

Modern Research on the Natural Life History of the Japanese Eel *Anguilla japonica*

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ABSTRACT

Life history studies on freshwater eels (*Anguilla* spp.) date approximately from 1920s. Due to the wide application of new otolith microchemistry and DNA techniques, the knowledge on the life history and ecology of the eel has remarkably increased in the last 15 years. This paper briefly reviews recent findings of the natural life history of the Japanese eel *Anguilla japonica*, particularly speciation and evolutionary processes, discovery of the spawning ground, DNA microsatellite analysis of population structure, the relationship between sex ratio and population density, and otolith research and its application to migratory environmental history of the species. Recently, populations of Japanese, American and European eels have dramatically decreased, which may relate to overfishing, habitat degradation and global climate change, but the reason for decline is uncertain. Knowledge of life history traits of the eel is essential for effective management and conservation.

Key words: *Anguilla japonica*, Speciation and Evolution, Spawning Ground, Otolith Microchemistry, Life History, Population Structure, Population Decline.

INTRODUCTION

The Japanese eel, *Anguilla japonica* Temminck and Schlegel, is a catadromous fish (Ege, 1939). It spawns in the tropical Pacific Ocean west of the Mariana Islands (Tsukamoto, 1992; Liao *et al.*, 1996). After hatching the leptocephali are transported by the North Equatorial Current and Kuroshio Current from the spawning ground to the continental shelves of Taiwan, China, Korea, and Japan. They metamorphose into glass eels in coastal waters and become pigmented elvers in estuaries (Ege, 1939). The elvers become yellow eels in rivers where they may live for 5-8 years until maturation (Tzeng *et al.*, 2000a). At the onset of maturation, the yellow eels metamorphose into silver eels and migrate back to the spawning area to

spawn and die (Tesch, 1977).

Japanese eel is an important aquaculture species in the Asian countries, such as Taiwan, China, Korea and Japan. Large numbers of elvers have been removed from estuaries for aquaculture purposes, preventing them from recruiting into the rivers (Tzeng, 1984; 1985). Due to over-exploitation and habitat degradation, the Japanese eel population has dramatically decreased to a very low level and many formerly important river fisheries are now closed. Understanding of the natural life history of this species is very important both for artificial propagation of eels for aquaculture, and for natural resource conservation.

EVOLUTIONARY SCENARIO OF *ANGUILLA* EELS

A total of 15 species and 3 subspecies

of *Anguilla* eels are found in the world (Castle and Williamson, 1974). Other than American (*A. rostrata*) and European (*A. anguilla*) eels in the Atlantic Ocean, all *Anguilla* species are found in the Indo-Pacific area. The eel ancestor is believed to have originated from the tropical Indo-Pacific. How eels migrated from the Indo-Pacific to colonize the Atlantic Ocean is an interesting question.

Examination of the molecular phylogenetic tree constructed from 16S rRNA and cytochrome *b* suggests that *A. borneensis* is the most ancient species; and Atlantic eels diverged from the ancestral stock approximately 50-60 and 10 million years (MY) ago, respectively (Aoyama *et al.* 2001). They adopted the former divergence time and proposed that Atlantic eels split off from their Indo-Pacific congeners and migrated through the ancient Tethys Sea to the present Atlantic Ocean before the closure of the Tethys Sea approximately 30 MY ago (Haq, 1984).

However, Lin *et al.* (2001) challenged the Tethys corridor hypothesis, on the basis of an alternative molecular phylogenetic tree reconstructed from mtDNA 12S rRNA and *cyt b* genes and by using an mtDNA substitution rate that is slower than the conventional rate. By this method the time of divergence of Atlantic and Indo-Pacific eels was estimated to be approximately 20 MY ago. Under this scenario, the Atlantic eel could not have moved through the Tethys Sea. Instead, Lin *et al.* (2001) suggested that Atlantic eels may have migrated from the Indo-Pacific to the Atlantic Ocean via the gap between North and South America, before the Isthmus of Panama was formed 5 MY ago.

Aoyama *et al.* (2001) proposed that eels spread from the Indo-Pacific to the Atlantic Ocean at the leptocephalus stage, drifting with the east-to-west circum-equatorial surface current, but Lin *et al.* (2001) considered that eels spread to the Atlantic at the migratory silver stage, via the deep west-to-east undercurrent of the Pacific Ocean.

