Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios

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Otolith Sr:Ca ratios were examined to evaluate the contribution of the stocked eel *Anguilla anguilla* elvers, which have been stocked in Lithuanian waters and mixed with naturally recruited eels for several decades, to the native eel population. Stocked eels were identified by the freshwater signature (Sr:Ca ratios $<2.24 \times 10^{-3}$) on the otolith after the glass eel stage. Naturally recruited eels, that had migrated through the North and Baltic Seas, were characterized by an extended seawater and brackish-water signature (Sr:Ca ratios $>3.23 \times 10^{-3}$) after the glass eel stage. Of 108 eels analysed, 21 eels had otolith Sr:Ca ratio profiles consistent with stocking while 87 showed patterns of natural recruitment. The ages of naturally recruited eels arriving in Lithuanian fresh waters varied from 1 to 10 years, with a mean ± s.d. age of 5.2 ± 2.1 years. Eels from the inland Lake Baluosˇai were all freshwater residents of stocked origin. Stocked eels, however, accounted for only 20% of the eels from the Curonian Lagoon and 2% of eels sampled in Baltic coastal waters. This finding does not support the hypothesis that the eel fishery in the Curonian Lagoon depends mostly on stocking.

Key words: *Anguilla anguilla*; European eel; migratory history; otolith microchemistry; stocking.

INTRODUCTION

Catadromous eels are commercially valuable species and support worldwide eel aquaculture and eel fisheries. The abundance of several species, e.g. *Anguilla anguilla* (L.), *Anguilla rostrata* (Lesueur) and *Anguilla japonica* Temminck & Schlegel, have declined throughout their distribution ranges due to overfishing, anthropogenic activities and changes of oceanic currents induced by global weather anomalies (Castonguay *et al.*, 1994; Dekker, 2003; Tatsukawa, 2003).
In addition, the eel’s mysterious life cycle further compounds its fate and makes conservation and recovery more difficult.

*Anguilla anguilla* inhabits coastal waters, estuaries, rivers and lakes in Europe and North Africa (Bertin, 1956; Tesch, 2003). Their leaf-like larvae, leptocephali, drift *via* the Gulf Stream and North Atlantic Current from oceanic spawning grounds in the Sargasso Sea to the continental shelves of Europe and North Africa or enter the Mediterranean Sea. The larvae metamorphose into glass eels on the continental shelf. Glass eels become pigmented elvers when they enter estuaries. Some elvers stay in salt or brackish water along the coast while others migrate upriver. Major elver runs occur into the Atlantic-facing estuaries of France, Spain, Portugal and the Bristol Channel and River Severn estuary in the U. K. Lesser migrations occur to other countries in the Baltic and Mediterranean Seas (Knights & White, 1998).

Declines in eel recruitment in Scandinavia have been noted since the 1940s (Moriarty, 1996), but the greatest decreases in the recruitment of eels throughout Europe have occurred since the early 1980s (Dekker, 2000). Recent recruitment of *A. anguilla* glass eel was estimated to be only 1% of the level before the 1980s (Dekker, 2004). Poor natural recruitment from the oceanic migration phase, exacerbated by habitat degradation, pollution, artificial physical barriers to migration and high fishing pressure on glass eels (Moriarty & Dekker, 1997) has led to the need for stocking to maintain, enhance, restore or establish stocks. Intensive stocking programmes have been undertaken in the Baltic Sea region over the past 50 years. The most intense stocking programmes have been implemented in the Baltic Sea drainage using eels originating from western Europe.

The first eel stockings in Lithuania occurred between 1928 and 1939 when 3.2 million elvers were released into lakes of the Vilnius region (c. 300 km from the Baltic coast). Since the mid 1960s, Lithuanian lakes have been stocked with c. 50 million elvers or young yellow eels at an average stocking rate of 1.1 million eels yearly (Ložys, 2002). Studies on stocking effectiveness, however, have not been carried out and the post-stocking movements of stocked eels remain largely unknown. Natural recruitment is unknown due to the lack of suitable locations to monitor recruitment in the main area of invasion, the Klaipėda strait (Curonian Lagoon). Therefore, statements by fishers and fisheries managers that the Curonian Lagoon eel fishery depends on eel stocking are speculative. The degree to which stocked and naturally recruited eels contribute to the eel fishery and eventually to the spawning stock is unknown. In the absence of tagging, it is difficult to discriminate stocked eels from naturally recruited eels since they are morphologically similar. Fish tagging can help identify different stocks, but most conventional tagging is not feasibly applied to small glass eels. Internal marking of the otolith, such as by tetracycline or alizarin complexone, is feasible (Tsukamoto, 1988). Most stocking programmes, as indicated by Cowx (1999), however, were carried out without evaluation of their potential success. Marks were not applied to the stocked eels before their release into lakes or the lagoon. The analysis of a natural tag, the otolith strontium (Sr):calcium (Ca) ratio, has been extensively used to study the migratory history of diadromous fishes and provides alternative resolution to discriminate stocked eel from naturally recruited eel (Elsdon & Gillanders, 2003).
The metabolically inert otolith records biological as well as environmental information throughout the fish's life. Fishes can absorb Sr in the ambient water and substitute for Ca in the process of CaCO3 deposition in the otolith. The positive relationship between salinity and otolith Sr:Ca ratios has been validated for different species including eels (Tzeng, 1996; Secor et al., 1998; Kraus & Secor, 2003). Accordingly, seawater-resident fish uptake and deposit more Sr in the otolith than do freshwater fishes. Otolith Sr:Ca ratios in combination with age data have been used to elucidate the migratory environmental history of diadromous fishes, including anguillids (Tsukamoto & Arai, 2001; Jessop et al., 2002; Shiao et al., 2003).

