 33‰-35‰ but can drop to 5‰-7‰ after large freshwater inputs. The Kaoping River is the largest river in southern Taiwan with a length of 171 km. Salinities in the estuary of the river vary with the tides from 0‰ to 33‰. The tidal influence extends 16.8 km upriver. The bay and river estuary are traditional fishing grounds for eel and shrimp. Much fishing gear such as shrimp nets is used to catch eels in the estuary, which provides an opportunity to conduct mark-recapture experiments to study small-scale movements and dispersal behavior of this eel.

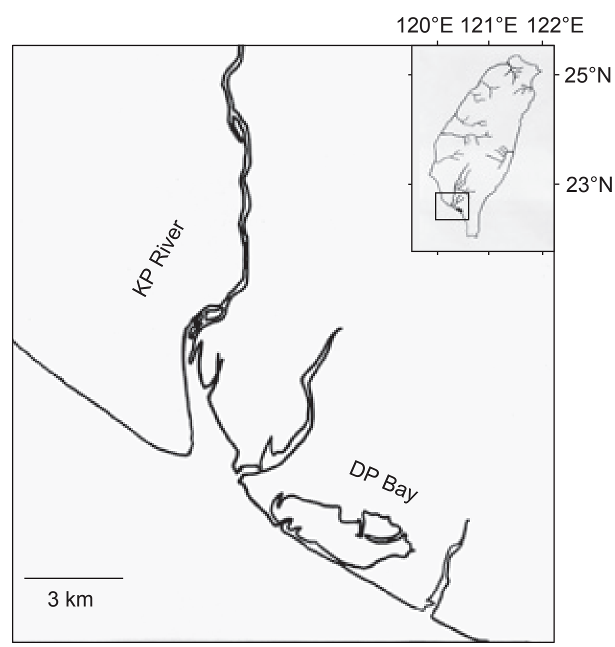

Fig. 1. Mark-recapture experimental sites for Japanese eels *A. japonica* in Dapong Bay (DP) and the estuary of the Kaoping River (KP), southwestern Taiwan.

Mark-recapture method

In total, 3263 Japanese eels in the yellow-eel stage were marked externally using either a coded wire tag (CWT), fin clip, or liquid nitrogen branding methods and internally by a tag with a microchip, as well as chemical marking of otoliths by an injection of oxytetracycline (OTC). The mark-recapture experiment with eels was conducted in Dapong Bay and the Kaoping River estuary in 2003, 2005, and 2006 (Table 1). Eels were recaptured by shrimp nets at 16 stations in the estuary of the Kaoping River (Fig. 2) and were recaptured by a great number of widely spread shrimp nets in Dapong Bay. The dimensions and construction of the shrimp nets were described by Lin and Tzeng (2008). The yellow eels used for the mark-recapture experiments came from 2 sources: 1) cultured eels from aquaculture ponds and 2) wild eels collected from the Kaoping River estuary. The cultured eels had been reared from elvers in fresh water for 2 yr and were acclimated in brackish water for 6 months at a salinity similar to that at the release site before marking. A muscle injection of 100 ppm OTC/kg of fish weight produced a fluorescent mark in the otolith (Fig. 3), which allowed its identification with a stereomicroscope (SMZ-10, Nikon, Japan) under ultraviolet light provided by a mercury lamp (HBO, 100w/2, Nikon) with an epifluorescence filter (BV-2A filter, at wavelengths of 400-470 nm, Nikon) to understand the initial increment deposited in otoliths of eels after OTC marking. Eels marked with chips or CWT were detected by commercial detectors (chip detector: All Weather Extended Range Multi Tag Reader, AVID, USA; CWT detector: Handheld Wand Detector, Northwest Marine Technology, USA). Other eels with external tags were recovered by sighting them with the naked eye. Otolith OTC marking of eels was identified by fluorescence microscopy. Based on the recapture data of eels from the widely spread shrimp nets, short-term movements and small-scale dispersal of the eel were evaluated.

Measurement of Sr/Ca ratios in otoliths

To understand habitat use by the eels, Sr/Ca ratios in otoliths of both wild and recaptured eels were measured from the primordium to the otolith edge by a wavelength dispersive x-ray spectrometer equipped with an electron probe microanalyzer (EPMA; JXA-8900R, JEOL, Japan) following the method of Tzeng et al. (2002). The

Table 1. Source, sample size, mean (± standard deviation; S.D.) total length (TL), and body weight (BW) by year of Japanese eels, *A. japonica*, marked by different methods (oxytetracycline (OTC), coded wire tag (CWT), microchip, fin clip, and liquid nitrogen (LN)), and release sites on the southern and northern coasts of Dapong Bay (DP) and upstream (KP-up) and downstream (KP-down) sections of the Kaoping River, Taiwan

