Life History and Evolution of Migration in Catadromous Eels (Genus Anguilla)

Jun Aoyama*

Ocean Research Institute
The University of Tokyo
1-15-1, Minamidai, Nakano
Tokyo 164-8639, Japan

Abstract
A variety of ecological information from both temperate and tropical eels of the genus Anguilla provided the first chance to evaluate the relationship between their life history patterns and phylogenetic relationships. Recent studies indicated that much shorter migrations of a few hundred kilometers are made by tropical eels to spawn in areas near their freshwater habitats, clearly contrasting with the long distance migrations of their counterparts in temperate regions, such as European A. anguilla, American A. rostrata and Japanese eels A. japonica. Molecular phylogeny indicated that the species inhabiting tropics such as A. borneensis in Borneo or A. mossambica in the Indian Ocean are likely to be the most ancestral. These findings suggested a scenario of these tropical species with short migration giving rise to temperate species with long migrations.

This paper outlines the recent findings on the ecology of anguillid species such as their spawning sites, larval migrations, recruitment, growth phase and down stream migrations as well as their molecular phylogenetic relationships and population genetics. Based on these findings, the present state of our understanding about the evolution of migration in the genus Anguilla and future perspectives are discussed.

1. Introduction
The freshwater eels of the genus Anguilla consist of 18 species/subspecies and are widely distributed throughout the world. They are found in most tropical, subtropical and temperate areas except for the South Atlantic and the west coasts of North and South America (Ege 1939; Watanabe 2003, Fig. 1). Freshwater eels are catadromous with their juvenile growth stage occurring in estuaries, rivers and lakes, and with their spawning areas being offshore in the ocean (Tesch 1977, 2003). Catadromous life histories are found in several other groups of fishes, but fewer species have this type of diadromy than have anadromous life histories in which spawning occurs in fresh water (McDowall 1987). The catadromous life history of anguillids is unique, because they have a relatively long larval development as a transparent leaf-like larva (leptocephalus) that is the peculiar larval form of elopomorph fishes and is thought to be highly adapted to a planktonic life in the open ocean (Smith 1989; Pfeiler 1999; Miller and Tsukamoto

*Corresponding author at:
Ocean Research Institute
The University of Tokyo
1-15-1, Minamidai, Nakano, Tokyo 164-8639, Japan
e-mail: jaoyama@ori.u-tokyo.ac.jp
After being transported back to their recruitment areas by ocean currents, they undergo metamorphosis into glass eels that then migrate across the continental shelf to estuaries. Historically, it was only known that the silver eels migrate out to the ocean and the glass eels return to fresh water, but where they spawned and where their larval development took place were great mysteries.

This changed at the beginning of the last century when the Danish fisheries biologist Johannes Schmidt first discovered that the breeding place of the Atlantic eels, *A. anguilla* and *A. rostrata*, was in the Sargasso Sea after about 20 years of intensive surveys all over the North Atlantic Ocean (Schmidt 1922, 1925, see also McCleave 2003). This finding clearly indicated that the European eels make a remarkably long migration of thousands of kilometers across the Atlantic Ocean. The American eels also make a long migration, but their spawning area in the Sargasso Sea is much closer to their species range in North America. Since that famous discovery, the long distance spawning migration of the Atlantic eels has fascinated many biologists and stimulated their research interests.

After Schmidt’s discovery of the spawning area of the Atlantic eels, the search for the spawning area of the Japanese eel began in the Pacific Ocean. The research effort started with a survey relatively close to Japan in the 1930s (see Tsukamoto et al. 2003a), and it ended with the determination of the spawning area in the waters west of the Mariana Islands in the region around 15°N, 140°E in the North Equatorial Current (NEC) (Tsukamoto 1992). The estimated spawning area was located about 2000 km to the south or southeast from the growth habitat of the Japanese eel in East Asia, and a long distance spawning migration of the genus *Anguilla* in the Pacific Ocean was confirmed for the first time.

The spawning areas of both the Japanese eel and the Atlantic eels were studied in more detail in subsequent years to clarify the precise locations and to determine the features that defined them (McCleave 2003; Tsukamoto et al. 2003a). In the Atlantic it was found that the northern limit of the spawning area appeared to be defined by distinct temperature fronts (Kleckner and McCleave 1988), and later a salinity front was suggested to play a role in defining the northern limit of the spawning area of the Japanese eel (Tsukamoto 1992; Kimura and Tsukamoto 2006). Following the discovery of the spawning area of Japanese eels, Kimura et al. (1994) hypothesized that northward Ekman transport driven by the trade winds in the NEC may play an important role in the migration of Japanese eel leptocephali enabling them to be transported to their species range in East Asia (see Kimura 2003). Then, based on a reexamination of all historical catch records of Japanese eel leptocephali, otolith analyses and regional oceanographic
conditions, Tsukamoto et al. (2003b) proposed two hypotheses for the determination of the exact timing and location of the spawning of Japanese eels. These hypotheses suggested that the Japanese eel has a lunar cycle of spawning during the new moon period, and their spawning area is associated with seamounts at the eastern edge of the Philippine Plate (Tsukamoto et al. 2003a, b). Support for these hypotheses was found in 1998 with small leptocephali being caught in the vicinity of the seamounts (Ishikawa et al. 2001a) and in 2005 by collections of a few hundreds newly hatched Japanese eel larvae during the new moon period to the west of one of the seamounts (Tsukamoto 2006).

Considerably less attention has been given to locating the spawning areas of the other species inhabiting various areas of the Indo–Pacific as well as the western South Pacific and the Indian Ocean. After the discovery of the spawning areas of the Atlantic eels, Schmidt and his colleagues further expanded their interest in the spawning areas of other anguillid species and conducted an expedition to study the distribution of anguillid leptocephali in the Indo–Pacific region from 1928 to 1930 (Jespersen 1942). This effort obtained a considerable amount of data including nearly 1500 anguillid leptocephali and some areas were suggested to be possible spawning areas of tropical anguillid species (Jespersen 1942). However, the clarity of their findings were reduced by an inability to identify most tropical eel leptocephali because of a major overlap in the key morphological characters used for species identification (Aoyama et al. 1999a; Kuroki et al. 2006a).

Several recent surveys have overcome that difficulty by using molecular genetic characters to identify anguillid leptocephali, which was made possible by recent progress in molecular techniques. Species identification methods using molecular characters have enabled anguillid leptocephali to be precisely identified, as well as eggs and newly hatched larvae (e.g., Wakao et al. 1999; Aoyama et al., 2000, 2001a; Watanabe et al. 2004a; Gagnaire et al. 2007).

In addition to learning about the spawning areas of anguillid eels, other studies have examined the otolith microstructure of leptocephali and glass eels to know their early life history and recruitment patterns. These studies started with the Japanese eel (e.g., Tsukamoto 1990) and the Atlantic eels (e.g., Castonguay 1987; Lecomte-Finiger 1992, 1994), and then expanded to include various other anguillid species. Research on the otolith microstructure of the glass eels found that the otolith increment width appeared to increase during metamorphosis, so that this could be used as an indicator of the age at which metamorphosis begins in anguillid larvae (Otake et al. 1994). Subsequent studies on glass eels have provided useful life history information about several species of tropical and temperate anguillid species.

Although the freshwater growth phase of the yellow eel and the downstream migrations of the silver eels of temperate anguillid species have been studied for many years (see Tesch 1977, 2003), a variety of recent advancements have been made on understanding these parts of the life histories. These studies have included acoustic telemetry or radio tracking of yellow and silver eels (e.g. Parker 1995; Aoyama et al. 1999b, 2002; Durif et al. 2003; Jellyman and Sykes 2003; Thibault et al. 2007), pop-up satellite tags for large sized silver eels (Jellyman and Tsukamoto 2002, 2005), spawning behavior (Dou et al. 2007) or swimming stamina trials in the laboratory (van Ginneken and van den Thillart 2000; van Ginneken et al. 2005a). Another important advancement was the use of otolith microchemistry to determine the type of habitat used by individual eels throughout their life. Tsukamoto et al. (1998) reported that some silver eels migrating to the spawning area had never entered fresh water based on the Sr content in their otoliths and termed these individuals as “sea eels”. It was then shown that many eels also remain in estuaries or even move back and forth between fresh water and the estuary. The life history of these eels appeared to be a form of “facultative catadromy” (Tsukamoto and Arai 2001). Subsequent research on other temperate anguillid species showed that this was a typical pattern for these eels (e.g. Tzeng et al. 2000; Jessop et al. 2002; Daverat et al. 2005) with a tendency for greater use of saltwater habitats at the higher latitude in the northern hemisphere (Daverat et al. 2006).

This variety of ecological information provided the first chance to evaluate the relationship between life history patterns of anguillid eels and their phylogenetic relationships (Tsukamoto et al. 2002). After some preliminary studies with only some of the species in the genus Anguilla,
analyses of the genetic relationships of all the species provided the first view of their possible phylogenetic relationships and evolutionary history (Aoyama et al. 2001b).

A more recent study using the sequences of the whole mitochondrial genome of all species of the genus then provided the best estimate of the phylogenetic relationships of anguillid eels (Minegishi et al. 2005). One consistent finding of these phylogenetic studies has been that some tropical species such as *A. borneensis* or *A. mossambica* appear to be the basal species of the genus. This suggests that the long spawning migration of temperate anguillids evolved from the shorter migrations of tropical species (Tsukamoto et al. 2002).

At a time when drastic declines in glass eel recruitment have been continuously observed in temperate anguillid eels in the northern hemisphere (Haro et al. 2000; Casselman 2003; Dekker 2003; Tatsukawa 2003), a synthesis of knowledge about the life histories and possible evolutionary history of these remarkable fishes may be useful to help understand what may be affecting the stability of these eel populations. Recruitment has declined drastically in much of the species ranges of the Atlantic eels (Casselman 2003; Dekker 2004), raising concern over the health of northern temperate eel stocks that likely have been affected by a variety of anthropogenic factors such as habitat loss, overfishing, pollution, and parasite introductions (Haro et al. 2000; Feunteun 2002; Robinet and Feunteun 2002; Dekker 2004), or changes in ocean–atmospheric conditions (Castonguay et al. 1994; Knights 2003; Friedland et al. 2007; Bonhommeau et al. 2008; Miller et al. 2009, in press).

In this paper, I overview recent findings about anguillid spawning sites, their larval migrations, recruitment, growth phase and silver eel migrations as well as their phylogeny and population genetics with an emphasis on the Japanese eel and tropical species for which much less has been known historically. These new findings are used as a background to discuss the present state of knowledge about the evolution of migration in the genus *Anguilla*. The management and conservation implications of this information are also discussed.

