

## Do Stocked Freshwater Eels Migrate? Evidence from the Baltic Suggests “Yes”

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*Abstract.*—In response to declining catches of eels in the brackish Baltic Sea, the Swedish government stocks eels *Anguilla anguilla* (L.), both in lakes (mainly glass eels/elvers) and in the sea itself (mainly yellow eels). However, the degree to which these fish contribute to the spawning stock, if at all, was unknown. We collected silver eels at the exit of the Baltic Sea and analyzed indices of their maturity status. In addition, we used electron (WDS) and nuclear (microPIXE) microprobes to map out the strontium and calcium contents of their otoliths, as Sr:Ca correlates with salinity. As a calibration, we analyzed otoliths from eels collected around the Swedish coast and fresh water (0–25 psu) and derived a relationship between salinity and Sr:Ca. Our results show that, of 86 silver eels analyzed, 17 eels had Sr:Ca profiles consistent with having been stocked into fresh water, six showed patterns consistent with stocking directly into the Baltic from marine waters, and 10 showed patterns indicative of natural catadromy. In all, 31.4% of silver eels showed histories of freshwater experience, including 24% of those found outside the Baltic. Silver eels caught exiting the Baltic had higher fat contents (21.1% of body weight) than those collected in the southern Baltic near Denmark (18.6%), but differences were not significant between wild and presumed stocked fish within geographic areas. The conclusions of Tsukamoto et al. (1998), i.e. that freshwater eels are not supported by catadromous individuals, do not appear to hold for the Baltic, although it is clear that noncatadromous fish composed the majority of our silver eel samples.

### Introduction

Baltic eel *Anguilla anguilla* (L.) catches have declined precipitously since the 1960s and a supplemental stocking program has been in effect in Sweden since the late 1970s (Svedäng 1996). The stocking program, at an annual cost of nearly 10 million SEK (~ US\$1 million; H. Wickström, personal communication), has consisted either of transplanting small eels (ca0.10–20 cm) collected as glass eels or elvers in the

Severn estuary in England, or transplanting yellow eels (35–48 cm) caught off the Swedish west coast (Wickström 1993). Today, stocking provides an estimated 8–9% of all young eels in Sweden. Whereas much has been learned about the biology of stocked eels from experiments (e.g., Wickström et al. 1996), there has been no direct evaluation of the contribution of stocked eels to Baltic catches, nor to their ultimate contribution to the spawning stock. However, previous work raised two testable hypotheses.

In one study, experimentally stocked eels on Gotland, that were tagged and allowed to migrate as silver eels, did not migrate through the outlet of the Baltic at Öresund (Figure 1) as did natural migrants, but rather ended up around the Danish islands in the Belt Sea (Westin 1990). In a second study, Svedäng and Wickström (1997) found no correlation between maturity stage and muscle fat concentration, and suggested that silver eels (a non-feeding stage) with low fat concentrations may temporarily halt migration, revert to a feeding stage, and "bulk up" until fat reserves are sufficient to carry out successful migration to the spawning area. Thus, by sampling silver eels at the exit point from the Baltic, measuring their fat reserves, and identifying stocked versus natural fish, one should be able to test whether: stocked eels can find

their way out of the Baltic (Westin 1990) and whether there is a correlation between stocked/natural status and low fat concentrations (Svedäng and Wickström 1997).

In a third study, Tsukamoto et al. (1998) used the method of strontium:calcium ratios in otoliths (for a review of the method and other otolith microchemistry, see Campana 1999) to determine whether or not catadromous European and Asian anguillids contribute to spawning stocks. Briefly, Sr entrained in aragonitic otoliths typically reflects environmental concentrations, and when normalized to otolith Ca it serves as a proxy for salinity because Sr is generally higher in marine waters than in fresh. Because otoliths accrete over time, a temporal record of Sr:Ca is maintained and can be assessed with various microprobe techniques



Figure 1. Map of the study region. Key: S = Salnö, G = Gotland, Å = Lake Ången, D = area sampled in Denmark for silver eels, K = Kullen, F = Fladen, M = Marstrand, and S-K = Skagerrak.

