9 Freshwater Eels and Humans in Taiwan

Wann-Nian Tzeng

Freshwater eels (*Anguilla* spp.) are an important food resource and support large-scale aquaculture in some oriental countries. Taiwan's climate is ideal for eel stocks living in the wild and for aquaculture. Indeed, the country's aquaculture industry, which was initiated in the 1960s and peaked in the early 1990s, contributed greatly to Taiwan's economic development at the time, though much of that production has since been transferred to mainland China. Despite their economic importance to humans, however, many people are not that familiar with eels, so this chapter supplements material presented elsewhere in this book by documenting aspects of eel distribution and biology, mythology, cuisine, etc, in Taiwan.

Eel Species in Taiwan

Of 19 species or subspecies of freshwater eel known worldwide (Watanabe et al. 2009), five have been reported in Taiwan, the Japanese eel (*Anguilla japonica*), the giant mottled eel (*A. marmorata*), *A. bicolor pacifica*, *A. celebesensis* and *A. luzonensis*. All except the last of these have been reported for some time as living naturally in Taiwan (Tzeng 1982, 1983; Tzeng and Tabeta 1983; Han et al. 2001), but relatively recently, two new species were identified by molecular analysis, *A. luzonensis* in a river of northern Luzon, the Philippines (Watanabe et al. 2009) and *A. huangi* at an aquaculture farm in Taiwan to which glass eels had been brought from northern Luzon for aquaculture (Teng et al. 2009). Those two new species are, however, synonymous (Leander et al. 2012), so according to Article 23 of the International Code for Zoological Nomenclature, the first nomenclatural act or the first published name receives precedence. In the case of the two new species, the name *luzonensis* was published in March 2009 and *huangi* in November 2009, so the species name *luzonensis* has priority. Further, the identification of *A. celebesensis*, described by Tzeng (1982), was placed in doubt because of the similarity of its external morphology with that of *A. luzonensis*, but with the recent simultaneous identification of both species as separate by DNA analysis (Chang et al. 2012), the two species have been maintained. Accordingly, it is confirmed that five species of *Anguilla* are found in Taiwan.

The colour pattern is uniform in *A. japonica* and *A. bicolor pacifica* and marbled in *A. marmorata, A. celebesensis* and *A. luzonensis. A. marmorata* can grow to >170 cm total length (Fig. 9.1), but the more common *A. japonica* does not reach that length in the wild. *A. bicolor pacifica* is a short-finned eel, the other four are longfinned, *A. japonica* is classified as temperate, and the other four as tropical (Tesch 2003). The geographic distribution of the five species differs too, with *A. japonica* of the two more common species dominating the lower reaches of rivers and *A. marmorata* preferring deep pools in upper reaches (Shiao et al. 2003). The other three species are rare (Tzeng et al. 1995). Clearly, though, the eels in Taiwan, their morphology, behaviour and habitat use, and the environment they inhabit, are diverse.

The Japanese eel is the most abundant of the five species known in Taiwan. Its glass eels recruit naturally to Taiwanese estuaries during winter, from November to February, and have traditionally been fished during their upstream migration to be ongrown in aquaculture farms (Tzeng 1985). Daily growth increments in the otolith (the ear stone) have revealed that Japanese eel leptocephalus larvae take some 120–140 days to arrive at the estuaries of Taiwan, mainland China, Korea and Japan (Cheng and Tzeng 1996), after the adult eels have spawned during the new moon of May/June west of the Mariana Islands (Tsukamoto 1992), the leptocephali being transported by the North Equatorial Current (NEC) and the Kuroshio Current (see the Japanese chapter in this book for more detail). However, despite anguillid eels being

W.-N. Tzeng (✉)
Institute of Fisheries Science, National Taiwan University, Taipei 10617, Taiwan

Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung 20224, Taiwan
e-mail: wnt@ntu.edu.tw

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Fig. 9.1 Colour patterns of *A. japonica* (*top left*) and *A. marmorata* (*bottom left*). The latter can grow to >170 cm (*right*, from Williamson and Boëtius 1993)

classified generically as catadromous, proven too by analysis of strontium/calcium (Sr:Ca) ratios in the otolith (Tzeng et al. 2000, 2003; Tsukamoto and Arai 2001; Thibault et al. 2007), part of the Japanese eel population completes its whole life cycle in seawater or at least in very brackish water.

The recent decline in the population of wild Japanese eels has resulted in there being an insufficient supply of glass eels for aquaculture in Taiwan and elsewhere. The reason for the decline is not absolutely clear, but as speculated elsewhere in this book and for other species of eel too, it may be related *inter alia* to overfishing, habitat degradation and/or global climate change (see below). Whatever the cause of the decline, though, and in an attempt to stimulate recovery of Japanese eels in the wild and concomitantly to increase glass eel production for aquaculture, the Taiwanese government ordered the release of hormone-induced mature eels (silver eels) into the open ocean from 1976 to 2002. Since the millennium, however, that programme has shifted its focus to releasing young eels into rivers.

In addition to the five species of eel found naturally in Taiwan, some exotic species of anguillid eel have also been found in the wild. Succinctly, faced with a reducing inflow of Japanese glass eels and a heavy demand for glass eels generally for aquaculture in the country, glass eels of non-endemic species such as the American eel *A. rostrata* were introduced from North America; some escaped from the aquaculture ponds into the wild and have since been caught occasionally during their spawning migration as adults (Han et al. 2002; Tzeng et al. 2009). Additionally, the Australian speckled longfin eel *A. reinhardtii* has been caught in Sun-Moon Lake in central Taiwan, having originally been imported from Australia for cuisine purposes because of its similarity to the *A. marmorata* eaten preferentially by Taiwanese (Chang et al. 2008).

Glass Eels

The species composition of glass eels differs between the eastern and the western coasts of Taiwan (Fig. 9.2). In the Hsiukuluan River estuary of eastern Taiwan (*A. marmorata* glass eels dominate to the tune of 97.1 % of the total catch and the other three species are scarce: *A. bicolor pacifica* (1.17 %), *A. japonica* (0.5 %), *A. luzonensis* (1.2 %). In contrast, *A. japonica* glass eels dominate along the northwestern coast of Taiwan, making up 81.0 % of the total glass eel catch, with *A. marmorata* (17.8 %), *A. bicolor pacifica* (1.0 %) and *A. luzonensis* (0.2 %) less or much less abundant. In the Donkang River estuary of southwestern Taiwan, the proportional representation by species of glass eel is between these two extremes: *A. marmorata* is most abundant (64.9 %), followed by *A. japonica* (29.7 %), *A. bicolor pacifica* (4.7 %) and *A. luzonensis* (0.7 %). The differences in geographic distribution and abundance among species around Taiwan are attributable to the spawning site of origin as well as the habitat (tropical or temperate) and the ocean currents around the island (warm Kuroshio Current or cold China Coastal Current) that transport the eel larvae in towards the coasts (Cheng and Tzeng 1996; Han et al. 2012; Leander et al. 2012).