Release date	Release site	Source	No. of eels marked by different methods						Mean (± S.D.)	
			OTC	CWT	Microchip	Fin clip	LN	Total	TL (cm)	BW (g)
9 Sept. 2003	DP-north	Culture	163		163		163	163		1200
		Culture		500				500		400
29 Sept.	KP-down	Culture		300				300		400
	KP-up	Culture	180	180				180		400
7 Oct.	DP-south	Culture	127		127			127		1200
28 Sept. 2005	KP-down	Culture	500		500	500		500	69.3 ± 4.9	508.3 ± 137.6
		Wild	152		152	152		152	69 ± 4.7	505.5 ± 129.2
3 Oct.	KP-up	Culture	150		150	150		150	68.9 ± 4.7	495.7 ± 134.6
13 Oct.	KP-down	Wild	68		68	68		68	44.2 ± 11.6	116.3 ± 109.9
15 Aug. 2006	KP-down	Culture	537		537	537		537	70.6 ± 10.6	578.1 ± 318.8
		Wild	246		246	246		246	67.5 ± 9.6	478.4 ± 280.1
16 Aug.	KP-up	Culture	100		100	100		100	72.7 ± 10.2	633.8 ± 320.7
25 Aug.	KP-down	Culture	140		140	140		140	66 ± 9	433.8 ± 259.1
		Wild	55		55	55		55	62.8 ± 10.1	356.8 ± 230.5
26 Aug.	KP-down	Culture	40		40	40		40	64.7 ± 9	389.2 ± 223.8
		Wild	5		5	5		5	48.2 ± 4.4	98.2 ± 45

EPMA beam conditions for the analysis were set to an accelerating voltage of 15 keV, an accelerating current of 3 nA, and a beam size with a rectangular area of 5 × 4 μm. Calcite ($CaCO_3$; NMNH 136321) and strontianite ($SrCO_3$; NMNH R10065) were used as standards for calibrating the Ca and Sr contents of otoliths. Quantitative data were calibrated by the ZAF method (Z, atomic number; A, absorption; and F, fluorescence correction). Sr/Ca ratios at 4‰ in weight percent were used as a criterion to discriminate freshwater and seawater contingents (Tzeng et al. 2002).

Data analysis

The dispersal distance of a marked eel was calculated from the latitude and longitude of the release and recapture sites measured by a hand-held global positioning system (GPS, PaPaGo, Taiwan) using the Haversine formula (Markou and Kassomenos 2010). Dispersal ranges of eels after release were estimated from the recapture rate at 24 h and 10 d after release. Twenty-four-hour and 10-d observations were used to monitor daily maximum movements and short-term dispersal.

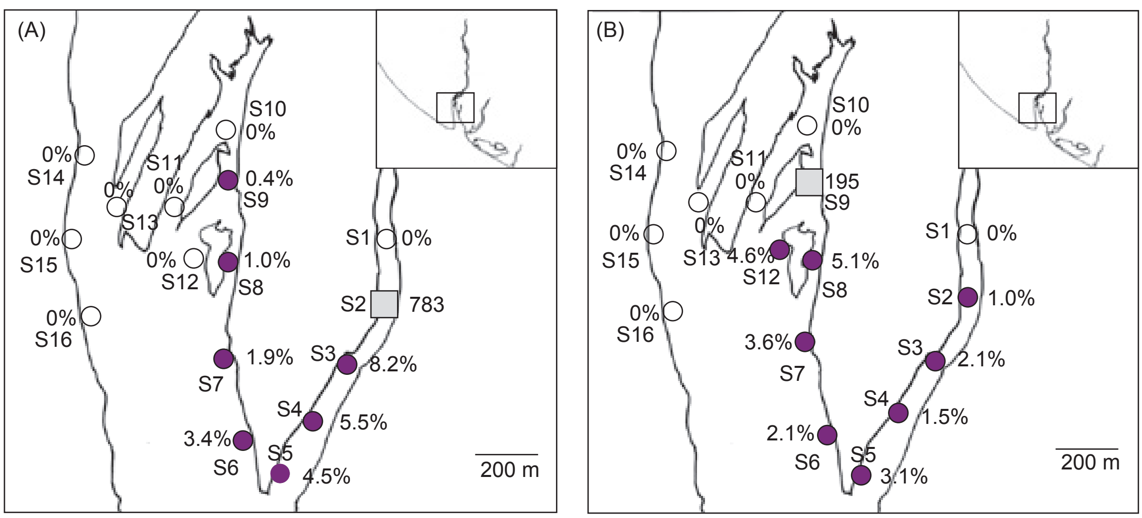

Fig. 2. Spatial variations in recapture rates of Japanese eels *A. japonica* in the Kaoping River, Taiwan (A) after 24 h for eels released at station 2 on 15 Aug. and (B) after 10 d for eels released at station 9 on 25 Aug. The square indicates the release site, and circles indicate recapture sites. S, station.

