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Original Article

Conservation restocking of the imperilled European eel does not necessarily equal conservation

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To stop the decline of the European eel population, one of the measures taken is translocating eels for restocking, despite its conservational value being largely unknown. We aimed to contribute to this knowledge gap by (i) investigating the origin of eels caught in coastal waters of Estonia and Finland using otolith microchemistry and (ii) directly estimating restocked eel escapement from Narva River Basin District (NRBD), which is part of the primary Eel Management Unit in Estonia. In Estonia, 74% of the sampled eels ($n = 140$) were natural recruits and 26% were restocked. In Finland, 27% of the sampled eels ($n = 235$) were natural recruits and 73% were restocked. Only 1% of all the coastally collected eels were originally restocked to NRBD. These new data together with the reported commercial landings from the escapement route conflict with the current silver eel escapement estimation for NRBD and question the accuracy and value of such indirect calculations compiled for most Eel Management Units throughout the European Union. It is concluded that restocking eels to freshwaters may be futile as a conservation measure in some situations, and better escapement is likely achieved in restocking eels to coastal waters or undammed freshwater systems with a direct connection to the sea.

Keywords: *Anguilla anguilla*, Eel Management Plan, migration, otolith microchemistry, provenance.

Introduction

European eel (*Anguilla anguilla*) is an iconic species that has been of scientific interest to humans since Aristotle and is currently considered as one of the symbols of the effects of the global change (e.g. Aristotle 350BC; Drouineau *et al.*, 2018). It has a remarkably complex life cycle and wide continental range stretching from the waters of eastern Mediterranean and northern Africa to northern Scandinavia (Moriarty and Dekker, 1997; Tesch, 2003). According to traditional text-book knowledge European eel is a classical catadromous species with terminal spawning in an unknown Sargasso Sea area (Tesch, 2003). However, starting from the ground-breaking observations of Tsukamoto *et al.* (1998) there has been a plethora of studies demonstrating that temperate

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eel species are actually facultatively catadromous (e.g. Limburg *et al.*, 2003; Daverat *et al.*, 2006).

The yields and recruitment indices of the highly valued pan-European eel stock have endured a drastic decline since the 1960–1970s peak (e.g. Castonguay *et al.*, 1994; ICES, 2019). Despite the significant increase in recruitment during recent years (ICES, 2019), the eel is still considered as critically endangered by IUCN. The single factors responsible for the decline of eel stock have been widely studied and discussed, including but not limited to overfishing, climate change, habitat loss, and alien parasites (e.g. Feunteun, 2002; Drouineau *et al.*, 2018). However, it is most likely the cumulative effect of these factors that has driven the stock to the present state (Jacoby *et al.*, 2015; Miller *et al.*, 2016). To stop and then reverse the stock decline, the European Eel Regulation was adopted (European Council, 2007) and Eel Management Plans (EMPs) were implemented all over Europe. For several years now, a general scientific recommendation has been that all anthropogenic impacts that decrease production and escapement of silver eels should be reduced to, or kept as close as possible to, zero (ICES, 2019). In reality, the implementation of the European Eel Regulation has come to a standstill and the agreed goals have not been fully realized (Dekker, 2016; European Commission, 2020). While it is obvious that reductions to zero-impact situation cannot happen over-night for anthropogenic pressures like hydropower turbines or pollution, banning or strongly limiting commercial and recreational fishing has the potential to have immediate within generation effects. However, a moratorium on eel fishing may have serious socio-economic consequences, especially in countries and communities that value eel fishing.

In the Baltic Sea and its freshwater basins, yellow and silver eel fishing has been, and in some places still is, an important part of the local small-scale commercial and recreational fisheries (ICES, 2019). As only limited amount of glass eels reach the Baltic compared to the North Sea, yellow eels are currently the main natural source of recruitment for most of the Baltic (Shiao *et al.*, 2006). With the general stock collapse the rates of glass and yellow eel natural immigration to the Baltic Sea are even lower as evidenced also by decreasing yellow eels numbers in coastal monitoring surveys (Bernotas *et al.*, 2016; ICES, 2019; Eschbaum *et al.*, 2020). To compensate for the low natural immigration levels and/or sustain the local fisheries, naturally recruited eels of different stage and origin are restocked into fresh and brackish waters all around the Baltic Sea (and beyond), a practice that in general started as early as the mid-1800s in Europe (Dekker and Beaulaton, 2016). While the numbers of the restocked eels have decreased drastically compared to historical levels, millions of eels are still restocked annually (ICES, 2019). However, the net conservational benefit of restocking eels from donor areas to distant freshwater habitats has been questioned by several studies (Westin, 2003; Sjöberg *et al.*, 2009, 2017; Marohn *et al.*, 2013) and remains a controversial issue. This is mainly because of concerns over glass eels catch and transport mortality and restocked eel escapement and spawning success. There is a general lack of studies evaluating the actual success of different restocking practices in terms of meeting the conservational goals. Similarly, there is a large deficit of knowledge of eel biology in coastal and transitional waters, relative to knowledge in fresh water (ICES, 2018).

One way to address various fish migratory life-history and provenance issues is to use the natural chemical information stored in the otoliths (e.g. Campana, 1999). For example, in migratory studies with temperate and tropical eels, otolith microchemistry has been one of the most applied methods (e.g. Tsukamoto *et al.*, 1998; Daverat *et al.*, 2006; Lin *et al.*, 2015). In the Baltic Sea, several studies have utilized otolith Sr:Ca profiles to infer migration patterns and occurrence of natural and restocked eels (Limburg *et al.*, 2003; Shiao *et al.*, 2006; Lin *et al.*, 2012; Marohn *et al.*, 2013; Sjöberg *et al.*, 2017). We are not aware of any provenance studies on European eels that combine multiple chemical markers and aim to determine the origin beyond the general freshwater vs. marine distinction. Therefore, the aims of this study were, using individual otolith microchemical profiles, to investigate: (i) the proportions of natural and restocked eels in the coastal waters of Estonia and Finland and (ii) the origin of brackish water collected restocked eels and especially the share of Narva River Basin District (NRBD) eels in the coastal seas of Estonia and Finland.