(Campana 1999). Otoliths from eels collected in the North Sea and the East China Sea revealed no evidence of freshwater experience, leading the investigators to question whether catadromous eels really do contribute their genes to future generations. Thus a third hypothesis—that only noncatadromous eels recruit to the spawning stock—should also be testable.

In the present study, we used the Sr:Ca method to trace the environmental histories of migrating Baltic eels. We first calibrated the method by measuring the Sr:Ca ratios in eel otoliths collected either in fresh water or along a stable salinity gradient, and then used these to examine and analyze otoliths of silver eels, collected either exiting the Baltic or down in its southern reaches. We found a substantial fraction of migrating silver eels whose Sr:Ca patterns are consistent with having been stocked, and further found fish showing catadromous patterns.

## Methods

### *Study Area*

Eels were collected at different places in the Baltic Sea, the Skagerrak-Kattegat area, and the Swedish west coast (Figure 1) either by trapping, trawling, or by purchase from fishermen. Eels that were experimentally stocked and monitored in two lakes (Lake Ången on the Swedish mainland, and Lake Fardume on the island of Gotland) served as known freshwater endmembers. Yellow eels collected from three areas of different salinity (Marstrand, approx. 25 psu, Gotland, approx. 7 psu, and Salnö, approximately 5 psu) were assayed to provide Sr:Ca ratios representative of those salinities. Finally, silver eels were collected at sites exiting the Baltic Sea (Kullen, Fladen, and in the Skagerrak) as well as in the southern Baltic in the vicinity of the Danish islands of Lolland and Falster. Eels were stored frozen until ready for analysis.

### *Laboratory Procedures*

Morphometric measures (total length, weight, eye diameter, jaw length, and pectoral fin lengths) were made on defrosted fish. A sample of tissue was taken just anterior of the anal vent and analyzed for lipid content as described in Svedäng and Wickström (1997). Eye diameters and total lengths were used to calculate an index ( $I$ ) of maturation status (Pankhurst 1982):

$$I = (25\pi/8TL) \times [(A + B)_L^2 + (A + B)_R^2],$$

where TL is total length, and A and B are the height and width of the left (L) and right (R) orbitals. Silver eels with values of  $I$  greater than 6.5 are classified as sexually maturing (Pankhurst 1982; Svedäng and Wickström 1997).

Sagittal otoliths were removed from the skull, cleaned, embedded in Spurr's epoxy, and sectioned in the sagittal plane by grinding to the core with a graded series of grinding papers, and finally polished to 0.5  $\mu\text{m}$  surface fineness. Following carbon coating, otoliths were analyzed for Sr and Ca by using either a wavelength-dispersive (WDS) electron microprobe at the Department of Geosciences, Uppsala University, or nuclear microscopy combined with proton induced X-ray emission analysis ( $\mu\text{PIXE}$ ) at the Department of Nuclear Physics, Lund Technical University. The latter method has the advantages of higher resolution and more rapid data collection and was therefore the method of choice, given availability of machine time. Thirty-eight otoliths were analyzed using WDS and 100 with  $\mu\text{PIXE}$ .

Analyses using WDS involved visually locating the core of the otolith with transmitted light, then laying out a transect of 30–50 points spaced 20–40  $\mu\text{m}$  apart traversing the otolith from the core to the outer posterior edge (a so-called "life-history transect"). The parameters for operation were: accelerating voltage, 20 kV; current, 20 nA; electron beam diameter, 15  $\mu\text{m}$ . Strontium was counted for 40 s on the peak and 40 s on the background (only on one side, to avoid the strong interference from a second order Ca K- $\alpha$  peak). Calcium was counted until a precision of at least 0.1% was reached (usually < 20 s), and background was counted for 10 s on each side of the peak. Strontianite ( $\text{SrCO}_3$ ) and calcite ( $\text{CaCO}_3$ ) were used as calibration standards. The detection limits were  $0.03 \pm 0.004$  weight percent for both elements.