Elvers purchased in the U. K. and France are directly released into Lithuanian freshwater lakes and the Curonian Lagoon. These stocked eels do not experience the long migratory journey through the North and Baltic Seas and thus they should show a freshwater signature of low otolith Sr:Ca ratios immediately after the elver stage. In contrast, eels naturally recruited to Lithuania must pass the North and Baltic Seas and should show an extended seawater and brackish-water signature of high (North Sea) and intermediate (Baltic Sea) otolith Sr:Ca ratios after the elver stage. Thus, a life-history scan of otolith Sr:Ca ratios should be able to discriminate between both stocked and naturally recruited eels. Clarification of the eel's migratory history will also help to evaluate the contribution and interaction of the two possible eel origins (stocked or naturally recruited) to each population along the Baltic coasts and in the Curonian Lagoon and inland lakes.

**MATERIALS AND METHODS**

**FISH COLLECTION AND SAMPLING SITES**

Silver and yellow-stage *A. anguilla* were collected by fyke nets and long lining from Baltic coastal waters, the Curonian Lagoon in western Lithuania and the freshwater Lake Baluosois in eastern Lithuania in 2003–2004 (Fig. 1). The lake is c. 300 km from the Curonian Lagoon and c. 350 km from the Baltic Sea to which it is connected via a system of small streams, lakes, the River Nemunas and the Curonian Lagoon. Natural recruitment to these lakes has never been reported and may not occur; however, the possibility cannot be excluded. Elvers have been regularly stocked since 1960 into the system of lakes in the Baluosois Lake region.

The shallow Curonian Lagoon (mean depth 3.7 m) is separated by a narrow sand spit (0.5–4.0 km wide) from the Baltic Sea and is connected to the Baltic Sea through the narrow (0.5 km-wide) Klaipeda Strait. The salinity of the Baltic Sea adjacent to Lithuania varies from 4.9 to 6.8 (Dubra & Dubra, 1998). The lagoon is 1584 km² in area and is a freshwater basin. Rivers supply the lagoon with c. 36 times more fresh water than the water volume in the lagoon itself and the mean water level in the lagoon is 15 cm higher than sea level. Therefore, brackish water penetration into the lagoon is rare. The salinity fluctuates from 0.03 in the southern part of the lagoon up to 2.7 in the Klaipeda Strait. During stormy inflows of brackish water, the salinity may episodically rise to 5–6 in the northern areas (Olenin, 1996). The Curonian Lagoon was stocked by young yellow eels during 1996–1997 (43 000), 2000–2003 (10 000) and by elvers in 1995 (150 000) and 2003 (60 000).

The total length (*L*ₜ) and mass (*M*) of each eel was measured to the nearest 1.0 mm and 1.0 g. Sexes were determined macroscopically from the gross morphology of the gonads, where eels with thin, regularly lobed organs (Syrski’s organ) were considered...
males, while individuals with more broad and folded curtain-like gonads were females (Tesch, 2003). The eels were classified as yellow and silver eels, by their external colour, fin shape and eye size.

Water Sr and Ca concentrations around the eel sampling locations were determined by atomic absorption spectrophotometer (Hitachi Z-5000). Standard solutions (Merck, Darmstadt, Germany) were used to make the standard curve. Sr and Ca concentrations of the water collected from the Baltic coast (salinity 5-8) were c. 1.67 × 10^{-5} and 2.60 × 10^{-3} M, respectively (6.44 × 10^{-3} for the Sr:Ca ratio). Water collected in
the Curonian Lagoon (salinity 0) contained $c. 1.36 \times 10^{-6}$ M of Sr and $1.51 \times 10^{-3}$ M of Ca ($0.90 \times 10^{-3}$ for the Sr:Ca ratio). Water Sr and Ca concentrations in the Baltic coast and Curonian Lagoon were in the range of normal brackish and fresh water.

