Growth differences between naturally recruited and stocked European eel *Anguilla anguilla* from different habitats in Lithuania

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European eels *Anguilla anguilla* from freshwater lakes in Lithuania had slower growth rates and lower backcalculated total lengths (*L*<sub>T</sub>) than those from lagoons and coastal waters, but no significant differences were found among fish with different migratory histories or between naturally recruited and stocked fish except a higher *L*<sub>T</sub> at age of stocked European eels at ages 5 to 8 years. The asymptotic *L*<sub>T</sub>(*L*<sub>T</sub><sup>N</sup>) did not differ among habitats or migratory histories, but the stocked eels in the lakes had smaller *K* (coefficient from the von Bertalanffy growth function) than did the both naturally recruited and stocked eels in the lagoon and coastal waters. The growth rate of European eels in Lithuania might be influenced mainly by different habitats rather than different migratory histories and stocking. The lower *L*<sub>T</sub> at age of naturally recruited fish at ages 5–8 years compared to stocked fish might result from the extra energy costs entailed in migration from the Atlantic and across the Baltic Sea.

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Key words: *Anguilla anguilla*; growth; habitats; migratory histories; Sr:Ca ratios; stocking.

INTRODUCTION

The European eel *Anguilla anguilla* (L.) is a facultatively catadromous fish. After hatching, the leaf-like leptocephali larvae drift from the Sargasso Sea to the continental shelf and metamorphose to glass eels. The fish may enter freshwater rivers, reside in coastal waters or migrate between habitats until sexual maturity and then die after returning to the Sargasso Sea to spawn (Tzeng *et al*., 1997, 2000, 2002; Tsukamoto *et al*., 1998; Tesch, 2003).

Due to the drastic decline of European eel populations since the 1980s (Moriarty & Dekker, 1997; Dekker, 1999, 2000, 2003a, b, 2004; Feunteun,
2002), stocking programmes have been extensively conducted in Europe. Post-stocking concerns, however, were concentrated on stocking efficiency (Feunteun, 2002), dispersion of parasites (Audenaert et al., 2003), bio-economical yield (Wickström et al., 1996), ecological consequences (Holmlund & Hammer, 2004) or behavioural differences compared to naturally recruited European eels (Westin, 1998, 2003; Limburg et al., 2003). Little is known, however, about possible effects on European eel growth.

In Lithuania, stocked European eels from the U.K. or France were released in inland freshwater lakes and the nearly freshwater Curonian Lagoon, whereas naturally recruited fish colonized the brackish Baltic Sea and the Curonian Lagoon (Shiao et al., 2006). Both stocked and naturally recruited European eels occupied two habitats, which might cause differences in European eel growth rates (Acou et al., 2003; Morrison & Secor, 2003). In addition, the growth of the fish was also affected by their migratory histories (Tzeng et al., 2003; Jessop et al., 2004; Daverat & Tomás, 2006), but the potential differences in growth rates among European eels with different migratory histories is unclear in the Baltic region.

Naturally recruited European eels take c. 5 years (range 1 to 10 years) to migrate from the eastern Atlantic coasts to the south-eastern Baltic, a distance of at least 1200 km (Shiao et al., 2006). In contrast, stocked European eels transported from other countries did not have such a migration across the Baltic Sea. Energy must be used to migrate, and it has been suggested that 40–60% of the fat stores of adult European eels are consumed during the spawning migration of c. 6000 km (van Ginneken & van den Thillart, 2000; van den Thillart et al., 2004). Therefore, the artificial transfer of stocked European eels might benefit somatic growth because they avoid the energy cost of long-distance migration.

This study evaluated: (1) habitat effects on European eel growth by comparing fish from the Baltic Sea, Curonian Lagoon and inland lakes, (2) effects of migratory histories on growth by comparing European eels with different migratory routes and (3) stocking effects on growth by comparing the growth trajectory of naturally recruited and stocked European eels.

**MATERIALS AND METHODS**

**COLLECTION OF SPECIMENS**

European eels were collected in Baltic Sea coastal waters, the Curonian Lagoon and the inland lakes Baluosai and Dringis in eastern Lithuania in 2003–2004 (Table I and Fig. 1). The total length ($L_T$) and mass ($M$) of each fish was measured to the nearest 1 mm and 1 g. Sexes of the fish were determined macroscopically from the gross morphology of the gonads. The developmental stages of the European eels were classified as yellow and silver according to their external colour, fin shape and eye size (Tesch, 2003).