Material and methods

Study area and eel sampling

Mainland Estonia can be divided into two main basins (also Eel Management Units, EMUs): West-Estonian River Basin District and East-Estonian River Basin District (Figure 1). The former is

Figure 1. Map of the study area and sampling locations in fresh and coastal waters of Estonia (1–14) and Finland (15–25). 1, Lake Võrtsjärv; 2, Triton PR AS eel farm; 3, Lake Lõõdla; 4, Lake Vagula; 5, Lake Kuremaa; 6, Lake Kaiavere; 7, Lake Saadjärv; 8, Lake Peipsi; 9, Käsmu Bay; 10, Matsalu Bay; 11, Virtsu; 12, Saarnaki Islet; 13, Kõiguste Bay; 14, Vilsandi Island; 15, Pori; 16, Taivassalo; 17, Inkoo; 18, Sipoo; 19, Kotka; 20, Virolahti; 21, Villikkalanjärvi; 22, Kuohijärvi; 23, Rusutjärvi; 24, Vesijärvi; 25, Toutonen. Note that Ivangorod Hydro Power Station on Narva River is marked with a black rectangle. The two Estonian EMUs are also displayed: West-Estonian River Basin District and East-Estonian River Basin District (sub-basin: NRBD).

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Table 1. Sampling locations, biological, and otolith microchemical parameters, and origin (natural or restocked) of eels collected from Estonian and Finnish inland lakes, an Estonian eel farm, and Swedish quarantine facility.

ID[a]	Location	*n*	TL[b]	M[b]	Sr:Ca[c] (mmol/mol)	Ba:Ca[c] (m/mol)	$^{87}Sr:^{86}Sr$[c]	Natural (%)	Restocked (%)
1	Lake Võrtsjärv	11	672 ± 87	648 ± 251	0.16 ± 0.02	0.0074 ± 0.0028	0.7134 ± 0.0007	0	100
2	Triton PR AS eel farm	17	266 ± 110	57 ± 65	0.47 ± 0.05	0.0158 ± 0.0046	0.7115 ± 0.0003	0	100
3	Lake Lõõdla	10	496 ± 68	219 ± 85	0.17 ± 0.02	0.0038 ± 0.0013	0.7135 ± 0.0009	0	100
4	Lake Vagula	11	741 ± 141	814 ± 544	0.17 ± 0.02	0.0063 ± 0.0018	0.7151 ± 0.0009	0	100
5	Lake Kuremaa	11	627 ± 83	465 ± 215	0.20 ± 0.02	0.0080 ± 0.0045	0.7164 ± 0.0005	0	100
6	Lake Kaiavere	12	685 ± 89	597 ± 277	0.19 ± 0.01	0.0058 ± 0.0015	0.7164 ± 0.0003	0	100
7	Lake Saadjärv	10	694 ± 59	619 ± 178	0.22 ± 0.01	0.0113 ± 0.0059	0.7159 ± 0.0003	0	100
8	Lake Peipsi	13	668 ± 174	580 ± 474	0.18 ± 0.03	0.0064 ± 0.0027	0.7151 ± 0.0012	0	100
21	Villikkalanjärvi	5	708 ± 36	660 ± 206	0.79 ± 0.02	0.0032 ± 0.0007	n/a	0	100
22	Kuohijärvi	5	898 ± 111	1425 ± 514	0.77 ± 0.11	0.0038 ± 0.0011	n/a	0	100
23	Rusutjärvi	5	801 ± 55	850 ± 194	0.72 ± 0.11	0.0049 ± 0.0019	n/a	0	100
24	Vesijärvi	5	891 ± 36	1410 ± 138	0.73 ± 0.09	0.0042 ± 0.0012	n/a	0	100
25	Toutonen	5	926 ± 33	1100 ± 0	0.36 ± 0.07[d]	0.0026 ± 0.0018[d]	n/a	60[e]	40
n/a	Swedish quarantine	29	103 ± 24	2 ± 2	0.71 ± 0.17	0.0006 ± 0.0002	0.7104 ± 0.0004	0	100

[a]ID numbers correspond to the numbers displayed also in Figure 1.
[b]Total length (TL, mm) and total body mass (M, g) given as mean ± *SD*.
[c]Mean ±*SD* otolith Sr:Ca, Ba:Ca, and $^{87}Sr:^{86}Sr$ values representing ambient lake or facility water chemistry.
[d]Data from two eels.
[e]Three eels were identified as natural recruits but were probably translocated from Denmark.

accessible to natural recruits, but recruitment success is assumed to be poor (Järvalt, 2008). In the sub-basin of the latter (i.e. NRBD), no natural eel recruitment occurs owing to a hydropower station located on Narva River which blocks the upstream migration for all diadromous fish since it was built in 1950–1955. Eels have been restocked to NRBD since 1956. Estonian EMP was adopted in 2008 and its main management measures have been restocking eels to NRBD and reducing the number of fishing licenses for small fyke nets in the coastal sea. Eels have been only occasionally restocked to the coastal waters (most recently in 1998, 1999, and 2004; Supplementary Material).

All the otoliths used in this study were obtained from the archive collections of the affiliated institutions, so no eels were directly sacrificed for this study. Estonian eels were sampled from NRBD lakes inaccessible to natural recruits and inhabited only by restocked eels, an eel farm responsible also for restocking, and from brackish coastal waters inhabited by natural and restocked eels (Figure 1; Tables 1 and 2; Supplementary Material). The freshwater collected eels were used to determine the baseline otolith chemical fingerprints for the restocked eels which were later checked against the otolith chemical fingerprints of restocked eels collected from brackish water to directly investigate the escapement from Estonian inland waters. All Estonian freshwater and brackish water eels were sampled with fyke-nets in the periods of 2001–2015 and 1993–2016, respectively.