$\mu\text{PIXE}$  analyses were made at the Lund Nuclear Microprobe facility, using a standard 2.55 MeV proton beam. X-rays were detected with a Kevex Si(Li) detector of 5  $\text{mm}^2$  active area and a measured energy resolution of approximately 155 eV at the 5.9 keV Mn K $_{\alpha}$  peak. A thick absorber (mylar + aluminum) was used during the analysis to suppress the Ca X-ray peaks; this permitted increasing the current to enhance the signals of Sr and other trace elements. The total charge was approximately 1 micro-Coulomb.

The normal procedure for a scan was to raster as much of the otolith as possible in a grid of  $128 \times 128$  pixels. Thus, we mapped out large areas of the otolith rather than being confined to a line transect, which facilitated interpretation of the data. Following data collection, the data sets were normalized to counts per charge.

### Data Analysis

Strontium:calcium ratios were calculated, graphed, and examined for patterns. Yellow eel otoliths that had been analyzed with  $\mu$ PIXE were used to calibrate Sr:Ca to salinity. Subsamples (two replicate  $6 \times 6$  groups of pixels) were chosen from near the outer growing edge on different parts of each otolith and mean Sr:Ca ratios were calculated. A nonlinear regression of Sr:Ca on salinity yielded the following relationship:

$$\text{Sr:Ca}_{\text{PIXE}} = a \times (1 - b e^{-K \times \text{Salinity}}), \text{ where}$$

$$a = 3.467 \pm 0.191 \text{ (standard error)}$$

$$b = 0.905 \pm 0.0254$$

$$K = 0.132 \pm 0.0251$$

$$N = 29, R = 0.97.$$

Because of the mylar absorber used to suppress Ca peaks in the  $\mu$ PIXE analyses, the Sr:Ca ratios do not reflect true mass ratios. Therefore, otoliths from six fish were analyzed with both methods, and regression analysis was used to relate electron microprobe Sr:Ca measurements to  $\mu$ PIXE:

$$\text{Sr:Ca}_{\text{WDS}} = 0.477 + 1.531 \times \text{Sr:Ca}_{\text{PIXE}}$$

$$(R^2 = 0.84, p < 0.05).$$

Based on otolith Sr:Ca and the associated estimated salinity histories, silver eels were classified into eight distinct groups. Five of these groups describe wild fish: entirely marine (M); marine moving into brackish water (MB); entirely brackish after the glass eel stage (B); "complex migration" (CM) when moving back and forth between waters of different salinities, but never into fresh water; and catadromous (CAT) when the movements following the glass eel stage included residence in fresh water. The last three groups are called "stocked," and show patterns that are consistent with either having been stocked as glass eels and remained virtually until capture in fresh water (S1), captured

along the Swedish west coast as yellow eels and transferred into the Baltic (S2), or having been stocked as glass eels but migrating out to brackish or marine waters to feed and grow (S3). Examples of these types are given in Figure 2.

Analysis of variance (ANOVA) and goodness-of-fit tests were conducted on silver eels to test the hypotheses that differences exist between fish caught exiting the Baltic and those caught in the southern Baltic (Denmark), and that differences exist between wild and stocked eels with respect to lipid content. All statistical analyses were conducted with Statistica (Statsoft 1999).

### Results

Collectively, the silver eels we analyzed displayed a wide repertoire of habitat use patterns. Many eels appeared to move around among different areas over the course of their lifetimes, among different salinity zones, up into fresh water, or both (Figure 2). Distributions of eel habitat use patterns differed between the eels caught exiting or outside the Baltic, and those collected in the Baltic around southeastern Denmark (Figure 3; goodness of fit  $\chi^2 = 32.06$ ,  $df = 7$ ,  $p < 0.001$ ). Categories that differed the most included MB (fish moving from marine to brackish water), CM (movement back and forth among zones of different salinity), catadromous, S1 (entirely freshwater, presumed to be stocked), and S3 (stocked but moved into saline waters), with all being more numerous in the Danish samples except for CM and S3.

