Management and Ecological Note

Does larval duration contribute to population genetic isolation of the Japanese eel Anguilla japonica?

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Japanese eel, Anguilla japonica Temminck & Schlegel, is a temperate catadromous fish with a long migratory loop and lengthy leptocephalus stage. Its freshwater distribution ranges from Taiwan, through Mainland China, Korea, and north to Japan (Tesch 2003). The spawning ground of this species is presumed to be in the western Mariana Islands near 14–16° N 142° E (Tsukamoto 1992, 2006). The leptocephalus larvae drift from their spawning grounds with the North Equatorial Current (NEC) followed by Kuroshio Current (KC) to reach the coasts of Northeast Asia (Tsukamoto 1992; Cheng & Tzeng 1996). They then metamorphose into glass eels along continental shelf and enter estuaries and fresh water for growth.

In the past, the concept of panmictic populations for Japanese eels was accepted based on evidence from mtDNA sequences (Sang et al. 1994; Ishikawa et al. 2001). However, Tseng et al. (2006) divided the genetic populations of the Japanese eel into low-latitude (South China and Taiwan) and high-latitude (Japan, Korea and North China) groups based on microsatellite DNA. They suggested that most progeny tend to be transported back to similar locations as their ancestors. The mechanism of how Japanese eel is separated into two stable populations remains a puzzle. Japanese eel appears to spawn in a restricted area and the larvae are passively transported by the NEC and KC, which exhibit considerable changes in speed, eddy structure and route at daily, monthly or even annual levels (reviewed in Aoyama 2009). If two genetic populations for the Japanese eel exist, there must be a mechanism for the non-random return of larvae to the place where their parents formerly resided. In the wild, populations of many organisms are composed of a mixture of individuals that reproduce at different times within a reproductive season.
(reviewed by Hendry & Day 2005). The heritable reproductive time is thought to contribute to this temporal restriction on gene flow between early and late reproducers, thus creating a pattern of isolation by time (IBT) (Hendry & Day 2005). However, studies on the Japanese eel have rejected this possibility, with the concept of IBT tested using microsatellite markers showing no evidence of genetic structuring among arrival waves. (Chang et al. 2007; Han et al. 2010). Conversely, studies for larval duration in the Japanese eel have been performed by calculating the otolith daily growth rings (Tzeng 1990; Cheng & Tzeng 1996). The geographical cline for the leptocephalus stage duration (larval duration), which increases from south to north, is well known. Accordingly, one possibility for genetic structuring of Japanese eel might be the heritable differences in larval durations between southern and northern groups. As the newly arrived recruits are similar in total length (Tsukamoto 1990; Cheng & Tzeng 1996), indicating size-dependent metamorphosis of the leptocephali in the Japanese eel, it is likely that leptocephali with a heritable short larval duration might mostly metamorphose in the south, while those with heritable long larval duration may mostly drift north along with the KC.

Genetic differentiations between eel groups with different larval duration were examined to test this possibility. Japanese glass eels were collected from an estuary in northern Taiwan between 2001 and 2008 using a fyke net (a stow net for glass eel) (Han et al. 2008). These were used for analysis of otolith daily growth increments using scanning electron microscopy (SEM) following the methods of Tzeng (1990). Photographs with faint images were excluded from analysis. Recruits with long (>125 days, n = 31), middle (100–125 days, n = 43) and short (<100 days, n = 30) larval durations were randomly selected from among these samples for subsequent microsatellite DNA analyses (Table 1). Genomic DNA extraction was carried out from a small piece of muscle tissue from each fish. Extraction was performed using a commercial DNA purification and extraction kit (Bioman Scientific Ltd., Bioman Scientific Ltd., Taipei, Taiwan), following the methods of Han et al. (2008). Seven polymorphic microsatellite DNA loci were assayed for genetic comparison for these three eel groups. These loci were selected from the GenBank (accession numbers AJ297601-3, AM062761-2, AB051084 and AB051094) with modest to high polymorphism and easy of use. As no genetic differentiation was found between annual samples (AMOVA, among samples 0.14%, P = 0.34), they were pooled for analysis. Hardy–Weinberg equilibrium (HWE) tests showed no significantly deviation after Bonferroni corrections among the three eel groups with different larval duration. There was no evidence of allele dropout, scoring errors and null alleles for these three groups. Overall genetic differentiations was very low without differences (\( F_{ST} = 0.0014, P = 0.34 \)) (Table 1). Pair-wise \( F_{ST} \) found insignificant genetic differentiations among them (Table 1). The statistical power was analysed with the program powsim (Ryman & Palm 2006) using Fisher’s exact tests. The powsim analysis revealed that seven microsatellite loci could provide >88% probability of detecting a significant differentiation of \( F_{ST} \) of 0.005 and >16% probability for \( F_{ST} \) of 0.001 when analysing 104 specimens within three groups. Although the likelihood of remaining undetected could not be excluded, the true degree of genetic differentiation among the three eel groups was nevertheless very small.

Larval duration is an important factor in determining the dispersal of a fish and, therefore, the amounts of genetic interchange among geographically distant populations (Riginos & Victor 2001). The flexibility in time of metamorphosis allows the larvae to disperse far distances to find a suitable habitat (Scheltema & Wilhams 1983) and also provides a potential way for speciation to occur. The heritable larval duration in the Japanese eel, if present, should limit gene flow and result in subsequently segregative migration of the leptocephali. Such a scenario is found in American, Anguilla rostrata LeSueur, and European, Anguilla anguilla (L.), eels, both of which spawn in the Sargasso Sea (Tesch 2003). Their offspring disperse separately on either side of the Atlantic Ocean because of different larval duration (Wang & Tzeng 2000). In the present study, there was no genetic differentiation among separate eel groups based on their larval durations, indicating little or no contribution of larval duration on population genetic isolation for the Japanese eel. The variation in larval duration of leptocephali is likely to be an acclimatisation, which depends on their nutrition status in the open ocean, with faster growing

<table>
<thead>
<tr>
<th>Eel groups</th>
<th>&lt;100 days (n = 30)</th>
<th>100–125 days (n = 43)</th>
<th>&gt;125 days (n = 31)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short:</td>
<td>0.1008</td>
<td>0.1291</td>
<td></td>
</tr>
<tr>
<td>&lt;100 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle:</td>
<td>0.0011; P = 0.41</td>
<td>0.0997</td>
<td></td>
</tr>
<tr>
<td>100–125 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long:</td>
<td>0.0043; P = 0.09</td>
<td>0.0005; P = 0.64</td>
<td></td>
</tr>
<tr>
<td>&gt;125 days</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall ( F_{ST} ): 0.0014, P = 0.34.</td>
<td></td>
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leptocephali metamorphosing and recruiting at younger ages (Shinoda & Tsukamoto 2009). In the European eel, it has been proven that temporal variations among recruits may be misinterpreted as geographical isolation (Dannewitz et al. 2005; Maes et al. 2006). For Japanese eel, when the samples were analysed in more detail and the temporal component was taken into consideration, the overall genetic variations were not consistent over time (Han et al. 2009). Therefore, one possibility for the genetic partitioning of spatial samples within an indicated year in Tseng’s study may be ‘chaotic genetic patchiness’, in which the random variation in parental contribution of reproductive activity and incomplete mixing of larvae may act in concert to produce offspring with a genetic heterogeneity for a certain year. Thus, the Japanese eel is thought to be one panmictic population. In conclusion, the variation on larval duration of the Japanese eel is likely an acclimatisation but not a heritable character.

Acknowledgments

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