Review Article

Skin coloration and habitat preference of the freshwater *Anguilla eels*

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Abstract

The genus *Anguilla* comprises 16 species and three subspecies of freshwater eels, which can be further divided into marbled and plain eels in terms of skin coloration on their backs. Owing to the overlap of geographical distributions between most marbled and plain eels in tropical/subtropical regions, the co-existence of marbled and plain eels in the same river is common. To understand the correlation between eel skin color and its habitat preference in the river, the distribution patterns of all anguillid eels were collected and analyzed. Results showed that all marbled eels distribute in tropical/subtropical areas and preferred the middle/upper reaches. The plain eels distributed both in temporal and tropical/subtropical areas, and preferred to inhabit the middle/lower reaches and estuaries. Plain skin coloration may help them easily remain hidden in a sandy and muddy environment, which is common in estuaries and lower reaches of rivers in tropical/subtropical areas, while mottled skin coloration more easily blends in with substrates such as cobble, gravel, and fallen leaves which are commonly found in the upper reaches of rivers in the tropical/subtropical areas. The different habitat preference between marbled and plain eels in the tropical/subtropical areas are likely a result of adaptive evolution to avoid potential interspecific competition, and this finding is meaningful for developing applicable management plans for eels.

Introduction

For centuries, the life history of freshwater eels (genus *Anguilla*) was a mystery to biologists. Freshwater eels are typical catadromous fish; they spend most of their lifetime in freshwater rivers and estuaries before finally migrating to their spawning grounds in the ocean for reproduction [1]. In total, there are 16 species and three subspecies of freshwater eels identified in the world [2-4], which can be categorized into two groups based on body coloration: mottled skin and uniformly-colored skin, called "marbled eels" and "plain eels" [5]. Marbled eels are typically distributed mainly in tropical and subtropical regions, whereas plain eels are distributed over tropical, subtropical, and temperate regions [1]. Marbled and plain eels coexist in some rivers in tropical and subtropical regions, where they may share the same niches, and forage for the same prey, thereby causing possible interspecific competition [4]. Thus, under selection pressure, eels may evolve some morphological and physiological characters to reduce interspecific competition and maximize their sustainability.

In recent years, several studies have been conducted on habitat choices of eels, and these revealed that they can be influenced by extrinsic environmental factors, such as salinity, water temperature, river size, and carrying capacity [6-8]. Other than these factors, the habitat preference of the eel in the river appears to be species-specific. For instance, the giant mottled eel (*A. marmorata*, a marbled eel) was inclined to inhabit the middle and upper reaches of rivers, but the Japanese eel (*A. japonica*, a plain eel) tended to dwell in the estuaries and lower reaches of rivers, as determined by analysis of trace elements (Sr/Ca ratios) in the otoliths taken from wild-captured eels in the same river [6,7,9], or by field investigation [10]. Body coloration of animals facilitates a number of important physiological and behavioral functions, including thermoregulation, mate attraction, rival deterrence, and predator avoidance [11]. To better understand the life history strategy of the anguillid eels, especially the role of eel skin color on its habitat preference in the river, data were collected and analyzed to summarize the phylogenetic relationship, geographical distribution and habitat preference between marbled and plain eels.

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Materials and methods

Body coloration, biogeographic distribution and habitat preference of *Anguilla* eels

The habitats of freshwater eels in the river can be classified into the upper reaches/mountain stream, middle reaches, and lower reaches/estuaries according to the hydrological conditions and the distance from the estuary. We searched online reference banks of Web of Science, Library of Congress, and Google Scholar till December 2019 to acquire habitat distribution information of anguillid eels. The search used combined key words like *Anguilla*, habitat, and distribution. We also searched specialist books and conference proceedings we had on hand regardless of the language. All acquired papers studying the biogeographic distribution and habitat preference of *Anguilla* eels were screened by manpower.

Evolutionary relationships of *Anguilla* eels

The evolutionary history of 19 *Anguilla* eels was inferred using the Neighbor–Joining method (Saitou & Nei, 1987) based on the complete mitochondrial genome (Table 1). The marine eel *Moringua edwardsi* was used as the outgroup species. The optimal tree with the sum of branch length = 0.66905714 was shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) was shown next to the branches [12]. The evolutionary distances were computed using the Maximum Composite Likelihood method [13] in the units of the number of base substitutions per site. This analysis involved 20 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions

Table 1: Accession numbers of 19 *Anguilla* eels and one outgroup marine eel.