Overall, eels presumed to have been stocked composed 26.7% of the silver eels collected for the study, not counting several fish that were used in the calibration. Aggregating the three stocked categories, there was no statistical difference between the ratios of wild and stocked eels between the geographic areas (Figure 4;  $\chi^2 = 0.723$ ,  $df = 1$ ,  $p < 0.39$ ). However, among the stocked categories, S1 fish were almost exclusively found in the Danish sample, and S3 fish were three-fold higher exiting the Baltic than in the Danish collection (Figure 3). Counts of eels classed as S2 were the same in both areas. In contrast, the proportion of silver eels that had spent time in fresh water, either stocked or wild, was marginally higher in the Danish sample (38% in Danish waters versus 24% outside;  $\chi^2 = 3.20$ ,  $df = 1$ ,  $p < 0.07$ ). Eels with freshwater experience composed 31.4% of all silver eels (excluding individuals used in calibration).

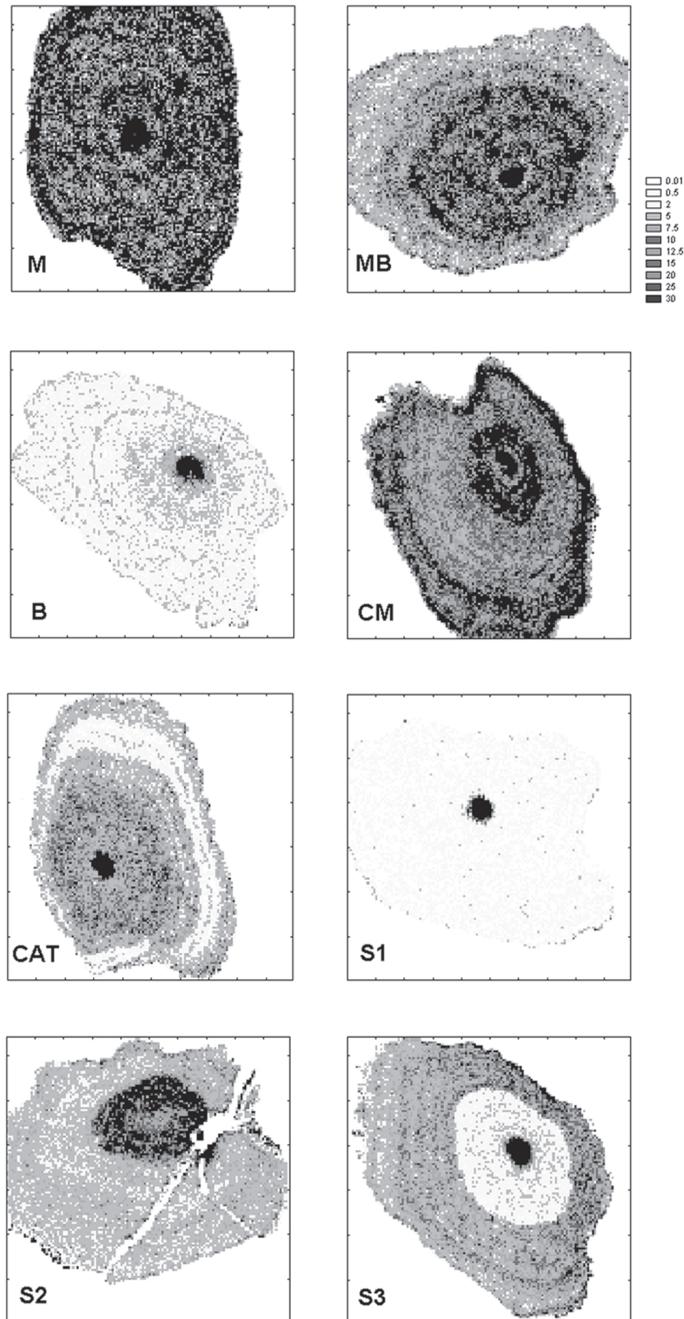


Figure 2. Examples of the eight habitat use categories as discerned by strontium:calcium ratios. Images are of  $\mu$ PIXE scans of otolith chemistry converted to estimated salinity values. Note that the high values in the otoliths' centers are due to high levels of Sr associated with the leptocephalus stage. Key to categories: M = entire life spent in marine waters; MB = moved from marine to brackish waters; B = spent entire postglass-eel life in brackish waters; CM = complex migration, moving back and forth between marine and brackish waters; CAT = catadromous; S1 = stocked into fresh waters and remaining there until maturation; S2 = stocked from marine waters into the Baltic Sea; S3 = stocked into fresh water and leaving to spend time feeding and growing in brackish and/or marine waters.

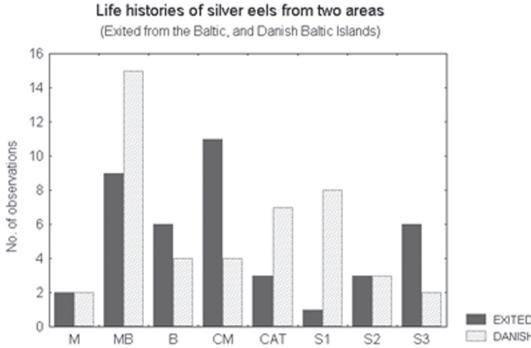