**SAMPLING SITES**

The Baltic Sea is the largest brackish-water body in the world with an area of 412 000 km$^2$. The salinity in the Lithuanian coastal waters of the Baltic Sea varies from
c. 1 in the outflow from the Curonian Lagoon to 7 in the offshore area (Vysˇniauskas, 2003). The Curonian Lagoon is 1584 km² in area. It is separated by a narrow sand spit (0.5–4.0 km) from the Baltic Sea and the narrow Klaipˇeda Strait. The lagoon is a freshwater basin with salinity varying from 0 in the southern part of the lagoon, up to 1.6 in the Klaipˇeda Strait. During stormy inflows of sea water, the salinity may episodically increase to 5–6 in the northern areas (Olenin, 1997). The average water level in the Curonian Lagoon is 15 cm higher than sea level, thus seawater penetration into the lagoon is rare. Lakes Dringis and Baluosˇai are located in the eastern part of Lithuania, 300 km distance from the Curonian Lagoon and the Baltic Sea. Both lakes are of glacial origin. The area of Lake Dringis is 731 ha and Lake Baluosˇai is 250 ha. Both lakes are connected to the Nemunas River, the longest river in Lithuania, and then connected to the Curonian Lagoon and Baltic Sea without dams or other migration obstacles for European eels.

Daily temperature data for the Curonian Lagoon and Baltic Sea in 2004 were provided by the Marine Research Centre (Ministry of Environment) and for Lake Tauragnai by the Lithuanian Hydrometeorological Service (Ministry of Environment). Temperatures in Lakes Dringis and Baluosˇai were based on those in Lake Tauragnai, c. 10 km distant and with similar hydrological features. Yearly water temperatures in Lake Tauragnai (mean 8.8°C) were significantly lower than in the Curonian Lagoon (mean 9.6°C) (ANOVA and Tukey’s test, P < 0.01) but did not differ from those in the Baltic Sea (mean 8.9°C) in 2004.

The Curonian Lagoon was stocked with elvers during 1996–1997 (43 000 fish), 2000–2003 (10 000 fish) and with glass eels in 1995 (150 000 fish) and 2003 (60 000 fish). Lakes Baluošai and Dringis belong to the lake system of eastern Lithuania and have been regularly stocked with glass eels since 1960. Even if only one lake in the lake system is stocked, released European eels were possibly able to spread to nearby lakes through streams or small rivers. Whether naturally recruited European eels occurred in these eastern Lithuanian lakes is unknown. Although reports of commercial landings did not indicate that fish could be found in these lakes before stocking, the possibility of naturally recruited fish occurring in the lakes could not be excluded.

### Table I

Sampling site, time, number, development stage, sex ratio and origin of Anguilla anguilla collected from Baltic coastal waters, Curonian Lagoon, Lake Baluosˇai and Lake Dringis in Lithuania

<table>
<thead>
<tr>
<th>Site</th>
<th>Baltic Sea</th>
<th>Curonian Lagoon</th>
<th>Lake Baluosˇai</th>
<th>Lake Dringis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling time</td>
<td>June to September 2003</td>
<td>June to August 2003</td>
<td>April 2004</td>
<td>August to September 2004</td>
</tr>
<tr>
<td>n</td>
<td>48</td>
<td>50 (49 used)</td>
<td>10</td>
<td>23</td>
</tr>
<tr>
<td>Stage</td>
<td>Yellow</td>
<td>Yellow except one silver</td>
<td>Silver</td>
<td>Yellow</td>
</tr>
<tr>
<td>Sex ratio (female: male)</td>
<td>48:0</td>
<td>50:0</td>
<td>9:1</td>
<td></td>
</tr>
<tr>
<td>IHS, number (%)</td>
<td>25 (52)</td>
<td>43 (88)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>SR, number (%)</td>
<td>23 (48)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>FR, number (%)</td>
<td>0 (0)</td>
<td>6 (12)</td>
<td>10 (100)</td>
<td>23 (100)</td>
</tr>
<tr>
<td>Origin of fish</td>
<td>Natural recruited, number (%)</td>
<td>47 (98)</td>
<td>40 (80)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Restocked, number (%)</td>
<td>1 (2)</td>
<td>10 (20)</td>
<td>10 (100)</td>
<td>23 (23)</td>
</tr>
</tbody>
</table>

FR, freshwater residents; IHS, inter-habitat shifter; SR, seawater resident.
OTOLITH PREPARATION, SR:CA RATIO MEASUREMENT AND CLASSIFICATION OF THE EELS

The otolith preparation followed Shiao et al. (2006) in that the largest otolith (sagitta) was collected and polished until the core was exposed. Sr and Ca concentrations in the otolith were measured from the core to the edge of the otolith at intervals of 10 μm by electron probe microanalyzer (EPMA; JEOL JXA-8900R, Tokyo, Japan).