Species	Accession No.
Anguilla japonica	NC_002707.2
Anguilla anguilla	NC_006531.1
Anguilla australis australis	NC_006532.1
Anguilla australis schmidti	NC_006533.1
Anguilla bicolor bicolor	NC_006534.1
Anguilla bicolor pacifica	NC_006535.3
Anguilla malgumora	NC_006536.1
Anguilla celebesensis	NC_006537.1
Anguilla dieffenbachii	NC_006538.1
Anguilla interioris	NC_006539.1
Anguilla marmorata	NC_006540.1
Anguilla megastoma	NC_006541.1
Anguilla mossambica	NC_006542.1
Anguilla bengalensis labiata	NC_006543.1
Anguilla bengalensis nebulosa	NC_006544.1
Anguilla obscura	NC_006545.1
Anguilla reinhardtii	NC_006546.1
Anguilla rostrata	NC_006547.2
Anguilla luzonensis	NC_011575.1
Moringua edwardsi	AP_010840.1

containing gaps and missing data were eliminated (complete deletion option). There were a total of 16350 positions in the final dataset. Evolutionary analyses were conducted by MEGA X [14].

Results

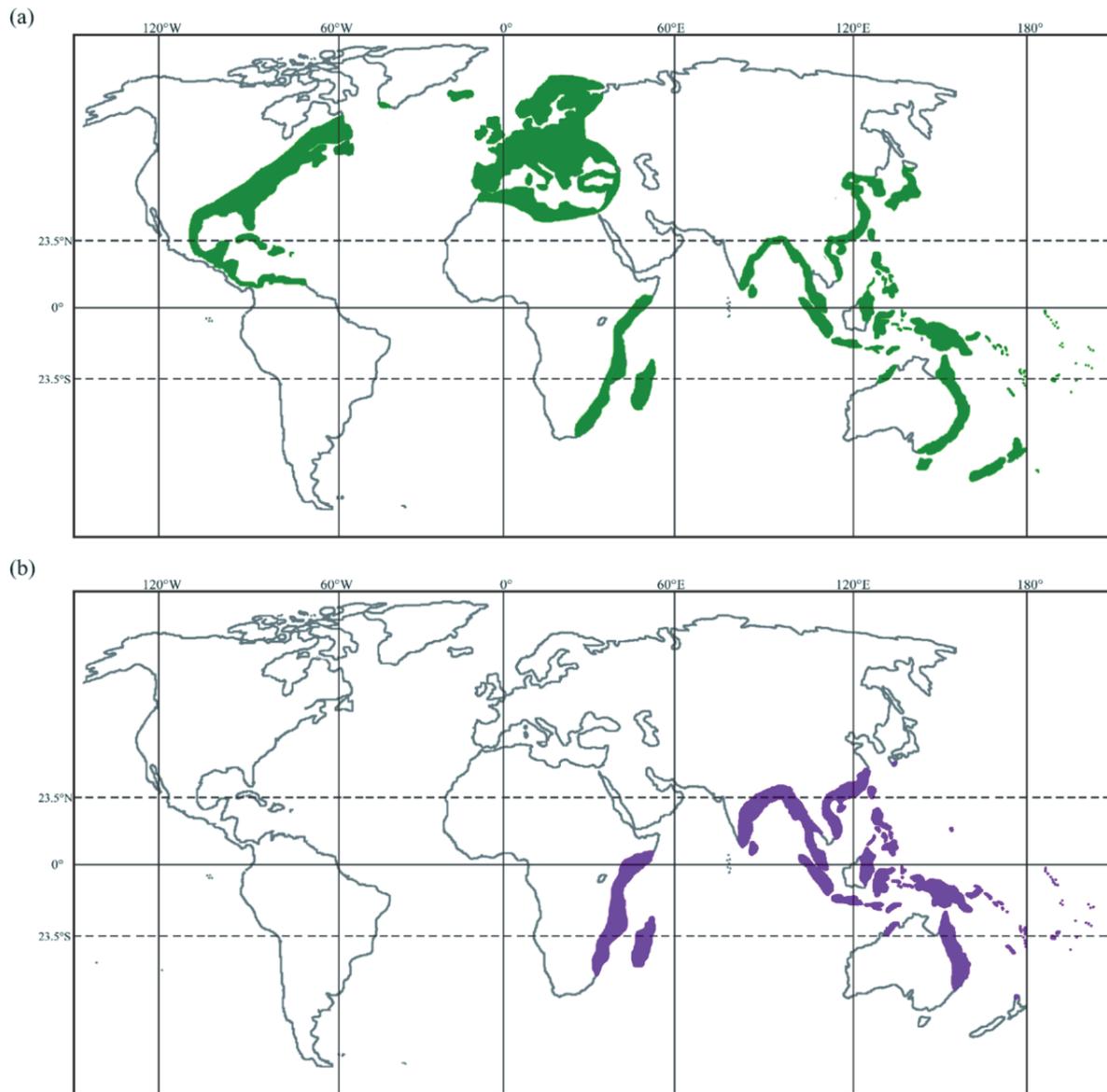### Relationship between body coloration and habitat usage of freshwater eels