Figure 3. Distributions of habitat use patterns by geographic area. Key to categories: M = entire life spent in marine waters; MB = moved from marine to brackish waters; B = spent entire postglass-eel life in brackish waters; CM = complex migration, moving back and forth between marine and brackish waters; CAT = catadromous; S1 = stocked into fresh waters and remaining there until maturation; S2 = stocked from marine waters into the Baltic Sea; S3 = stocked into fresh water and leaving to spend time feeding and growing in brackish and/or marine waters.

Trends were observed in the lipid contents of silver eels. Lipids tended to be higher among wild versus presumably stocked eels, and greater in eels exiting the Baltic than those collected in Denmark (Figure 5). Although there was no statistical difference between wild and stocked eels, eels exiting the Baltic were significantly fatter than Danish-caught eels (ANOVA,

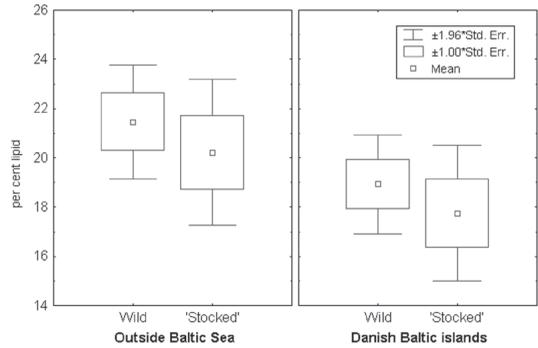


Figure 5. Box plots of lipid contents of silver eels, by geographic area and stocking status.

$F_{1,77} = 4.14, p < 0.05$ ). Differences also existed among eels presumed to have different stocking histories ( $F_{2,19} = 3.39, p < 0.055$ ). Of the nine eels that spent their entire lives in fresh water (S1), only one exceeded 20% lipid content, whereas ten out of thirteen S2 and S3 eels had lipid levels of at least 20% (Figure 6).

Silver eels collected in the Danish Baltic islands varied differently from exiting eels with respect to Pankhurst's maturation index (Table 1). In the Danish collection, catadromous eels had the highest mean *I* of 7.86, while two eels classified as marine had the lowest (mean *I* = 5.92). Exited catadromous eels, conversely, had the lowest *I*-values (mean 6.26), but were also the most fatty (mean per cent lipid = 27.5). *I*-values less than or equal to 6.5 are generally interpreted as sexually immature. *I*-values were

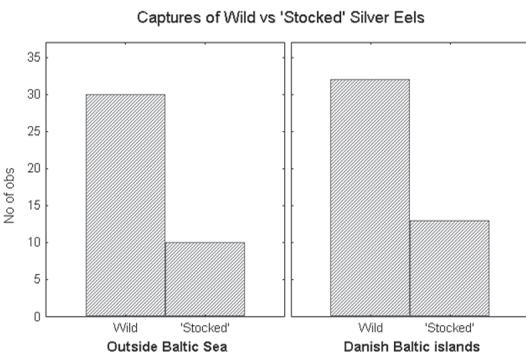


Figure 4. Wild versus stocked silver eels by geographic area.