2. Phylogeny of the genus *Anguilla*

2-1. Morphological studies

The history of morphological studies of the genus *Anguilla* has been reviewed recently by Watanabe (2003), who found that these eels are difficult to completely separate into clear species in some cases using only morphological characters. Therefore, although morphological studies have generally achieved remarkable success in identifying groups of evolutionarily related species and have provided the foundation for all current work on the systematics of fishes (Stepien and Kocher 1997), eels may be a difficult group to study using only morphological characters. In the case of the genus *Anguilla*, the first and only comprehensive systematic study until Watanabe (2001) was carried out by Ege (1939).

Ege (1939) estimated the evolutionary relationships of all the anguillid species on the basis of his morphological observations. He first divided the genus into four groups that were: the first species group (*A. celebesensis*, *A. interioris* and *A. megastoma*), the second species group (*A. nebulosa nebulosa*, *A. nebulosa labiata*, *A. marmorata*, *A. reinhardtii* and *A. ancestralis*, which was subsequently synonymized with *A. celebesensis* by Castle and Williamson 1974), the third species group (*A. borneensis*, *A. japonica*, *A. dieffenbachii*, *A. anguilla*, *A. rostrata*, and *A. mossambica*), and the forth species group (*A. bicolor bicolor*, *A. bicolor pacifica*, *A. obscura*, *A. australis australis*, and *A. australis schmidtii*). If the scheme of species relationships proposed by Ege (1939) is to be interpreted as a phylogeny and the node species are considered to be the most likely ancestral species, then the scheme can be explained as follows (Fig. 2): The first group is morphologically distinctive from the other groups and was suggested to be the most ancestral in the genus. *Anguilla nebulosa* and *A. borneensis* were proposed to have been derived from this group to form the second and third groups, respectively. Later, a member of the third group, *A. japonica*, may have given rise to the fourth group, with *A. bicolor* being the most ancestral species. These groupings were highly constrained by the external morphological characters examined, and their relationships were reconstructed based on a few objective criteria.
Watanabe et al. (2004b) recently reexamined the taxonomy of the genus *Anguilla*, using a total of 14 morphological characters that included 12 of those used by Ege (1939) and two new characters with a total of 1713 specimens that consisted of 1497 newly collected samples and 216 museum specimens (see also Watanabe 2001). It was concluded that the combination of color markings, width of maxillary bands, and origin of the dorsal fin divided the genus *Anguilla* into four groups, as was suggested by Ege (1939). However, the similar morphology of all species in the same group indicated that it would be necessary to revise the taxonomy of the freshwater eels with new characters and methods, because a few species could not be clearly separated using morphological characters without using their collection locality as a key factor (Watanabe et al. 2005a). Then, these authors did not evaluate the systematics or phylogenetic relationships of the genus *Anguilla* based on their morphological data.

However, recent genetic studies (described below) that have mostly been based on Ege’s (1939) traditional taxonomy showed no critical inconsistency. This suggested that the taxonomy of the genus *Anguilla* that was proposed by Ege (1939), which has long been accepted, correctly recognized the evolutionary units in this genus. However, the present knowledge about their morphological differences is not good enough to correctly identify the species as shown by Watanabe et al. (2004b).

### 2-2. Molecular phylogenetic approaches

The first molecular phylogenetic approaches to the genus *Anguilla* were conducted by Tagliavini et al. (1995, 1996) and Aoyama et al. (1996), Aoyama and Tsukamoto (1997), although all these studies analyzed only some species of the genus. Aoyama and Tsukamoto (1997) conducted a phylogenetic analysis using *A. celebesensis* as an outgroup, based on Ege’s conclusion that *A. celebesensis* was the most ancestral species (Ege 1939). This would be problematic because the monophyletic relationship of the remaining seven anguillid species was implicit in this assumption (Bastrop et al. 2000). However, this was the first attempt to know the branching order of the species that indicated the evolutionary history of the anguillid species. Aoyama and Tsukamoto (1997) suggested a clade made of species inhabiting the North Atlantic Ocean and East Africa (*A. mossambica*). Based on this close relationship of the geographically distant species, they proposed the “Tethys Corridor Hypothesis” in which anguillid eels entered the Atlantic Ocean through the Tethys Sea from their place of origin (Fig. 3), which was thought to be present day Indonesia (Aoyama and Tsukamoto 1997; Tsukamoto and Aoyama 1998; Aoyama et al. 2001b).

Thereafter, two molecular phylogenetic studies of the genus *Anguilla* have been published, in which Lin et al. (2001) examined mitochondrial 12S rRNA and cytochrome *b* genes of 12 species, and Aoyama et al. (2001b) examined 16S rRNA and cytochrome *b* genes from all species of the genus (Fig. 4). The major difference between these two studies was the position of *A. borneensis* (*malgumora*), which is an endemic species on the east side of Borneo, Indonesia. Aoyama et al. (2001b) concluded that *A. borneensis* was the most likely basal species, but it was a nodal
species forming a clade with *A. marmorata* and *A. nebulosa* (*bengalensis*) in the topology presented by Lin et al. (2001). Lin et al. (2001) could not reveal the most basal species because their phylogenetic tree was initially divided into two large clades. Such discrepancies were likely caused by the many reasons such as problems in the identification of individual species, the differences in taxon sampling, the analyzed genes, amounts of sequence data, and the outgroup settings (Aoyama 2003; Minegishi et al. 2005).

In recent years the complete mtDNA sequences of many taxa including teleosts have been determined and used for phylogenetic analyses, which have successfully resolved some controversial phylogenetic relationships (e.g. Inoue et al., 2001). The complete mtDNA sequences of all species of the genus *Anguilla* were recently determined for the molecular phylogenetic analysis

---

**Fig. 3.** A diagram showing the Tethes Corridor hypothesis for how the Atlantic anguillid species may have moved through the ancient Tethes Sea into the Atlantic basin, and other possible radiations of species out from central Indonesia where anguillid eels may have originated.

**Fig. 4.** Molecular phylogenetic trees of anguillid eels in two previous studies.
by Minegishi et al. (2005). The resultant topology suggested that *A. mossambica* was the most likely basal species, and the remaining species formed the following two large clades at basal nodes (Fig. 5; Minegishi et al. 2005). In the former group, *A. borneensis* was derived first, and subsequently, followed by the geographically widely separated groups of the two Atlantic species (*A. anguilla* and *A. rostrata*) and three Oceania species (*A. dieffenbachii*, *A. australis australis* and *A. australis schmidtii*) were split. In the latter group with eleven species, *A. celebesensis* and *A. megastoma*, *A. nebulosa nebulosa* and *A. nebulosa labiata*, *A. bicolor bicolor* and *A. bicolor pacifica* showed sister relationships (Minegishi et al. 2005).

The presence of species groups corresponding to their geographic distribution and their relationships were almost the same as those of Aoyama et al. (2001b) with a few exceptions (see Aoyama 2003; Minegishi et al. 2005). However, the most ancestral or basal species suggested by these studies were different. Furthermore, the sister relationship of the Indian Ocean species of *A. mossambica* and the Atlantic eels that was the key for the Tethys Corridor Hypothesis of Aoyama et al. (2001b) was not found in the topology presented by Minegishi et al. (2005). The molecular phylogenetic tree presented by Minegishi et al. (2005) was constructed based on the complete mtDNA sequences of all species of the genus *Anguilla*, and it showed mostly 100% statistical supports for the nodes in the tree that were much higher than in any previous studies. However, as Minegishi et al. (2005) pointed out, the statistical supports for the nodes presented in their study were not simply comparative with the previous studies, because the phylogenetic analysis methods and molecular evolution models or parameters used in these studies were different.

Aoyama et al. (2001b) concluded that *A. borneensis* was the most basal species based on their MP (maximum parsimony) analyses of the TS (transition)/TV (transversion) parameter of five that was estimated from the actual data set, and using only TV data to enhance more ancient divergence (Brown et al. 1982; Desalle et al. 1987; Murphy and Collier 1996). Although their analyses showed *A. borneensis* to be the most basal species in the strict consensus tree, the basal position of *A. mossambica* as suggested by Minegishi et al. (2005) was also found among a total of 12 equally parsimonious trees derived from the TV data (data not shown). Similarly, although Minegishi et al. (2005) suggested *A. mossambica* to be the most basal species by the updated Baysian analysis of the complete mtDNA data, if the same data set is analyzed by the MP method under a variety of parameter settings, the basal position of *A. borneensis* was also shown in many cases (data not shown). These facts strongly suggested that the molecular phylogenetic analyses conducted so far clearly indicated the relationships of the anguillid species as has been stated by each authors. However, it must be noted that these results were supported only under the given conditions such as taxon sampling, amount of data and analytical settings etc.

![Fig. 5. The molecular phylogenetic relationships of all species of the genus Anguilla estimated using the entire mtDNA genome. Drawn after Mol. Phylogen. Evol., 34, Minegishi et al., Molecular phylogeny and evolution of the freshwater eels genus Anguilla based on the whole mitochondrial genome sequences, 134–146, © 2005, with permission from Elsevier.](image-url)
The variations in the molecular phylogenetic estimates at the basal parts of the trees strongly suggested that the mtDNA of the genus *Anguilla* does not include enough information for a robust phylogenetic reconstruction. It is reasonably assumed that lineages of the genus *Anguilla* have experienced particular evolutionary events such as rapid radiation and extinction of phylogenetically critical species, which may have caused the difficulties in making their molecular phylogenetic estimates. Careful consideration of the phylogenetic relationships of the anguillid species are needed, not only with statistical supports of the given phylogeny, but also from a zoogeographic perspective considering the geography of landmasses and ocean basins over evolutionary time.

2-3. A new species in the genus *Anguilla*

As mentioned above, Aoyama *et al.* (2001b) and Lin *et al.* (2001) showed considerably different phylogenetic positions of their specimens that were presumed to be *A. borneensis* (*malgumora*, see Smith 1999) based on their morphological characters. Aoyama (2003) examined the mitochondrial sequence data from these two studies published in the DDBJ/EMBL/GenBank (Aoyama *et al.* AB021779; Lin *et al.* AF006718) and found that there is a considerable difference (92/1140 site), which was equivalent to that normally found between other species (42-101/1140 site). Aoyama *et al.* (2001b) analyzed morphologically well-developed adult specimens collected from the type locality (Borneo, Indonesia, see Ege 1939), and the leptocephali genetically identified as this type of *A. borneensis* including specimens as small as 8.5 mm TL that were found near their freshwater growth habitat in Indonesian waters (Aoyama *et al.* 2003; Miller 2003; Kuroki *et al.* 2006a). Furthermore, Minegishi *et al.* (2005) examined this species later and obtained an entirely identical sequence. In contrast, specimens sequenced by Lin *et al.* (2001) were morphologically undeveloped glass eels collected in the Philippines, which is far from the species range of *A. borneensis*. These facts strongly suggested that the specimen used by Lin *et al.* (2001) was not *Anguilla malgumora* (*A. borneensis*) and was different from any other anguillid species presently recognized.