Evolutionary histories of Anguillid eels are difficult to prove directly, and these two hypotheses must be examined from different viewpoints including fossil records, paleo-oceanography, biogeography and the distribution, life history and ecology of extant eel species.

SPAWNING GROUND

The search for the spawning area of the Japanese eel began in the 1930s, approximately 10 years after Schmidt (1922; 1925) discovered the spawning area of the Atlantic eels (Tsukamoto *et al.*, 2003a). At the beginning of the search, information on the life history and ecology of the Japanese eel was scanty. Thus, Matsui (1957) considered that the Japanese eel spawned in the area east of Taiwan and south of Okinawa because the adult Japanese eel reached the southernmost limit of its continental distribution near Taiwan. Kuo (1971) argued that the Japanese eel of Taiwan should spawn locally in the waters off south-western Taiwan on the grounds that elver catches were higher on the west coast of Taiwan than on the east coast. The spawning ground proposed by Matsui (1957) is plausible only if the east coast of Taiwan is supplied with eel larvae that have been transported by the Kuroshio Current from south to north.

These two hypotheses misled the search for the spawning area of the Japanese eel for more than 50 years (Tanaka, 1975). In the 1980s, daily growth increments of eel otoliths were counted to determine the age of elvers, which indicated that elvers had lived in the ocean more than half a year before arriving in the estuary (Tabeta *et al.*, 1987; Tsukamoto, 1990; Tzeng, 1990; Tzeng and Tsai, 1992; Cheng and Tzeng, 1996). If eel larvae are passively transported from the spawning ground in the open ocean to the estuary by oceanic currents, their spawning area should be more south and east than that proposed by Matsui (1957). Thus, research cruises to search for the spawning area of

the Japanese eel, which began in 1965, shifted from north and west to more south and east in the Pacific (Tsukamoto *et al.*, 2003a). At last, the smallest (7.9 - 34.2 mm TL) and most abundant leptocephali (958 specimens) were collected in the west Mariana Islands on 14 June - 22 July 1991, and the spawning area of the Japanese eel was thus narrowed down to the waters around 15°N 140°E in the Equatorial Current of the western Pacific (Tsukamoto, 1992).

However, the exact site where eels actually spawn remains to be located. Two different approaches were proposed by Tsukamoto *et al.* (2003a). One is to follow silver eels along their spawning migration route all the way to their spawning place using ultrasonic telemetry or the newly developed pop-up data logger tags (Jellyman and Tsukamoto, 2002); the other way is the conventional method of moving backward to the spawning site along the larval transport route seeking smaller and smaller leptocephali, until freshly spawned eggs are located.

QUESTIONING PANMIXIA

On the basis of mtDNA analysis the Japanese eel in the western Pacific was proposed to be a panmictic population (Sang *et al.*, 1994; Ishikawa *et al.*, 2001). However, the allele frequency at some loci of elvers collected across the dispersal range of the species exhibited a geographic cline (Chan *et al.*, 1997). This suggested that genetic heterogeneity exists in the population. A similar discrepancy was reported in the American eel, i.e., mtDNA analysis suggested a single population (Avise *et al.*, 1986) whereas a geographic cline was found at a few allozyme loci (Williams *et al.*, 1973; Koehn and Williams, 1978). The geographic cline detected by allozyme analysis was considered to be derived from natural selection within the generation after hatching (Nishida, 2001).

Recently, a more sensitive DNA marker, microsatellite DNA, was applied to explore the problem of population structure of the

Japanese (Ishikawa *et al.*, 2001; Tseng, 2003; Tseng *et al.*, 2001a; b) and European eels (Wirth and Bernatchez, 2001). These workers found that both Japanese and European eels had weak but significant genetic differentiation. Analysis of the microsatellite DNA indicated that Japanese eels collected from 7 locations from Taiwan, China, Korea and Japan can be divided into 3 genetically-differentiated subpopulations, namely Japan, north China and Korea, and south China and Taiwan groups (Tseng, 2003). The panmixia paradigm for the Japanese eel must therefore be reconsidered.