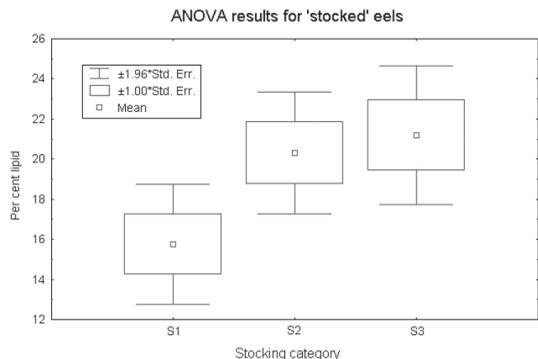


Figure 6. Box plots of lipid contents of silver eels classified as stocked.

Table 1. Mean ( $\pm$  s.e.) values of Pankhurst's index (I) of maturation status and mean muscle tissue lipid contents of silver eels collected either exiting the Baltic or in Danish Baltic waters. Habitat use categories are described in the Methods section.

| Habitat use category | Exited eels          |                   |   | Danish eels          |                   |    |
|----------------------|----------------------|-------------------|---|----------------------|-------------------|----|
|                      | Maturation index (I) | Lipid content (%) | N | Maturation index (I) | Lipid content (%) | N  |
| M                    | 9.54 (0.05)          | 14.0 (4.0)        | 2 | 5.92 (0.58)          | 12.92 (4.23)      | 2  |
| MB                   | 8.28 (0.53)          | 21.1 (1.6)        | 9 | 6.60 (0.40)          | 19.63 (0.78)      | 14 |
| B                    | 8.74 (0.39)          | 22.4 (2.1)        | 6 | 6.71 (0.30)          | 18.38 (0.77)      | 4  |
| CM                   | 8.01 (0.77)          | 22.0 (2.8)        | 8 | 6.80 (0.49)          | 15.89 (4.00)      | 4  |
| CAT                  | 6.26 (1.21)          | 27.5 (1.5)        | 2 | 7.86 (0.55)          | 21.61 (2.59)      | 7  |
| S1                   | 8.56 (—)             | 16.0 (—)          | 1 | 6.67 (0.32)          | 15.81 (1.73)      | 8  |
| S2                   | 8.31 (0.69)          | 20.3 (1.4)        | 3 | 7.11 (0.92)          | 20.28 (3.17)      | 3  |
| S3                   | 8.16 (0.16)          | 21.0 (2.6)        | 5 | 6.57 (1.06)          | 21.68 (0.68)      | 2  |

significantly higher (mean  $8.28 \pm 0.24$  s.e.) in the exited eels when compared to those collected in the Danish islands (mean  $6.91 \pm 0.18$  s.e.; ANOVA  $F_{1,81} = 21.7, p < 0.0001$ ). Four of the nine S1 stocked eels had I-values greater than 6.5, but all had low fat values (11–15%). There was no correlation between I-values and lipid contents for Danish silver eels (Pearson  $r = 0.009$ ), although there was a very slight positive trend in the data. In contrast, there was a significant negative correlation (Pearson  $r = -0.47, p < 0.001$ ) between these parameters in eels exiting the Baltic.

van Ginneken and van den Thillart (2000) report that the energy cost of swimming for eels is 0.137 cal per gram wet weight and kilometer. Based on data in their paper, the caloric value of eel fat is 10.68 kcal  $g^{-1}$ . Knowing an eel's wet weight and fat content, one can therefore compute a "migration potential," assuming that 60% of the lipids are reserved for gonadal development (van Ginneken and van den Thillart 2000). Results of such calculations indicate that catadromous eels in this study had the highest migration potential (mean = 7149 km) and stocked eels that spent their entire lives in fresh water (S1) had the lowest (mean = 4938 km; Table 2).