Finnish eels were sampled from brackish coastal waters in the period of 2006–2017 using pound-nets, fyke-nets and longlines (Figure 1; Tables 1 and 2). A sub-sample of freshwater eel otoliths was also obtained from several Finnish lakes (1992–2015) inaccessible to natural recruits and inhabited only by restocked eels, but these were not included into the statistical analyses because of the small sample size and the fact that no $^{87}Sr:^{86}Sr$ analysis was conducted on them. The latter were an opportunistic addition and were not part of the original sample collection plan. Finland restocks eels almost equally to fresh and brackish waters (Supplementary Material). Finally, chemically marked eels

Table 2. Sampling locations, biological parameters, and origin (natural or restocked) of eels collected from the Estonian (9–14) and Finnish (15–20) coastal sea.

ID[a]	Location	*n*	TL[b]	M[b]	Natural (%)	Restocked (%)
9	Käsmu Bay	17	771 ± 97	908 ± 361	35	65
10	Matsalu Bay	13	690 ± 86	644 ± 266	77	23
11	Virtsu	12	585 ± 119	486 ± 313	67	33
12	Saarnaki Islet	16	624 ± 105	489 ± 346	94	6
13	Kõiguste Bay	28	778 ± 124	951 ± 431	54	46
14	Vilsandi Island	54	700 ± 74	670 ± 266	89	11
	Total	140			74	26
15	Pori	37	810 ± 117	1058 ± 321	24	76
16	Taivassalo	36	839 ± 106	1176 ± 503	83	17
17	Inkoo	36	849 ± 102	1370 ± 415	58	42
18	Sipoo	35	682 ± 76	615 ± 252	9	91
19	Kotka	52	789 ± 102	1037 ± 392	0	100
20	Virolahti	39	783 ± 109	985 ± 540	0	100
	Total	235			27	73

[a]ID numbers correspond to the numbers displayed also in Figure 1.
[b]Total length (TL, mm) and total body mass (M, g) are given as mean ± *SD*.

sampled from the quarantine facility in Helsingborg ($n = 29$) were obtained to establish the otolith chemical signature corresponding to the quarantine facility. These samples were needed because all eels restocked in Sweden since 1983 and in Finland since 2009 undergo this mandatory procedure. Otoliths from a period of 2002–2011 were used to account for potential variability in water chemistry caused by a switch in the water source feeding the facility. Total length (TL) and mass (M) of each fish was measured to the nearest 1 mm and 1 g. Silvering stage in all the eels collected from the coast was recorded visually (i.e. body colour and enlargement of the eyes and pectoral fins was inspected). Sixty-five and zero per cent of the Finnish and Estonian eels, respectively, were assigned as silver eels. As no silver eels were available from the latter, individuals with TL >600 mm were

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preferably chosen from the archive collection to increase the likelihood for an escapee from NRBD. This was done for cases if the eel had been mistakenly assigned as a yellow eel or silver eels had reverted back to yellow eel stage in the sea.

Otolith preparation and chemical analysis

Both sagittal otoliths were removed, cleaned and stored dry in plastic tubes or paper envelopes. For chemical analysis, one randomly chosen otolith per individual was embedded into epoxy resin. Each epoxy block was then manually grinded on a grinding machine with silicon carbide grinding papers size P400, P1200, and P2500 until the core was visible. Final polish was given with size P4000 grinding paper. Individual sagittal thin sections were finally glued onto standard glass slides and stored in clean plastic containers for later analysis. Before the chemical analyses, all otoliths were ultrasonically cleaned for 15 min in ultrapure water and subsequently dried in a laminar flow hood. Otolith thin-sections were analysed for ^{24}Mg, ^{43}Ca, ^{55}Mn, ^{88}Sr, and ^{137}Ba using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) (Supplementary Material). Additional otolith ^{87}Sr:^{86}Sr analyses were conducted on all Estonian freshwater and Swedish quarantine eels and on a sub-sample of Estonian brackish water collected eels that possessed a freshwater Sr:Ca signal next to the core (and were therefore considered to be restocked) (Supplementary Material). This was conducted to further strengthen our ability to determine the freshwater origin of the brackish water unknowns.

Data interpretation and analysis

Otolith chemical signatures representative of the eel farm and the quarantine facility were extracted from the entire available region next to the primordium, but before the artificially induced Sr or Ba mark, if one existed (Figure 2a and b). Otolith chemical signatures representative of the water body where the specific eel was restocked to were extracted from the region next to the primordium (ca 100 µm), but excluding the region corresponding to the farm or quarantine period, if one existed (Figure 2c and d).

Wild caught eels were assigned as natural recruits if their otolith Sr:Ca values stabilized at >2.0 mmol/mol (reflecting the North Sea) just after the primordium Sr:Ca peak and continued to decrease steadily to <2.0 mmol/mol (reflecting the Baltic Sea and/or its freshwater basins) (Figure 4a and h). If the values just after the initial Sr:Ca peak dropped abruptly to <2.0 mmol/mol, a specific eel was regarded as restocked (e.g. Figure 4b and c). In comparison, life-time otolith Sr:Ca values in sea water resident eels sampled from the North Sea (Southern Norway; $n = 23$) were all >2.0 mmol/mol (M. Rohtla, unpublished data). So, a natural eel moving to eastern Baltic Sea should display a gradually declining otolith Sr:Ca profile as a result of large salinity difference between the North and the Baltic Sea, and an existing salinity gradient within the Baltic Sea (Shiao *et al.*, 2006). Such eels may display otolith Sr:Ca values of ~0.5 to 2.5 mmol/mol depending mostly on ambient water chemistry, whereas Ba:Ca and ^{87}Sr:^{86}Sr values in areas with no direct freshwater influence should be relatively homogenous at <0.002 mmol/mol and ~0.7094, respectively (Åberg and Wickman, 1987; M. Rohtla, unpublished data). Whereas an eel moving or translocated to the freshwater basins of the Baltic Sea may display otolith Sr:Ca values of ~0.1 to 1.8 mmol/mol, Ba:Ca of ~0.002 to 0.03 mmol/mol and ^{87}Sr:^{86}Sr of ~0.7095 to 0.7451, depending mostly on bedrock composition (Löfvendahl *et al.*, 1990; M. Rohtla, unpublished data). All this means that providing freshwater and brackish water elemental and isotopic otolith thresholds for the entire Baltic Sea is a difficult task, which was not the aim of this study. Distinguishing natural eels from the restocked eels is, however, straightforward in large majority of cases as described above, but also below.