Once the Sr:Ca ratio of the otoliths was measured, the migratory histories of the European eels were classified according to Shiao et al. (2006) as (1) seawater resident type, (2) freshwater resident type and (3) inter-habitat shifter. In addition, the origins of the European eels (naturally recruited or stocked) were distinguished by otolith Sr:Ca ratios according to Limburg et al. (2003) and Shiao et al. (2006).

OTOLITH MEASUREMENT AND BACKCALCULATION PROCEDURES

After microchemical analysis, the otoliths were polished to remove the carbon layer and etched with 5% ethylene diamine tetraacetic acid (EDTA) for 1–2 min to reveal the annual rings for age determination. The radius was measured by image software (SigmaScan Pro 5.0; SPSS Inc., Chicago, IL, U.S.A.) to the nearest 1 μm along the longest radius from the core to edge. The duration of time spent in fresh and sea water was then estimated by relating the Sr:Ca ratios profile to the otolith annuli. The $L_T$ at age at age $i$ ($L_T^i$) was estimated by the Dahl-Lea method (Francis, 1990): $L_T^i = L_T^c R_i R_c^{-1}$, where $L_T^c$ is the $L_T$ at capture, $R_i$ is the $i$th otolith radius and $R_c$ is the otolith radius from core to the edge. The backcalculation was started from age 2 (1 year after the glass eel stage), as suggested by Poole et al. (2004). The backcalculated $L_T^i$ were compared among habitats and migratory groups and between naturally recruited and stocked European eels.
GROWTH INDICATORS

The mean growth rate ($G_M$) was derived from $L_T$ divided by the age ($A$): $G_M = L_T A^{-1}$. The $M$ and $L_T$ relationship was represented by the formula: $M = aL^b_T$, where $a$ and $b$ are constants derived by linear regression using the formula: $\ln M = \ln a + b \ln L_T$. Then, the slope ($b$) was used to describe the degree of the increase in $\ln M$ per unit increase in $\ln L_T$.

The growth coefficient ($K$) and asymptotic length ($L_{T}^{\infty}$) in the von Bertalanffy growth function (VBGF) and the corresponding S.E. were calculated by the non-linear fitting method in FiSAT (version 1.2.0; Gayanilo et al., 1996). Accordingly, the 95% CI of the two parameters were calculated by assuming normal distribution of estimates (Hogg et al., 2005): 95% CI = estimate ± 1.96 S.E.

$K$ was used to describe European eel growth after becoming elvers and $L_{T}^{\infty}$ was regarded as an indicator of $L_T$ of the silver eels (Beverton, 1963) because the fish stop increasing in $L_T$ when sexually mature (silver eel stage; Tesch, 2003). Meanwhile, plots of the $L_T$ at age at each age were also compared to reveal the trend of the growth trajectory among site and migratory history groups. In addition, those of naturally recruited European eels between the elver stage and initial freshwater entry were compared to those of stocked fish to evaluate stocking effects.

DATA ANALYSIS

All numerical variables being compared by parametric statistical tests were first examined for compliance with the assumptions of normality of distribution and homogeneity of variance using the Kolmogorov–Smirnov test and Bartlett’s test, respectively. Variables that met these assumptions were compared by ANOVA and Tukey’s test was conducted for multiple comparison among groups. If these assumptions could not be satisfied, variables were compared by non-parametric methods (Mann–Whitney test and Kruskal–Wallis test). The slope of the linearized (by ln transformation) $M$ and $L_T$ relationship was compared by ANCOVA. To examine the stocking effects, data of the naturally recruited European eels from the Baltic Sea and Curonian Lagoon were pooled because these fish all stayed and grew in the Baltic Sea in the period from the elver stage to freshwater entrance. All statistical procedures were conducted by SAS® (version 8.01), and significance level $\alpha$ was set at 0.05.