**OTOLITH PREPARATION AND SR:CA ANALYSIS**

The largest pair of eel otoliths (sagittae) was removed, dried in air, embedded in Epo-fix resin, ground and polished until the core was exposed. For electron probe microanalysis, the polished otoliths were coated with carbon under a high-vacuum evaporator. Sr and Ca concentrations in the otolith were measured from the otolith core to the edge at 10 $\mu$m intervals. Quantitative analyses were conducted with an electron probe microanalyzer (JEOL JXA-8900R), using beam conditions of 15 kV for the acceleration voltage, 3 nA for the current, and a $5 \times 4 \mu$m rectangular scanning beam. The quantitative data were corrected by the PRZ (phi-rho-z) method to calculate oxide compositions (Goldstein et al., 1984; Reed, 1993). The peak concentration of Sr $L\alpha$ was counted for 80 s with background measurements for 20 s on each side. The peak concentration of Ca $K\alpha$ was counted for 20 s and each background for 10 s. A synthesized aragonite ($CaCO_3$) and strontianite [(Sr$_0.95$Ca$_{0.05}$)CO$_3$; NMNH R10065] were used as calibration standards. Since aragonite-structure carbonates are similar to otoliths, the standards have smaller matrix corrections than other types of standards such as oxide or silicate (Jarosewich & White, 1987). The standards were mounted in epoxy resin and polished. The carbon coating for the standards and otoliths had the same thickness (25–35 nm). After microchemical analysis, the otolith was polished to remove the carbon layer, then etched with 5% EDTA for 1–2 min to reveal the annual rings for age determination (Fig. 2). The duration of the eel in fresh waters and sea and brackish waters was estimated by relating the otolith Sr:Ca ratio profile to the otolith annuli.

**DATA ANALYSIS**

Data are expressed as means ± s.D. ($n =$ number of fish). Statistical differences among groups (locations) were evaluated by one-way ANOVA or Mann–Whitney rank sum test. Differences among groups were identified by Tukey’s pair-wise multiple comparison test. Significance was set at $P < 0.05$.

**RESULTS**

**TOTAL LENGTH, BODY MASS, AGES AND SEXES OF THE EELS AMONG LOCATIONS**

All 48 eels collected in the coastal waters of the Baltic Sea were at the yellow eel stage as were the 49 eels collected at the Curonian Lagoon, with the exception of one silver eel (Table I). All 10 eels collected in the Lake Baluosoai were migrating silver eels. All eels collected in the three sites were all females except one male in Lake Baluosoai. There were no significant differences in mean $L_F$ ($F_{2,105}$, $P > 0.05$) and $M$ ($F_{2,105}$, $P > 0.05$) among sampling locations. The mean ages of the eels from Lake Baluosoai, however, were significantly greater than those from the Curonian Lagoon and the Baltic coast ($F_{2,105}$, $P < 0.001$). This implied that the eel grew faster in the Baltic coasts and Curonian Lagoon than in Lake Baluosoai.

**LIFE-HISTORY SCAN OF OTOLITH SR:CA RATIOS**

Sr:Ca ratios in eel otoliths increased from $c. 8–10 \times 10^{-3}$ in the core to a peak of $c. 18–24 \times 10^{-3}$ c. 60–100 $\mu$m from the core. Otolith Sr:Ca ratios
then sharply decreased (Figs 3–6), which corresponded to the metamorphosis from leptocephalus to glass eel (Arai et al., 1997). Otolith Sr:Ca ratios before the elver stage were similar among individuals since the eels have similar migratory histories at the leptocephalus and glass eel stages. The patterns of otolith Sr:Ca ratios beyond the elver stage were variable, indicating diverse migratory histories during the yellow eel to silver eel stages. The migratory patterns of the eels were classified as follows.

**Freshwater pattern**

There were 16 eels (10 from Lake Baluošai and six from the Curonian Lagoon), which showed consistently low otolith Sr:Ca ratios from the elver
and through their life span (Fig. 3). No eels collected in the Baltic Sea had a pattern of consistently low otolith Sr:Ca ratios. The mean otolith Sr:Ca ratio of these 16 eels after the elver stage was $0.72 \pm 0.76 \times 10^{-3}$, which is consistent with previous studies on European and American eels (Tzeng et al., 1997; Cairns et al., 2004). This pattern suggested that these eels resided in fresh water from the elver to the yellow or silver eel stage.

**Seawater and brackish-water pattern**

Twenty-three eels (48%) collected in the Baltic coastal waters had otolith Sr:Ca ratios consistently $>3 \times 10^{-3}$ between the elver check and the otolith edge (Fig. 4). The consistently high otolith Sr:Ca ratios suggested that these eels resided in fresh water from the elver to the yellow or silver eel stage.

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**Table I. Biological characteristics (mean ± s.d.) of *Anguilla anguilla* collected from Lithuanian sites**

<table>
<thead>
<tr>
<th>Sampling location</th>
<th>Sampling period</th>
<th>Developmental stage</th>
<th>n*</th>
<th>$L_T$ (cm)</th>
<th>Body mass (g)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baltic coasts</td>
<td>June to September</td>
<td>Yellow eel</td>
<td>48</td>
<td>$63.0 \pm 7.3$</td>
<td>$582.4 \pm 274.6$</td>
<td>$11.0 \pm 1.8$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(47.5–81.0)</td>
<td>(180.0–1400.0)</td>
<td>(8–16)</td>
</tr>
<tr>
<td>Curonian Lagoon</td>
<td>June to August</td>
<td>Yellow eel except one silver eel</td>
<td>50</td>
<td>$66.3 \pm 10.4$</td>
<td>$691.4 \pm 441.7$</td>
<td>$10.8 \pm 1.7$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(49.0–92.0)</td>
<td>(201.0–2126.0)</td>
<td>(6–15)</td>
</tr>
<tr>
<td>Lake Baluosoai</td>
<td>April</td>
<td>Silver eel</td>
<td>10</td>
<td>$64.7 \pm 11.0$</td>
<td>$519.9 \pm 266.2$</td>
<td>$19.0 \pm 3.0$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(43.3–80.0)</td>
<td>(127.0–930.0)</td>
<td>(15–24)</td>
</tr>
</tbody>
</table>

*All female except one male in Lake Baluosoai.

n, sample size; $L_T$, total length.