ANOVA and MANOVA were used to investigate otolith element-to-calcium and ^{87}Sr:^{86}Sr differences among Estonian lakes restocked with eels. Fisher's exact test of independence was conducted to test if the distributions of natural and stocked eels differed among brackish water sampling locations. Canonical analysis of principal coordinates (CAP test using PRIMER PERMANOVA+) was used to visualize the variation in Sr:Ca and ^{87}Sr:^{86}Sr values among Estonian freshwater locations. Data was square-root transformed and normalized before the analysis.

Results

Freshwater collected eels

Mean otolith chemical ratios mirroring the representative values in the sampled Estonian and Finnish lakes, eel farm and quarantine facility demonstrated considerable among-site variation with the latter two standing out the most. Eels sampled from the Estonian eel farm in 2002–2015 had relatively high Sr:Ca and Ba:Ca and low ^{87}Sr:^{86}Sr otolith mean values compared to the Estonian lakes (Table 1 and Figure 2a). Eels sampled from the Swedish quarantine facility in 2008–2011 had also relatively high Sr:Ca, but extremely low Ba:Ca and low ^{87}Sr:^{86}Sr mean otolith values (Table 1 and Figure 2b). In both facilities, mean otolith Sr:Ca (coefficient of variation CV = 11–23%) and Ba:Ca (CV = 30–37%) varied considerably more compared to ^{87}Sr:^{86}Sr (CV = 0.04%). All Swedish quarantine eels were either marked with Sr or a combination of Sr and Ba (Figure 2b). Otolith Sr mark in one individual from the Estonian eel farm was also confirmed (Figure 2a).

Significant statistical differences among Estonian lakes that are restocked with eels were found for otolith Sr:Ca ($F_{5,59} = 17.5$, $p < 0.001$), Ba:Ca ($F_{5,59} = 5.7$, $p < 0.002$), and ^{87}Sr:^{86}Sr ($F_{5,44} = 34$, $p < 0.001$), but not for Mg:Ca ($F_{5,59} = 0.88$, $p = 0.49$) and Mn:Ca ($F_{5,59} = 0.52$, $p = 0.76$) (Figure 2c and d). The latter two were therefore excluded from further analysis, but Mg:Ca was used for detecting vateritic inclusions. Among the Estonian lakes three distinct groups with minimum over-lap in otolith Sr:Ca and ^{87}Sr:^{86}Sr were detected (MANOVA: $F_{2,47} = 13$, $p < 0.001$; Figure 3): (i) Võrtsjärv–Lõõdla group with relatively low Sr:Ca and ^{87}Sr:^{86}Sr values; (ii) Vagula group with medium Sr:Ca and ^{87}Sr:^{86}Sr values, and (iii) Saadjärv–Kaiavere–Kuremaa group with relatively high Sr:Ca and ^{87}Sr:^{86}Sr values. As expected, eels sampled from Lake Peipsi ($n = 13$) had the most variable otolith chemical signatures (Table 1), suggesting multiple restocking origins. It was estimated that six eels originated from Saadjärv–Kaiavere–Kuremaa group, four from Võrtsjärv–Lõõdla group and two from Vagula group.

In the Finnish lakes sub-sample ($n = 25$), 88% of the eels were restocked and 12% were of natural origin (Table 1). Various Sr:Ca profiles were detected, probably reflecting different restocking histories and environmental exposures (Figure 2e and f). Most interestingly, three eels from Lake Toutonen (which is inaccessible to natural recruits) were identified as natural recruits (Figure 2e). However, it later turned out that these individuals

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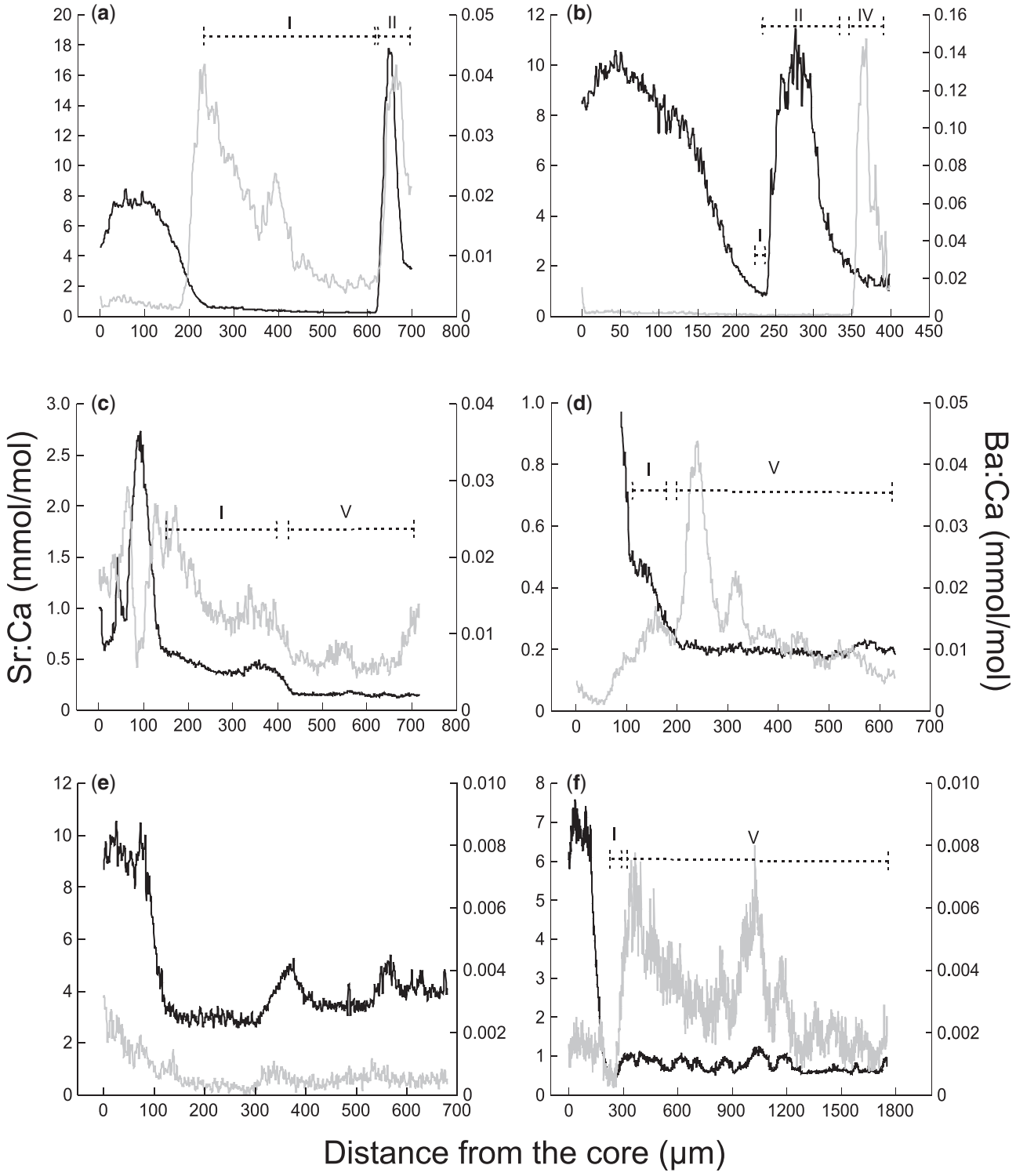