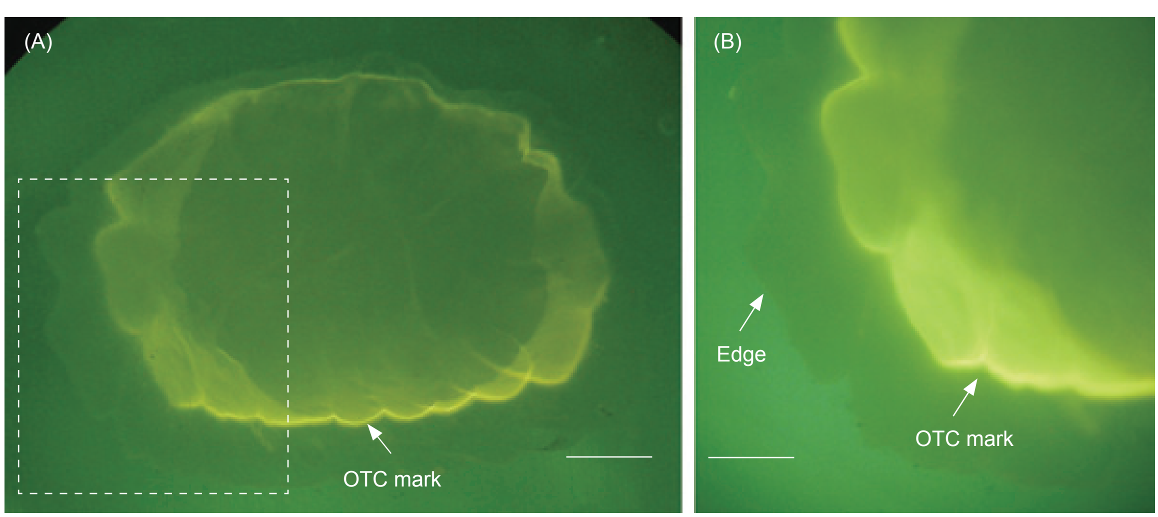

Fig. 3. (A) Oxytetracycline (OTC) mark in an otolith of a Japanese eel *A. japonica* released on 28 Sept. 2005 and recaptured on 25 May 2006 in the estuary of the Kaoping River, Taiwan. (B) The newly deposited increment after the OTC mark magnified from (A). Scale bars: A = 500 μm; B = 300 μm.

The recapture rate (%) of eels was calculated as (the number recaptured/number released) × 100%. Differences in recapture rates of eels between upstream and downstream release sites, and cultured and wild origins were compared using the Wilcoxon rank-sum test to understand if the migratory behavior differed between release sites or between eels with different origins. Temporal and spatial changes in recapture rates were also analyzed to evaluate the exploitation status of eels in the estuary.

RESULTS

Sr/Ca ratios in otoliths of eels cultured in a controlled environment

Figure 4 show temporal changes in the Sr/Ca ratio in an otolith of a cultured eel, reared in fresh water for 2 yr after the elver stage, acclimated in brackish water for 6 mo before release into the estuary of the Kaoping River on 28 Sept. 2005 and recaptured on 25 May 2006. Changes in the Sr/Ca ratio in the otolith of the eel corresponded to the actual rearing conditions. The Sr/Ca ratio in the otolith was $< 4 \times 10^{-3}$ when the eel was reared in fresh water for 2 yr after the elver stage and then fluctuated $(3\text{-}6) \times 10^{-3}$ when the eel was acclimating in brackish water for 6 mo before release. This indicated that the otolith Sr/Ca ratios can be used as a proxy to reveal the migratory environment of the eel.

Migratory patterns of wild eels

The pattern of Sr/Ca ratios in otoliths between the primordium and elver check (EC) was similar among eels because they migrated in the same marine environment from the spawning ground to the estuary. However, beyond the EC, migratory patterns of wild eels could be classified into 1) freshwater, 2) seawater, and 3) estuarine contingents (Fig. 5). The estuarine contingent was the most abundant, constituting 75.5% of eels from the Kaoping River (n = 209) and 60% from Dapong Bay (n = 60), followed by the freshwater contingent (22% for the river and 25% for the bay) and the seawater contingent (2.5% and 15%, respectively). The migratory patterns of the recaptured eels were also classified into 3 contingents:

1) Seawater contingent, such as an eel recaptured in Dapong Bay in 2003, the otolith Sr/Ca ratios of which fluctuated between $(4 \text{ and } 6.5) \times 10^{-3}$, indicating that the eel had remained in a seawater environment after release (DP2003 in Fig. 6A);

2) Estuarine contingent, such as an eel released into the Kaoping River in 2005, the otolith Sr/Ca ratios of which fluctuated around 4×10^{-3} (KP2005 in Fig. 6A); and

3) Freshwater contingent recaptured 2006, the otolith Sr/Ca ratios of which were $< 4 \times 10^{-3}$ (KP2006 in Fig. 6A). This indicated that the marked eel also showed facultative migratory behavior. Among 143 recaptured eels from Dapong Bay, 93.9% were recaptured in