There are several possible explanations for this apparent contradiction. One is that due to a particular molecular evolutionary process in the genus *Anguilla*, there exists mitochondrial pseudogenes (see Bensasson *et al.* 2001) or introgressions (Smith 1992). However, from an ecological view point, it could also be possible that the examined specimen was a new species or some kind of cryptic species which is only genetically distinguishable from a morphologically similar species.

We then conducted a reexamination of all mitochondrial sequences of the genus *Anguilla* determined so far, we found one yellow eel specimen and two leptocephali that have the same mitochondrial sequence with Lin *et al.* (2001). Considering their geographic distribution and possible spawning areas inferred from the larval collection data, we concluded that this is a new species of the genus *Anguilla* and named this new species as the Luzon mottled eel, *Anguilla luzonensis*. The yellow eel of this species was found from the Cagayan River system, of northern Luzon Island in the Philippines (Watanabe *et al.* unpublished data) and the leptocephali were from the waters west of the Mariana Islands (16°59.343N 140°57.986E, and 15°58.543N 138°58.625E, Aoyama *et al.* unpublished data). The morphological characters of the yellow eel were as follows: coloration marbled dark brown, broad maxillary band, total length 682 mm, preanal length 301 mm, head length 95 mm, predorsal length 220 mm, length of trunk 206 mm, distance between the verticals through the anus and origin of the dorsal fin 81 mm, length of the lower jaw 39.1, total number of vertebrae 104 and the number of prehaemal vertebrae 42.

This species was morphologically indistinguishable from *A. celebesensis* and *A. interioris* (Watanabe 2003) whereas they differ significantly in mitochondrial DNA sequences from all known 18 anguillid species (Minegishi *et al.* unpublished data). The sizes of the leptocephali collected from the western Pacific were large enough for metamorphosis (51.2 and 41.6 mm in TL, Aoyama *et al.* unpublished data). It is reasonably supposed that *A. luzonensis* inhabits the Philippines and possibly in adjacent areas and has a spawning area in the NEC region in the western North Pacific. Detailed ecological information about this new species is not available yet, so an intensive survey of the growth habitats and spawning area of *A. luzonensis* is needed.
3. Life histories of temperate anguillids

3-1. Spawning areas of temperate eels

The first anguillid eels having had their spawning area determined were the two species of the Atlantic eels (Schmidt 1922, 1925; Boëtius and Harding 1985; McCleave 2003). The smallest leptocephali were discovered in the southern Sargasso Sea, and larvae <10 mm were later shown to be widely distributed in the overlapping areas of the south of about 30°N (Fig. 6), with the European eel spawning slightly to the east of the American eel (Schoth and Tesch 1982; McCleave et al. 1987). The distribution of small leptocephali in relation to the hydrographic structure in the southern Sargasso Sea showed that spawning occurred south of distinct temperature fronts that were formed during the spawning season in late winter and early spring (Kleckner and McCleave 1988). The leptocephali of both species appear to become widely distributed with various sizes being present in the summer and early fall across the southern Sargasso and in the Florida Current (Kleckner and McCleave 1982, 1985; Boëtius and Harding 1985; McCleave and Kleckner 1987; McCleave et al. 1987; Kettle and Haines 2006).

Research on the spawning area of the Japanese eel also has been extended over many years with the location eventually being well defined. After the first collection of a 57-mm fully-grown leptocephalus in 1967 off the southern tip of Taiwan, subsequent research efforts in the 1970’s collected a total of 55 leptocephali of about 50–60 mm TL, mainly in the waters east of

Fig. 6. Maps showing the collection of leptocephali of Japanese eels in the Pacific (left) and European and American eels in the Atlantic (right). Areas where the leptocephali of ≤10 mm of Atlantic eels were collected indicated as the overlapping shaded oval in the right panel, as shown by McCleave et al. (1987). The areas sampled within one degree squares for the Japanese eel between 1956 and 2002 showed as black dots, and the catches of Japanese eel leptocephali were black circles.

The area where leptocephali ≤10 mm have been collected indicated as the shaded oval in the left panel. The black squares in the right panel showed the locations where leptocephali ≤7 mm of both species were collected at the same station. The inset shows the locations where larvae ≤7 mm of the Japanese eel have been collected (the stations inside the box west of the Suruga Seamount larger larvae are also shown in the circles outside of the box) in the left panel. The number of genetically identified specimens at each station is shown in circles in the inset, and the left panel also shows the catch locations of metamorphosing leptocephali (black triangles) and oceanic glass eels (black squares). Reprinted from Macmillan Publishers Ltd: Nature, 439, Tsukamoto K. Spawning of eels near a seamount, 929, © 2006.
Taiwan (see Tsukamoto et al. 2003a). Smaller leptocephali of about 40–50 mm TL were collected in more southern waters east of Luzon Island of the Philippines, and then even smaller 19–25-mm specimens were collected further offshore in June 1990 (Ozawa et al. 1991). Based on these collection data and the current patterns in this region, spawning of *A. japonica* was predicted to occur somewhere west of the Mariana Islands (Fig. 6). An extensive sampling survey covering a large area between 10–22°N, 131–155°E was then conducted by the R/V *Hakuho Maru* to determine the regional distribution of Japanese eel leptocephali in the western North Pacific. This resulted in a large collection of 958 leptocephali including the smallest larva ever collected at that time (7.7 mm TL), which placed the estimated spawning area at around 15°N, 140°E in the North Equatorial Current (NEC) (Tsukamoto 1992). This spawning area was found to be just south of a weak salinity front that is typically present in the region as a result of tropical rainfall (Tsukamoto 1992; Kimura et al. 1994, 2001) and this salinity front was hypothesized to act as a cue for eels to help find the spawning area.

To determine a precise location where actual spawning occurs, two other hypotheses were proposed based on the reexamination of all the previous collection data of Japanese eel leptocephali and their hatching dates estimated from otolith daily rings (Tsukamoto et al. 2003a, b). Because all the small leptocephali had been collected in the waters west of three seamounts of the West Marina Ridge, the “Seamount Hypothesis” was proposed. This hypothesis suggested that these shallow seamounts reaching up to depths less than about 40 m from the surface could provide landmarks to help migrating eels find the spawning area. The second new hypothesis was developed from an otolith microstructure analysis of the daily age of the leptocephali collected in the NEC in July 1991 (see Fig. 7). The back-calculated hatching dates of these leptocephali of about 10–30 mm TL were clearly separated into two groups, which consisted of May-

---

**Fig. 7.** SEM photograph of the otolith microstructure of 51 mm anguillid leptocephalus collected in the North Equatorial Current region in 2002.
born and June-born individuals, and both groups roughly coincided with the new moon period of each month (Fig. 8a; Tsukamoto et al. 2003b). Hatching dates of other leptocephali collected in 1998 also back-calculated to the new moon periods of late May, June and July (Fig. 8b; Ishikawa et al. 2001a). These findings indicated that the Japanese eel had not been spawning continuously throughout their spawning season during the spring and summer that had been indicated by otolith analysis of glass eels collected from Japanese coastal waters (Tsukamoto 1990). This led to the formulation of the “New Moon Hypothesis” suggesting that the Japanese eel may spawn periodically once a month during a new moon (Tsukamoto et al. 2003a, b).

This hypothesis was then used to time the sampling surveys during new moons, and the Seamount Hypothesis guided sampling to the region at and to the west of the West Mariana Ridge. Then in 2005 more than 400 tiny pre-leptocephali and small leptocephali were collected to the southwest of the Suruga Seamount (14°13.7N, 142°53.0E) of the West Mariana Ridge in June (Fig. 9, Tsukamoto 2006). The Suruga Seamount is the southernmost extension of the West Mariana Ridge, which is located 200 km northwest of Guam, and it towers up high from the ocean floor of depths of about 3000–4000 m up to 40 m from the sea surface. Some of the specimens collected during the 2005 cruise were identified as A. japonica on board by a specially developed real-time PCR method (Watanabe et al. 2004a), which was confirmed again later by their mitochondrial DNA sequences in the laboratory on land. Their ages were determined using otolith daily rings to be 2 and 4–5 days old after hatching for eye-unpigmented and eye-pigmented preleptocephali, respectively, suggesting that the spawning occurred about 4 days

![Fig. 8](image_url)

*Fig. 8. The hatching dates estimated from the number of otolith increments in Japanese eel leptocephali collected in the North Equatorial Current region in 1991 (a; top panel) and in 1998 (b; bottom). Top, reprinted partially from *Environ. Biol. Fish.*, 66(2), 2003, 221–229, Seamounts, new moon and eel spawning: the search for the spawning site of the Japanese eel, Tsukamoto et al., Figure 2, © 2003, Kluwer Academic Publishers, with kind permission of Springer Science and Business Media; bottom, reprinted with permission from *Fish. Sci.*, 67, Ishikawa et al., Spawning time and place of the Japanese eel, *Anguilla japonica*, in the North Equatorial Current of the western North Pacific Ocean, 1097–1103, © 2001, the Japanese Society of Fisheries Science.*
before the new moon (Tsukamoto 2006). This first capture of tiny recently hatched preleptocephali during the new moon period provided further confirmation of the New Moon Hypothesis and supported for the Seamount Hypothesis for Japanese eel spawning.

The next major progress about the spawning areas of temperate anguillids came in 1995 when leptocephali collected at about 15°N and 160°E in the South Equatorial Current (SEC) in the western South Pacific (WSP) were genetically identified as being the larvae of *A. australis* (Fig. 10, Aoyama *et al.* 1999a), which is a temperate anguillid inhabiting both eastern Australia and New Zealand. These nine leptocephali (20.5–32.2 mm) were the first clear evidence of spawning in the SEC by this species because the previous collections of only a few large size morphologically identified leptocephali did not provide good evidence about the location of their spawning area (Castle 1963; Jellyman 1987; Kuroki *et al.* 2008a). Further support of spawning by this species in the SEC was provided by Kuroki *et al.* (2008a) that examined the distribution of the historically collected specimens and analyzed the otolith microstructure of the leptocephali collected in 1995, and in subsequent surveys conducted in 2000 and 2005 (Fig. 10). The distributions of leptocephali and their ages suggested that the spawning area of this species was likely in the SEC somewhere between Vanuatu and Fiji (Kuroki *et al.* 2008a). Also, a front formed by different temperature and salinity water masses along the southern edge of the SEC was suggested during the 1995 survey, that could help to define the spawning area to the west of Fiji (Miller *et al.* 2006, 2009 (in press)). But further collections of small leptocephali are needed to
clearly understand the location of the spawning area of *A. australis* (but see also Jellyman and Bowen 2009 (in press)).