Long-term catch data (1972–2011) have indicated a significant decadal change in peak catches of Japanese glass eels coinciding with solar activity reflected in an 11.2 year periodic change in sunspot number (Fig. 9.3a; Tzeng et al. 2012a). The catch of glass eels seems to increase with a concomitant increase in the number of sunspots, and although the cause–effect relationship between glass eel numbers and sunspots is not a direct one, the climate change index WPO (Western Pacific Oscillation) that influences

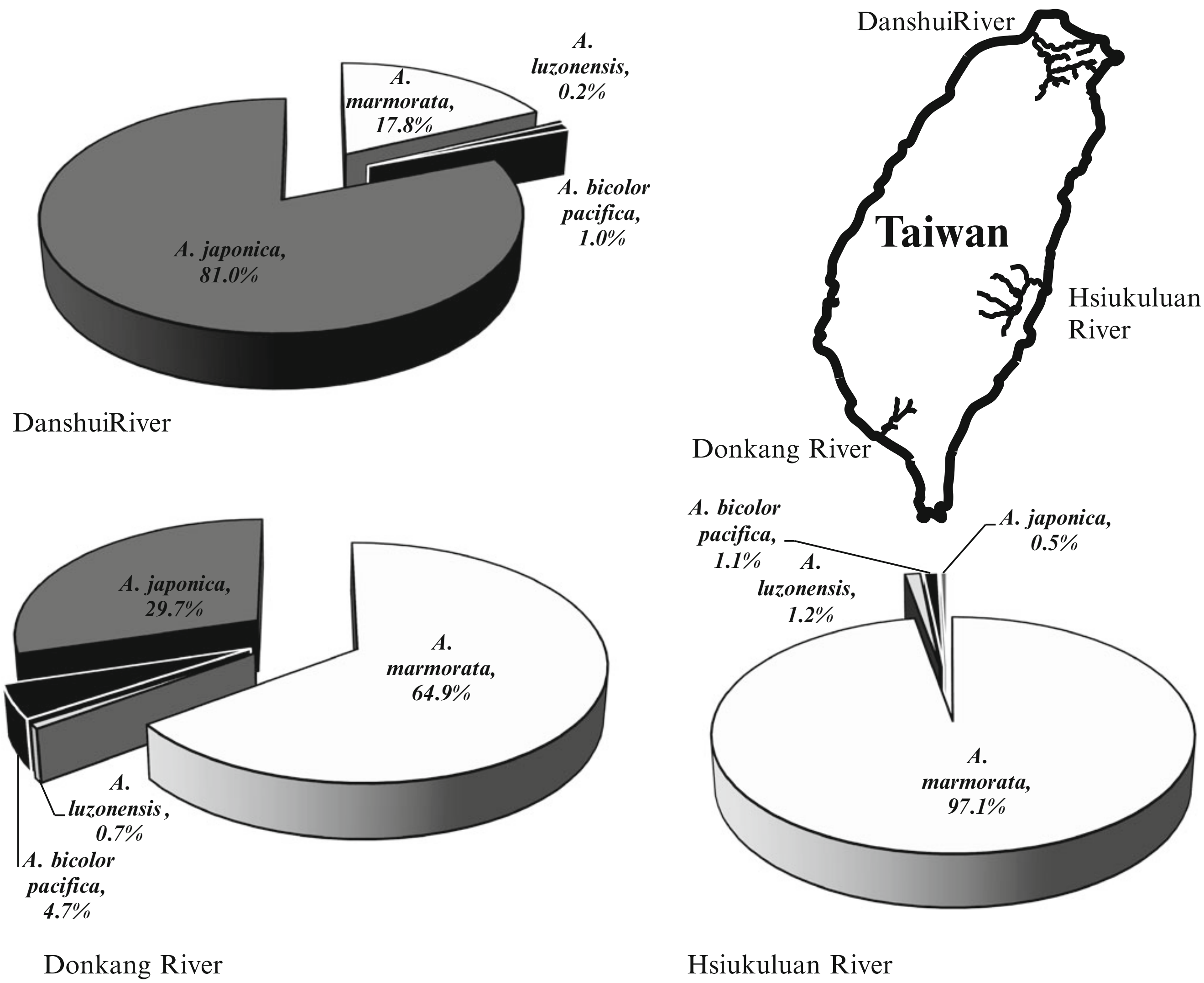

Fig. 9.2 Species compositions of glass eels caught in the Hsiukulan River estuary of eastern Taiwan ($n = 3{,}035$), the Tanshui River estuary of northwestern Taiwan ($n = 2{,}583$) and the Donkang River estuary of southwestern Taiwan ($n = 148$; Y-S. Han, unpublished data)

the two currents (NEC and Kuroshio) that transport eel larvae from the spawning grounds to the coasts and subsequently affects the Taiwanese glass eel catch is clearly a link (Tzeng et al. 2012a). After peaking in 1979, the Taiwanese glass eel catch gradually declined to a lower peak in 2001, since when it declined further until the most recent lower peak in 2011, mirroring similar decreases in the population size of the Japanese, American and European eels (Fig. 9.3b). All this is taken as evidence that fluctuations in the catches of glass eels in Taiwan reflect not only the overall population size of *A. japonica* but also ocean–atmosphere interactions exemplified by the climate change indices of sunspots and WPO.