## Discussion

The strontium-calcium "tag" provides a powerful means to examine salinity histories, given caveats. Although otolith Sr:Ca ratios have not been related to salinity under controlled experimental conditions for European eels, the calibration using geographic locations along a stable salinity gradient yielded a good fit to an

asymptotic curve, similar in shape to one derived for striped bass by Secor and Piccoli (1996) and also similar to results presented for *A. japonica* (Tzeng 1996). Because of the asymptotic shape of the curve, it is difficult to distinguish between strongly brackish and marine salinities, but resolution improves at lower salinities. Other confounding influences on otolith Sr:Ca ratios include the effects of growth rate (Sadovy and Severin 1992) and temperature (Campana 1999). Aside from the slow-growing leptocephalus stage, during which time otolith Sr accumulates to very high levels (Figure 2), we could not distinguish the influence of growth rate per

Table 2. Mean ( $\pm$  s.e.) migration potentials (km) for silver eels collected exiting the Baltic and around the Danish islands in the southern Baltic, by habitat use type. Assumes caloric value of 10.68 kcal  $g^{-1}$  eel fat and that 40% of the lipid reserves may be used in migration (i.e., that 60% of reserves is required for spawning; van Ginneken and van den Thillart 2000). Habitat use categories are described in the Methods section.

| Habitat use category | Migration potential (km) | N  |
|----------------------|--------------------------|----|
| M                    | 5126 (1046)              | 3  |
| MB                   | 6292 (234)               | 22 |
| B                    | 6430 (533)               | 9  |
| CM                   | 6100 (745)               | 10 |
| CAT                  | 7149 (1091)              | 9  |
| S1                   | 4938 (476)               | 9  |
| S2                   | 6334 (486)               | 6  |
| S3                   | 6611 (552)               | 7  |

se in our specimens. On the other hand, Sr:Ca ratios could be seen to increase during winter, when temperatures drop and growth rate slows. These showed up as bands of higher Sr:Ca and were only visible outside of freshwater environments. Thus, classification of eels depended on examination of the entire "gestalt" pattern, and comparisons to known-origin eels. As with other studies (e.g., Tzeng 1996; Tzeng et al. 1997; Tsukamoto et al. 1998), however, the discrimination of freshwater and nonfreshwater residency was not a problem.

Recently it has been suggested (Tsukamoto et al. 1998) that catadromous forms of freshwater eels do not migrate to the spawning grounds, and therefore do not contribute to maintenance of populations. The conclusion was based upon a survey of 18 *A. anguilla* individuals from the North Sea, of which only seven were silver, and 12 *A. japonica* individuals (all silver stage). It is well known that eels of all ages and developmental stages are found in marine waters (Tesch 1977), and this was confirmed by our study as well. However, we found that over 30% of all the silver eels (total N = 86) in our collections had spent at least some time in fresh water, including 24% of eels exiting the Baltic.

Aside from otolith Sr:Ca patterns, we have no other independent means of telling whether an eel was stocked or wild; therefore we can only classify our eels as having habitat use patterns that are consistent with having been stocked. For eels displaying the S2 pattern, an alternative explanation is that the eels swam very quickly from marine to brackish water. An alternative for the S3 pattern could be that glass eels entered a river somewhere outside of the Baltic, spent several years in that system, and then migrated into the Baltic or marine waters. However, there is no good alternative explanation for the S1 pattern, because historically eels have reached the Baltic as bootlace eels (small and pigmented) rather than as glass eels (Svärdson 1976). Due to time and labor constraints, eel ages were not determined, but in other studies of Baltic eels, age did not correlate with maturation (Svedäng et al. 1996; Svedäng and Wickström 1997) or growth (Holmgren 1996).

