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.
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 = 0.66995714 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 to the outgroup species. 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 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 costs [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,
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 cryptis...
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.

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.

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

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 long-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**

The authors thank the Ministry of Science and Technology, Executive Yuan, Taiwan (NSC 102–2628–B–002–023–MY3, MOST 105–2313–B–002–030, MOST 106–2313–B–002–036–MY3), and the Council of Agriculture, Executive Yuan, Taiwan (106AS–11.3.4–FA–Fi) for funding this project.

**Author contributions**

Hsiang-Yi Hsu and Yin-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.

**References**


**Citation:** Hsu HY, Lin YT, Huang YC, Han YS (2020) Skin coloration and habitat preference of the freshwater *Anguilla* eels. Int J Aquac Fish Sci 6(3): 096-101. DOI: [https://dx.doi.org/10.17352/2455-8400.000063](https://dx.doi.org/10.17352/2455-8400.000063)