If the panmixia assumption for the European (or Japanese) eel is not valid, what are the implications for our knowledge of spawning areas and times? Three models were suggested by Wirth and Bernatchez (2001); 1) There may be a difference in time of adult eel arrival from different latitudes at a single spawning area (temporal allopatry); 2) There may be more than one spawning area (spatial allopatry); 3) There may be assortative mating in a single spawning area. All three models imply that the offspring from particular times, areas, or matings must return to the freshwater habitats of the parents with some degree of fidelity by unknown mechanisms involving ocean currents and perhaps oriented swimming (McCleave, 2003; McCleave *et al.*, 1998).

LIFE HISTORY EVENTS AS RECORDED IN OTOLITH

Otoliths (ear stones) are paired calcified structures that function in balance and hearing in all teleost fishes. The otolith has long been known as a time-keeper because growth checks in otoliths are periodically deposited on a daily and yearly schedule. Otoliths have been used to determine fish ages for more than a century since Reibisch's observation of otolith annuli in 1899 (Campana, 1999). More recently, the precision of otolith ageing advanced to a daily level after Pannella (1971) discovered daily growth increments. This brought fish

ageing techniques forward to a new milestone. The incorporation of many chemical elements (at least 31) in otoliths leads to even more research possibilities. The concentration of strontium (Sr) is approximately 100-fold higher in seawater than in fresh water (Campana, 1999). Thus otolith Sr/Ca ratios are widely used to study the migratory history of diadromous fish between freshwater and the marine environment. Accordingly, fish otoliths are a metaphor of the CD-ROM or the Rosetta stone. The elements deposited in the otolith are metabolically inert, and can be carefully retrieved with EPMA (Electron Probe MicroAnalyzer) or LA-ICPMS (laser-ablation Inductively Coupled Plasma Mass spectrometry) to reconstruct the migratory environmental history of the fish (Campana *et al.*, 2000; Tzeng and Tsai, 1994).

Since daily growth increments in otoliths of the Japanese eel were first described by Tabeta *et al.* (1987), the use of otolith microstructure to study the early life history of the eel increased rapidly (Tzeng, 1990; Tsukamoto, 1990; Cheng and Tzeng, 1996; Arai *et al.*, 1997). The Japanese eel spawns in the New Moon of May and June as back-calculated from the otolith daily growth increments of leptocephali collected near the spawning area (Liao *et al.*, 1996; Tsukamoto *et al.*, 1998b; Tsukamoto *et al.*, 2003b). Upstream movement of elvers is linked to the lunar cycle and tidal rhythms (Tzeng, 1985; McCleave and Wippelhauser, 1987). This indicates that the spawning and upstream moving behaviours of the eel are controlled by an internal clock driven by the lunar cycle. Furthermore, an obvious check appears in the elver otolith during its metamorphosis from leptocephalus to glass eel (Wang and Tzeng, 1998; Tzeng, 2003). The daily ages calculated from the daily growth increments in elver otoliths by developmental stages indicate that both ages at metamorphosis from leptocephalus to glass eel and ages at estuarine arrival increase with the distance from the spawning areas. The timing of metamorphoses from leptocephalus to glass eel

and the Kuroshio Current play important roles in determining the ultimate estuarine arrival in the long-distance dispersal of the Japanese eel (Cheng and Tzeng, 1996).

After metamorphosis from leptocephalus to glass eel, the migration of the Japanese eel is probably influenced less by the Kuroshio Current and more by coastal currents. Examination of the daily growth increments from the metamorphosis check to the otolith edge of elvers indicated that the age of elvers was approximately 4 -7 days greater in the southern than the northern estuaries of Taiwan (Cheng and Tzeng, 1996). This suggests that Japanese eel elvers were transported by the China coastal current from the north to the western coast of Taiwan. These results invalidate the suggestion by Kuo (1971) that Japanese eels spawn off south-western Taiwan.

Casselmann (1982) pioneered the measurement of Sr/Ca ratios in otoliths of Atlantic eels. He found that Sr/Ca ratios in eel otoliths decreased when they migrate from the marine environment to freshwater. However, the otolith microchemistry study of Japanese eel was neglected until the 1990s, when Tzeng and Tsai (1994) measured Sr/Ca ratios in otoliths of the elvers of Japanese eels that were migrating from the ocean to the river. Sr/Ca ratios in otoliths of the elver gradually increased from the primordium during marine life, reached a peak approximately 1 month before upstream migration, and then dramatically decreased. It was proposed that peak ratios corresponded to metamorphosis from leptocephalus to glass eel as the young animals migrated from Kuroshio Current to coastal waters (Otake *et al.*, 1994; Arai *et al.*, 1997).