A greater mystery is the location of the spawning area of the New Zealand longfinned eel, *A. dieffenbachii*, which is endemic to New Zealand (Jellyman 1987, 2003; Jellyman and Tsukamoto 2002). Its spawning area is unknown because no larvae have ever been identified as belonging to that species. Its silver eels leave fresh water at a higher stage of gonadal maturation (Jellyman 1987) and its glass eels return at an older age than does *A. australis* (Marui et al. 2001), which has increased the mystery about where they spawn. So the mysterious question about where temperate anguillid eels spawn is continuing still today.

### 3-2. Larval migration of temperate eels

Tsukamoto (2006) compared the distribution of small leptocephali <10 mm of the Japanese eel to the same size of the Atlantic eels shown by McCleave *et al.* (1987) and found that the spawning area of the Japanese eel appeared to be vastly smaller than those of the Atlantic eels (Fig. 6). The likely reason is that the Japanese eel spawns in a current that clearly bifurcates into both north and south flows, with only the north branch being appropriate for transporting larvae to their recruitment areas. In contrast, there is no bifurcation leading leptocephali to totally inappropriate regions after leaving the Atlantic eel spawning area. This suggests that for the larval migration of the Japanese eel to be successful in reaching East Asia, their spawning area must be very precisely located in relation to the specific oceanographic conditions, whereas natural selection pressure has been much less for a very precise spawning area in the Atlantic eels.

Northward Ekman transport in the NEC and behavioral mechanisms such as vertical migration also have been considered to be essential for Japanese eel leptocephali to enter the Kuroshio at the bifurcation point (Kimura *et al.* 1994). Ekman transport is known to shift waters northward (in the northern hemisphere), particularly in depth layers shallower than 70 m. After hatching, Japanese eel leptocephali are transported westward by the NEC and later they likely
start a diel vertical migration. Thus, they are shifted westward by the NEC during daytime while staying in deeper layers with less Ekman transport, but once swimming up to the shallow layers during nighttime, they would be transported to the north by Ekman transport. This mechanism may facilitate Japanese eel leptocephali entering the northward flow and avoiding being entrained into the strong southward flow of the Mindanao Current. Thus, the exact location of the spawning site is critical, not only in the latitude in relation to the NEC, but also longitudinally in relation to the distance from the bifurcation point to allow successful recruitment of the Japanese eel to East Asia.

Other factors that can affect recruitment of eels are related to changes in ocean conditions. Ocean–atmosphere changes such as El Niño and the North Atlantic Oscillation (NAO) have been proposed as having an effect on the successful larval migration and recruitment of temperate anguillid eels (see Miller et al. 2009, in press). In the WNP, El Niño has been suggested to alter the latitude of a salinity front that could be one of the factors defining the exact location of Japanese eel spawning and could also affect the successful transportation of larvae to East Asia (Kimura et al. 2001; Kimura 2003). A recent modeling study has evaluated the effects of El Niño conditions on the larval transport of the Japanese eel (Kim et al. 2007). Changes in ocean conditions also have been proposed as possible factors affecting the recruitment success of the European eel in the WNA (Castonguay et al. 1994; Knights 2003; Bonhommeau et al. 2008).

Although relatively few oceanic glass eels have been collected (Kleckner and McCleave 1985; Sakakura et al. 1996; Otake et al. 2006), glass eels can easily be collected as they recruit to the estuaries, and this enabled their otolith microstructure to be studied. The glass eels of the Japanese eel were studied from a variety of locations by Tsukamoto (1990), and this study was followed by various others (Cheng and Tzeng 1996; Kawakami et al. 1998, 1999; Shinoda 2004). Several studies were done on the Atlantic eels from a variety of locations (Lecomte-Finiger 1992, 1994; DeSaunay and Guérault 1997; Arai et al. 2000a; Wang and Tzeng 2000; Powles and Warlen 2002; Sullivan et al. 2006) including most recently Iceland (Kuroki et al. 2008b). The glass eels of the temperate species in Australia and New Zealand also have been studied (Arai et al. 1999a; Shiao et al. 2001, 2002), and the glass eels of A. dieffenbachii were found to have the greatest number of increment of any Pacific Ocean species of anguillid eel (Fig. 11; Marui et al. 2001).

Fig. 11. The estimated ages and durations of the various life history stages of several species of temperate (A. dieffenbachii, A. australis) and tropical (A. bicolor pacifica, A. marmorata, A. celebesensis) glass eels from the Australasia and the Indo–Pacific regions that were obtained from the otolith microstructure of each species. Reprinted partially with permission from Mar. Ecol. Prog. Ser., 213, Marui et al., Comparison of early life history between New Zealand temperate eels and Pacific tropical eels revealed by otolith microstructure and microchemistry, 273–284, Figure 8, © 2001; Inter-Research.
Daily deposition of otolith increments has been validated in temperate and tropical glass eels after they have reached their recruitment areas (Umezawa et al. 1989; Martin 1995; Arai et al. 2000b; Sugeha et al. 2001a) and in the early stage larvae of artificially matured eels (Shinoda et al. 2004). It has been recently suggested that the estimates of the total number of otolith increments in some temperate species of glass eels may not accurately represent their total age. This possibility has arisen from the consistent mismatch of the back-calculated hatching dates estimated from the total number of otolith increments in glass eels from the Atlantic, where there have been estimates of the spawning season based on collections of small leptocephali (McCleave et al. 1998). It was proposed that there may not be deposition of daily rings during metamorphosis from the leptocephalus to the glass eel stage (Cieri and McCleave 2000). However, subsequent studies with other anguilliform (Powles et al. 2006) or elopomorph (Chen and Tzeng 2006) species have clearly shown that otolith deposition continues through metamorphosis. This was also supported by the examination of all the different stages (leptocephalus, metamorphosing leptocephalus, and oceanic glass eel) of the tropical eel Anguilla marmorata (Kuroki et al. 2005). Further research into behavioral and environmental effects on otolith deposition in glass eels would help to clarify this issue.

The studies on glass eel otoliths have been very useful, because the otolith increments were found to increase in width during metamorphosis. This enabled most of these studies to determine the approximate duration of the leptocephalus stage and provide estimates of the larval migrations of each species. Large variations in the larval duration of glass eels recruiting to different latitudes have been observed for the Atlantic eels (Wang and Tzeng 2000) and their ages and sizes were suggested to be seasonally varied (DeSaunay and Guérault 1997). Similar patterns have also been observed for Anguilla australis, which were older in New Zealand than in Australia, which is closer to the spawning area based on their larval migration route (Arai et al. 1999a; Shiao et al. 2002; but see also Jellyman and Bowen 2009, in press).

Studies on the glass eels of the Japanese eel have also suggested the existence of a cline in age at metamorphosis (Cheng and Tzeng 1996). However, the rapid speed of the Kuroshio that extends through most of the latitudinal range of the species seems to reduce such age differential among sites. Shinoda (2004) who analyzed a total of 307 glass eels collected from nine localities covering the whole species range reported that the average larval duration of the Japanese eel was 156 days, but there was a large variation ranging from 98 to 227 days. There was also variation in the larval duration of nearly 90 days among glass eels that recruited to the same place in the same time (Shinoda 2004). These results suggested that although anguillid species have some different ranges of larval durations, the length of time spent as leptocephali of each individual can vary widely depending on its transport and recruitment history.

3-3. Growth phase and spawning migration

Once glass eels reach coastal waters and migrate upstream in fresh water, the growth phase of their life history begins. Several recent laboratory studies have examined the behavior and growth of glass eels of the Japanese eel (Dou et al. 2003; Dou and Tsukamoto 2003). Other studies have examined the temperature at which Atlantic glass eels in Iceland begin their upstream migration behavior (Linton et al. 2007). Studies on European and New Zealand glass eels also have examined the interactions between environmental conditions and their behavioral responses (e.g. Edeline et al. 2005a, b, 2006; August and Hicks 2008; McCleave and Jellyman 2002).

However, an important question about the behavior of glass eels or elvers is how they may decide to enter fresh water as in the typical catadromous migration, or to remain in estuaries for their growth phase. This question has received increasing attention since studies on the otolith microchemistry have shown that Japanese and European eels display a facultative catadromy, with some individuals never entering fresh water (Tsukamoto et al. 1998; Tsukamoto and Arai 2001). The concentrations of Strontium (Sr) in otoliths have been used to evaluate the likely levels of salinity experienced by eels during their life, because the concentration of Sr is much higher in seawater than in fresh water, and this is reflected by the amount of Sr incorporated into
the otoliths (Tsukamoto and Arai 2001; Daverat et al. 2005). Both Sr:Ca ratios in line transects across the otoliths showing changes in the habitats used by the eels and whole otolith Sr concentration maps have been common techniques (Fig. 12). In the Sr concentration maps, the blue color shows freshwater residency, the yellow brackish water exposure in estuaries, and the orange shows likely contact with higher salinities, such as in coastal marine waters (Fig. 12). Subsequent studies evaluating the habitat use history in the Japanese eel (Tzeng et al. 2002, 2003; Arai et al. 2003a; Kotake et al. 2003, 2005), the American eel (Jessop et al. 2002, 2004; Morrison et al. 2003; Cairns et al. 2004; Lamson et al. 2006), European eel (Tzeng et al. 2000; Arai et al. 2006; Daverat and Tomás 2006), and New Zealand eels (Arai et al. 2004) have confirmed that facultative catadromy is a common characteristic of temperate anguillid eels.

For the Japanese eel it also was suggested that there may be a latitudinal cline in the proportion of eels that stay in marine habitats instead of entering fresh water (Tsukamoto et al. 2009b, in press). A higher proportion of eels may stay in marine habitats in the northern parts of their range, because there is lower productivity in fresh water than in the marine environment. Similarly, the relative productivity of freshwater habitats will be higher in more southern areas compared to the marine habitats. This pattern of a higher degree of use of estuarine or marine habitats in the northern areas has been suggested to be a common feature of all three of the Northern Hemisphere anguillid species (Daverat et al. 2006).