RESULTS

STAGE, SEXES, MIGRATORY HISTORIES AND ORIGINS

One hundred and thirty European eels were caught in Lithuania during 2003–2004, with 48, 49, 10 and 23 fish from the Baltic coast, Curonian Lagoon, Lake Baluosošai and Lake Dringis, respectively. Fish from the Curonian Lagoon and Baltic coast and Lake Dringis were all yellow eels while fish from Lake Baluosošai were all silver eels. All fish collected were females except for one male caught in Lake Baluosošai. This male was excluded from all analyses (Table I).

The European eels from the Baltic coast were seawater residents (48%) and inter-habitat shifters (52%) and no freshwater residents were found. The European eels from the Curonian Lagoon were mainly composed of inter-habitat shifters (88%) while freshwater residents accounted for 12%. The otolith Sr:Ca ratios in fish from the inland lakes Baluosošai and Dringis all showed a freshwater pattern. The European eels in the Baltic Sea coasts and Curonian Lagoon were mostly naturally recruited fish (98 and 80%, respectively) while the fish from both lakes were all stocked European eels (100%; Table I).
GROWTH COMPARISONS AMONG HABITATS

Data for naturally recruited and stocked European eels in the Curonian Lagoon were pooled because of insignificant differences in the mean \( A, L_T \) and \( M, G_M \) and backcalculated \( L_T \) at age (Mann–Whitney \( U \)-test, \( P > 0.05 \); Table II). Mean \( A, L_T, M \) and \( G_M \) differed significantly among habitats (Kruskal–Wallis test for mean \( A \) and ANOVA for other variables, all \( P < 0.01 \); Table III). The European eels from Lake Dringis were smaller and weighed less than fish from other sites and the fish from both inland lakes were older with slower \( G_M \).

The values of \( b \) differed significantly among habitats, with the highest slopes for European eels caught in the Baltic Sea, followed by fish caught in the Curonian Lagoon and fish from both lakes (ANCOVA, \( P < 0.01 \)). This might suggest that the coastal European eels gain mass faster than do those in the lagoon and the lakes (Table III). The backcalculated \( L_T \) at age were similar at ages 2 and 3 years among all habitats but became significantly different from ages 4 to 13 years (Kruskal–Wallis test, \( P < 0.05 \)) [Fig. 2(a)]. The \( L_T \) at age of European eels from Baltic coastal waters and the Curonian Lagoon were similar at all ages (Kruskal–Wallis test, \( P > 0.05 \)) while fish in both lakes were smaller \( (P < 0.05) \) than in the Baltic Sea and Curonian Lagoon. In other words, the growth rate of the European eels from the coast and the lagoon were faster than those from the lakes, regardless of their origins (wild or stocked).

GROWTH COMPARISONS BETWEEN MIGRATORY HISTORIES

No significant differences were found in mean \( A, G_M, L_T, M \) and \( L_T \) at age in all ages between European eels from the Baltic Sea coast and Curonian Lagoon with different migratory histories (Mann–Whitney tests, all \( P > 0.05 \); Table IV) [Fig. 2(b)]. Although not statistically significant, the \( L_T \) at age of freshwater resident fish (stocked fish) in the lagoon seemed to be larger than those of the inter-habitat shifters (naturally recruited fish) at each age and some individuals continued growing at an age of 14 or over [Fig. 2(b)].

| Table II. Comparisons of means ± s.d. and range (parentheses) of number (n), age before entering fresh water (\( A_F \)), total length (\( L_T \)), total mass (\( M \)), age and mean growth rate (\( G_M \)) between naturally recruited European eels which entered fresh water at least once and stocked fish in the Curonian Lagoon. All differences were not statistically significant (\( P > 0.05 \)) |
|---|---|---|
| \( n \) | Naturally recruited | Stocked |
| \( n \) | 85 | 10 |
| \( A_F \) (years) | 5.2 ± 2.1 (1–10) | Since elver (age set to 1) |
| \( L_T \) (mm) | 642 ± 91 (475–880) | 694 ± 101 (605–920) |
| \( M \) (g) | 621.4 ± 346.6 (180.0–1735.0) | 804.5 ± 542.3 (382.0–2126.0) |
| Age (years) | 10.8 ± 1.7 (6–16) | 10.9 ± 3.1 (9–18) |
| \( G_M \) (mm year\(^{-1}\)) | 61 ± 11 (38–91) | 66 ± 11 (51–83) |
Table III. Comparisons of mean ± s.d. and range (in parentheses) of total length ($L_T$), mass ($M$), age ($A$), mean growth rate ($G_M$) and intercept ($a$) and slope ($b$) in the relationship between ln $L_T$ and ln $M$ ($r^2$ values are given) for European eels from different habitats. All fish were female. Different superscript lower case letters indicate statistically significant differences ($P < 0.05$).