The Sr/Ca ratios in otoliths of eels were validated to be positively correlated with the salinity of ambient water (Tzeng, 1996; Kawakami *et al.*, 1998; Kraus and Secor, 2003). Thus, Sr/Ca ratios have been widely used to reconstruct the migratory environmental history of the European (Tzeng *et al.*, 1997; 1999), Japanese (Han *et al.*, 2003; Shiao *et al.*, 2003; Tsukamoto

et al., 1998a; Tsukamoto and Arai, 2001; Tzeng *et al.*, 2000b; 2002a; 2003a; b) and American eels (Jessop *et al.*, 2002; 2004; Morrison *et al.*, 2003; Cairns *et al.*, 2004). These studies broadly indicate that the life cycle of the eel has been over-simplified, and that the estuarine and freshwater migratory behaviour of the eel is more flexible and complicated than previously believed. Some eels in the yellow (growth) phase stage skip freshwater life and live in marine coastal waters until maturation (Tsukamoto and Arai, 2001). Migratory behaviours of yellow eels were classified into marine, estuarine and freshwater eel migratory contingents (Tzeng *et al.*, 2003a; b). The freshwater eel contingent has a well-known migratory pattern of growth in the river and migration downstream for spawning as silver eels. The marine eel contingent remains in coastal waters and never invades freshwater. The estuarine contingent wanders between freshwater and seawater. Whether the evolution of migratory contingents is genetically or environmentally determined is not clear. The evolution of the marine migratory contingent of the Japanese eel was proposed to have resulted from the latitudinal difference in productivity (Tsukamoto *et al.*, 2002) and from congeneric competition with the tropical eel *A. marmorata* (Shiao *et al.*, 2003). Production was higher in freshwater than in seawater at the lower latitude but it was opposite (higher in seawater than freshwater) at the higher latitude (Gross 1987). *A. marmorata* is a more ancient species that may invade the tropical freshwater habitat earlier than the temperate eel *A. japonica*. This led the Japanese eel to evolve a marine migratory contingent to effectively use the productive marine habitat at the higher latitude. These findings raise questions about the conventional definition of catadromy in anguillid eels, i.e. ocean spawning and freshwater growth (Myers, 1949; Gross, 1987; Tzeng *et al.*, 2000b).

POPULATION DECLINE

Recently, it was found that the sex ratio of the Japanese eel in Taiwanese rivers was unbalanced with more than 80% of the eels being female (Tzeng *et al.*, 2002b). The female-loaded sex ratio may cause some females to reproductively fail when stock size is low, if they are unable to find mates, or if the fertilization rate of broadcast spawners depends on sperm concentration.

Before the yellow stage the sex of the eel is undifferentiated; whether sex is genetically or environmentally determined is not certain. Most studies point to population density as the probable principal factor determining the sex of the eel, with habitats having high densities of eel dominated by males and low density habitats dominated by females (Colombo *et al.*, 1984; Krueger and Oliveira, 1999). Elver restocking experiments further support this conclusion (e.g. Parsons *et al.*, 1977; Roncarati *et al.*, 1997. Degani and Kushnirov (1992) demonstrated that European eels maintained at higher densities produced more males than those maintained at lower densities. Likewise, Tzeng *et al.* (2002b) found that females predominated in low density habitats in the rivers of Taiwan while males dominated in a superintensive culture ponds. Thus, eel sex determination may be due primarily to environmental factors, particularly density. Alternatively, the sex of elvers in high-density captivity can be feminized by the treatment of estradiol-17 β (Degani and Kushnirov, 1992; Satoh *et al.*, 1992; Chiba *et al.*, 1993). We do not know if pollutants in rivers contain environmental hormone analogues capable of influencing the gender of eels.