Fishing for Eels in Taiwan

The types of fishery and fishing gear are diverse and reasonably unique to Taiwan. Both traditional and modern types of gear are deployed (Fig. 9.4). To catch inwardly migrating glass eels, *dipnets* with lights are used during flood tides at night by fishers standing on river banks or small fishing boats (Fig. 9.4a). Apparently, newly recruiting glass eels (Stages V_A and V_B) are relatively inactive and can be caught more easily than the pigmented stages (Stages VI_A or older) that have already adapted to an estuarine environment (Tzeng 1985). Also to catch glass eels, *handnets* are hauled through coastal waters near estuaries, held open by a stainless steel

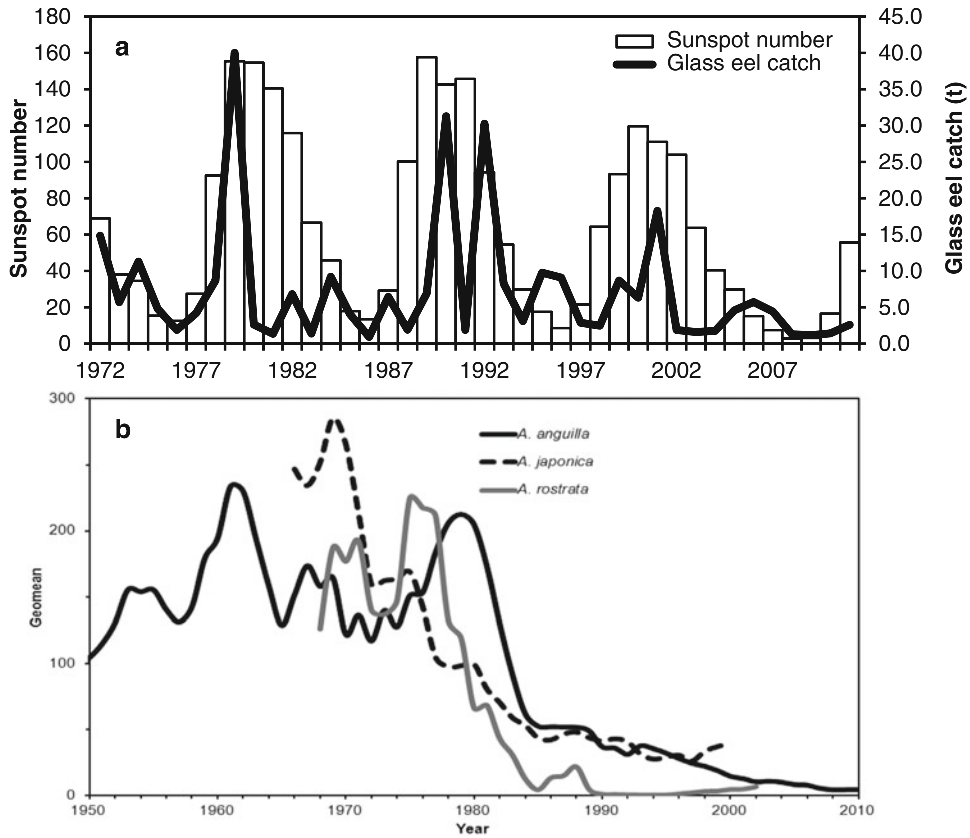

Fig. 9.3 (**a**) Annual trend in the Taiwanese catch of glass eels overlying a plot of the number of sunspots, 1972–2011. (**b**) Recruitment (3-year running averages of geomeans of indices as % 1979–1994 means) of glass European (*A. anguilla*), American (*A. rostrata*) and Japanese (*A. japonica*) eels (B. Knights, unpublished data). Note that the data for American eel are derived from yellow eels trapped at the Moses–Saunders Dam (St Lawrence River, Canada) and that the *plotted line* allows for the estimated 7-year lag between recruitment as glass eels and capture as yellow eels

frame (Fig. 9.4b) or by floaters and sinkers (Fig. 9.4c), and *triangular nets* (Fig. 9.4d) are operated by fishers pushing them against the current in estuaries and along nearby coasts. Finally, glass eels are captured by nets set across estuaries during flood tides at night (Fig. 9.4e), and because many such *setnets* are often laid out together at river mouths, boat passage can be impeded.

To catch adult eels, other types of gear are used. *Bamboo eel tubes* (Fig. 9.4f) have a long history of use, being designed before World War II and commonly used in the Nantou Prefecture, an area in central Taiwan well known for its bamboo production. The fishing gear is designed with a hole at one end of the bamboo into which the water flows to spread the smell of the bait (usually an earthworm) used to lure an eel into the funnel-shaped entrance at the other end. Recently, an alternative to bamboo in the form of a *PVC eel tube* has become more common; it is light and convenient to use, and one end of the tube is covered with a net while the other is left open. Unlike the bamboo tube, the *PVC* eel tube does not require bait, simply providing a ready-made shelter for the eel, and is set in both upper and lower reaches of rivers and in estuaries. Another means of catching adult eels uses the *shrimpnets* originally designed to catch river prawns but taking eels as a bycatch; eels are now targeted, however, and are caught in the nets when they enter in search of the prawns as food (Fig. 9.4g). The net is made of light nylon and contains several smaller units, each with a funnel-like opening that stops the eels inside from escaping. It is a highly effective means of catching adult eels and is moved around rivers easily by a small boat. Finally, *electrofishing* for eels in Taiwan used to be very popular (Fig. 9.4h) largely because it was a method that could be used irrespective of water currents, but it is now illegal in the country.

Eel Life History Determined from the Otolith

Although huge strides in knowledge have been made over the past few decades, the early life history of the Japanese eel while the leptocephali are being carried in the NEC and the Kuroshio Current from the spawning ground west of the Mariana Islands to estuaries along the coasts of East Asia is

Fig. 9.4 A montage of the various fishing gears used to catch eels in Taiwan: for glass eels in estuaries, (**a**) dipnet, (**b**) handnet with a stainless steel frame, (**c**) handnet with sinkers and floaters, (**d**) triangular net, (**e**) setnets; for yellow and silver eels in rivers, (**f**) bamboo eel tube (B, bottom; E, entrance), (**g**) shrimpnet, (**h**) electrofishing