<table>
<thead>
<tr>
<th>Site</th>
<th>Baltic Sea</th>
<th>Curonian Lagoon</th>
<th>Lake Baluošai</th>
<th>Lake Dringis</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_T$ (mm)</td>
<td>630 ± 73$^a$ (475–810)</td>
<td>663 ± 104$^a$ (490–920)</td>
<td>647 ± 110$^a$ (433–800)</td>
<td>526 ± 110$^b$ (387–695)</td>
</tr>
<tr>
<td>$M$ (g)</td>
<td>582.4 ± 274.6$^a$ (180.0–1400.0)</td>
<td>691.4 ± 441.7$^a$ (201.0–2126.0)</td>
<td>519.9 ± 266.2$^a$ (127.0–930.0)</td>
<td>263.9 ± 112.9$^b$ (78.0–560.0)</td>
</tr>
<tr>
<td>$A$ (years)</td>
<td>11.0 ± 1.8$^a$ (8–16)</td>
<td>10.8 ± 1.7$^a$ (6–15)</td>
<td>19.0 ± 3.0$^b$ (15–24)</td>
<td>16.0 ± 2.6$^b$ (12–22)</td>
</tr>
<tr>
<td>$G_M$ (mm year$^{-1}$)</td>
<td>59 ± 9$^a$ (41–79)</td>
<td>63 ± 13$^a$ (38–91)</td>
<td>36 ± 6$^b$ (27–43)</td>
<td>33 ± 5$^b$ (23–42)</td>
</tr>
<tr>
<td>ln ($a$)</td>
<td>−20.25</td>
<td>−17.36</td>
<td>−15.34</td>
<td>−15.37</td>
</tr>
<tr>
<td>$b$</td>
<td>4.11$^a$</td>
<td>3.66$^b$</td>
<td>3.32$^c$</td>
<td>3.34$^c$</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.895</td>
<td>0.958</td>
<td>0.954</td>
<td>0.947</td>
</tr>
</tbody>
</table>
FIG. 2. The growth curve of mean ± s.d. backcalculated total lengths at age and age for European eels among (a) habitats [Baltic Sea (BS; □; n = 48), Curonian Lagoon (LG; ●; n = 49), Lake Balušai (LAB; △; n = 10) and Lake Dringis (LAD; ▶; n = 23)], (b) migratory environmental histories [BS seawater resident (○; n = 23), BS inter-habitat shifter (IHS) (●; n = 25), LG freshwater resident (□; n = 6), LGIHS ( ■; n = 43), LAB (△; n = 10) and LAD (▶; n = 23)] and (c) between naturally recruited (●; n = 85) and stocked (○; n = 10) fish.
Table IV. Comparisons of mean ± s.d. and ranges (in parentheses) in total lengths ($L_T$), mass ($M$), ages and growth rates ($G_M$) among European eels with different migratory histories from different sites. Comparisons of variables between migratory groups were all statistically insignificant ($P > 0.05$).