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**Fig. 3.** Transects of mean ± s.d. otolith Sr:Ca ratios ($0.72 \pm 0.76 \times 10^{-3}$) from 16 freshwater-resident eels, illustrating consistent low values after the glass eel stage. Eels were collected from the Curonian Lagoon ($n = 6$) and Lake Baluosoai ($n = 10$). The transition of freshwater and sea and brackish residence (—) is indicated.
Fig. 4. Otolith Sr:Ca ratio transects illustrating some eels with seawater and brackish-water residence after the glass eel stage. 1 and 4, the annuli corresponding to the peaks of Sr:Ca ratios; EC, elver check. Eels were collected from the Baltic Sea: (a) number 34, 55.5 cm total length, $L_T$, age...
Eels resided in brackish or sea waters without entering fresh water from the elver stage through to the yellow eel stage. Eels with this kind of otolith Sr:Ca ratio pattern were considered to be seawater and brackish-water eels (Tsukamoto et al., 1998; Tzeng et al., 2000). The mean otolith Sr:Ca ratio from the elver check to the otolith edge of the seawater–and brackish water–resident eels was $4.84 \pm 1.61 \times 10^{-3}$, which was significantly higher than that of the freshwater-resident eels ($0.72 \pm 0.76 \times 10^{-3}$) (Fig. 3). Therefore, the mean otolith Sr:Ca ratios of the eels collected in the freshwater Lake Baluoˇsai and in the Baltic Sea were used as criteria to classify different migratory environmental histories of the eel. Eels with otolith Sr:Ca ratios $<2.24 \times 10^{-3}$ (mean otolith Sr:Ca ratios of 16 freshwater eels $+ 2$ S.D.) were considered as freshwater residents while eels with ratios $>3.23 \times 10^{-3}$ (mean otolith Sr:Ca ratios of 23 seawater and brackish-water eels $- 1$ S.D.) were considered as seawater and brackish-water residents. Intermediate values were regarded as a transition between fresh and sea water. No eels collected in the Curonian Lagoon demonstrated the seawater and brackish-water pattern; all showed freshwater residency ($<2.24 \times 10^{-3}$) for all or part of their life span.

Some seawater–and brackish water–resident eels showed relatively high otolith Sr:Ca ratios between the elver and the yellow eel stages and gradually decreased to lower otolith Sr:Ca ratios in the later part of the yellow stage (Fig. 4). For example, eel number 34 had higher Sr:Ca ratios ($5–12 \times 10^{-3}$) before 600 μm (age 5 years) and lower ratios ($3–5 \times 10^{-3}$) between 700 and 1000 μm (age 6–10 years) [Fig. 4(a)]. Eel number 44 showed otolith Sr:Ca ratios that decreased from $6–10 \times 10^{-3}$ at 350 μm (age 2 years) to $3–4 \times 10^{-3}$ c. 800 μm (age 8 years) [Fig. 4(d)]. Decreasing trends of otolith Sr:Ca ratios were found in 20 seawater and brackish-water eels that indicated a habitat shift from high to low salinity by these eels (Figs 4 and 5). The pooled profile of these 20 seawater–and brackish water–resident eels showed a relatively large mean otolith Sr:Ca ratio ($5.51 \pm 1.57 \times 10^{-3}$, range $4.8 \times 10^{-3}$, $n = 1240$) between 160 and 770 μm from the core and a small otolith Sr:Ca ratio ($3.64 \pm 1.10 \times 10^{-3}$, range $3–5 \times 10^{-3}$, $n = 1119$) between 780 and 1500 μm (Fig. 7). The gradient of mean otolith Sr:Ca ratios (Fig. 7) may reflect the migratory history of the eel from the full-strength sea water in North Sea to the brackish waters in the south-eastern Baltic coasts.

**Patterns of interhabitat shifters**

Most eels caught in the Curonian Lagoon (88%) and half from the Baltic Sea (52%) migrated between habitats (Table II), i.e. their otolith Sr:Ca ratios fluctuated between freshwater and seawater levels. Most interhabitat shifters (eels migrating between fresh water and sea and brackish water) showed high otolith Sr:Ca ratios ($>3.23 \times 10^{-3}$) for several years after the elver stage that

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Fig. 4. (Continued) 11 years, (b) number 39, 65.5 cm $L_T$, age 13 years, (c) number 41, 70 cm $L_T$, age 14 years and (d) number 44, 57.5 cm $L_T$, age 14 years. The transition of freshwater and sea and brackish residence (—) is indicated.
were then followed by relatively low ($<2\cdot24 \times 10^{-3}$) or fluctuating ratios between the freshwater and the seawater levels (Fig. 5). Eel number 1 resided in sea and brackish water for the first 5 years (otolith Sr:Ca ratios range: 4–12 $\times 10^{-3}$) and invaded fresh water at age 5 years [Fig. 5(d)]. This eel showed seasonal peaks in otolith Sr:Ca ratios at each annulus, suggesting that it win-tered in brackish water but spent the remainder of each year in fresh water (Tzeng et al., 1997, 1999). The coincidence of otolith Sr:Ca ratio peak and annulus was also found in other eels, e.g. number 4, 34 and 41 (Figs 4 and 5). In light of the high plasticity of eel phenotypes, an explicit description or classification of the diversified migratory behaviours is not feasible and seems not necessary. Briefly, these varying patterns suggested that the eels recruited to fresh water and resided there until being caught or moved seasonally and irregularly between fresh and sea water.