With reference to previous studies, *A. marmorata*, *A. luzonensis*, *A. bengalensis bengalensis*, *A. bengalensis labiata*, *A. interioris*, *A. celebesensis*, *A. megastoma*, and *A. reinhardtii* were classified as marbled eels, and all other 11 species/subspecies were classified as plain eels. The worldwide geographical distribution of marbled eels and plain eels showed that the marbled eels often overlapped with those of plain eels (Figure 1) in tropical/subtropical areas.

Body coloration, geographical distribution, and habitat distribution data of all eel species were listed (Table 2). *A. marmorata* was inclined to inhabit the upper reaches of rivers, while *A. japonica*, *A. bicolor bicolor*, and *A. bicolor pacifica* (all plain eels) tended to inhabit the lower reaches (brackish/sea waters) [6,7,10,15,16]. *A. bengalensis bengalensis*, the Indian mottled eel, was reported to reside from the upper- to midstream areas with cooler water temperatures and higher elevation [8,17]. The African mottled eel, *A. bengalensis labiata*, mainly inhabited areas far inland by surmounting formidable barriers in their upstream migration [18,19]. The Luzon mottled eel, *A. luzonensis*, mainly found in Luzon Island of the Philippines (Han et al. 2016), inhabited the upper reaches and pure freshwater areas suitable for its growth [20]. *A. interioris*, the long-finned marbled eel, was mainly found in the freshwater of highlands in New Guinea [21], but the glass eels of *A. interioris* were ever detected at Java Island and southern Mindanao Island [22,23]. Another marbled eel, *A. celebesensis*, was reported to reside from the upper reaches of rivers in Sulawesi Island [24,25]. In addition to the Sulawesi Island, the glass eels of *A. celebesensis* were ever detected at Philippines coasts [26]. *A. megastoma*, the Pacific long-finned marbled eel, was found only in the middle or upper reaches near the headwaters of freshwater rivers [27,28]. The Australian long-finned marbled eel, *A. reinhardtii*, was one of main eel species at East Coast of Australia [29], and commonly found in many freshwater areas, including the upper reaches of rivers, dams, and lakes [30].

A. mossambica, a species of plain eel, is an inter-habitat migrant, moving between freshwater and seawater habitats, as indicated by microchemical analysis of their otoliths [31]. In another study, *A. mossambica* was found to inhabit coastal and estuarine areas without migration upstream into inland freshwater areas [32]. *A. malgumora* (*A. borneensis*), also called Indonesian longfinned eel, was a common plain eel inhabiting the lower and middle reaches of rivers in Borneo and Sulawesi Island of Indonesia and Sabah of Malaysia [33,34]. *A. obscura*, the Pacific short-finned plain eel, was distributed primarily over the lower reaches of rivers and coastal lagoons at western South Pacific, including Papua New Guinea, Fiji, and French Polynesia [27,35,36]. The other two short-finned plain eels,

Figure 1: Worldwide biogeographical distribution of freshwater eels (a) Plain-colored eels were mainly distributed in temperate, subtropical, and tropical areas (green). (b) Marbled eels were distributed in subtropical and tropical areas (purple). This figure was redrawn by the authors using Adobe Illustrator CS6 (Adobe Systems Incorporated, USA) with reference to a world map (WRLD-EPS-01-0006), which was downloaded from the Free Vector Maps website (https://www.freevectormaps.com/).

A. australis australis and *A. australis schmidtii*, were distributed mainly over eastern Australia and New Zealand, respectively, where their predominant habitats were lower reaches of rivers and estuaries [8,20,37]. In New Zealand, *A. dieffenbachi* (a plain eel) was commonly found in pure freshwater near the middle and lower reaches of rivers . Most populations of *A. rostrata* and *A. anguilla* were found in estuaries, lower reaches of rivers, and lowland lakes, where they usually completed their growth phase. However, they also appeared in the middle and upper reaches of rivers [38–40].