<table>
<thead>
<tr>
<th>Migratory group</th>
<th>SR</th>
<th>IHS</th>
<th>FR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baltic Sea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>23</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>$L_T$ (mm)</td>
<td>627 ± 77 (480–810)</td>
<td>632 ± 75 (475–740)</td>
<td>—</td>
</tr>
<tr>
<td>$M$ (g)</td>
<td>533.3 ± 269.6 (195.0–1170.0)</td>
<td>632.6 ± 305.3 (180.0–1400.0)</td>
<td>—</td>
</tr>
<tr>
<td>Age (years)</td>
<td>10.9 ± 1.7 (8–14)</td>
<td>10.8 ± 1.8 (8–16)</td>
<td>—</td>
</tr>
<tr>
<td>$G_M$ (mm year$^{-1}$)</td>
<td>59 ± 9 (41–74)</td>
<td>60 ± 10 (41–79)</td>
<td>—</td>
</tr>
<tr>
<td>Curonian Lagoon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$n$</td>
<td>0</td>
<td>43</td>
<td>6</td>
</tr>
<tr>
<td>$L_T$ (mm)</td>
<td>—</td>
<td>694 ± 101 (605–920)</td>
<td>657 ± 106 (490–880)</td>
</tr>
<tr>
<td>$M$ (g)</td>
<td>—</td>
<td>804.5 ± 542.3 (382.0–2126.0)</td>
<td>655.6 ± 405.1 (201.0–1735.0)</td>
</tr>
<tr>
<td>Age (years)</td>
<td>—</td>
<td>10.9 ± 3.1 (9–18)</td>
<td>10.8 ± 1.6 (6–14)</td>
</tr>
<tr>
<td>$G_M$ (mm year$^{-1}$)</td>
<td>—</td>
<td>66 ± 11 (51–83)</td>
<td>62 ± 13 (38–91)</td>
</tr>
</tbody>
</table>

FR, freshwater residents; IHS, inter-habitat shifter; $n$, sample size; SR, seawater resident.
GROWTH COMPARISON BETWEEN ORIGINS

There were no significant differences in the mean $A$, $G_M$, $L_T$ and $M$ between naturally recruited and stocked European eels (Mann–Whitney $U$-test, all $P > 0.05$; Table II). Moreover, the $L_T$ at age of naturally recruited fish at each age were not significantly different than for stocked fish in the lagoon (Mann–Whitney $U$-test, $P > 0.05$) [Fig. 2(c)] except that naturally recruited eels were significantly smaller at ages 5 to 8 years.

VON BERTALANFFY PARAMETERS

Because the 95% CI of $L_T\infty$ were found to overlap between migratory history groups of European eels in the Baltic Sea and Curonian Lagoon, the data were pooled (Fig. 3). The 95% CI of $L_T\infty$ overlapped among all habitats, which indicated the differences in $L_T\infty$ were not significant. The $K$ value of European eels in the Baltic Sea, however, was significantly higher than that of fish in the lakes, while that of fish in the lagoon was in the middle. In general, the fish on the brackish coast had smaller $L_T\infty$ and higher $K$, the fish in inland freshwater lakes had a median $L_T\infty$ and a smaller $K$, while the fish in the lagoon had the highest $L_T\infty$ and a median $K$ value.

DISCUSSION

EFFECTS OF HABITATS

The growth of anguillids in different habitats is affected by different migratory behaviours (Edeline & Elie, 2004), population density, water temperature, food availability (Tesch, 2003), productivity (Gross, 1987), salinity (Tzeng et al., 2003) and feeding preferences (Edeline et al., 2005). Stocked $A. \text{anguilla}$ released in the Curonian Lagoon grew faster than those in two inland lakes. This result supports the assumption by Shiao et al. (2006) that the eutrophic
water body and longer growing season of the Curonian Lagoon and the Baltic
coasts might benefit European eel growth more than living in mesotrophic
inland lakes with a shorter growing season. This observation is also consistent
with other related studies (Naismith & Knights, 1993; Acou et al., 2003;
Daverat & Tomás, 2006) that A. anguilla were found growing faster in the estu-
found that the growth rate and production of American eels Anguilla rostrata
(Lesueur) caught in brackish water was higher than for fish from upstream
freshwater sites. On the other hand, A. anguilla glass eels fed more intensely
and grew faster in salt than in fresh water (Edeline et al., 2005). This indicated
a habitat effect on locomotor activity and behaviour response and growth
(Edeline & Elie, 2004). In the Baltic Sea region, Svedäng et al. (1996) found
that the growth rate of silver fish from the Baltic Sea was not significantly dif-
ferent from that of fish from the Swedish west coast. Moreover, the naturally
recruited fish, either collected in the Baltic Sea or Curonian Lagoon, experi-
enced similar habitats moving through the Baltic, and some naturally recruited
fish might move between the coast and the lagoon. Therefore, it is not surpris-
ing that the growth of naturally recruited European eels did not differ signifi-
cantly between the Baltic coasts and the lagoon.