**Fig. 5.** Otolith Sr:Ca ratio transects illustrating eel movement into fresh water after a period of seawater and brackish-water residence: (a) eel number 19, 62.4 cm total length, $L_T$, age 13 years and (b) number 4, 63.8 cm $L_T$, age 9 years. (c) Eel number 15, 83 cm $L_T$, age 11 years demonstrates a gradual decline of the otolith Sr:Ca ratio profile corresponding to the movement from high salinity through low salinity to fresh water. (d) Eel number 1, 56 cm $L_T$, age 11 years, shows seasonal migration between high salinity and low salinity or fresh waters. 1 and 1–10, the annuli corresponding to peaks in the otolith Sr:Ca ratios; EC, elver check. (e) The X-ray intensity mapping displays high Sr content from age 1 to 5 years and high Sr rings at annuli 6–10 in eel number 1. All eels were collected from the Curonian Lagoon. The transition of freshwater and sea and brackish residence (——) is indicated.
MIGRATORY PATTERNS AND ORIGIN OF THE EELS AMONG LOCATIONS

The eels collected along the Baltic coast were either seawater–and brackish water–resident eels (48%) or interhabitat shifters (52%); none were freshwater eels (Table II). The eels collected from the Curonian Lagoon were primarily interhabitat shifters (88%) while freshwater-resident eels accounted for c. 12% (Table II). Eels from the freshwater Lake Baluošai were all freshwater eels (Table II).

The presence or absence of an extended seawater and brackish-water signature (otolith Sr:Ca ratios $>3 \times 10^{-3}$) after the glass eel stage was used to
Fig. 6. Otolith Sr:Ca ratio profiles of interhabitat shifters. Otolith Sr:Ca ratio transects illustrating movement between fresh water and sea and brackish water: (a) eel number 5, 62.3 cm total length, LT, age 11 years and (b) number 7, 74.5 cm LT, age 10 years (eels number 5 and 7 were collected from...
distinguish stocked eels from naturally recruited eels. The six eels from the Curonian Lagoon and 10 eels from Lake Baluošai showing a consistent freshwater signature throughout their life after the glass eel stage must have been the stocked eels. Another 85 eels with extended large otolith Sr:Ca ratios after glass eel stage should have been the naturally recruited eels if the stocked elvers had not migrated immediately to sea water.

In a few interhabitat shifters \( (n = 7) \), a period of low otolith Sr:Ca ratios \( (<2.24 \times 10^{-3}) \) appeared before the extended high otolith Sr:Ca ratio \( (>3.23 \times 10^{-3}) \) making it difficult to tell whether these seven eels were stocked eels or naturally recruited eels (Fig. 6). This may indicate that the eels had invaded fresh water at the elver stage for a period of time, then returned to sea and brackish water. Eels number 5, 6 and 7 resided in fresh water for c. 2 years, returned to sea and brackish waters for 1–4 years, and then moved back to fresh water [Fig. 6(a), (b)]. Eels number 14, 45 and 100 resided in fresh water for 1–4 years and subsequently returned to sea and brackish waters for their remaining life [Fig. 6(c), (d)]. Differences in their migratory histories were evident. Eels number 45 and 100, collected on the Baltic coast, [Fig. 6(c), (d)] showed relatively high otolith Sr:Ca ratios \( (400–700 \mu \text{m for eel number 45 and 350–800} \mu \text{m for eel number 100}) \) at the early stage and a decreasing trend in otolith Sr:Ca ratio in the later stage, which is very similar to the pattern of naturally recruited eels. Therefore, eels number 45 and 100 might be naturally recruited eels that have entered fresh water somewhere prior to entering Lithuanian waters. In contrast, eels number 5, 6, 7 and 14 collected in the Curonian Lagoon [Fig. 6(a), (b)] and eel number 60 from Baltic coast might be stocked eels that stayed in a fresh water for a few years then returned to the Baltic coast or migrated between both sites. This interpretation was based on otolith Sr:Ca ratios for the seawater and brackish-water signature that were smaller, intermittent or shorter than that for naturally recruited eels and that showed no decline in otolith Sr:Ca ratios. Overall, 87 individuals were naturally recruited eels while 21 individuals were stocked eels among the samples collected in the Curonian Lagoon \( (n = 10) \), Baltic coasts \( (n = 1) \) and Lake Baluošai \( (n = 10) \) (Table III). Stocked eels accounted for c. 20% of the eels in the Curonian Lagoon and 2% on the Baltic coast; however, the eels in the Lake Baluošai were 100% of stocked origin (Table III).