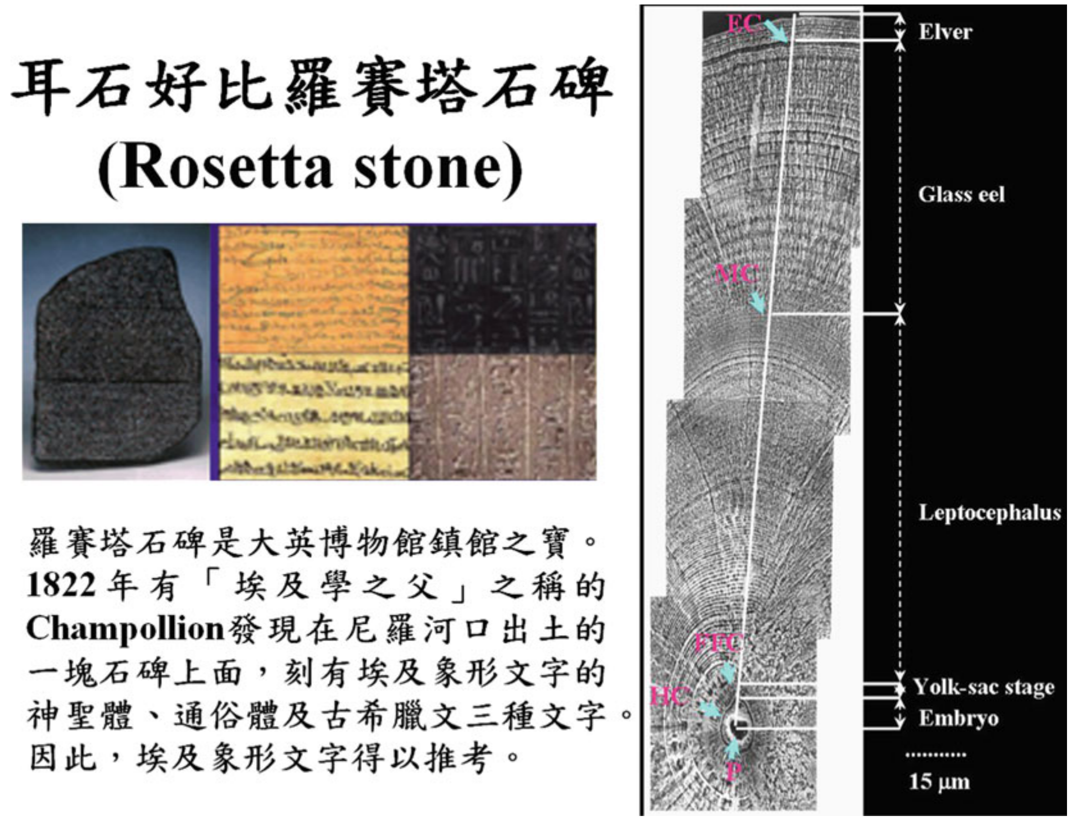

Fig. 9.5 Comparison of the archaeological records of ancient Egyptians displayed on the Rosetta stone (*left*) with records of the life history events of a young eel displayed in its otolith (*right*)

not yet fully understood. Some migratory life history information recorded in the otolith can be decoded through analyses of microstructure (Fig. 9.5). A fish otolith records life history events in a manner analogous to the Rosetta Stone (a well-known archaeological artefact currently housed at the British Museum in London, which has been used to unlock the mysteries of the hieroglyphs of ancient Egyptians).

An otolith is a biomineralized crystal of calcium carbonate ($CaCO_3$), functioning as an aid to hearing and balance in teleost (bony) fish, within which group eels are found. It acts as a time-keeper by depositing an annulus and daily growth increments (DGIs; Fig. 9.6) that allow one to determine the age of the fish in the form of annual zones and daily rings. A DGI is an unique structure, deposited in a circadian rhythm and allowing back-calculation of the birthdate and daily life of a fish by reading the rings (Tzeng 1990), so is regarded as a diary of the activities of a fish (Pannella 1971). An otolith is very like a CD-Rom, because the life history information of an eel recorded in its otolith can be retrieved in a manner similar to how one extracts data from a CD with a computer (Fig. 9.7). From DGIs identified in a scanning electron microscopic image of an otolith of a Japanese eel leptocephalus collected east of the Philippines (Fig. 9.8), it was discovered that the eel had been spawned during a new moon period (Liao et al. 1996), similar to that of the eel leptocephalus

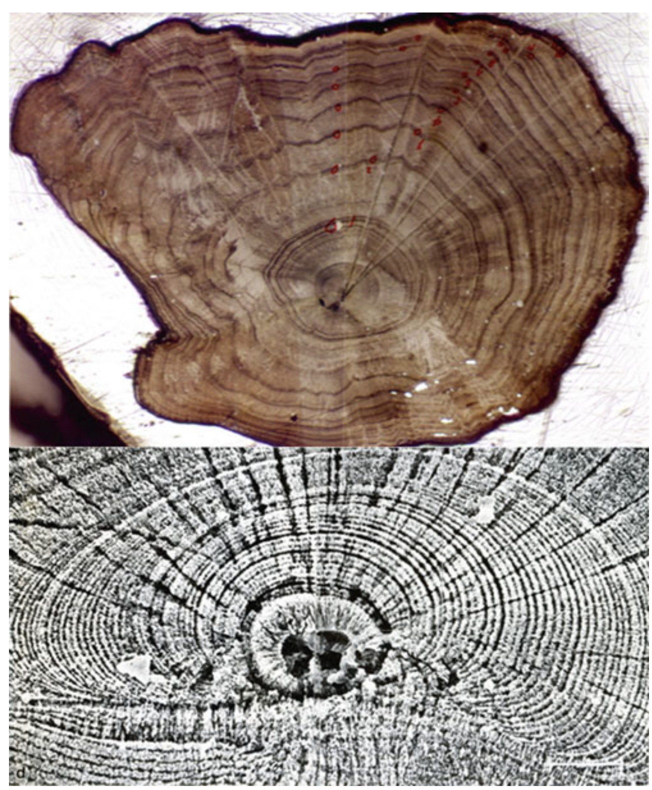

Fig. 9.6 *Top:* Annuli and *Bottom:* daily growth increments (DGIs) in otoliths of a Japanese eel

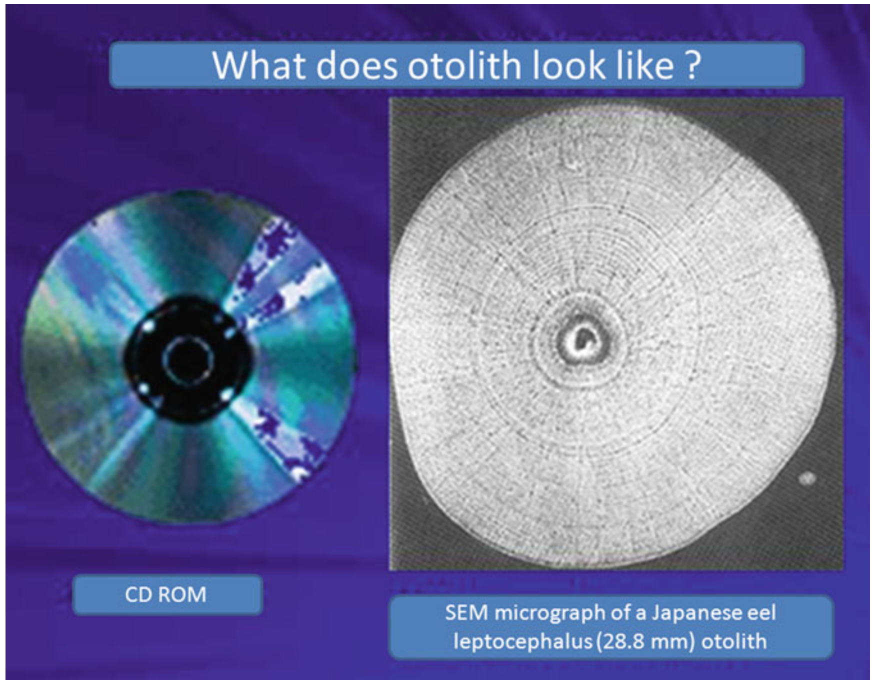

Fig. 9.7 A CD-Rom (*left*) and daily growth increments on a section of a sagittal otolith of a Japanese eel leptocephalus (*right*)