EFFECTS OF MIGRATORY HISTORIES

Three migratory patterns, seawater residents, freshwater residents and inter-
habitat shifters, were identified from the Curonian Lagoon and Baltic coasts.
No significant growth differences among migratory groups, however, were
found although such growth differences occur in other anguillids (Jessop et al.,
2002, 2004; Tzeng et al., 2003). This suggests that migratory history
may have minor effects on the growth of European eels recruited to Lithuanian
waters. These results might be due to the minor salinity difference between
the Baltic coast (c. 7/00) and Curonian Lagoon (0/01) compared with other
studies in river systems connecting to the ocean or manipulative laboratory
experiments (Edeline et al., 2005).

EFFECTS OF STOCKING

Not only habitat affects stocked European eels; the stocking process itself
seemed to affect the growth of stocked fish in the Curonian Lagoon. The
$L_T$ at age between 4 and 7 years were significantly larger for stocked fish than
for naturally recruited fish. The water temperature was similar in Lithuanian
Baltic coastal waters and in the Curonian Lagoon. As previously discussed,
the small salinity difference between the Baltic Sea coast and Curonian Lagoon
might be a minor influence on the growth difference. Moreover, the genetic
structure of the European eel populations are still under debate (Lintas et al.,
1998; Wirth & Bernatchez, 2001; Pujolar et al., 2006), and a genetically
driven growth difference among European eel stocks cannot be supported.
Evidently then, temperature, salinity and genetic structure cannot satisfactorily
explain the differences in $L_T$ at age between stocked fish and naturally recruited
fish over a specific age range.
The time that naturally recruited fish spend in the Baltic Sea before entering fresh water in Lithuania is c. 5–2 years (range: 1–10 years; Shiao et al., 2006), which is encompassed by the age 5–8 year range where significant differences in $L_T$ at age were observed between naturally recruited and stocked European eels. Naturally recruited fish have to allocate energy for long-distance migration that stocked fish do not. The energy savings due to non-migration may accumulate over c. 5 years until the fish reach Lithuania. After the arrival of naturally recruited fish in the Baltic Sea, any differences in $L_T$ might be reduced by compensatory growth (Graynoth & Taylor, 2000) or by better energy transformation efficiency from feeding (Bernatchez & Dodson, 1987). A zoobenthos study in the lagoon and the Lithuanian coastal zone down to a depth 40 m (Olenin, 1997) demonstrated that invertebrate biomass (molluscs excluded) was greater in the lagoon, which could affect growth of the European eels. More evidence is needed to test whether the extra energy expenditure on migration would cause the differences in growth of the fish.

$K$ AND $L_{T_n}$ IN VBGF

The growth coefficient $K$ was found to be different among habitats rather than between migratory histories and origins. The trend in $K$ was in accordance with previous results and other related studies (Naismith & Knights, 1993; Acou et al., 2003; Morrison & Secor, 2003; Cairns et al., 2004; Daverat & Tomás, 2006) in that the growth of the European eels might be more enhanced in estuary and coastal waters than in fresh water. In this study, it was further suggested that the productivity and longevity of the growing season, rather than the salinity, might play a more important role in growth of the European eels because that of the fish in the nearly freshwater lagoon was higher than in freshwater lakes.

On the other hand, the $L_{T_n}$ of the European eels in the lagoon was largest, followed by that in the lakes and that in Baltic coastal waters was smallest, although not statistically different. This suggests that the size of silver eels might be different among habitats. For example, Svedäng et al. (1996) found that the silver eels from the Baltic Sea were both larger and older than those from the Swedish west coast which has a higher salinity. Because the fecundity of the silver eels with larger size was higher (Vollestad & Jonsson, 1986; Barbin & McCleave, 1997; Hoyle & Jellyman, 2002), different reproductive output among habitats might result (Goodwin & Angermeier, 2003; Morrison & Secor, 2003). More studies, however, are needed to evaluate this hypothesis.

In summary, the growth rate of European eels in Baltic Sea coastal waters was not significantly different from that of fish caught in the Curonian Lagoon, regardless of the migratory histories and origins (naturally recruited and stocked), but they were all significantly higher than those in the two lakes, which indicated that the growth rate of the European eel was influenced by the habitat more than the migratory histories and origins in Lithuania. The higher $L_T$ at age at ages 4–7 years might be due to different energy allocations for migration. Differences in $K$ but not in $L_{T_n}$ were detected, which was in accordance with previous growth comparisons.
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