In the past two decades, Japanese eel elvers have been overexploited for aquaculture across the species range (Tzeng, 1984; 1997). Consequently, population densities of yellow eels upriver is very low. Thus, the high proportion of female eels in Taiwanese rivers may support the density-dependent environmental sex determination hypothesis (Colombo *et al.*, 1984; Krueger and Oliveira, 1999). Males at metamorphosis from the yellow to the

migratory silver eel stage are smaller and younger than females, i.e. male eels exhibit a time-minimizing growth strategy by maturing as soon as possible, while females postpone maturation with a size-maximizing growth strategy to attain higher fecundity (Vollestad and Jonsson, 1986; Helfman *et al.*, 1987; Vollestad, 1992). Thus, density-dependent sex determination is a key mechanism in eel population regulation. In high-density habitats, food resources are limited and the earlier differentiation of males may promote an earlier spawning migration. This could reduce intraspecific competition and mortality. In contrast, in low-density stocks, food resources are relatively plentiful and eels differentiating into females would have enough time to fully utilize the resources and grow larger to achieve higher fecundity and increased reproductive success. This could help in eel population recovery. However, the mechanism by which population density generates the signal to begin sexual differentiation of the eel requires further study.

CONCLUSION AND RESEARCH PROSPECTS

The world-wide decline of anguillid eels was one of the major theme of the International Eel Symposium held at the annual meeting of the American Fisheries Society in Quebec City, Canada, August 2003. Delegates were very concerned about dramatic decreases in populations of American, European and Japanese eels which have plummeted to approximately 1-10% of their levels in the 1970-1980s (Dekker, 2003; Casselman, 2003; Tatsukawa, 2003). The effective population size of Japanese eel decreased (Tseng *et al.*, 2003). Current populations are far below the biologically safe limit, and extinctions in the near future are a distinct possibility. The reasons for the population declines are still uncertain, but may relate to changes in oceanic currents and global climate, degradation of habitat (e.g. dam construction and pollution), exotic parasite infec-

tion, and over-fishing. Population levels of the Japanese, American and European eels are at the edge of collapse and the need for management and conservation is urgent.

Knowledge of life history traits (such as growth and survival rates, age and size at maturity, fecundity) of the eel is essential for effective stock assessment, management and conservation. The Japanese eel is widely distributed from Taiwan in the south, through China and Korea to Japan in the north. Within this range, different sub-populations have evolved, in like manner to the European eel (Wirth and Bernatchez, 2001). Life history traits of these subpopulations may differ, hence data specific to sub-populations are required for population dynamic analysis. In addition, each of the subpopulations may have evolved 3 different migratory contingents: freshwater, sea and estuarine eels at the yellow growth phase stage. The relative contribution of the 3 migratory contingents to the adult stock is unclear and needs to be investigated.

Low eel populations may produce compensatory effects in the spawner-recruit relationship by maximizing the intrinsic rate of increase at the lowest spawner abundance (Quinn and Deriso, 1999). The Japanese eel in Taiwan has a female-skewed sex ratio, which may favour population recovery due to higher egg production. However, the continuing population decline could mean that stock levels are now in the depensation zone, where production of young at low population levels is lower than expected. If this is the case, fishery managers have cause for grave concern because fished stocks do not always recover after being fished to very low abundance, even when fishing is stopped (Quinn and Deriso, 1999). The life history of the eel is still veiled in mystery, particularly in the marine habitat where it spawns. To achieve the knowledge required for sustainable utilization of the eel, research in eel life history must continue and expand.

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日本鰻自然生活史研究的進展

曾萬年

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鰻魚(*Anguilla* spp.)生活史的研究，可以回溯到 1920 年代。近年來，由於耳石微化學及基因技術的導入，使得蒙上一層神秘面紗的鰻魚的生活史及生態之研究有了突破性的進展。本研究簡要回顧近 15 年來日本鰻生活史研究的發現，特別是種化及演化過程、產卵場的探索、族群的遺傳結構、性比的偏歪分布與族群密度關係、耳石的研究及其在洄游環境歷史的應用。日本鰻、美洲鰻及歐洲鰻的資源量，目前已經下降到只剩 1-10%，正處於生物安全警戒線之下。資源減少與過漁，棲地惡化及氣候變遷有關，但真正原因仍然不確定。為了有效地管理及保育，鰻魚生活史的研究必需持之以恆。

關鍵詞：日本鰻，種化及演化，產卵場，耳石微化學，生活史，族群結構，資源衰竭。