Fig. 9.8 At around 21:00 local time on 22 August 1995 at 12°30′N 131°30′E, Taiwanese researchers caught their first Japanese eel leptocephalus (27.40 mm total length) using an Isaacs–Kidd midwater trawl at a depth of 250 m

found at the Mariana Islands (Tsukamoto et al. 2003). It is from DGIs too that it was discovered that Japanese eel larvae take about 6 months to move passively with the NEC and Kuroshio Current over the ~5,000 km from the spawning grounds at the Mariana Islands to the estuaries of East Asia (Cheng and Tzeng 1996).

The otolith also records environmental information; its chemical composition is influenced by the ambient environment through which the fish passes during its migration or passive drift (Tzeng and Tsai 1994; Tzeng 1996). The otolith is inert, so once a trace element has been incorporated into its structure it will remain there for the life of the fish (Campana 1999), allowing one to reconstruct the past environmental history of an eel, for instance. That is the source of the recent discovery (mentioned above) that some Japanese eels spend their whole life in seawater; there are three types of residence determinable from temporal change in the Sr:Ca ratio in otoliths, seawater contingent, freshwater contingent and estuarine contingent (Fig. 9.9; Tzeng et al. 2002, 2003). In other words, part of the eel population can skip its freshwater phase (seawater contingent eels). Similar behaviour has since been found for the European eel (Tzeng et al. 1997, 2000; Daverat et al. 2006; Shiao et al. 2006) and the American eel (Jessop et al. 2006; Thibault et al. 2007; Lamson et al. 2009), and it is therefore likely that such facultative migratory behaviour is advantageous to a fish adapting over time to a changing natural environment.

Evolution of the Eel Aquaculture Industry in Taiwan

The development of Taiwan's aquaculture industry for *A. japonica* can be divided into seven stages (Fig. 9.10; Hsue 2012). Most culture is carried out outdoors (Fig. 9.11). It started in 1952, initially at a small scale, but from 1970, production increased rapidly and peaked at about 55,000 t with a value of ~NT$15 billion (equivalent to US$518 million at the 2012 exchange rate) in the early 1990s. Of the total production of Japanese eels in Taiwan then, ~90 % was exported to Japan and the other 10 % consumed locally. However, annual production in Taiwan then dropped dramatically, to <20,000 t

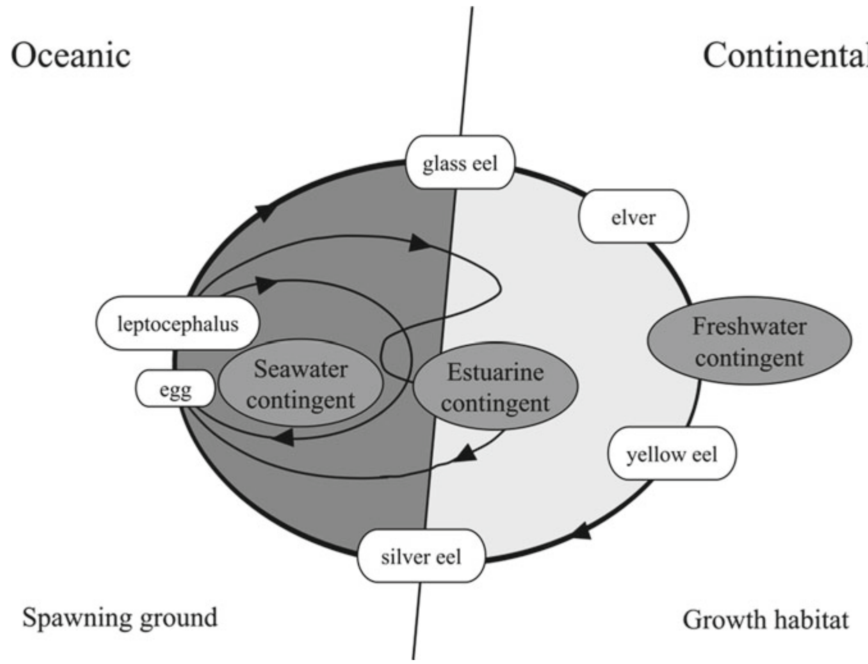

Fig. 9.9 The life history of freshwater eels displayed showing the three migratory patterns possible, freshwater contingent, estuarine contingent and seawater contingent