Phylogeny analysis of *Anguilla* eels in relationship to skin color and habitat type

The phylogenetic relationships, skin color and temporal/tropical characters of 19 *Anguilla* eels were constructed in Figure 2. Generally, eels with closer phylogenetic relationships

possess similar morphological and distribution characteristics. Most marbled eels shared a close phylogenetic relationship, and, likewise, most of the plain eels shared a close phylogenetic relationship. All marbled eels distribute in tropical/subtropical areas, and all temporal eels have plain skin colors.

Discussion

Teleost fish develop at least six classes of pigment cells (chromatophores) leading to a fascinating diversity of colors [41]. anguillid eels are characterized with a dark or marbled back produced by black/brown melanophores and yellow/orange xanthophores at the inner and outer boundaries of the dermis [42]. The mechanism in controlling skin color pattern of the anguillid eels may be related to Agouti signaling protein [41]. Some animals adapt to their environment through body coloration. For example, chameleons maintained crypsis

and communicated by changing their body coloration [43]. Cephalopods, such as octopuses, can rapidly change their body coloration to mimic visual characteristics of the background [44]. Another method of camouflage, known as countershading, has been reported in fish species [11,45]. Some body coloration of fish, including eels, is darker on the upper side and brighter on the underside. When seen from the underside, the brighter ventral body would blend in with the light background. In contrast, when seen from the top in daylight, the darker dorsal surface would blend in with the dark background of the deep water or substrate below [46]. Freshwater eels may also have evolved different body colorations (marbled and plain) in order to blend in with their habitat.

Figure 2: Phylogenetic tree and skin color of the genus *Anguilla*.

The comprehensive analysis of this study indicated that, in tropical/subtropical areas where marbled and plain eels coexist, marbled eels tended to inhabit the middle to upper reaches of rivers while plain eels prefer the habitats located from the middle reaches to estuaries (Table 2). In a typical river system of tropical/subtropical areas, the substrates found in upper reaches are primarily boulders, bedrock, cobble, and gravel, which are quite different from the substrates of the lower reaches, which are more sandy and muddy because rivers deposit eroded materials carried from the upper reaches [47]. The countershading of plain eels may help them remain hidden in a sandy and muddy environment, allowing them to avoid being detected by predators/prey. On the other hand, marbled eels can blend in with substrates such as cobble, gravel, and fallen leaves in the upper reaches.

In rivers located in tropical/subtropical areas, they were usually cohabited by at least one dominant plain eel and one dominant marbled eel. For example, *A. japonica* (plain) and *A. marmorata* (marbled) were dominant and coexisted in the rivers of Taiwan [3,10]; *A. bicolor pacifica* (plain) and *A. luzonensis* (marbled) were dominant and coexisted in rivers on East Luzon Island [48]; *A. australis australis* (plain) and *A. reinhardtii* (marbled) were dominant and coexisted in rivers of eastern Australia [29]; *A. mossambica* (plain) and *A. marmorata* (marbled) were dominant and coexisted in rivers of Mozambique [31]; and *A. bicolor bicolor* (plain) and *A. bengalensis bengalensis* (marbled) were dominant and coexisted in rivers of Peninsular Malaysia and India [4,17]; and *A. marmorata* (marbled) and *A. bicolor pacifica* (plain) were dominant and coexisted in rivers of Vietnam [16]. In addition, *A. obscura* (plain) using the lower reaches of rivers, *A. marmorata* (marbled) using the middle
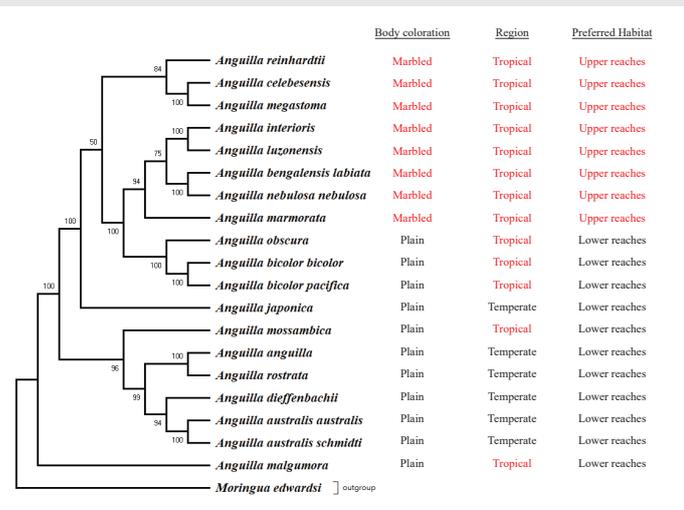
Table 2: Body coloration, biogeographical distribution and preferred habitats of *Anguilla* spp.