Figure 2. Representative otolith Sr:Ca (black line, left y-axis) and Ba:Ca (grey line, right y-axis) profiles of eels collected from freshwater lakes, eel farm and quarantine facility: a) Estonian eel farm, TL 145 mm, core-to-edge transect, Sr marked; b) Swedish quarantine facility, TL 127 mm, core-to-edge transect, Sr and Ba marked; c) Lake Võrtsjärv, TL 570 mm, ca 700 µm transect from the core; d) Lake Saadjärv, TL 723 mm, ca 600 µm transect from the core; e) Lake Toutonen, TL 970 mm, ca 700 µm transect from the core; f) Lake Villikkalanjärvi, TL 695 mm, core-to-edge transect. I - pre-marking eel farm or quarantine period; II - first Sr-marking; III - second Sr-marking; IV - Ba-marking; V - waterbody where the eel was restocked to.

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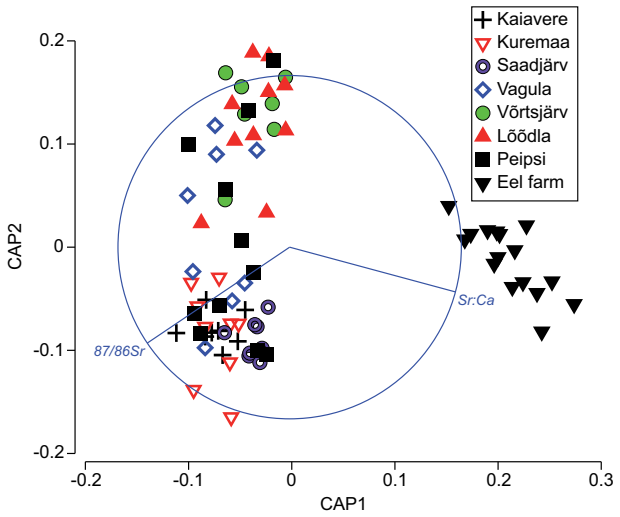

Figure 3. Canonical analysis of principal coordinates of European eel otolith Sr:Ca and ^{87}Sr:^{86}Sr values from Estonian freshwaters.

were probably translocated from Denmark as yellow eels in 1970s.

Brackish water collected eels

Of all the eels sampled from the coastal waters of Estonia ($n = 140$), 74% were natural recruits and 26% were restocked (Table 2 and Figure 4a–h). One restocked eel was also probably translocated later in life (Figure 4f). Distributions of restocked and naturally recruited eels among brackish water sampling locations were significantly different (Fisher's exact test, $p < 0.0001$; Table 2). Proportion of restocked individuals was the highest among eels collected from Käsmu Bay (65%), whereas natural recruits were proportionally most widespread in Vilsandi Island (91%) and Saarnaki Islet (94%).

Three per cent of all the Estonian brackish water sampled eels were identified as being originally restocked to Estonian inland lakes. Three of them were caught from Käsmu Bay (Figure 4b) and one from Vilsandi (Figure 4c). Two of them had been restocked to Võrtsjärv and Saadjärv (Figure 4c). Two of them only possessed the eel farm signature (with no lake signature) and had probably descended immediately to the sea during the first and second continental year (Figure 4b). Two of them had probably escaped NRBD as silver eels but reverted back to yellow eel stage in the Baltic Sea (Figure 4c). Seven Kõiguste Bay caught eels were identified as originally restocked to the same region (Arju Bay and Suurlaht in 1998–1999) as their otolith Sr:Ca profiles decreased to <2.0 mmol/mol after the primordium and their age corresponded to the time of restocking (Figure 4d). Eight other individuals also possessed otolith Sr:Ca <2.0 mmol/mol after the primordium, followed by an increase to values of 2.5–4.0 mmol/mol and final decrease again to <2.0 mml/mol (Figure 4g). Such individuals were considered as restocked to Swedish or Danish estuaries or rivers, and it is hypothesized that these eels did not settle there and eventually moved to the Baltic Sea. At this point it cannot be fully excluded that at least some of them were natural recruits. Other restocked eels that were identified from the Estonian coastal sea were restocked to brackish or freshwaters of the Baltic Sea, probably mostly to Finland as evidenced by similar quantitative and qualitative properties of the profiles.