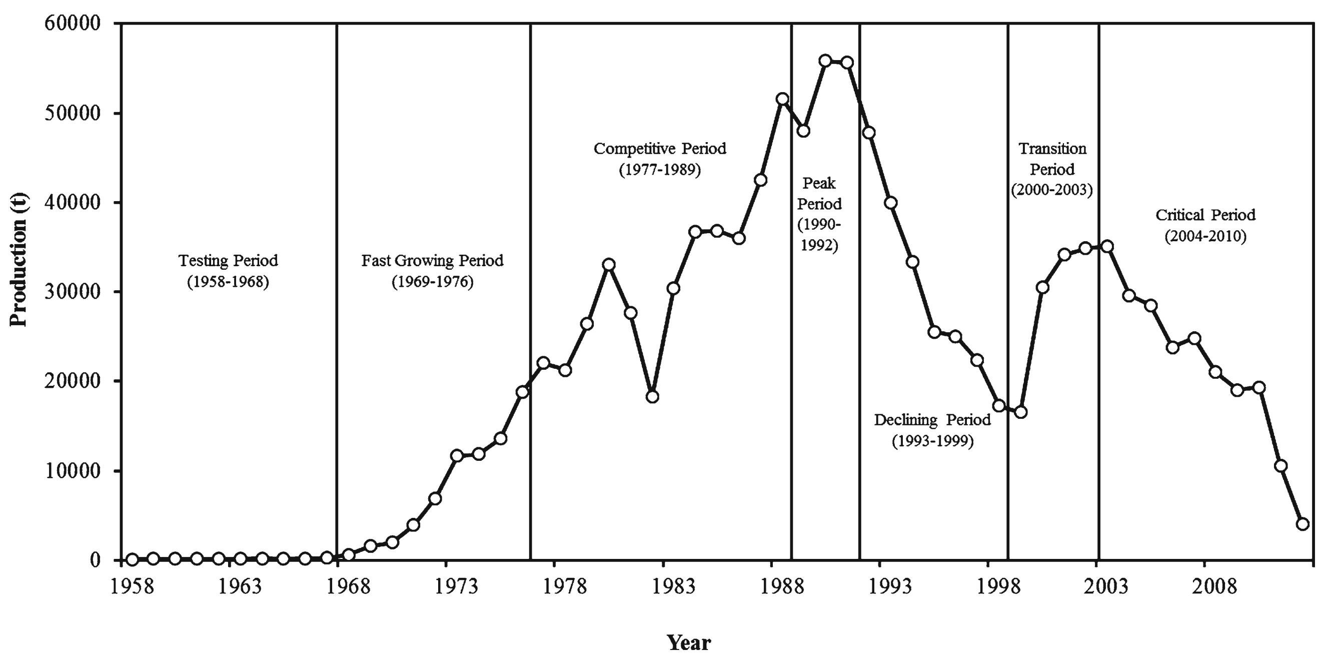

Fig. 9.10 Aquaculture production of Japanese eels in Taiwan, 1958–2012, showing the seven phases mentioned in text (updated from Hsue 2012)

by 1999, almost certainly influenced by the reduction in imports of glass eels from China that resulted from the rise of eel aquaculture there for export to Japan following China's economic revolution in 1980. The annual aquaculture production of eels in mainland China was ~165,000 t in 1999, of which ~95,000 t was exported to Japan, so mainland China over time clearly replaced Taiwan as the source of material destined for consumption in Japan. With land and labour costs cheaper in China than in Taiwan, it was obviously economically beneficial for Taiwanese eel farmers to relocate their businesses to mainland China. Taiwanese eel production did rise again slightly, concomitant with increasing catches of glass eels, between 2000 and 2003, but it thereafter decreased again to an annual value of <10,000 t (Fig. 9.10).

Fig. 9.11 Outdoor aquaculture of Japanese eels in Taiwan: (**a**) a water wheel used to increase the dissolved oxygen; (**b**) artificial feed being provided in a cage; (**c**) eels competing for food

On average, China and Japan account for ~80 % of the glass eel catches by Asian countries and Taiwan and Korea the remaining ~20 %. The annual catches of glass eels by all Asian countries combined have varied over the years, but Taiwan's catch peaked in the 1970s before gradually decreasing to its very low level today (Fig. 9.3a). Some 50–75 % of the glass eels taken in Taiwan are harvested before upstream migration (Tzeng 1984), but the catch has traditionally been much less than the demand, so imports from other countries have been part of the eel aquaculture industry since it burgeoned in the 1960s and 1970s. Overall, the relatively limited local catch and increased competition among producers of glass eels for the increasingly expensive (local and imported) raw material has been behind the general reduction in eel aquaculture in Taiwan over the past two decades. Eel aquaculture contributed greatly not only to Taiwan's national economic development, but also notably to the development of local fishing villages. However, it did have some negative environmental consequences: the overextraction of underground freshwater for eel aquaculture caused widespread land subsidence, and the use of seawater for aquaculture raised the salinity of the soil in some adjacent rice fields. Such adverse effects have been less evident since the late 1990s, though, the area under aquaculture now being less, by recycling water, and by the use of surplus ponds for rainwater collection and storage.

Taiwanese Conservation and Restocking Programmes

In an attempt to supplement the production of Japanese eel eggs and larvae in the wild and thence hopefully to stimulate the recruitment of glass eels to Taiwanese estuaries for aquaculture as well as to promote a sustainable fishery for adult eels, the Taiwan Fisheries Research Institute (TFRI) released hormone-induced eel spawners into the Shiau-Liu-Chio Trench (120°20′–36′E 22°15′–30′N) off the country's southwestern coast. Between 1976 and 2001, a total of 29,921 adult eels weighing >50 t was released during 23 cruises made to the trench between October and March each year (mostly during December). The trench was thought at that time to be the spawning ground for the Taiwanese population of Japanese eels (Kuo 1971; Kimura et al. 1999). However, the Japanese eel is now known to be a panmictic population (Han et al. 2010), and its only known spawning ground is in waters west of the Mariana Islands (142°E 14°N; Tsukamoto 1992). It is unknown whether those releases of adult eels had any positive effect on the population, and in May/June of 1999–2001, three additional TFRI cruises were made to the now-known spawning site, releasing another 1,500 hormone-induced spawners weighing >2 t. To date, it has proven impossible to evaluate the effect of this release programme on the recruitment of Japanese glass eels to Taiwan, and the fate of individual eels remains unknown. Certainly, however, there is no significant relationship between the annual numbers of spawners released at sea between 1976 and 2001 and the annual catches of glass eels in Taiwan (Tzeng et al. 2012b).

In the early 2000s, following criticism by the international scientific community that such a release programme in the open ocean might induce genetic pollution, the programme was stopped, and since 2003, the TFRI has restocked freshwater streams only. During the months July–November of 2003–2008, 35,636 young eels weighing >76 t were released into three of Taiwan's main rivers, one each in the northwest, the northeast and the southwest. These young eels have been relatively easy to monitor, and mark–recapture data have been collected to evaluate the effects of the restocking programme on exploitation status and to collect information and parameters important in furthering understanding of the species' population dynamics and migratory behaviour. Following analysis using a standard yield-per-recruit model, it was evident that growth-overfishing was taking place in Kao-Ping River in southwestern Taiwan, i.e. too many small eels were being caught before optimal growth had been attained. A spawner-per-recruit model demonstrated recruit-overfishing too, i.e. insufficient silver eels escaping from the river back to sea to spawn (Lin et al. 2009, 2010; Lin and Tzeng 2010; Tzeng 2012).

Eel Cuisine in Taiwan

More than half of Taiwan's production of Japanese eels is converted into "kabayaki" and "shirayaki" for export to Japan (Fig. 9.12a, b). Japanese people generally celebrate "Ushinohi" in July by consuming eels. In Taiwan, however, dishes of eel meat, which are high in energy because of the fat content, are enjoyed by locals throughout winter, particularly on the day of the winter solstice (21 or 22 December), to keep the body warm; although the country is classified as subtropical, Taiwanese winters can be very cold.