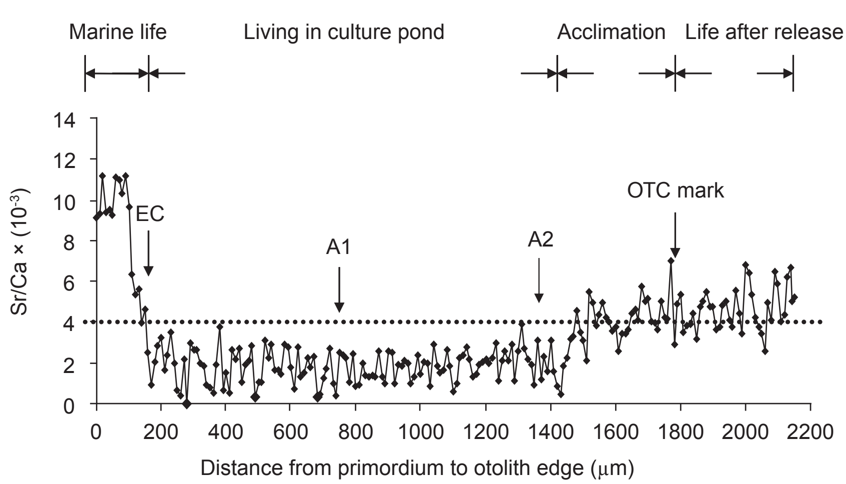

Fig. 4. Temporal changes in otolith Sr/Ca ratios for a cultured Japanese eel *A. japonica* reared in a controlled saline environment and marked with oxytetracycline (OTC) before release in the estuary of the Kaoping River, Taiwan on 28 Sept. 2005. The eel was recaptured in the estuary on 25 May 2006. EC, elver check; A, annuli.

areas of the freshwater outlets where salinities were low (5‰-7‰). Similarly, 99% of the 296 eels recaptured from the Kaoping River were recaptured near their release site in the estuary. This tendency of habitat preference is similar to the composition of migratory patterns of wild eels as indicated in figure 5.

On the other hand, 1 eel released in an upstream section of the Kaoping River moved to the downstream estuarine area over a period of 194 d, and its otolith Sr/Ca ratios increased from < 2 × 10^{-3} at release in the freshwater upstream section to 6‰-7‰ at recapture in the estuary (Fig. 6B).

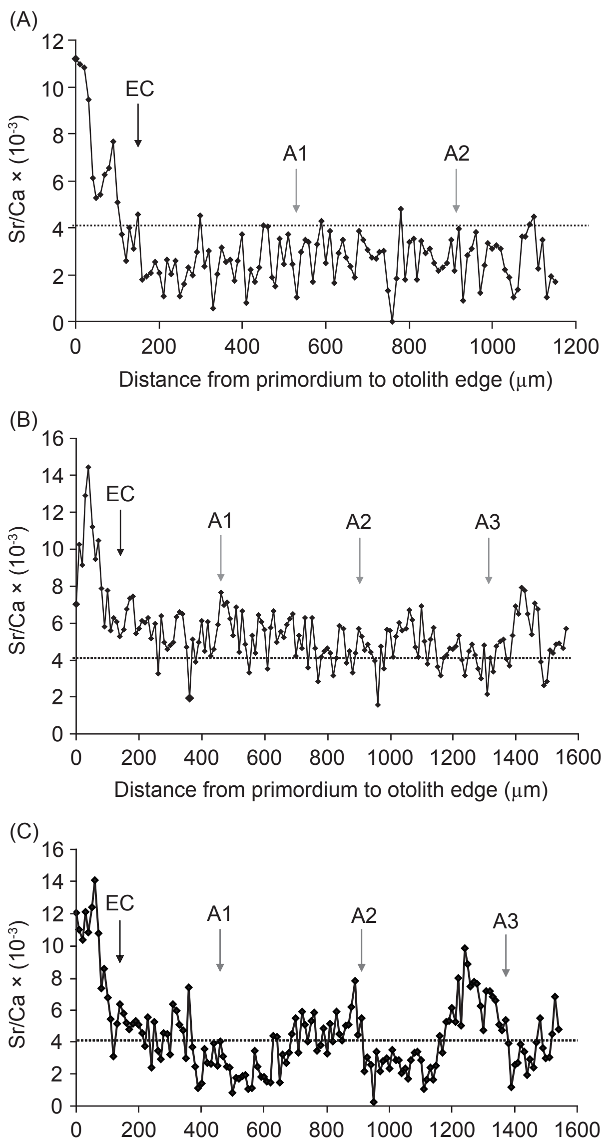

Fig. 5. Migratory patterns of wild Japanese eels *A. anguilla* collected in the Kaoping River, Taiwan. (A) Freshwater contingent with Sr/Ca ratios of < 4 × 10^{-3}, (B) seawater contingent with Sr/Ca ratios of > 4 × 10^{-3}, and (C) estuarine contingent with Sr/Ca ratios that fluctuated between those of the freshwater and seawater contingents. EC, elver check; A1-3, annuli.

Spatial and temporal changes in recapture rates

Recapture rates of eels were 18.1% in Dapong Bay in 2003, and 2.9%, 3.4%, and 22.4% in the Kaoping River in 2003, 2005 and 2006, respectively (Table 2). The recapture rate in the river was significantly higher downstream than upstream ($p < 0.05$), but did not significantly differ between cultured and wild eels ($p > 0.05$). The recapture rate decreased with an increasing distance from the release site (Fig. 7).

Recapture rates were generally the highest in the 1st month after release and decreased sharply after the 2nd month except in the Kaoping River in 2003 (Fig. 8). Few eels were recaptured in the 2nd half of the year.