Ecological characters of the eels staying in estuarine and marine habitats are poorly known compared to those in freshwater habitats. Yellow eels are opportunistic predators on invertebrate preys and on small fishes when they reach larger sizes (Moriarity 2003), so their growth

---

**Fig. 12.** Strontium maps of the otoliths of three Japanese eels that show the likely types of habitats where they lived with a dark blue color for fresh water, light blue for low salinities, and yellow and orange for higher salinities in the left panel, and line transects of Sr:Ca ratios along the length of the same otoliths show the patterns of change in Sr levels during the life of each eel (right panel).
rates likely vary depending on the types and amount of food available in each area. In some areas that have been studied recently, there are indications from otolith studies that the growth rates of yellow eels may be higher in estuarine habitats than in pure freshwater regions of river systems (Jessop et al. 2004; Kotake et al. 2005; Daverat and Tomás 2006). Other studies on the demographic characteristics of yellow and silver eels have continued with the Atlantic eels (e.g. Oliveira and McCleave 2000, 2002; Goodwin and Angermeier 2003; Morrison and Secor 2003; Chadwick et al. 2007; Costa et al. 2008; Lasne et al. 2008; Weeder and Hammond 2009, in press) and the New Zealand eels (see Jellyman 2007, 2009 in press).

Until recently though, comparatively less research has been done on the Japanese eel, perhaps in part because of an emphasis on early life history studies and research on the physiology and artificial production of larvae for aquaculture purposes (Aida et al. 2003; Tsukamoto et al. 2009b, in press). However, the first study on the structure of the burrows of yellow eels was conducted recently (Aoyama et al. 2005), and the first acoustic tracking study of estuarine yellow and silver eels was also carried out (Aoyama et al. 2002). Studies on the magnetosensitivity of Japanese eels have shown that glass eels, yellow eels and silver eels are sensitive to magnetic fields (Nishi et al. 2004; Nishi and Kawamura 2005) and that the sensory organ for detecting these fields is apparently located near the olfactory organ (Nishi et al. 2005). Other interesting recent studies on the otolith aging from the Hamanaka Lake system, Japan and several other locations in Japan (Amakusa, Mikawa Bay, Sanriku Coast) have consistently shown that the Japanese eels has a faster growth than other temperate anguillid species (Yokouchi 2005; Kotake et al. 2007; Yokouchi et al. 2008).

The migratory behavior of silver eels have been recently studied in Mikawa Bay, Japan, in relation to environmental conditions that may trigger the onset of the migration to the spawning area (Okamura et al. 2002). Other research examined the reproductive characteristics of the eels caught in Mikawa Bay (Utoh et al. 2004) and also examined their age, growth and general habitat use based on the Sr:Ca ratios in their otoliths (Kotake et al. 2005). Okamura et al. (2007) examined the morphology and coloration of yellow and silver eels to define the characteristics of the silver eel stage of the Japanese eel. This provided very useful criteria to distinguish the life stages of the Japanese eel, as Y1 and Y2 for the yellow eel stage and S1 and S2 for the silver eel stage. This provided a morphological basis for classifying the silvering process of the Japanese eel, and similar approaches in physiology, ecology and behavior will give a much better understanding of this most mysterious life stage of the Japanese eel.

Studies on the other species of temperate silver eels also have been contributing to the understanding of the ecology of silver eels. With reduced recruitments of the temperate anguillid eels in some areas there also has been increasing research on the downstream migration of silver eels and the passage of eels at dams that can act as barriers to migration (Boubée et al. 2001; Durif et al. 2003; Watene et al. 2003; Boubée and Williams 2006; Iansen et al. 2007; Klein Breteler et al. 2007). New studies also have been conducted on the migrations of silver eels in the Baltic Sea using data storage tags (Westerberg et al. 2007). This study showed that the eels moved at shallow depths mostly within 0.5 m of the surface at night and rested on the bottom during the day at depths of 2–36 m (Westerberg et al. 2007). The oceanic migrations of the New Zealand longfinned eel, which is one of the largest size species of Anguilla, was recently studied using satellite popup tags (Jellyman and Tsukamoto 2002). Because this approach successfully provided the first ocean swimming depth and direction data (Jellyman and Tsukamoto 2002, 2005), the satellite popup tags will be a powerful tool for studying spawning migration of the silver eels in the ocean. However, the typical popup tags are still too large for the use in other temperate anguillid species that do not reach the massive sizes of the New Zealand longfinned eel. In the laboratory, a variety of swimming stamina studies have been conducted on European silver eels to assess their ability to reach the spawning area. These studies found that the energy stores in the silver eels is likely enough to reach the spawning area by continuous swimming (van Ginneken and van den Thillart 2000; van Ginneken et al. 2005a) and such swimming behavior may stimulate gonadal maturation (van Ginneken et al. 2005b; Palstra et al. 2007a). Also it is suggested that parasite and virus infections could severely damage the eels during migration and result in spawning failure (van Ginneken et al. 2004, 2005c; Palstra et al. 2007b).
4. Population structure of temperate eels

Anguillid eels have long been accepted to have panmictic population structures because sexually matured silver eels from their wide species range migrate to a single spawning site and their larvae appear to be passively transported back randomly to their growth habitats by ocean currents (Schmidt 1925; DeLigny and Pantelouris 1973; Tesch 1977; Avise 1994; see also Maes and Volckaert 2002). For the most part, this concept has been supported because the majority of genetic studies carried out so far have suggested panmictic population structures for Japanese (Sang et al. 1994; Ishikawa et al. 2001b; but see also Tseng et al. 2003, 2006), American (Mank and Avise 2003; Wirth and Bernatchez 2003), and European eels (Dannewitz et al. 2005; but see also Wirth and Bernatchez 2001) despite their species ranges being spread over thousands of kilometers.

Wirth and Bernatchez (2001) were the first to use highly polymorphic microsatellite DNA markers for population analysis of the European eel (see also Daemen et al. 2001). They found a weak, but highly significant genetic differences among specimens collected from the North Atlantic, Baltic and North Seas and Iceland, suggesting restricted gene flow between the geographic or maritime units (Wirth and Bernatchez 2001). However, more recent studies (Dannewitz et al. 2005; Albert et al. 2006; Pujolar et al. 2006; Maes et al. 2006) found considerable temporal variation of the microsatellite markers in samples from different cohorts, suggesting that such genetic variation might have appeared as a spatial pattern in the study by Wirth and Bernatchez (2001). Therefore, the panmixia hypothesis for the European eel is presently still the most likely possibility.

The Japanese eel also has been suggested to be panmictic by numerous studies (Taniguchi and Numachi 1987; Sang et al. 1994; Ishikawa et al. 2001b). But the existence of multiple populations in the Japanese eels was suggested for the first time by Chan et al. (1997) based on their finding of a geographic cline in allele frequency of some isozyme loci. Tseng et al. (2006) recently reported two genetically different groups which were separated into a low-latitude group (southern China and Taiwan) and a high-latitude group (Japan, Korea, and northeast China) by the analysis of eight polymorphic microsatellite loci. Subsequently, Chang et al. (2007) found that glass eels of consecutive monthly cohorts estimated by the otolith microstructure that recruited to the same habitat exhibited subtle genetic patchiness, although they did not find overall significant temporal genetic variations. These recent findings clearly indicated that Japanese eels likely have different populations in its species range.

As mentioned above, however, Japanese eels appear to spawn at a very restricted location in synchrony with new moon periods (Tsukamoto 2006), and their larvae are transported passively by the NEC and Kuroshio, which likely has considerable changes in its speed, eddy structure, and route at daily, monthly or even decadal scales (Kimura et al. 2001; Miller et al. 2009, in press). If Japanese eels actually have two different genetic populations in their species range, which is directly connected by the strong Kuroshio, there must be a mechanism for larvae to consistently return back to similar latitudes where their parents formerly resided. But the present knowledge about the larval migration of the Japanese eel and oceanographic conditions in its route has not suggested any mechanisms so far to consistently divide them into different population. Contrary, the highly polymorphic population genetic markers has recently been suggested to vary spatially and temporally even within a panmictic population, and sometimes it leads the misunderstanding for the population genetic structure as is mentioned above (Pujolar et al. 2006; Maes et al. 2006). Considering these facts, it seems to be reasonable at the moment, to suppose that at least the temperate species of anguillid eels, which migrate back to their growth habitats in strong currents such as eastern boundary currents, are basically panmictic. This type of ecological perspective should also be used to help evaluate the population structure of the shortfinned eel, A. australis, which has been historically divided into two subspecies by Ege (1939). No statistical difference in mtDNA markers has been found between these two subspecies (Dijkstra and Jellyman 1999), but Shen and Tzeng (2007a) found some statistical differences in these two subspecies using microsatellite markers. These two subspecies also have a slight, but statistically different numbers of total vertebrae (Watanabe et al. 2006) that
originally resulted in their separation into different subspecies. How these differences appear to be maintained and why there are no greater genetic differences between the two subspecies are unknown, so further population studies beyond a simple snapshot in time are needed.

5. Life histories of tropical anguillids

5-1. Spawning areas of tropical eels

Compared to the many research cruises conducted in the WNA and WNP to study the spawning areas and larval distributions of the Northern Hemisphere temperate anguillids, only one expedition had been carried out to specifically find the spawning areas of tropical anguillids prior to the year 2000 (Miller 2003). This only historical expedition was the Carlsberg Foundation’s Oceanographical Expedition Round the World by the Danish in 1928–1930 (Jespersen 1942). A large number of shortfinned eel leptocephali were collected during this expedition off West Sumatra, which suggested that *A. bicolor bicolor* had a spawning area in this region (Jespersen 1942; but see also Miller 2003, Aoyama *et al.* 2007). However, because other small leptocephali collected by that expedition could not be identified exactly using only morphological characters and no tiny leptocephali were found, only a limited amount of information about the spawning areas of tropical anguillids could be gained from their collection data.

This situation changed however, after the establishment of a genetic species identification method for anguillid leptocephali, and new research cruises were conducted to study the spawning areas and larval distributions of tropical anguillids. In February 2000 a few small *A. celebesensis* (12–20 mm TL) and *A. borneensis* (8–13 mm) leptocephali, which were the smallest larvae of these species ever collected, were found in the Celebes Sea, suggesting that these two species spawned in this region (Aoyama *et al.* 2003; Fig. 13). Then during a cruise of the R/V *Baruna Jaya VII* in the waters around Sulawesi Island in May 2001, 53 tropical eel leptocephali were collected (Aoyama *et al.* 2003). These included small *A. celebesensis* leptocephali (13–15 mm) collected in Tomini Bay, which is a relatively closed but deep bay south of the northern arm of Sulawesi Island. Another survey by the *Baruna Jaya VII* around Sulawesi Island in September of 2002 also collected anguillid leptocephali of several species, but *A. celebesensis* were interestingly absent in Tomini Bay where they had been during May of the year before (Wouthuyzen *et al.* 2009). These cruises showed the presence of different spawning areas of *A. celebesensis* in the Celebes Sea and Tomini Bay that are located just a few hundred kilometers apart (Aoyama *et al.* 2003). This indicated that *A. celebesensis* likely spawned in two different ocean basins depending on which side of Sulawesi Island they were living on. By spawning in these two basins, this species likely has a totally different migratory ecology and population structure than any other anguillid species that has been studied. Because both *A. celebesensis* and *A. borneensis* have small species ranges, the nearby locations of their spawning areas indicated that they had only made very short spawning migrations, which is in clear contrast to their temperate counterparts (Aoyama *et al.* 2003).