### The Ages on Arrival in Lithuanian Waters

Sixty-three naturally recruited eels initially entered fresh water at ages of 1–10 years with a mean age of \( 5.2 \pm 2.1 \) years (Fig. 8). This implies that after reaching the Baltic, the eels spent a number of years in marine and brackish waters before entering fresh water. Twenty-two of these 63 eels showed consistent low otolith Sr:Ca ratios after extended high Sr:Ca ratios, indicating that they

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Fig. 6. (Continued) the Curonian Lagoon) and rapid entry into freshwater at the elver stage (EC, elver check) then a return to sea and brackish water; (c) eel number 45, 64 cm \( L_T \), age 12 years and (d) eel number 100, 81 cm \( L_T \), age 12 years (eels number 45 and 100 were collected from the Baltic Sea). The transition of freshwater and sea and brackish residence (—) is indicated.
continuously resided in fresh water after freshwater entry [Fig. 5(a), (b)]. Mean age of these 22 eels at freshwater entry was 4.6 ± 2.2 years [Fig. 8(b)], not significantly different from the mean ± s.d. ages of the other 41 eels (5.6 ± 1.9 years) that entered fresh water but showed subsequent movements between fresh and sea and brackish waters (P = 0.16, Mann–Whitney rank sum test). This indicated these eels spent several years in the Baltic Sea then entered fresh water at the area of capture. After the initial freshwater entry, the eels spent 5–6 years (range: 1–10 years) in the Curonian Lagoon or Baltic coast before capture (Fig. 8).

**DISCUSSION**

**INTERPRETATION OF EEL MIGRATION BY OTOLITH SR:CA RATIOS**

Bath *et al.* (2000) and Kraus & Secor (2004) pointed out that it was Sr:Ca ratios in the water rather than salinity that primarily determined the incorporation of Sr into otoliths. These ratios can be used to infer migration patterns of eels. Table II summarizes the migratory patterns of *Anguilla anguilla* as inferred from otolith Sr:Ca ratios. Freshwater residents, Sr:Ca ratios consistently <2.24 × 10^{-3}; seawater and brackish-water residents, Sr:Ca ratios consistently >3.23 × 10^{-3}; interhabitat shifters, otolith Sr:Ca ratios covering the ranges of freshwater and seawater values.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Sample size</th>
<th>Freshwater residents</th>
<th>Seawater and brackish-water residents</th>
<th>Interhabitat shifters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baltic coast</td>
<td>48</td>
<td>—</td>
<td>48</td>
<td>52</td>
</tr>
<tr>
<td>Curonian Lagoon</td>
<td>50</td>
<td>12</td>
<td>—</td>
<td>88</td>
</tr>
<tr>
<td>Lake Baluošai</td>
<td>10</td>
<td>100</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>108</td>
<td>14.8</td>
<td>21.3</td>
<td>63.9</td>
</tr>
</tbody>
</table>

Fig. 7. The mean ± s.d. otolith Sr:Ca ratio profile of 20 European eels that showed a gradual decline pattern, indicating the movement from the full strength of salinity in the North Sea into brackish water of the Baltic Sea (phase I: mean Sr:Ca ratio = 5.51 ± 1.57 × 10^{-3}, n = 1240) and ultimately arrived at the coastal waters of Lithuania (phase II: mean Sr:Ca ratio = 3.64 ± 1.10 × 10^{-3}, n = 1119). The transition of freshwater and sea and brackish residence (—) is indicated.
of Sr into the otolith. This finding implied that otolith Sr:Ca ratios, as the proxy of salinity, should be interpreted based on knowledge of the ambient water chemistry. This is because fishes living in Sr-rich fresh water may incorporate Sr at the same level or even higher than the fishes living in normal sea and brackish water. Kraus & Secor (2004), however, also admitted that natural Sr-rich fresh water, if it can be found, is rarely seen. Generally, Sr is c. 100-fold greater in sea water \( (8 \times 10^{-5} \text{ M}) \) than in fresh water \( (9 \times 10^{-7} \text{ M}) \) (Campana,

### Table III. Relative contribution of stocked and naturally recruited *Anguilla anguilla* in different habitats

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Sample size</th>
<th>Stocked</th>
<th>Naturally recruited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baltic coasts</td>
<td>48</td>
<td>2</td>
<td>98</td>
</tr>
<tr>
<td>Curonian Lagoon</td>
<td>50</td>
<td>20</td>
<td>80</td>
</tr>
<tr>
<td>Lake Balušai</td>
<td>10</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>108</td>
<td>19</td>
<td>81</td>
</tr>
</tbody>
</table>

**Fig. 8.** The naturally recruited eels showed a variable range of the ages at first freshwater entry (■) as well as the duration between first freshwater entry and capture (□). (a) The eels showed more than one freshwater entry. The mean ± S.D. age at the first freshwater entry was 5·6 ± 1·9, years \( (n = 41) \) (■) and the age between the first freshwater entry and the capture was 5·3 ± 1·9, years \( (n = 41) \) (□). (b) The eels only showed one freshwater entry. The mean age at first freshwater entry was 4·6 ± 2·2, years \( (n = 22) \) (■) and the age between the first freshwater entry and the capture was 6·1 ± 2·1, years \( (n = 22) \) (□).
More than 10-fold higher water Sr concentration or seven-fold higher water Sr:Ca ratios were measured in the Baltic coast than in the Curonian Lagoon. Elsdon & Gillanders (2005) found significantly increased otolith Sr:Ca ratios by enhancing ambient water Sr:Ca ratios by two- to four-fold. Their experimental results justified the use of otolith Sr:Ca ratios in interpreting migratory history of the eels across different salinity environments.