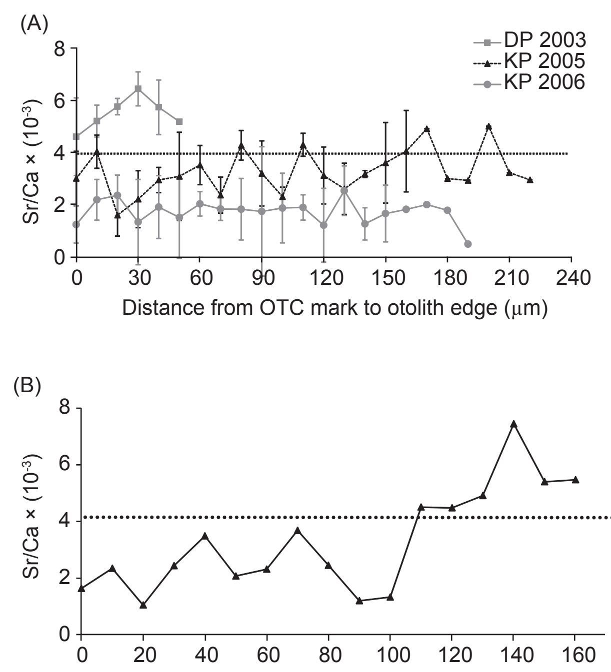

Fig. 6. (A) Migratory patterns of recaptured Japanese eels *A. japonica* released in Dapong Bay (DP) in 2003 and the Kaoping River (KP), Taiwan in 2005 and 2006; and (B) 1 eel released upstream in the Kaoping River in 2004 and recaptured downstream 194 d later in 2005.

Dispersal of marked eels and habitat preferences

From the mark and recapture data, the maximum dispersal distance of this eel was estimated to be approximately 2.48 and 2.21 km/d for eels released in the northern and southern areas of Dapong Bay, respectively, and 2.09 km/d in the Kaoping River. In the Kaoping River, eels with release durations of 24 h and 10 d exhibited the same dispersal distances (Fig. 7).

Approximately 70% of eels were recaptured within 1 km of the release sites, regardless of whether they were released up- or downstream of the fishing ground in the river.

DISCUSSION

Otolith Sr/Ca ratios as an environmental proxy

The relationship between otolith Sr/Ca ratios and the ambient water salinity has been examined by many laboratory-controlled experiments (Tzeng 1996, Kawakami et al. 1998, Lin et al. 2007). In this study, temporal changes in Sr/Ca ratios in

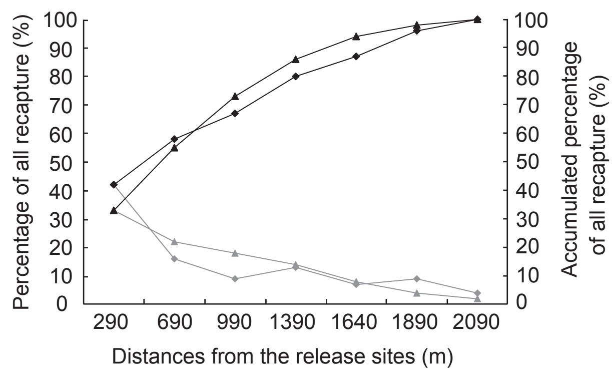

Fig. 7. Recapture rates after 24 h for Japanese eels *A. japonica* in relation to distance from the release site in the Kaoping River, Taiwan. Triangles represent the 195 eels released on 25 Aug. and the 45 recaptured on 26 Aug. 2006, and diamonds represent the 783 eels released on 15 Aug. with 204 eels recaptured on 25 Aug. 2006.

Table 2. Spatial and temporal changes in the recapture rate (RR = (no. recaptured/no. released) × 100%) by site (Dapong Bay north (DP-north) and south (DP-south) and Kaoping River upstream (KP-up) and downstream (KP-down)) and the source of Japanese eels *A. japonica* in Taiwan. RRs of eels between upstream and downstream sections, and cultured and wild origins were compared by the Wilcoxon rank-sum test

Release date		Release site	Source	No. released	No. recaptured (RR in %)
9 Sept. 2003		DP-north	Culture	163	34 (20.9)
			Culture	500	59 (11.8)
29 Sept.		KP-down	Culture	300	14 (4.7)
		KP-up	Culture	180	0 (0)
7 Oct.		DP-south	Culture	127	50 (39.3)
28 Sept. 2005		KP-down	Culture	500	25 (5)
			Wild	152	4 (2.6)
3 Oct.		KP-up	Culture	150	1 (0.6)
13 Oct.		KP-down	Wild	68	0 (0)
15 Aug. 2006		KP-down	Culture	537	146 (27.2)
			Wild	246	58 (23.6)
16 Aug.		KP-up	Culture	100	0 (0)
25 Aug.		KP-down	Culture	140	40 (28.6)
			Wild	55	5 (9.1)
26 Aug.		KP-down	Culture	40	2 (5)
			Wild	5	1 (20)
Total	DP	2003		790	143 (18.1)
	KP	2003		480	14 (2.9)
		2005		870	30 (3.4)
		2006		1123	252 (22.4)

otoliths of cultured eels corresponded to the known salinity history of the eels before their release. This validated that Sr/Ca ratios in otoliths can be used to construct the migratory environmental history of the eel. Sr/Ca ratios after the OTC mark indicated that marked eels stayed in brackish water after release until recapture. The known environmental information for cultured eels validated that the use of otolith Sr/Ca ratios to reconstruct the past migratory environmental history of eels is reliable.