Of all the eels sampled from the coastal waters of Finland ($n = 235$), 27% were natural recruits and 73% were restocked (Table 2; Figure 4h–l). Distributions of restocked and naturally recruited eels among brackish water sampling locations were significantly different (Fisher's exact test, $p < 0.0001$; Table 2). Proportion of restocked individuals was the highest among eels collected from Kotka and Virolahti (100%), whereas natural recruits were proportionally most widespread in Taivassalo (83%). In the Gulf of Finland (GoF) the share of natural recruits clearly decreased from west to east. No Estonian origin freshwater restocked eel were identified as the otolith chemical fingerprints of coastally collected restocked Finnish eels did not match the respective values from Estonian freshwaters. Mean ($\pm SD$, min–max) otolith Sr:Ca and Ba:Ca values next to the primordium Sr:Ca peak in the Finnish coastally collected restocked eels ($n = 172$) were 0.71 (± 0.27; 0.41–1.81) and 0.0018 (± 0.0018; 0.0002–0.0099) mmol/mol, respectively. It was estimated that 76% of Finnish restocked eels were restocked directly to brackish water (possessing quarantine otolith signature and/or a short V or U-shaped dip in Sr:Ca values) (Figure 4f and i), 21% were quarantine eels restocked to freshwater (possessing a long otolith freshwater signature reflecting the water body the eels were restocked into) and 3% were of ambiguous restocked origin. Large majority of the freshwater restocked eels came from Pori, where 68% of the sampled eels had been originally restocked to freshwater as evidenced by their long otolith freshwater signatures (Figure 4j). In other locations such eels were less abundant.

Five coastally collected Finnish eels had also been Sr-marked (Figure 4i). Two Sr-marked and two double Sr-marked eels were observed in Kotka and one double Sr-marked eel was observed in Pori. All these marked eels were relatively small (TL 244–325 mm) and caught in 2014–2015.

Discussion

Proportions of restocked and natural eels in coastal waters of Estonia and Finland

We demonstrated that natural recruits prevail over restocked eels in the Estonian coastal sea, but the opposite was true for Finnish coastal sea where restocked eels prevail over natural recruits. Such disparity was not expected given that the sampling regions are geographically close and the fact that other similar studies conducted elsewhere in the Baltic Sea have demonstrated the prevalence of natural recruits. For example, Limburg *et al.* (2003) and Sjöberg *et al.* (2017) reported that the proportions of natural and restocked eels among brackish water collected individuals in Sweden were 73% vs. 27% and 90% vs. 10%, respectively. In Lithuania the same proportions were 78% vs. 22% and in Latvia 98% vs. 2% in favour of the natural recruits (Shiao *et al.*, 2006; Lin *et al.*, 2012). All these findings point towards strong prevalence of natural recruits in the Baltic Sea. But what can explain the opposite pattern found among eels sampled from coastal waters of southern Finland?

All but one brackish water sampling sites displaying restocked eel prevalence in this study were in the GoF. We propose that these results are in concordance with the current eel restocking practices and available CPUE data in the region. Eel natural recruitment to eastern Baltic Sea is at historical lows as evidenced by CPUE time-series data from Estonian coastal survey sites of which most are located far from known eel restocking locations (Bernotas *et al.*, 2016; Eschbaum *et al.*, 2020). Since eels tend to

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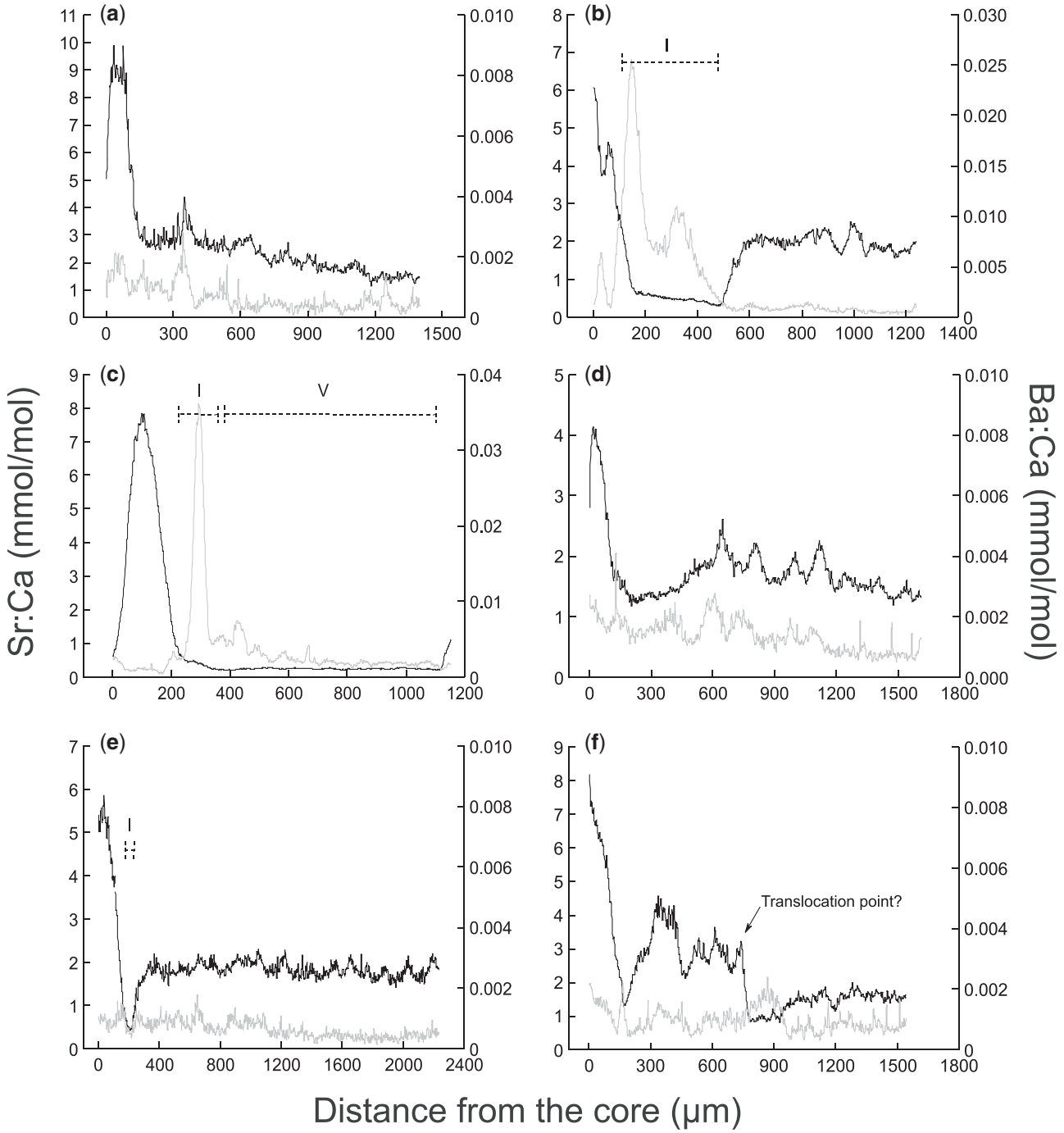