To accommodate local consumption, a diversity of eel dishes has developed over the years. Taiwanese people generally prefer the giant mottled eel over the Japanese eel as food, but the former species was listed as endangered from 1989 to 2009 and its culture, sale and fishing banned. Recently, however, the ban has been lifted and the giant mottled eel has again become a popular food and is listed on the menus of many of the popular restaurants on the island (Fig. 9.12c–f).

Arts and Mythology

The eel is an important religious icon in Taiwanese folklore. The Japanese eel and the giant mottled eel are regarded, respectively, as river and sea gods, and this can be seen in the design and paintings of gate god statues commonly placed at the entrance to traditional Taiwanese village dwellings. Many villagers believe that the gate gods protect them against the devil and evil spirits, and protect the security of their family (Fig. 9.13a). Additionally, eels appear in the design of "ong-bao" (Fig. 9.13b), the red bags containing money that parents give children to seek good fortune during the Chinese Lunar New Year. Eels are important also for Taiwanese native (aboriginal) peoples, but those people do not kill and eat the eels because they believe that they are the embodiment of celestial beings.

The eel is also considered to be a propitious creature in Taiwan (and elsewhere), and this can be seen from its depiction on things used commonly in daily life, such as necktie pins, company logos and souvenirs (Fig. 9.14).

The Future of Eels in Taiwan

Both the fishery and aquaculture of Japanese eels in Taiwan have a long history, contributing greatly to local economic development, and eel dishes have been developed to satisfy the needs of people in their daily lives. However, the natural population of Japanese eels has decreased dramatically over the past three decades, similar to the situation with the American eel and the European eel, and the catch of glass eels has decreased to a level much lower than that needed to meet aquaculture demand. To sustain eel aquaculture into the future, therefore, it is essential that enhanced effort be put into developing the means of artificially propagating the seed eels for aquaculture (see the Japanese and Danish chapters for

Fig. 9.12 Some examples of cuisine offered in Taiwanese restaurants: (**a**) kabayaki, (**b**) shirayaki, (**c**) fried eel, (**d**) eel prepared in a casserole with ginger, basil and wine, (**e**) eel boiled with Chinese herbal medicine, (**f**) shabu-shabu (**a** and **b**, Japanese eel; **c**–**f**, Giant mottled eel). Photographs reproduced with permission (**a** and **b**) Just Champion Enterprise Co. Ltd, (**c**–**e**) Ji-Peng Chen/Super Utmost, (**f**) Jun-Ren Chen

information on progress to date), to preclude overfishing glass eels in east Asia and elsewhere. In addition, it is crucial that the fisheries for yellow and silver eels in rivers be better regulated and that anthropogenic effects on the habitats of eels be minimized if any recovery of wild eel stocks is to materialize in future.

Finally, although it is abundantly clear that eels are hugely important to the people of Taiwan, as they are in much of the rest of East Asia, serious collaborative research and development efforts and definitive management are needed if eel populations are to be preserved for the benefit of future generations of humankind.

a

b

Fig. 9.13 (**a**) Gate gods depicting *A. japonica* (*left*) and *A. marmorata* (*right*), and (**b**) red bags with A. *marmorata* (*left*) and *A. japonica* (*right*) shown as symbols of good fortune for Chinese New Year celebrations. Reproduced with permission (**a**) De-Hong Shih/Super Utmost and (**b**) You-Sen Wang/Super Utmost

Fig. 9.14 A gold-plated necktie pin depicting a Japanese eel (*top left*), the logo of an eel marketing company in Northern Ireland (*bottom left*), and a commemorative mug with an eel design presented to the author on his retirement (*right*)

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References

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188: 263–297

Chang S-T, Yeh M-F, Chen R-T, Tsai C-L, Shen K-N, Tsai C-F (2008) A giant exotic speckled longfin eel (*Anguilla reinhardtii* Steindachner, 1867) captured from the Sun Moon Lake. Endem Species Res (Taipei) 10(2):59–64

Chang K-C, Huang Y-S, Liu F-K (2012) How many *Anguilla* species in the Taiwan waters? In: Proceedings of the 15th East Asia eel resource consortium, National Taiwan Ocean University, Keelung, Taiwan, p 35

Cheng P-W, Tzeng W-N (1996) Timing of metamorphosis and estuarine arrival across the dispersal range of the Japanese eel *Anguilla japonica*. Mar Ecol Prog Ser 131:87–96

Daverat F, Limburg KE, Thibault I, Shiao J-C, Dodson JJ, Caron F, Tzeng W-N et al (2006) Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. Mar Ecol Prog Ser 308:231–241

Han Y-S, Chang C-W, He J-T, Tzeng W-N (2001) Validation of the short-finned eel *Anguilla bicolor pacifica* in natural waters of Taiwan. Acta Zool Taiwanica 12:9–19

Han Y-S, Yu C-H, Yu H-T, Chang C-W, Liao I-C, Tzeng W-N (2002) The exotic American eel in Taiwan: ecological implications. J Fish Biol 60:1608–1612

Han Y-S, Hung C-L, Liao Y-F, Tzeng W-N (2010) Population genetic structure of the Japanese eel *Anguilla japonica*: panmixia at spatial and temporal scales. Mar Ecol Prog Ser 401:221–232

Han Y-S, Zhang H, Tseng Y-H, Shen M-L (2012) Larval Japanese eel (*Anguilla japonica*) as sub-surface current bio-tracers in East Asia continental shelf. Fish Oceanogr 21:281–290

Hsue W-C (2012) Cost and benefit analysis of *Anguilla japonica* and *A. marmorata* aquaculture in Taiwan. Master thesis, Institute of Fisheries Science, College of Life Science, National Taiwan University

Jessop BM, Shiao J-C, Iizuka Y, Tzeng W-N (2006) Migration of juvenile American eels *Anguilla rostrata* between freshwater and estuary, as revealed by otolith microchemistry. Mar Ecol Prog Ser 310:219–233

Kimura S, Döös K, Coward AC (1999) Numerical simulation to resolve the issue of downstream migration of the Japanese eel. Mar Ecol Prog Ser 186:303–306

Kuo H (1971) Approach of eel elvers to the land in Taiwan. Fish Cult 8:52–56 (in Japanese)