Comparison of advantages between otolith Sr/Ca ratios and conventional tagging methods

In this study, multiple traditional tagging methods including tags and marks were used.

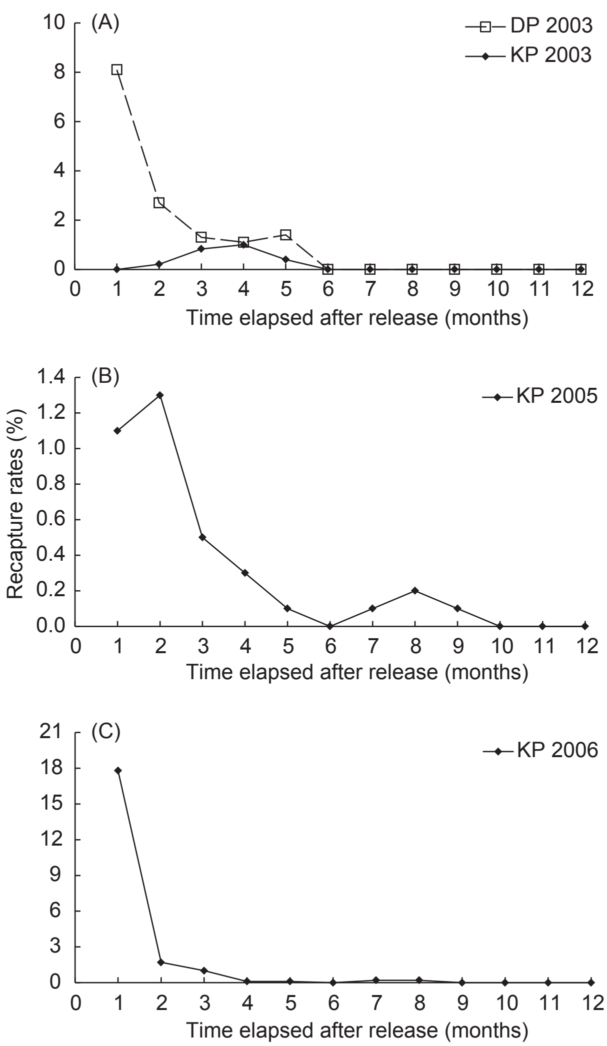

Fig. 8. Temporal changes in the mean (± standard deviation) recapture rate in the 1st year after release in (A) Dapong Bay and the Kaoping River, Taiwan in 2003 and (B) in the Kaoping River in 2005 and (C) 2006.

Mortalities of eels subjected to different marking methods during the acclimation period were all < 0.1%, indicating that these tags and marks did not cause mass mortality which could have biased the results of the mark and recapture experiment. External tags enabled local fishermen to easily identify marked eels from unmarked ones and helped increase recapture rates. Meanwhile from the daily returned data, we could determine short-term and small-scale movements. Liquid nitrogen marking of the epidermis disappeared after 3 mo. That is sufficient time for short-term observations. Internal tags such as chips could provide information on individual behavior, while the OTC on otoliths provided information of progressive migratory environments from release to recapture through the Sr/Ca-ratio analysis. Otolith Sr/Ca ratios can only track seasonal and yearly migratory patterns of eels because the daily deposition rate of otoliths of eels is less than the time-resolution limitation of the EPMA beam size of 5 × 4 μm. Changes in otolith element/Ca ratios of sufficient magnitude may reflect a change in habitat salinities achieved either by eel movement between habitats or a resident eel which experienced changing salinities. However, approximately 30 d is required to incorporate an Sr signal into an American eel otolith (Jessop et al. 2002), and perhaps a similar period for barium (Ba). So the relatively large analytical "spot" size means that short-term fluctuations in ambient element/Ca ratios are less relevant than seasonal or annual patterns in ambient water chemistry, which are often less variable. Changes in otolith element/Ca ratios of longer duration, of say > 2-3-fold which depend on the "spot" size and interval, suggest a movement between habitats because changes in habitat salinities at a single location are rarely of extended duration in open tidal estuaries such as the study sites. The issue is not whether water chemistry varies temporally or geographically, but whether by doing so it creates conditions, subsequently reflected in otolith chemistry, that may make otolith element/Ca ratios data difficult to interpret when categorizing fish habitat residence and inter-habitat movements into broad categories such as freshwater, estuarine, and marine residence and determining movements between these categories. Each method has respective advantages and disadvantages. Combining both conventional tagging methods and a natural tag, i.e., otolith Sr/Ca ratios, indicated that the Japanese eel preferred an estuarine habitat and showed detailed migratory behavior.

The nature of facultative catadromy of the Japanese eel

Facultative catadromy in a freshwater eel was first defined in the Japanese eel from otolith Sr/Ca ratios by Tsukamoto and Arai (2001). A similar phenomenon was defined as semi-catadromy in the European eel by Tzeng et al. (2000) and as conditionally facultative catadromy in the American eel by Thibault et al. (2007). Meanwhile, the proportion of the seawater contingent increased with latitude in all 3 eel species (Daverat et al. 2006). This indicates that habitat use by eels is phenotypically plastic and not genetically determined (Han et al. 2010). Dapong Bay is a highly saline habitat with a small freshwater input, and the brackish-water region is small. But the proportion of the estuarine contingent in Dapong Bay was still greater than the seawater contingent, similar to the situation in the Kaoping River. This indicates that the nature of the habitat preference of the eel in the yellow-eel stage does not easily change with the environment, although habitat availability may differ.