Figure 4. Representative otolith Sr:Ca and Ba:Ca profiles of eels collected from brackish coastal waters of Estonia and Finland: a) Vilsandi Island, TL 789 mm, core-to-edge transect, natural recruit b) Käsmu Bay, TL 863 mm, core-to-edge transect, restocked Estonian eel farm eel with no lake signature and fast descent to the sea; c) Vilsandi Island, TL 731 mm, core-to-edge transect, Estonian eel farm eel restocked to Lake Saadjärv, note the long freshwater residency period and formation of seawater signature at the end; d) Kõiguste Bay, TL 695 mm, core-to-edge transect, eel restocked to brackish waters of Estonia; e) Käsmu Bay, TL 863 mm, core-to-edge transect, quarantine eel restocked directly to brackish waters; f) Käsmu Bay, TL 601 mm, core-to-edge transect, eel that was probably restocked to North Sea estuary, but migrated back to the sea where it was caught and translocated to the Baltic Sea; g) Virtsu, TL 646 mm, core-to-edge transect, eel that was probably restocked to North Sea estuary, but migrated back to the sea and entered the Baltic Sea; h) Taivassalo, TL 801 mm, ca 800 µm transect from the core, natural recruit; i) Kotka, TL 296 mm, ca 500 µm transect from the core, double Sr-marked eel restocked to fresh water as evidenced by high Ba:Ca levels after the Sr-marks; j) Pori, TL 752 mm, ca 1050 µm transect from the core, eel that was restocked to freshwater and remained there until silvering; k) Inkoo, TL 800 mm, ca 400 µm transect from the core; eel that was restocked directly to brackish water, with a stabilized quarantine signature; l) Virolahti, TL 865 mm, core-to-edge transect, eel that was restocked directly to brackish water, with an unstabilized quarantine signature. I - pre-marking eel farm or quarantine period; II - first Sr-marking; III - second Sr-marking; IV - Ba-marking; V - waterbody where the eel was restocked to.

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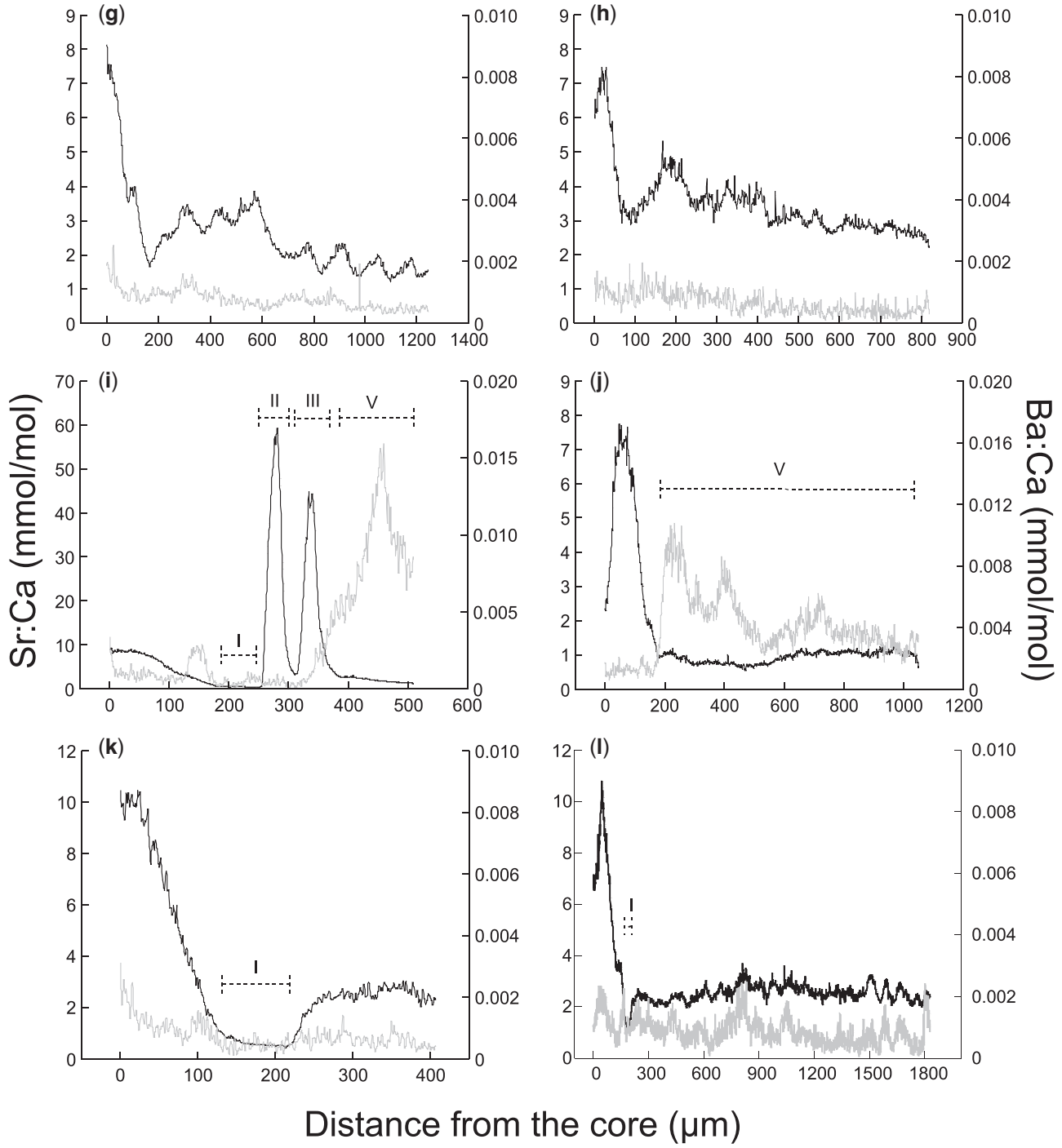

Figure 4. continued

adopt a relatively sedentary behaviour once home range is established (e.g. Walker *et al.*, 2014), it is reasonable to expect that restocking will inflate the proportion of restocked eels in locations otherwise void of eels. As Finland restocks ca half of the yearly restocking quota directly to the northern coast of the GoF this is probably the main factor responsible for the prevalence of restocked individuals. While Estonia does not currently restock eels to brackish waters, an unconfirmed number of restocked eels from NRBD will also eventually reach the GoF (see more below). In conclusion, all this creates a situation where restocked eels are more abundant than natural eels in the GoF region.

