Sex-dependent habitat use by the Japanese eel *Anguilla japonica*

in Taiwan (CM 2006/J:09)

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**ABSTRACT**

The eel’s life history strategy is not only complicated but also plastic. Some of

the American, European and Japanese eels may skip the freshwater phase and can
grow up in the brackish water and seawater until silver eel stage (Tzeng et al. 1997,

1999, 2000a, Tsukamoto et al. 1998, Jessop et al. 2002, 2004), which should be

regarded as a facultatively catadromous fish (Tsukamoto and Arai 2001, Jessop et al.


behavior of the eel is well documented, differences in habitat preference between the

sexes, however, are still poorly understood.

The sex composition of wild eels in each habitat varies widely, ranging from

almost all males to predominantly females (Matsui 1972, Parsons et al. 1977, Tzeng


2001, Tesch 2003, Han and Tzeng 2006). The sex of the eel is labile and thought to

be environmentally determined (Colombo and Grandi 1996, Krueger and Oliveira


growth rate (Helfman et al. 1987, Holmgren and Mosegaard 1996), population

density (Krueger and Oliveira 1999, Tesch 2003, Han and Tzeng 2006), temperature
(Holmgren 1996), latitude (Vladykov 1966, Helfman et al. 1987) and river types
(Sinha and Jones 1967, Oliveira et al. 2001) are possible extrinsic cues. The higher
percentage of males in estuarine habitat than in freshwater in some studies had led to
the suggestion that higher salinity water might favor male development (Sinha and
Jones 1967, Helfman et al. 1987, Tesch 2003). However, many studies observed the
opposite distribution, with males predominant in freshwater and females
predominant in brackish water (Sinha and Jones 1967, Hansen and Eversole 1984,
Naismith and Knights 1990, Holmgren 1996). Thus, the use of chronologies of
salinity history recorded in the otoliths of individual eels as revealed by Sr/Ca ratios
(Campana 1999, Tzeng et al. 1994, 1997) may enable assessment of whether
habitats with different salinity will affect eel sex-determination.

Wild Japanese eels were collected with eel traps in the lower reaches of the
Kaoping River in southwestern Taiwan (120°50’E, 22°40’N) during the period from
1998 to 2005. A total of 39 silver males, 64 yellow females, 87 silver females, and
29 unknown-sex juveniles were randomly chosen for analysis. Sagittal otoliths were
used for Sr/Ca ratio analysis and age determination following Tzeng et al. (1997).

The Sr/Ca ratios in eel otoliths before the elver stage, approximately 0-150 μm from
the primordium, were similar among individuals (Fig. 1). However, otolith Sr/Ca
ratios beyond the elver stage varied markedly, ranging from 0-10 ‰. Previous
studies identified a 4 ‰ Sr/Ca ratio as the boundary between freshwater and
seawater habitats (Tzeng et al. 2003a,b). Based on this, the eel was classified into 4
types of migratory contingents:

Type 1 (freshwater resident), the >90 % of Sr/Ca ratios in the otolith beyond
the elver check fluctuated below 4 ‰ (Fig. 1a). Type 2a (brackish water resident with
freshwater preference), an intermediate type between types 1 and 3. From 50-90 %
of Sr/Ca ratios in the otolith beyond the elver check were lower than 4 ‰ (Fig. 1b).
Type 2b (brackish water resident with seawater preference), an intermediate type between types 1 and 3. From 50-90 % of Sr/Ca ratios in the otolith beyond the elver check were higher than 4 ‰ (Fig. 1c). Type 3 (seawater resident), the >90 % of Sr/Ca ratios in otolith beyond the elver check fluctuated above 4 ‰ (Fig. 1d).

The distribution of the 4 type life histories of the eels varied between sexes (Table 1). Silver stage males and females differed significantly in habitat use ($\chi^2 = 21.83$, df = 3, $p = 0.0013$). There was no significant difference between females of yellow and silver stages ($\chi^2 = 8.5$, df = 3, $p = 0.20$). Male silver eels predominated in the Type 1 (54%) and Type 2a (38%) contingents and silver females were dominant in the Type 2a (47%) and 2b (32%) contingents. Eels of the Type 3 contingent were rare for both sexes (Table 1).