Lamson HM, Cairns DK, Shiao J-C, Iizuka Y, Tzeng W-N (2009) American eel, *Anguilla rostrata*, growth in fresh and salt water:

implications for conservation and aquaculture. Fish Manag Ecol 16:306–314
Leander NJ, Shen K-N, Chen R-T, Tzeng W-N (2012) Species composition and seasonal occurrence of recruiting glass eels (*Anguilla* spp.) in the Hsiukuluan River, eastern Taiwan. Zool Stud 51: 59–71
Liao I-C, Kuo C-L, Tzeng W-N, Hwang S-T, Wu C-L, Wang C-H, Wang Y-T (1996) The first time of leptocephali of Japanese eel *Anguilla japonica* collected by Taiwanese researchers. J Taiwan Fish Res 4(2):107–116
Lin Y-J, Tzeng W-N (2010) Vital population statistics based on length frequency analysis of the exploited Japanese eel (*Anguilla japonica*) stock in the Kao-Ping River, southern Taiwan. J Appl Ichthyol 26:424–431
Lin S-H, Chang S-L, Iizuka Y, Chen T-I, Liu F-G, Su M-S, Su W-C (2009) Use of mark-recapture and otolith microchemistry on the study of the migratory behavior and habitat use of Japanese eels (*Anguilla japonica*). J Taiwan Fish Res 17(2):47–65
Lin Y-J, Chang Y-J, Sun C-L, Tzeng W-N (2010) Evaluation of the Japanese eel fishery in the lower reaches of the Kao-Ping River, southwestern Taiwan using a per-recruit analysis. Fish Res 106:329–336
Pannella G (1971) Fish otoliths: daily growth layers and periodical patterns. Science 173:1124–1127
Shiao J-C, Iizuka Y, Chang C-W, Tzeng W-N (2003) Disparities in habitat use and migratory behavior between tropical eel *Anguilla marmorata* and temperate eel *A. japonica* in four Taiwanese rivers. Mar Ecol Prog Ser 261:233–242
Shiao J-C, Ložys L, Iizuka Y, Tzeng W-N (2006) Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. J Fish Biol 69:749–769
Teng H-Y, Lin Y-S, Tzeng C-S (2009) A new *Anguilla* species and a reanalysis of the phylogeny of freshwater eels. Zool Stud 48: 808–822
Tesch F-W (2003) The eel, 5th edn. Blackwell Publishing, Oxford, 408 pp
Thibault I, Dodson JJ, Caron F, Tzeng W-N, Iizuka Y, Shiao J-C (2007) Facultative catadromy in American eels: testing the conditional strategy hypothesis. Mar Ecol Prog Ser 344:219–229
Tsukamoto K (1992) Discovery of the spawning area for Japanese eel. Nature 356:789–791
Tsukamoto K, Arai T (2001) Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. Mar Ecol Prog Ser 220:265–276
Tsukamoto K, Otake T, Mochioka N, Lee T-W, Fricke H, Inagaki T, Aoyama J et al (2003) Seamounts, new moon and eel spawning: the search for the spawning site of the Japanese eel. Environ Biol Fishes 66:221–229
Tzeng W-N (1982) Newly record of the elver, *Anguilla celebesensis* Kaup, from Taiwan. Chin Biosci (Taipei) 19:57–66 (in Chinese with English abstract)
Tzeng W-N (1983) Species identification and commercial catch of the anguillid elvers from Taiwan. China Fish Mon 366:16–23 (in Chinese with English abstract)
Tzeng W-N (1984) An estimate of the exploitation rate of *Anguilla japonica* elvers immigrating into the coastal waters off Shuang-Chi River, Taiwan. Bull Inst Zool, Academia Sinica 23:173–180
Tzeng W-N (1985) Immigration timing and activity rhythms of the eel, *Anguilla japonica*, elvers in the estuary of northern Taiwan, with emphasis on environmental influences. Bull Jap Soc Fish Oceanogr 47(48):11–28
Tzeng W-N (1990) Relationship between growth rate and age at recruitment of *Anguilla japonica* elvers in a Taiwan estuary as inferred from otolith growth increments. Mar Biol 107:75–81
Tzeng W-N (1996) Effects of salinity and ontogenetic movements on strontium: calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica* Temminck and Schlegel. J Exp Mar Biol Ecol 199:111–122
Tzeng W-N (2012) A review of the population structure, life history strategy, and sustainable fishery of the Japanese eel *Anguilla japonica* in Taiwan. J Fish Soc Taiwan 38(1):1–19
Tzeng W-N, Tabeta O (1983) First record of the short-finned eel *Anguilla bicolor pacifica* elvers from Taiwan. Bull Jap Soc Scientific Fish 49:27–32
Tzeng W-N, Tsai Y-C (1994) Changes in otolith microchemistry of the Japanese eel, *Anguilla japonica*, during its migration from the ocean to the rivers of Taiwan. J Fish Biol 45:671–683
Tzeng W-N, Cheng P-W, Lin F-Y (1995) Relative abundance, sex ratio and population structure of the Japanese eel *Anguilla japonica* in the Tanshui River system of northern Taiwan. J Fish Biol 46:183–200
Tzeng WN, Severin KP, Wickström H (1997) Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Mar Ecol Prog Ser 149:73–81
Tzeng WN, Wang CH, Wickström H, Reizenstein M (2000) Occurrence of the semi-catadromous European eel *Anguilla anguilla* (L.) in the Baltic Sea. Mar Biol 137:93–98
Tzeng WN, Shiao JC, Iizuka Y (2002) Use of otolith Sr:Ca ratios to study the riverine migratory behaviours of Japanese eel *Anguilla japonica*. Mar Ecol Prog Ser 245:213–221
Tzeng W-N, Iizuka Y, Shiao J-C, Yamada Y, Oka HP (2003) Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*). Aquaculture 216:77–86
Tzeng W-N, Han Y-S, Jessop BM (2009) Growth and habitat residence history of migratory silver American eel transplanted to Taiwan. Am Fish Soc Symp 58:137–147
Tzeng W-N, Han Y-S, Tsukamoto K, Kuroki M (eds) (2012a) Story of eel. Lanyang Museum, Taiwan, 232 pp (in Chinese)
Tzeng W-N, Tseng Y-H, Han Y-S, Hsu C-C, Chang C-W, Di Lorenzo E, Hsieh C-H (2012b) Evaluation of multi-scale climate effects on annual recruitment levels of the Japanese eel, *Anguilla japonica*, to Taiwan. PLoS One 7(2):e30805. doi:10.1371/ journal.pone.0030805
Watanabe S, Aoyama J, Tsukamoto K (2009) A new species of freshwater eel *Anguilla luzonensis* (Teleostei: Anguillidae) from Luzon Island of the Philippines. Fish Sci 75:387–392
Williamson GR, Boëtius J (1993) The eels *Anguilla marmorata* and *A. japonica* in the Pearl River, China, and Hong Kong. Asian Fish Sci 6:129–138