Leptocephali of other tropical anguillid species were collected in the Indonesian Seas during these surveys, but not all species were found to have the same types of spawning and larval migration strategies. In total, the genetic species identification of all the anguillid leptocephali from the three cruises around Sulawesi Island distinguished them into 28 *A. marmorata* (33.1–50.7 mm and one glass eel, 47.8 mm; Fig. 14), 42 *A. celebesensis* (12.3–47.8 mm), 3 *A. borneensis* (8.5, 13.0, 35.4 mm), 7 *A. bicolor* (42.6–49.2 mm), and 4 *A. interioris* (43.4–48.9 mm). These collection data in the central Indonesian Seas during three different times of the year clearly indicated that there were no small leptocephali of *A. marmorata* or *A. bicolor pacifica* despite small specimens of other species being collected. In the case of *A. marmorata*, the northern population of this species that was identified genetically as being distributed from Sulawesi Island north through the Philippines to southern Japan (Ishikawa *et al.* 2004; Minegishi *et al.* 2008), has a spawning area in the NEC to the west of the Mariana Islands (Miller *et al.* 2002). In fact, *A. marmorata* leptocephali have been collected during many different years in the region to the west of the Mariana Islands (Fig. 15; Miller *et al.* 2002; Kuroki *et al.* 2005, 2006a). However,
no small leptocephali of *A. bicolor pacifica* have ever been collected, so its spawning area is presently only a matter of speculation. The geographic range of this subspecies extends across northern Indonesia, the Philippines and New Guinea (Ege 1939; Watanabe et al. 2004b, 2005b), so it may also spawn somewhere offshore in the WNP. The lack of small leptocephali of both *A. bicolor pacifica* and *A. marmorata* in the Indonesian waters supports the hypothesis that both species spawn in the WNP.

A spawning area of the other subspecies *A. bicolor bicolor* that is distributed on both sides of the Indian Ocean has been suggested to be off West Sumatra (Jespersen 1942; see Miller 2003), although the exact species identity of the smaller sized leptocephali are questionable. A recent survey by the *Baruna Jaya VII* in the same region in June 2003 confirmed the presence of leptocephali there, but no small specimens were collected (Aoyama et al. 2007). Due to the presence of strong equatorial current jets that could transport leptocephali towards the area off West Sumatra (Aoyama et al. 2007), more collection data including areas further offshore are needed to better define the spawning area of this species.

Some progress also has been made in beginning to learn about the spawning areas of tropical anguillids in the WSP. The collection of 12 genetically identified leptocephali of
A. reinhartii (20.0–34.0 mm) in the same area in the SEC as A. australis leptocephali (Aoyama et al. 1999a; Kuroki et al. 2008a; see Jellyman and Bowen 2009, in press) has indicated that this species also migrates far offshore to spawn. However, only a few specimens were collected from this region in previous years and its species identification were not clear except for one specimen of A. obscura from further east near Tahiti (Fig. 10; Jespersen 1942; Castle 1963). The three surveys by the Hakuho Maru in 1995, 2001 and 2004, were also able to clearly identify only a few individuals of A. marmorata (N = 15, 19.0–50.9 mm), A. obscura (N = 1, 36.7 mm), and A. megastoma (N = 2, 41.7, 42.8 mm) as summarized by Kuroki et al. (2008a) (Fig. 10).

The recent population genetic analyses described below suggested that there may be more than one spawning area of A. marmorata in the region, with the eels found in French Polynesia being a different population from those in Fiji and perhaps in New Caledonia (Ishikawa et al. 2004; Minegishi et al. 2008). However, not enough leptocephali have been collected so far to speculate about the exact locations of the spawning areas of A. marmorata, or of the other two species, which have mostly overlapping distributions from New Guinea across the tropical islands of the WSP to French Polynesia (Ege 1939; Watanabe et al. 2004a, b). Further sampling surveys in conjunction with population genetic studies on each species are needed to determine

---

Fig. 14. Photographs of all four larval stages of Anguilla marmorata showing the young leptocephalus (17 mm TL), fully grown leptocephalus (49 mm), metamorphosing leptocephalus (46 mm), and oceanic glass eel (47 mm) stages. The top two larvae are from the North Equatorial Current region, and the bottom two are from the central Indonesian Seas.
if these tropical eels have multiple local spawning areas, or if any of them have single spawning areas as panmictic populations.

5-2. Larval migration of tropical eels

The knowledge gained from the collections of small leptocephali of tropical eels has indicated that their larval migrations can range from very short to distances similar to some temperate species. The larval migration distances for *A. marmorata* in the northern edge of the species range in the North Pacific are similar to those of the Japanese eel (Fig. 15). The migration distances of some *A. reinhartii* also may be similar to the shorter distances of migration of *A. australis* in the WSP. In contrast, the distances for *A. celebesensis* from the center of Tomini Bay to the surrounding coastlines are less than 100 km.

These variations in migration distances are also reflected in the maximum sizes of their leptocephali and larval growth rates. Leptocephali of tropical eels have smaller maximum sizes of about 50–55 mm (Jespersen 1942; Kuroki et al. 2005, 2006a; Aoyama et al. 2007), whereas the temperate species can reach about 70 mm and even greater than 80 mm in the case of the European eel (Table 1). Several otolith studies have recently been conducted to learn about the early life history and larval migrations of tropical eels. These studies have been carried out on several species, such as *A. marmorata* (Kuroki et al. 2005), *A. interioris* (Kuroki et al. 2006b), and *A. bicolor bicolor* (Kuroki et al. 2007). Then in a larger study of four species of
**Table 1.** List of all species of the genus Anguilla and the present knowledge about their ecological characters.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spawning area</th>
<th>Ref.</th>
<th>Migration distance (km)</th>
<th>Full grown size (mm)</th>
<th>Ref.</th>
<th>Growth rate (mm/day)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Temperate species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anguilla</em></td>
<td>Sargasso Sea</td>
<td>1, 2</td>
<td>5000</td>
<td>75</td>
<td>1, 2, 7</td>
<td>0.38*</td>
<td>15</td>
</tr>
<tr>
<td><em>A. rostrata</em></td>
<td>Sargasso Sea</td>
<td>1, 2</td>
<td>2500</td>
<td>70</td>
<td>1, 2, 7</td>
<td>0.38*</td>
<td>15</td>
</tr>
<tr>
<td><em>A. japonica</em></td>
<td>West of Mariana</td>
<td>3</td>
<td>2500</td>
<td>60</td>
<td>16</td>
<td>0.43*</td>
<td>16</td>
</tr>
<tr>
<td><em>A. dieffenbachii</em></td>
<td>Westen SEC region</td>
<td>4, 5</td>
<td>?</td>
<td>?</td>
<td></td>
<td>—</td>
<td></td>
</tr>
<tr>
<td><em>A. australis australis</em></td>
<td>Westen SEC region</td>
<td>4, 5, 6</td>
<td>?</td>
<td>?</td>
<td>7</td>
<td>0.51</td>
<td>17</td>
</tr>
<tr>
<td><em>A. australis schmidtii</em></td>
<td>Westen SEC region</td>
<td>4, 5, 6</td>
<td>?</td>
<td>?</td>
<td>7</td>
<td>0.51</td>
<td>17</td>
</tr>
<tr>
<td><strong>Tropical species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. reinhardtii</em></td>
<td>Westen SEC region</td>
<td>4, 5, 7</td>
<td>?</td>
<td>?</td>
<td></td>
<td>—</td>
<td>17</td>
</tr>
<tr>
<td><em>A. celebesensis</em></td>
<td>Celebes Sea, Tomini Bay</td>
<td>8</td>
<td>50</td>
<td>50</td>
<td>18</td>
<td>0.56</td>
<td>18</td>
</tr>
<tr>
<td><em>A. borneensis</em></td>
<td>Celebes Sea</td>
<td>8</td>
<td>100</td>
<td>50</td>
<td>18</td>
<td>0.52</td>
<td>18</td>
</tr>
<tr>
<td><em>A. interioris</em></td>
<td>East of New Guinea, West of Sumatra</td>
<td>7, 9</td>
<td>?</td>
<td>50</td>
<td>9</td>
<td>0.49–0.52</td>
<td>9</td>
</tr>
<tr>
<td><em>A. marmorata</em></td>
<td>West of Mariana, Indonesia, East of Madagascar Island, SEC</td>
<td>7, 10, 11, 12</td>
<td>1000</td>
<td>50</td>
<td>18, 12</td>
<td>0.44</td>
<td>18</td>
</tr>
<tr>
<td><em>A. bicolor pacifica</em></td>
<td>Equatorial Pacific region</td>
<td>7</td>
<td>1000</td>
<td>50</td>
<td>18</td>
<td>0.47</td>
<td>18</td>
</tr>
<tr>
<td><em>A. bicolor bicolor</em></td>
<td>West of Sumatra, East of Madagascar Island</td>
<td>7, 11, 13, 14</td>
<td>?</td>
<td>?</td>
<td>14</td>
<td>0.36</td>
<td>14</td>
</tr>
<tr>
<td><em>A. marmorata</em></td>
<td>Westen SEC region</td>
<td>4, 5, 7</td>
<td>?</td>
<td>?</td>
<td></td>
<td>—</td>
<td></td>
</tr>
<tr>
<td><em>A. marmorata</em></td>
<td>Westen SEC region</td>
<td>4, 5, 7</td>
<td>?</td>
<td>?</td>
<td></td>
<td>—</td>
<td></td>
</tr>
<tr>
<td><em>A. marmorata</em></td>
<td>Westen SEC region</td>
<td>4, 5, 7</td>
<td>?</td>
<td>?</td>
<td></td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>


*growth rate based on the regression of TL and age (see 18)
tropical eel leptocephali, Kuroki *et al.* (2006a) found that *A. borneensis* and *A. celebesensis* with the shortest migration distances appeared to have faster growth rates than *A. marmorata* and *A. bicolor pacifica* that had longer migrations. Similarly, *A. reinhartii* had a slightly faster growth rate than *A. australis* in the WSP (Kuroki *et al.* 2008a). These findings suggested that tropical anguillids with short migrations may have a larval strategy of fast growth and metamorphosis at a relatively small size compared to the temperate species, and then recruit at a young age (Kuroki *et al.* 2006a; Reveillac *et al.* 2008).