Although all silver eels classified as stocked did not vary in their proportions whether inside the Baltic or out, most of the S1 eels were captured in the Danish Baltic islands. Whereas half of these fish are classified as mature by Pankhurst's index of maturity, all but one of

them had lipid contents less than 20% of body weight (one of them had a lipid content of 27%, however). This means, if the assumption that 40% of muscle lipid is available for migration is valid (van Ginneken and van den Thillart 2000), that the S1 eels have shorter migration potentials and on the whole would not have the energy reserves to make the greater than 6000 km journey to the spawning grounds in the Sargasso Sea. Interestingly, whereas no relationship existed between Pankhurst's index and lipid content in the Danish eels, lipid content declined with increasing eye size in the exiting eels. This may be consistent with eels burning off energy reserves as they migrate into deeper waters, this last necessitating enlargement of their eyes.

One of the ongoing debates about stocked eels in the Baltic is whether or not they can orient their way out to spawn (Westin 1990; 1998; Tesch et al. 1991). In successive tagging studies, Westin found that stocked eels took months to years longer to reach the southern Baltic than eels presumed to be wild in origin, and also found that a high proportion of stocked individuals did not orient properly to locate the closest exit from the Baltic at Öresund. Rather, many stocked eels were recaptured in the southern Baltic along the coasts of Poland, Germany, and Denmark (Westin 1998). It was also shown that wild eels rendered anosmic by plugging up either both nostrils or only the left nostril had poorer navigation abilities. From this Westin (1998) suggested that stocked eels, lacking olfactory imprints for their way across the Baltic to freshwater sites, cannot use smell as a cue and instead must use the less reliable cue of declining water temperature.

Although we cannot tell how long the eels in this study had migrated in the silver stage, the fact that most of the S1 eels were collected at the Danish site appears to corroborate Westin (1990, 1998). However, the eels with highest fat contents (catadromous eels), and therefore highest migration potentials, were also mostly found at this site. Further, as eels are stocked in southern Baltic countries such as Poland (Moriarty et al. 1990; Bartel and Kosior 1991), it is also possible that the eels we identified as S1 did not originate in Sweden and were undertaking a coastal migration from Poland, Germany, or Denmark.

The results of our study are at odds with those reported by Tsukamoto et al. (1998) in that we did find eels with freshwater histories, and many of these showed evidence of maturity and

of being able to undertake the long migration to the spawning grounds. Nevertheless, it is striking that nearly 69% of the silver eels showed no evidence of freshwater residency. One possible reason is suggested by Tsukamoto et al. (1998), i.e., that catadromy is but one of many habitat use strategies employed by eels, which have high plasticity in many of their life history characters (e.g., Panfili and Ximenes 1994; Holmgren 1996; Glova et al. 1998; Secor and Rooker 2000). Another possibility is that dams and other artificial obstructions within the Baltic Sea drainage may be preventing young eels from ascending many rivers. Such barriers have been implicated in reducing the numbers of eels migrating upstream in British rivers (White and Knights 1997). Although glass eels and elvers can climb vertical surfaces such as dam walls (Tesch 1977), bootlace eels, such as those entering the Baltic, cannot. The hypothesis that dams serve as barriers to eel recruitment might be tested by assessing the frequencies of catadromous silver eels in drainages differing with respect to barriers, distance from the spawning grounds (affecting the life stage at which eels arrive at rivers), or both.

### Conclusions

A most striking result of this study was the confirmation of the remarkable plasticity of habitat use patterns among European eels. Eels that migrate in the silver stage show a life history (based on otolith microchemistry) of exploiting all forms of aquatic habitat ranging from marine to fresh waters. Our results indicate that Baltic drainage eels that spend all their lives in fresh water are less likely to be able to make the spawning migration, unless they remain in the system for a number of years to feed, as suggested by Svedäng and Wickström (1997). However, contrary to Tsukamoto et al. (1998), our study strongly suggests that catadromous eels indeed begin the spawning migration, and show strong potential for reproductive success.

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