Species	Body coloration	Main geographical distribution	Preferred habitat	Main References
A. marmorata	Marbled	Taiwan, Indonesia, Philippines, East Africa, French Polynesia, Malaysia, Vietnam	Upper reaches	[6,7,10,15,16,31]
A. bengalensis bengalensis	Marbled	India, Peninsular Malaysia	Upper reaches	[8,17]
A. bengalensis labiata	Marbled	East Africa, Kenya	Upper reaches	[18,19]
A. luzonensis	Marbled	Luzon Island (Philippines)	Upper reaches	[20,48]
A. interioris	Marbled	Papua New Guinea, Mindanao Island (Philippines), Java & Sulawesi Island (Indonesia)	Upper reaches	[21-24]
A. celebesensis	Marbled	Sulawesi Island (Indonesia), Philippines	Upper reaches	[24-26]
A. megastoma	Marbled	Solomon Islands, Fiji, New Caledonia, French Polynesia	Upper reaches	[27,28]
A. reinhardtii	Marbled	Eastern Australia, Northern New Zealand	Upper reaches	[29,30]
A. malgumora	Plain	Borneo and Sulawesi (Indonesia), Sabah of Malaysia	Lower reaches	[33,34]
A. mossambica	Plain	East Africa, Madagascar, South Africa	Lower reaches	[31,32]
A. obscura	Plain	Papua New Guinea, Fiji, French Polynesia (western South Pacific)	Lower reaches	[27,35,36]
A. bicolor bicolor	Plain	India, Java Island, East Africa, Peninsular Malaysia	Lower reaches	[7,8,15]
A. bicolor pacifica	Plain	Philippines, Sulawesi (Indonesia), Vietnam	Lower reaches	[7,16,22]
A. australis australis	Plain	Eastern Australia, New Zealand	Lower reaches	[37,38,20]
A. australis schmidtii	Plain	New Zealand	Lower reaches	[20,37,38]
A. dieffenbachi	Plain	New Zealand	Lower reaches	[38]
A. rostrata	Plain	Eastern North and Central America	Lower reaches	[39]
A. anguilla	Plain	Europe, North Africa	Lower reaches	[28]
A. japonica	Plain	Taiwan, China, Korea, Japan	Lower reaches	[6,10,32]

reaches, and *A. megastoma* (marbled) using the upper reaches in rivers of French Polynesia [27]. The potential for interspecific competition between eel species in these rivers could be effectively reduced by this habitat partitioning strategy. Interestingly, recent study indicated that hybridization and gene exchange are pervasive in tropical eel species, but that these species have nevertheless remained distinct entities for several million years. Cytonuclear incompatibilities and hybrid breakdown may be powerful mechanisms which help maintaining species boundaries [49].

Phylogenetic tree revealed that most marbled eels shared a close phylogenetic relationship, and, likewise, most of the plain eels shared a close phylogenetic relationship (Figure 2). The eels with closer phylogenetic relationships possessed similar skin coloration, which probably results from their long-term adaptive evolution. It is also worth noting that only plain eels inhabited the temperate areas. In temperate areas, the upper reaches of rivers are usually characterized by low primary productivity and low temperature, thus lacking suitable habitats for eels. Subsequently, eels usually inhabit the estuaries and lower reaches of rivers in temperate areas. Marbled eels which have evolved to adapt tropical/subtropical areas were thus rare in temperate area.

Previous study indicated that American eels could be distributed over the middle reaches of rivers in temperate areas [39]. A recent study has also revealed that the giant mottled eel is distributed throughout estuaries and the middle and upper reaches of some short tropical rivers [50-54]. These large-scale habitat distributions may result from a lack of interspecific competition. That is, eels may be able to expand their habitat range to some extent if no competitive species exist. Even so, the habitat partitioning between plain and marbled eels in the same river is a common phenomenon in almost all geographical areas.

The differences in body coloration between marbled eels and plain eels are likely a result of adaptive evolution which may help to reduce potential interspecific competition when they coexist in the tropical/subtropical rivers. This finding is important for developing applicable management plans for eels with different skin color types, with lower reach/estuary for protecting plain eels and middle/upper reaches for conserving marbled eel species.

Acknowledgments

Author contributions

Hsiang-Yi Hsu and Yen-Ting Lin mainly conducted the experiments, analyzed the results, and wrote the manuscript. Yi-Cheng Huang and Yu-San Han designed and supervised the experiments and participated in manuscript writing and interpretation of results.

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