Support for this hypothesis has been seen in studies on the glass eels of these species. Arai *et al.* (1999b, 2001) examined the otolith microstructure of three species of tropical anguillid glass eels that recruited to the northern part of Sulawesi Island (Poigar River) on the Celebes Sea side. This study found that *A. celebesensis* had consistently younger ages of about 90 days at the onset of metamorphosis and 120 days at recruitment (counted from the total number of increments) than did *A. marmorata* and *A. bicolor bicolor* (both species were higher than 120 days at metamorphosis and 150 days at recruitment, Fig. 16). Comparisons of these two parameters show clear contrasts in the ages of the locally spawned species *A. celebesensis* and *A. marmorata/A. bicolor pacifica* whose leptocephali likely migrate from the NEC far to the north. Otolith examinations of these three species showed similar patterns of younger ages of *A. celebesensis* in all cases (Arai *et al.* 1999c, d; Marui *et al.* 2001) except for glass eels thought to be *A. celebesensis* that were collected at the northern tip of Luzon Island of the Philippines (Arai *et al.* 2003b).

Studies on the temporal abundance of glass eels recruiting to the Poigar River on Sulawesi Island also have provided some indirect information about the larval migrations of these tropical eels. The collections were quantitatively made with the same method every month over a period of

---

Fig. 16. Plots of the estimated ages at metamorphosis and recruitment of glass eels of two species of tropical anguillid eels that recruited to the Poigar River of northern Sulawesi Island (Celebes Sea side) throughout 1997, which were obtained from examinations of their otolith microstructure. Reprinted with permission partially from *Mar. Ecol. Prog. Ser.*, 216, Arai *et al.*, Recruitment mechanisms of tropical eels, *Anguilla* spp. and implications for the evolution of oceanic migration in the genus *Anguilla*, 253–264, © 2001, Inter-Research.
four years. Arai et al. (1999b) first reported that the glass eels of *A. celebesensis* and *A. marmorata* were caught in large numbers throughout much of the year, but in smaller numbers during some months. Sugeha et al. (2001b) confirmed this pattern by sampling continuously for three years at the Poigar River and also showed that there were big catches of *A. celebesensis* during June and small catches especially in February and March of all three years. There also was some variability in the recruitment patterns among years such as in 1998, which may have been related to the large 1997–1998 El Niño event, but it is unclear if the larval migration was disrupted, or if downstream migration or spawning by the silver eels had been affected. The glass eel catches at this site were also large in 2000, with at least a few *A. celebesensis* and *A. marmorata* being collected throughout the year (Bataragoa et al. 2001). These findings of big catches only in some months suggest that there may be peak spawning seasons in the region around the Celebes Sea for *A. celebesensis*.

There also have been some studies on the glass eels of tropical anguillids in the Indian Ocean that have provided information about their larval durations and recruitment patterns. The glass eels of *A. bicolor bicolor* collected near the mouth of the Cimandiri River on the Indian Ocean side of Java Island were also found to be older than those of *A. celebesensis* described above (Setiawan et al. 2001). Otolith analyses of specimens collected year round in the Cimandiri River in 1998 and 1999 had mean ages ranging from 144 to 196 days, showing that glass eels at that location were relatively old consistently (Setiawan et al. 2001). However, a sample of the glass eels of this species from Réunion Island to the east of Madagascar showed a much younger average age at recruitment of about 80 days (Robinet et al. 2003a). Further research on this species at a number of other sites in the western Indian Ocean have found older mean ages of recruitment ranging from 130 to 142 days (Robinet et al. 2008). Another species endemic the southwest Indian Ocean, *A. mossambica*, was found to have a shorter age at recruitment than the averages of *A. bicolor bicolor* and *A. marmorata* (Robinet et al. 2008).

5-3. Growth phase and spawning migration

Compared to temperate eels, very little is known about the freshwater growth phase or downstream migration of tropical anguillid eels. There have been a few studies examining the freshwater distributions of the species in the WSP (Marquet and Galzin 1991; see Jellyman 2003) and of *A. marmorata* on Réunion and Mauritius islands in the western Indian Ocean (Robinet et al. 2003b, 2007). Some information is also available about eels in eastern Africa (Jubb 1960, 1961; Balon 1975) and elsewhere (Wickstrom and Enderlein 1988; Williamson and Boetius 1993). More recent studies have examined the gonadal development, demographic characteristics, and growth of *A. reinhartii* in eastern Australia (Walsh et al. 2003, 2004, 2006). Other studies used Sr:Ca ratios to study tropical eels in Taiwan (Shiao et al. 2003) and the northern Philippines (Briones et al. 2007).

Perhaps the first major effort to study tropical anguillids was that of Sugeha (2003), which found high growth rates of *A. marmorata* yellow eels on Sulawesi Island (mean: 137 mm/year). These growth rates were even considerably higher than have been observed for the Japanese eel, which appears to have a higher growth rate than other temperate anguillids (see Kotake et al. 2007; Yokouchi et al. 2008). The study by Sugeha (2003) also examined catches of eels attempting to leave Poso Lake of central Sulawesi Island, which flows into Tomini Bay, to start their spawning migration. An entire lack of downstream migrating silver eels from the lake was observed from mid-August to early November of 2001, suggesting that the spawning season was not continuous throughout the year at that location. Another interesting finding was that the two primary species migrating out of the lake had different GSI values. Examinations of their relative gonad sizes showed that *A. celebesensis* had much higher GSI values than *A. marmorata* (Sugeha 2003). This is understandable because the former species spawns in the bay after a short migration and the latter species still had a long migration to go back to its NEC spawning area as discussed above. Similar observations of silver eels with high GSI values were made in *A. bicolor bicolor* and *A. marmorata* on Réunion Island suggesting that their spawning migrations were not particularly long (Robinet et al. 2003c). But it is alternatively possible to
suppose that GSI on departure from their growth habitat is not directly related to the migration distance because larger species probably swim faster than smaller species and are able to reach their spawning site far off shore despite their high GSI, as has been suggested by Jellyman and Bowen (2009, in press). Also if the GSI values at the final stage, just before the spawning or the end of the spawning migration, are different in each species, simple comparisons of GSI on departure give no information about their relative sexual maturation stages.

Considerably less attention has been paid for the spawning migration of tropical anguillid so far in comparison with temperate species that show spectacular long distance migration. However, information on the spawning migration of tropical anguillid species that included the most ancestral lineage in the genus are fundamental to understand the origin and evolution of the spawning migration of the freshwater eels.

6. Population structure of tropical eels

Similar to life history studies, research on the population structures of tropical species of anguillid eels are only just beginning in recent years. The first population genetic study on a tropical species was conducted by Ishikawa et al. (2004) on the widely distributed species A. marmorata, which was unlikely to be panmictic because they are distributed throughout most of the Indo–Pacific ranging from the eastern side of Africa to French Polynesia. This study used 449 eels collected from 10 localities throughout the species range and found five apparent populations using mitochondrial and AFLP markers. These populations included a northern population that spawns in the NEC as discussed above, and other likely populations in the western Indian Ocean, the eastern Indian Ocean, the Fiji region, and French Polynesia (Tahiti).

A subsequent more extensive study by Minegishi et al. (2008) used longer sequences of mtDNA and eight microsatellite DNA loci from eels collected at 13 sites, including five sites not used by Ishikawa et al. (2004). Minegishi et al. (2008) basically supported the result of the previous study but suggested metapopulation structure for A. marmorata in the Indian Ocean and the WSP, respectively (Fig. 17). Further they found a clearly different new population at Guam in the Mariana Islands of the WNP (Fig. 17). Watanabe et al. (2009, in press) also found strong evidence of a separate population in Guam and some of the other islands of Micronesia in

![Map showing the four major population groups of Anguilla marmorata estimated using eels collected at 13 locations (small white circles) throughout the species range in the genetic analysis of Minegishi et al. (in press). The eels in the Indian Ocean and South Pacific regions may each consist of metapopulations with some genetic differentiation in each region, but the North Pacific and Guam populations appear to be distinctly different from each other.](image)
an analysis of the total number of vertebrae (Fig. 18). The eels from Guam were found to have a significantly higher number of vertebrae than eels in any other region (Fig. 18). Another interesting finding was that individuals from at least two populations (North Pacific, South Pacific) appeared to be mixing in Ambon, which is a small island to the east of Sulawesi Island (Minegishi et al. 2008).

Other studies have focused on the population structure of *A. marmorata* and *A. bicolor* just in the Indian Ocean, or that of *A. reinhartii* in the WSP. One recent study of *A. marmorata* has focused on the detailed gene flow within the Indian Ocean basin using ten microsatellite loci and 444 eels from a wider range of locations (Gagnaire et al. unpublished data). The results of that analysis found evidence of east–west differentiation as was found in the previous studies, and indications of unidirectional gene flow from Sumatra to the Madagascar region. A less intensive examination of *A. bicolor* from eight different areas around the Indian Ocean found no differences in the number of total vertebrae or in the mtDNA control region (Watanabe et al. 2005b). The tropical eel *A. reinhartii* has a more limited species range in the northwest margin of the WSP and along the east coast of Australia. A recent study using

![Fig. 18. Frequency distributions of the total number of vertebrae of Anguilla marmorata from 13 locations throughout the species range. The numbers of vertebrae observed in the eels from various locations were statistically different in many cases, and the range at Guam and other Micronesian islands can be seen to be distinctly higher than in other areas. Data plotted from Watanabe et al. (2009, in press). The collection localities were: Réunion Island (REU), and Sumatra (SUM) in the Indian Ocean, the Japanese Archipelago (JPN), Luzon Island (LUZ), Sulawesi Island (SUL), Ambon Island (AMB), and Guam and Micronesia (MIC) in the western North Pacific, and New Guinea (NGU), New Caledonia (NCA), Fiji (FIJ), Samoa (SAM), and Tahiti (TAH) in the western South Pacific region.](image-url)
microsatellite DNA suggested that this species may consist of a single panmictic population (Shen and Tzeng 2007b). These first few studies on the population structures of tropical eels are suggestive that a variety of types of spawning and recruitment strategies and resulting population structures may have evolved among tropical species of the genus *Anguilla*. Future studies on the life histories and population structures of tropical species with much more limited geographic ranges and those inhabiting widely spread out small island groups will be important for gaining insight into migratory ecology and speciation mechanisms of anguillid eels.