The sex differentiation of the eels occurs during the juvenile stage around 15-35 cm for the temperate eel species of Japanese, American and European eels (Matsui, 1972; Helfman et al., 1987; Kruger and Oliveira, 1999). This approximately corresponded to the region of eel otoliths 200-400 μm from the primordium, as evaluated by back-calculated growth histories from annual otolith increments (Tzeng et al. 2000b). The mean Sr/Ca ratio of female eels was significantly higher ($F = 10.8$, df = 1, $p = 0.001$) than for males during the supposed eel sex-differentiated period (Table 2). Mean otolith Sr/Ca ratios beyond the elver check also differed between the sexes, with higher mean values for females than for males ($F = 24.5$, df = 1, $p < 0.001$).

Different habitat use by eels of each sex might have an adaptive advantage. Female and male eels have evolved different life history strategies, with male eels exhibiting a time-minimizing growth strategy by maturing as soon as possible at a smaller size, while females postpone maturation with a size-maximizing growth strategy so as to attain higher fecundity (Vollestad and Johnson 1986, Helfman et al.,
In summary, sex-undetermined eels in the Kaoping River estuary tended to develop as females in a brackish water habitat and as males in a freshwater habitat. Sexually differentiated individuals continued to show a sex-specific habitat preference. Phenotypic-dependent eel sex determination together with sex-specific habitat choice may have evolved as an adaptation to a spatially heterogeneous habitat to maximize population fitness.

LITERATURE CITED


Helfman GS, Facey DE, Stanton HL, Bozeman EL (1987) Reproductive ecology of
the American eel. Am Fish Soc Symp 1:42-56


Larsson P, Hamrin S, Okla L (1990) Fat content as a factor inducing migratory behavior in the eel (*Anguilla anguilla* L.) to the Sargasso Sea. Naturwissenschaften 77:488-490


Table 1. Composition of life history types (%) of the Japanese eels between sexes

<table>
<thead>
<tr>
<th>Sex</th>
<th>n</th>
<th>Type 1</th>
<th>Type 2a</th>
<th>Type 2b</th>
<th>Type 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex unknown</td>
<td>29</td>
<td>12 (41)</td>
<td>9 (31)</td>
<td>6 (21)</td>
<td>2 (7)</td>
</tr>
<tr>
<td>Female yellow silver</td>
<td>64</td>
<td>23 (36)</td>
<td>24 (37)</td>
<td>16 (25)</td>
<td>1 (2)</td>
</tr>
<tr>
<td>Male silver</td>
<td>39</td>
<td>21 (54)</td>
<td>15 (38)</td>
<td>1 (3)</td>
<td>2 (5)</td>
</tr>
</tbody>
</table>

Table 2. Comparison of mean Sr/Ca ratios (‰) (range) between sexes in otolith regions of 200-400 μm from the primordium and that from elver check to the otolith edge (> 150 μm) in silver Japanese eels

<table>
<thead>
<tr>
<th>Sex</th>
<th>200-400 μm</th>
<th>&gt;150 μm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>0.26 ± 0.11 (0.10 – 0.55)</td>
<td>0.27 ± 0.09 (0.16 – 0.54)</td>
</tr>
<tr>
<td>Female</td>
<td>0.34 ± 0.14 (0.16 – 0.59)</td>
<td>0.35 ± 0.08 (0.18 – 0.50)</td>
</tr>
</tbody>
</table>
Fig. 1. Temporal changes in the Sr/Ca ratios of Japanese eel otoliths from different migratory contingents collected from the estuary of the Kaoping River. (a) Type 1, (b) Type 2a, (c) Type 2b, and (d) Type 3. M: metamorphosis from leptocephalus to glass eel; EC: elver check from glass eel to elver.