On the other hand, micro-habitats at the 16 stations where eels were recaptured in the Kaoping River were not homogeneous, which might have led to an uneven distribution of eel recapture rates. Anguillid eels undergo extensive marine migrations, but their freshwater migrations are more limited, both spatially and temporally (Jellyman et al. 1999). Eels in freshwater habitats have restricted habitats and little migration. Jellyman and Sykes (2003) found that New Zealand eels seldom crossed the channel of the Cust River or the South Branch of the Waimakariri River.

The eels released in this study were also rarely found to cross tributaries. Their short-term movements showed considerable fidelity to particular habitats. The onset of activity at dusk was related to feeding in both shortfinned and longfinned eels in New Zealand (Ryan 1984, Glova and Jellyman 2000). A similar activity rhythm was also found in wild *A. anguilla* (Baras et al. 1998). American eels are more active at night (Thibault et al. 2007). Our study also validated that the Japanese eel is inactive during the day, because shrimp nets set overnight and recovered in the morning revealed better harvests than shrimp nets set in the morning and recovered in the evening.

Dispersal and home range of the eels after release

The recapture rate in the river was significantly higher downstream than upstream, but did not significantly differ between cultured and wild eels. This indicates that the sources of the eel, regardless of being cultured or wild, were well mixed and did not influence the recapture rate. The recapture rate decreased with increasing distance from the release site, indicating that the eels did not migrate far from the release site. Approximately 70% of eels were recaptured within 1 km of the release sites, regardless of whether they were released upstream or downstream of the fishing ground in the river. This indicates that eels dispersed quickly after release, but only small distances from the release site.

The maximum distance of daily movements of eels released in both the Kaoping River and Dapong Bay was estimated to be around 2 km. The recapture rate decreasing with distance showed similar tendencies between 24 h and 10 d after release. This indicates that the eels settled down very quickly after release and did not move far from the released site again, which implies that the eels may have home range behavior and establish a territorial area after transplantation to a new environment. Tagging processes often produce some aberrant behaviors as evidenced by the initial extensive movements in European eels and shortfinned and longfinned New Zealand eels (Baras et al. 1998, Jellyman and Sykes 2003). However in this study, we did not find a similar phenomenon because the distribution patterns between 24 h and 10 d after release were similar. The average home range was found to be approximately 10-30 m for New Zealand shortfinned and longfinned eels (Jellyman and Sykes 2003) and 0.1-1 km for American eels in Canada (Thibault et al. 2007). In Taiwan, the daily maximal movement could reach 2 km. Differences in distances of home ranges and territories among species might be due to varied stream and landforms causing behavioral performances to differ.

However, the particular eel in figure 6B, which was released upstream in the river and collected in the estuary, moved a distance of approximately 42.1 km. If the eel had moved the maximum daily movement distance of 2 km/d, it would have required only about 21 d. However, the observed duration between its upstream release and estuarine recapture was 194 d. Evidently, the eels remained stationary for a period once they found suitable habitat before moving further downstream. Otolith Sr/Ca ratios indicated that 1 eel had spent more than 100 d in fresh water and then moved to a highly saline environment during the last 50 d. Consequently, the eel moved from upstream to downstream over about 2-3 mo rather than passively with the current. Compared to other phases, eels in the yellow-eel phase have small, restricted movements.

Otolith Sr/Ca ratios indicated the phenotypic plasticity of habitat use by wild eels in the yellow-eel stage, and migratory patterns could be divided into 3 contingents. The estuarine contingent was more abundant than the freshwater and seawater contingents. The mark-recapture data also indicated that eels preferred estuarine brackish rather than fresh or seawater environments. This eel exhibited home range behavior and did not move far from the release sites. The conventional marking and tagging techniques and otolith elemental signatures can supplement limitations of each method to better understand the migratory behaviors of and habitat use by eels.

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REFERENCES

Baras E, D Jeandrain, B Serouge, JC Philippart. 1998. Seasonal variations in time and space utilization by radio-tagged yellow eels *Anguilla anguilla* (L.) in a small stream. Hydrobiology **371/372:** 187-198.

Cairns DK, JC Shiao, Y Iizuka, WN Tzeng, CD MacPherson. 2004. Movement patterns of American eels in an impounded watercourse, as indicated by otolith microchemistry. North Am. J. Fish. Manage. **24:** 452-458.

Campana SE. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms, and applications. Mar. Ecol. Progr. Ser. **188:** 263-297.

Cheng PW, WN Tzeng. 1996. Timing of metamorphosis and estuarine arrival across the dispersal range of the Japanese eel *Anguilla japonica*. Mar. Ecol. Progr. Ser. **131:** 87-96.

Daverat F, KE Limburg, I Thibanlt, JC Shiao, JJ Dodson, F Caron et al. 2006. Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. Mar. Ecol. Progr. Ser. **308:** 231-241.

Degens ET, WG Deuser, RL Haedrich. 1969. Molecular structure and composition of fish otoliths. Mar. Biol. **2:** 105-113.