7. Discussion

7-1. Evolution of migration in anguillid eels

From the preceding brief review of these subjects, it is clear that the spawning sites, larval migrations, other ecological traits, and the phylogenetic relationships of anguillid eels are still far from completely elucidated. However, the information available for both temperate and tropical species provides some insights into the evolution of migration in anguillid eels. Because anguillid eels appear to return to the spawning site in the ocean where they were born, Tsukamoto and Aoyama (1998) proposed a model for the speciation of anguillid eels using the “migration loop” concept to consider how range expansion and speciation occur in these fishes (see Tsukamoto et al. 2002).

Catadromous migration loops of anguillid eels between their offshore spawning areas and freshwater or estuarine growth habitats have evolved from a completely marine ancestor. Except for anguillid eels and a few rare ophichthid or muraenid species that enter freshwater habitat in the tropics, all other eels of the Anguilliformes are completely marine species. In addition, anguillid eels appear to be most closely related to the Serrirovermeridae (Inoue unpublished data), which is a completely mesopelagic family. Furthermore, the members of the Elopomorpha, which includes the true eels of the Anguilliformes and their close relatives such as the tarpons, bonefishes and notacanths, all share the common trait of having a marine leptocephalus larval stage (Fig. 19; Nelson 1994; Inoue et al. 2004). It has been suggested that anguillid eels originated in tropics (Aoyama et al. 2001b; Minegishi et al. 2005) and would have evolved the ability to migrate into fresh water to take advantage of resources where there were no other eel species to compete with. In contrast to eels, life history patterns and phylogenetic relationships suggest a freshwater ancestry of the Salmoniformes, with salmon and trout originating in fresh water in temperate regions and then gaining the ability to migrate into the ocean (Gross 1987; McDowall 2002; Ishiguro et al. 2003).

Having the catadromous life history, ancestral anguillid eels were diverged into many species. Ishikawa et al. (2004) proposed two simple models to illustrate the basic process of anguillid speciation based on the migration loop concept (Fig. 20). In model I the expansion of freshwater growth habitats of anguillid eels takes place first and then reproductive isolation follows when their spawning areas become separated spatially or temporally (Fig. 20[I]). This model can explain speciation within an ocean current system and may be exemplified in part by the Atlantic eels. In the case of the two anguillid species that live along both sides of the North Atlantic basin, it has been proposed that as the basin expanded due to continental drift, eventually two genetically distinct larval development patterns with different timing of metamorphosis were required to successfully recruit to both sides of the basin, which led to speciation, despite both species still sharing a spatially and temporally overlapping spawning area (Tsukamoto et al. 2002; Kuroki et al. 2008b). Alternatively, speciation beyond the margins of an ocean current system was proposed to be represented by model II (Fig. 20[II]), assuming that a new spawning site is established first and then (or simultaneously) a separation of growth habitats occurs. This type of model may apply to new species or populations forming within tropical species.

Evidence is now accumulating to indicate that the long distance spawning migrations of anguillid eels are made by temperate species, and have evolved from short scale migrations of their tropical ancestral congeners. Tsukamoto et al. (2002) proposed a model for explaining the
Fig. 19. Mitochondrial genomic evidence for the monophyly of the superorder Elopomorpha whose members all possess a leptocephalus larva. Adult and larval forms are shown for most species. Reprinted from *Mol. Phyl. Evol.*, 32, Inoue et al., Mitogenomic evidence for the monophyly of elopomorph fishes (Teleostei) and the evolutionary origin of the leptocephalus larva, 274–286, © 2004, with permission from Elsevier.
evolution of long distance migration in anguillid eels (Fig. 21). As was revealed recently, anguillid species inhabiting tropics appear to have faster larval growth rates and smaller maximum larval size than temperate species, and then, they tend to have shorter larval durations (Kuroki et al. 2006a; Tsukamoto et al. 2009a in press). This suggested the ancestral eels that originated in the tropics probably had small scale migrations between their freshwater or estuarine growth habitats and ocean spawning sites. However, their leptocephali would have dispersed not only to their original species range in the tropics, but could also accidentally disperse to higher latitudes.

Fig. 20. Two models for how changes in the migration loops of anguillid eels could lead to the creation of new populations and eventual speciation through the establishment of new migration loops. Reprinted with permission from Ichthyol. Res., 51, 2004, 343–353, Genetic evidence for multiple geographic populations of the giant mottled eel Anguilla marmorata in the Pacific and Indian Oceans, Ishikawa et al., Figure 6, © 2004, The Ichthyological Society of Japan.

Fig. 21. A diagram showing shifts in the migration loop of an anguillid species that could lead to speciation. The leptocephali are dispersed and recruit to higher latitudes causing an eventual change in growth habitats, whereas the adults still return to spawn at tropical latitudes.
over an evolutionary time scale (Fig. 21). If these eels that colonized higher latitudes migrated back to the original spawning area, then it could eventually result in the creation of a new large scale migration loop between their tropical spawning area and higher latitude growth habitat (Fig. 21; Tsukamoto et al. 2002).

This scenario of tropical species with short migration giving rise to temperate species with long migrations can be inferred from the phylogenetic tree in Fig. 5, where the basal species A. mossambica and A. bornenesis could have given rise to both the Atlantic eels (Atlantic Group) and the temperate eels in the WSP (Oceanian Group). However, it could also be inferred from the molecular phylogeny in Fig. 5, that the basal species of the large Indo–Pacific Group, the Japanese eel with a large scale migration and the tropical species A. reinhardtii with a mid-scale migration, could have given rise to species such as A. celebesensis which have very short distance migrations. This implies that it is possible for different migration scales to evolve from both long and short migration loops in anguillid eels. Kuroki (2007) found that even the individuals of the same species that recruited to the same location showed considerably large variation in their larval periods (e.g., A. celebesensis, 85–126 days; A. marmorata, 127–246; A. bicolor bicolor, 127–154; A. japonica, 153–230; A. australis, 210–281; A. dieffenbachii, 231–295; A. rostrata, 248–365; A. anguilla, 248–459). This indicated that anguillid eels possess an intrinsically wide variation in their larval periods. This variation may be related to a mechanism such as delayed metamorphosis that has been reported for coral reef fishes (McCormick 1999) and a carapid fish (Parmentier et al. 2004). Kuroki et al. (2006a) suggested that the key for determining the migration scale of anguillid species is their larval growth and maximum larval size, which directly influences their planktonic period and their species range. However, the maximum larval sizes of each species are inferred from a limited number of metamorphosing leptocephali that have ever been collected and the larval periods vary widely even in the same species. Leptocephali of large scale migration species that have lower growth rates and larger maximum larval sizes may have the potential to grow much faster and metamorphose earlier to finish their larval periods in a shorter time, if they were exposed to different environmental conditions such as higher temperatures or productivity in their larval migration routes.

Anguillid eels have a long evolutionary history that is estimated to have extended over 40–70 million years (Aoyama et al. 2001b) during which time many changes in the distributions of landmasses and current patterns have occurred. These changes have likely played important roles in the diversification of new species and populations of both tropical and temperate eels that have a variety of migration distances and larval durations. Future studies on more species of tropical anguillid eels that inhabit areas with unique patterns of growth habitat geography and ocean currents will surely add valuable new perspectives on the evolution of migration in this remarkable group of fishes found in many parts of the world.

7-2. Management and conservation of eel resources

The new perspective about the variable life histories and population structures of anguillid eels is important for beginning or expanding management and conservation efforts at a time when many species have been reported to be showing declining recruitment. Freshwater eels have shown drastic decreases worldwide for the last three decades and the European eel was listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II in 2007 (CITES 2007). Recruitment of the European eel and American eel have fallen to levels possibly as low as 1% of their highest levels, and the Japanese eel also has seen declines in recruitment and commercial catches of yellow and silver eels (Fig. 22) at a time when there is increasing economic demand for these fishes as food (Dekker 2003; Tsukamoto et al. 2009b, in press). The causes for these declines have not been clearly established because they likely include both anthropogenic effects on the growth phase and the escapement of silver eels (Haro et al. 2000; Feunteun 2002), and the effects of ocean–atmospheric changes on the larval growth and survival in the ocean (Bonhommeau et al. 2008; Miller et al. 2009, in press).

Because anguillid species were historically thought to each consist of a single panmictic population, the new realizations of multiple populations of the same species that have resulted from early life history and population genetic studies indicate that new, more regionally focused
management strategies are needed for tropical species (Miller et al. 2009, in press). For example with a panmictic population structure, overharvesting eels in one area likely will not affect subsequent recruitment to that particular area because new recruits will arrive randomly from spawners that originated from other areas. However, in the case of local populations, such as those around Sulawesi Island for *A. celebesensis* and in Micronesia for *A. marmorata*, each local population probably has a very specific migration loop, and almost no recruitment from other areas may occur. This means that overharvesting eels in each of these areas may have a major impact on recruitment back to that particular area by each local population.

The risk that habitat loss or degradation in combination with overharvesting could threaten some local eel populations with extinction, must be seriously considered in the case of tropical eels in many regions of the Indo–Pacific and Indian Ocean where the life histories of most species are still very poorly known. Although many mysteries about the complexities of the life histories and evolution of anguillid eels remain to be solved, actions must be taken now to ensure that the eels in each particular area survive so that the unseen biodiversity of these fascinating catadromous fishes can be preserved.

References


Bonhommeau S, Chassot E, Rivott E. Fluctuations in European eel (Anguilla anguilla) recruitment resulting from environmental changes in the Sargasso Sea. Fish. Oceanogr. 2008; 17: 32–44.


Chadwick S, Knights B, Thorley JL, Bark A. A long-term study of population characteristics and downstream migrations of the European eel Anguilla anguilla (L.) and the effects of a migration barrier in the Girnock Burn, north-east Scotland. J. Fish Biol. 2007; 70: 1535–1553.


Dekker W. Synthesis and Analyses. In Slipping through our hands–Population dynamics of the European


Schmidt J. The breeding places of the eel. Phil. Trans. R. Soc. Lond. 1922; 211: 179–208.


Setiawan IE, Mochioka N, Amarullah H, Nakazono A. Inshore migration and spawning season of the

Shen KN, Tzeng WN. Genetic differentiation among populations of the shortfinned eel *Anguilla australis* from East Australia and New Zealand. *J. Fish Biol.* 2007a; **70**: 177–190.


Thibault I, Dodson JJ, Caron F. Yellow-stage American eel movements determined by microtagging and acoustic telemetry in the St Jean River watershed, Gaspé, Quebec. *Can. J. Fish Biol.* 2007; **71**: 1095–1112.


**References**