Salinity decreases gradually from c. 35 in the North Sea to c. 15 in the southwestern Baltic Sea and to c. 6 in the coastal waters of the south-eastern Baltic Sea. The migration from a high salinity (North Sea) to low salinity environment (south-eastern Baltic) was clearly imprinted in 20 naturally recruited eels with decreasing otolith Sr:Ca ratios (Fig. 7). Owing to the asymptotic relationship between otolith Sr:Ca ratios and salinity (Tzeng, 1996; Limburg et al., 2003), there is limited ability to distinguish full-strength and half-strength seawater salinities by otolith Sr:Ca ratios. Freshwater eels, however, showed very low otolith Sr:Ca ratios, distinct from those in seawater and brackish-water eels. This result is consistent with the finding of Zimmerman (2005) that salmonid otolith Sr:Ca ratios were linearly related to salinity, but the sensitivity of otolith Sr:Ca ratios was only enough to discriminate between fresh, brackish and sea water.

CONTRIBUTION OF STOCKED AND NATURALLY RECRUITED EELS TO THE POPULATION

The composition of stocked and naturally recruited eels differed among locations. Based on the patterns of otolith Sr:Ca ratios, eels caught in Lake Baluosoai are all of stocked origin, suggesting that few, if any naturally recruited eels reach this area and that eel fisheries in the inland lakes are all based on the stocked eels. Further studies with larger sample sizes are required to determine if there is any natural recruitment to the inland waters of eastern Lithuania. The proportions of stocked eels decreased to 20 and 2% in the Curonian Lagoon and Baltic coast, respectively (Table III). There was no evidence to suggest that stocked eels from inland lakes of eastern Lithuania will emigrate downriver and contribute to the eel stock in the Curonian Lagoon or the Baltic coast. It seems unlikely that stocked eels undergo the long migration, c. 300 km, from Lake Baluosoai or other lakes from the same water basin to the Curonian Lagoon during the yellow eel growth-phase. The eels caught in Lake Baluosoai showed narrow otolith annuli [Fig. 2(b)], which is distinct from that of residents in the Curonian Lagoon and Baltic coast [Fig. 2(a)]. The narrow annuli indicate a slow growth rate due to the limited prey available in Lake Baluosoai, determined by higher eel population density based on catch-per-unit effort in the stocked lakes of eastern Lithuania. The growth differences might also be determined by lower lake productivity and by feeding differences at the sampling sites. The Curonian Lagoon is eutrophic (Jaśinskaite, 1998) while Lake Baluosoai is mesotrophic to oligotrophic (K. Arbačiauskas, pers. comm.). Eel dietary studies demonstrated that the lagoon and Baltic Sea eels eat a high proportion of fishes while Lake Baluosoai eels eat largely invertebrates (E. Bacevičius, pers. comm.). None of the 11 stocked eels found in the Curonian Lagoon and Baltic coast showed narrow otolith annuli, suggesting that few,
if any, stocked eels migrate downriver to the Curonian Lagoon or Baltic coast waters until the spawning migration. A reasonable hypothesis is that the eel populations in inland lakes of eastern Lithuania and the Curonian Lagoon are independent during the growth phase. Energy costs, density-dependent migration and variable habitat quality could influence the geographic distribution as well as the migration of eels within the river (Feunteun et al., 2003).

Some glass or small yellow eels have been released in Curonian Lagoon, but the stocking rate has been low: (only 1·7 eels ha$^{-1}$ in 1995–2003). Only one stocked eel (number 60) was found to have emigrated from the Curonian Lagoon to the nearby Baltic coast while four stocked eels (number 5, 6, 7 and 14) eventually returned to the Curonian Lagoon after short movements to the Baltic coast. This suggests that stocked eels prefer to settle in the location where they are released. Accordingly, 91% ($n = 10$) of the stocked eels ($n = 11$) remained in the Curonian Lagoon where they were released, assuming that no or very few eels had descended from lakes via the Nemunas River. In addition, c. 9% ($n = 1$) of the stocked eels in the Curonian Lagoon emigrated to the Baltic coast and constituted c. 2% of the local eel population.