Dekker W. 2003. Epilogue: worldwide decline of eel resources necessitates immediate action. Fisheries **28:** 28-30.

Dekker W. 2004. Synthesis and analyses. In slipping through our hands-population dynamics of the European eel. PhD dissertation, Faculteit Natutuurweten Schappen, Wiskunde an Informatica, the Netherlands.

Feunteun E. 2002. Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. Ecol. Engin. **18:** 575-591.

Glova GJ, DJ Jellyman. 2000. Size-related differences in diel activity of two species of juvenile eel (*Anguilla*) in a laboratory stream. Ecol. Freshw. Fish. **9:** 210-218.

Han YS, Y Iizuka, WN Tzeng. 2010. Does variable habitat usage by the Japanese eel lead to population genetic differentiation. Zool. Stud. **49:** 392-397.

Haro A, W Richkus, K Whalen, A Hoar, WD Busch, S Lary et al. 2000. Population decline of the American eel: implications for research and management. Fisheries **25:** 7-16.

Jellyman DJ, BL Chisnall, ML Bonnett, JRE Sykes. 1999. Seasonal arrival patterns of juvenile freshwater eels (*Anguilla* spp.) in New Zealand. NZ J. Mar. Freshw. Res. **33:** 249-262.

Jellyman DJ, JRE Sykes. 2003. Diel and seasonal movements of ratio-tagged freshwater eels, *Anguilla* spp., in two New Zealand streams. Environ. Biol. Fishes **66:** 143-154.

Jessop BM, DK Cairns, I Thibault, WN Tzeng. 2008. Life history of American eel *Anguilla rostrata*: new insights from otolith microchemistry. Aquat. Biol. **1:** 205-216.

Jessop BM, JC Shiao, Y Iizuka, WN Tzeng. 2002. Migratory behaviour and habitat use by American eels *Anguilla rostrata* as revealed by otolith microchemistry. Mar. Ecol. Progr. Ser. **233:** 217-229.

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

Lin SH, CW Chang, Y Iizuka, WN Tzeng. 2007. Salinities, not diets, affect strontium/calcium ratios in otoliths of *Anguilla japonica*. J. Exp. Mar. Biol. Ecol. **341:** 254-263.

Lin YJ, WN Tzeng. 2008. Effects of shrimp net and cultured eels on the wild population of Japanese eel *Anguilla japonica* in Kao-Ping River, Taiwan. J. Fish. Soc. Taiwan **35:** 61-73.

Markou MT, P Kassomenos. 2010. Cluster analysis of five years of back trajectories arriving in Athens, Greece. Atmosph. Res. **98:** 438-457.

Pannella G. 1971. Fish otolith: daily growth layers and periodical patterns. Science **173:** 1124-1127.

Robinet T, E Feunteun. 2002. Sublethal effects of exposure to chemical compounds: a cause for the decline in Atlantic eels. Ecotoxicology **11:** 265-277.

Ryan PA. 1984. Diel and seasonal feeding activity of the shortfinned eel, *Anguilla australis schmidtii*, in Lake Ellesmere, Canterbury, New Zealand. Environ. Biol. Fishes **11:** 229-234.

Tesch FW. 1977. The eel. Biology and management of anguillid eels. London: Chapman and Hall.

Thibault I, JJ Dodson, F Caron, WN Tzeng, Y Iizuka, JC Shiao. 2007. Facultative catadromy in American eels: testing the conditional strategy hypothesis. Mar. Ecol. Progr. Ser.

344: 219-229.
Tsukamoto K. 1992. Discovery of the spawning area for Japanese eel. Nature **356:** 789-791.
Tsukamoto K. 2006. Spawning of eels near a seamount. Nature **439:** 929.
Tsukamoto K, T Arai. 2001. Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. Mar. Ecol. Progr. Ser. **220:** 265-276.
Tzeng WN. 1984. An estimate of the exploitation rate of *Anguilla japonica* elvers immigrating into the coastal waters off Shuang-Chi River, Taiwan. Bull. Inst. Zool. Acad. Sin. **23:** 173-180.
Tzeng WN. 1985. Immigration timing and activity rhythms of the eel, *Anguilla japonica*, elvers in the estuary of northern Taiwan, with emphasis on environmental influences. Bull. Jpn. Soc. Fish. Oceanogr. **47:** 11-28.
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. J. Exp. Mar. Biol. Ecol. **199:** 111-122.
Tzeng WN, KP Severin, H Wickström. 1997. Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Mar. Ecol. Progr. Ser. **149:** 73-81.
Tzeng WN, JC Shiao, Y Iizuka. 2002. Use of otolith Sr: Ca ratios to study the riverine migratory behaviours of Japanese eel *Anguilla japonica*. Mar. Ecol. Progr. Ser. **245:** 213-221.
Tzeng WN, CH Wang, H Wickström, M Reizenstein. 2000. Occurrence of the semi-catadromous European eel *Anguilla anguilla* (L.) in the Baltic Sea. Mar. Biol. **137:** 93-98.
Tzeng WN, HF Wu, H Wickström. 1994. Scanning electron microscopic analysis of annulus microstructure in otolith of European eel, *Anguilla anguilla*. J. Fish Biol. **45:** 479-492.