Eels are important commercial and recreational species in central and eastern Europe and make important contributions to local and regional economies. Hence, the original aim of stocking programmes in the Lithuania and other Baltic countries was enhancement of inland fisheries. Intensive exploitation of the stocked eels presumably led to high fishing mortality and a low rate of escapement by silver eels. Limburg et al. (2003), however, found that 26·7% of the migrating silver eels in the area connecting the Baltic Sea with the North Sea were of stocked origin, comparable to the present finding that stocked eels account for 20% of the population in the Curonian Lagoon. Without related information on natural recruitment as well as the survival rate of the stocked eels, it is difficult for this first evaluation of the contribution of stocked eels to the naturally recruited population in the south-eastern Baltic Sea to determine stocking effectiveness. It is possible, however, that the stocked glass eels in Lithuania (e.g. stocked to the Curonian Lagoon) or other Baltic countries migrate to the Baltic Sea too soon after release to allow the freshwater signature to be recorded in the otolith. If so, the proportion of stocked eels in the Baltic Sea will be underestimated. Alternatively, most stocking programmes in the Baltic countries are focused on fisheries enhancement in inland lakes and quick migration over long distances to the Baltic Sea without creating a freshwater signature in the otoliths seems unlikely.

Seawater–and brackish water–resident eels accounted for only 23% of eels examined from Baltic coastal waters and the lagoon, while interhabitat shifters comprised c. 70% of the eels. The proportion of naturally recruited eels that have experienced fresh water is more than twice as high as found in the migrating silvers in the area connecting the Baltic Sea to the North Sea (Limburg et al., 2003). If only the eels collected in the Lithuanian Baltic coast were considered, the proportion of the eels experiencing fresh water is still as high as 50%. The differences between these two independent studies may be due to the different geographical and habitat constraints or different behaviours of the eels. Long-distance migratory eels may be more active in exploring different habitats than their counterparts that settle down earlier. After entry into Baltic Sea, eels
trapped in this closed system may explore optimal habitats at minimal energy cost to benefit maximal growth. Diversified habitats usually provide more food and shelter than does a less diversified habitat, which presumably encourages euryhaline fishes to explore different habitats. This may explain the flexible and complex migratory behaviour of the eels, which reflects their environmental and evolutionary adaptation.

**AGES OF EEL ON ARRIVAL IN SOUTH-EAST BALTIIC SEA**

As far as is known, this is the first study that estimates the ages of the eels arriving in the south-eastern Baltic area. Most naturally recruited eels showed an initial freshwater entry at age 1–10 years (mean ± s.d. 5.2 ± 2.1 years). High variability in the age at initial freshwater entry indicates that some eels might migrate quickly through the Baltic Sea and into fresh water within 1 or a few years, while some eels showed very slow migration eastward. The broad ranges of age at initial freshwater entry also suggest a random distribution of the eels in the Baltic Sea rather than size- or age-dependent distribution. The eel density in the North Sea and Skagerrak and Kattegat Sounds may influence ages at arrival in the south-eastern Baltic. Low eel density in the Baltic Sea due to low recruitment of young eels (Westin, 2003) may discourage eastward migration due to low intraspecific competition, so the eels arrive at older ages. It is known that populations in the lower reaches of rivers achieve high densities, but as eels grow, relative biomass and hence competition for food and space increase. Agonistic encounters may then act as a stimulus for further upstream migration (Knights, 1987). Interestingly, on the Baltic coast of Denmark, at the monitoring site of eel recruitment at the Harte hydropower station, 50% of trapped eels were glass eels in the 1960s, while glass eels are rarely seen today. Thus, the mean size of recruiting eels has probably increased over the years due to the delayed recruiting process. In Vester Vedsted brook on the Danish North Sea coast, glass eels, elvers and yellow eels are found, however, pigmented glass eels are most common at the lower part of the brook and are considered as new recruits (Pedersen, 2002). More to the south of the European coast, in the Netherlands, new recruits are partly but never fully pigmented glass eels (Dekker, 2002), while in coastal Germany at recruitment monitoring sites both true glass eel and fully pigmented elvers are found (Kuhlmann et al., 2002). In south-west Norway in the River Imsa, all sampled eels are fully pigmented elvers or young yellow eels that have stayed for one winter or more in marine or estuarine waters (Vollestad, 2002). In Sweden, the catch in the River Viskan discharging to the North Sea consists mainly of elvers; however, at other rivers of the same coast age ranged from 0 to c. 8 years (Wickström, 2002). Overall, eels from rivers along the eastern coast of Sweden (Baltic Sea) are older than in rivers closer to the coast of the Skagerrak and Kattegat Sound (Wickström, 2002), i.e. the sound between the Baltic and the North Seas. Hence, presumably eels to the south-eastern Baltic should not be glass eels on arrival. The present observed arrival ages clearly support the hypothesis of eel recruitment to the south-eastern Baltic at the yellow eel stage, and explains why regional ichthyologists and managers were so uncertain about the contribution of natural recruitment, i.e. the absence of truly glass eels.
in the coastal waters led to hypotheses of natural recruitment weakness or even overall absence in the region.

Stocking programmes are a common and usually effective strategy to mitigate population decline, restore fisheries or to create new fisheries. The majority of stocked lakes in Latvia, Lithuania and Poland were almost devoid of eels before intensive stocking programmes began in the 1950s. The stocking programmes did create new eel fisheries in these inland lakes and also partially support the eel population in the Curonian Lagoon. Many stocking programmes, including eel stocking, however, are carried out without evaluation of their effectiveness or actual success (Cowx, 1999). The use of otolith Sr:Ca ratios enabled this study to discriminate stocked eels from naturally recruited eels and to evaluate their contribution to the population.

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