Origins of the restocked eels collected from the coastal waters

Three per cent of Estonian and zero per cent of Finnish brackish water collected eels were originally restocked to inland waters of Estonia. When combined, this dissolves to 1% of brackish water

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Table 3. Reported commercial landings (kg) of eel in different Estonian waterbodies covering the entire escapement route from Lake Võrtsjärv (i.e. the primary lake where eels are restocked in Estonia) to the Gulf of Finland.

Year	Lake Võrtsjärv	River Emajõgi	Lake Peipsi	Narva reservoir and river	GoF (Estonia)	Estimated escapement
2010	9698	94	5	0	1373	na
2011	10 820	1	12	0	772	na
2012	12 219	15	13	0	16	na
2013	12 473	14	33	0	609	na
2014	13 336	13	38	0	388	na
2015	12 277	4	30	0	330	na
2016	13 024	14	17	0	330	86 563
2017	13 832	26	32	0	132	64 681
2018	16 678	34	77	0	57	52 341
2019	19 599	29	97	0	54	65 779

Estimated silver eel escapement from NRBD is also provided.

collected eels originating from freshwaters of Estonia. In comparison, 15% of the eels collected from Finnish coastal waters were originally restocked to (probably Finnish) freshwaters. The low share of Estonian freshwater origin restocked eels in coastal waters is surprising as ∼52 to 86 tons of silver eels should escape NRBD annually according to the escapement calculations from 2016 to 2019 (ICES, 2019; Bernotas *et al.*, 2020; Table 3). Estimated escapement would have been even higher in 1990s and 2000s as the number of restocked eels was higher back then. We acknowledge that as only yellow eel otoliths were available from the Estonian coast, this sub-sample may not be ideal for identifying the escaping silver eels because the latter usually avoid shallow coastal areas. However, the reason why we lack silver eel samples from the Estonian coast is simply because there are no targeted yellow and silver eel fisheries anymore (as there is hardly any eels), and national surveys target only yellow eels. As silver eels are still fished on the Finnish coast, at least some NRBD silver eels should also end up there because the prevailing currents in the GoF move counterclockwise. Furthermore, some yellow eels can escape the NRBD and silver eels can also revert back to the yellow eel growth phase if delays in migration occur (Figure 4b and c; Svedäng and Wickström, 1997). We argue that the latter is very likely for eels descending from NRBD as eels face a complicated navigational task and hydropower station at the end. It has also been demonstrated that eels infected with *Anguillicola crassus* (as in majority of NRBD eels) were more vulnerable to recapture because their ability to perform vertical migrations in the water column was probably impaired, and therefore they avoided deeper waters and stayed in shallower water (Sjöberg *et al.*, 2009). But perhaps most importantly, the pertinent commercial catch data presented herein (Table 3) support the conclusion that only limited amount of silver and yellow eel escape from NRBD. What could be the reason behind these conflicting results?

We propose that most restocked eels are harvested within the NRBD. Current silver eel escapement calculations (B_{curr}) are largely based on eel abundance estimation in Lake Võrtsjärv, natural mortality (M), and anthropogenic mortality ($\sum$A) which consists of fishing ($\sum$F) and other human related mortality ($\sum$H) (ICES, 2011; Bernotas *et al.*, 2020). Because eels are relatively stationary once home range is established (e.g. Walker *et al.*, 2014), highest fishing mortality in absolute terms occurs in lakes that are restocked with eels. Significant part of the total cost for restocking eels comes directly or indirectly from commercial eel fishers fishing the restocked lakes. As most of them depend heavily on eel fishing, there is probably an increased motivation towards maximizing the yields and not reporting all catches. We suggest that this has resulted in strongly underestimated $\sum$F value in a situation where fishing pressure is *de facto* high and most individuals are exposed to this fishery for prolonged period (mean silvering age is 8–10 years in Lake Võrtsjärv, but significantly more in other NRBD lakes; Silm *et al.*, 2017). In addition, eels that disperse away from recipient lakes soon after restocking or survive to start the spawning migration are subjected to additional commercial and recreational fishing pressure in other parts of the system. Escapement calculations are also heavily dependent on the average mortality value, which can reportedly vary between 0.02 and 0.47 per annum for different eel stocks (Bevacqua *et al.*, 2011). For NRBD mortality is fixed at 0.1 following Dekker (2015), but it has not been estimated *per se* for NRBD.

The invisible 'conflict' between eel conservation and state affairs

Besides the international obligations associated with eel conservation, the issue has also a socio-economic side. Eel fishing in Estonia tends to be very profitable, if there are eels to fish. Eel restocking in Lake Võrtsjärv started in 1956, and the yields peaked in 1988 at 104 tons. Currently applied policies aim to keep these traditions alive to sustain life in rural areas, but in the meantime also to help the eel. Considering the new data, we argue that in this specific case we probably cannot have both, at least not in the current (eel) regulative framework. It is therefore advisable to modify the current eel restocking practice in Estonia.

Eel regulation dictates that eels should be only restocked to waterbodies where they have high probability of escapement (European Council, 2007). This general recommendation is corroborated by several case studies conducted in the Baltic Sea and beyond that all arrived at a general conclusion that restocking eels to some freshwater habitats may not be beneficial to eels in terms of population sustainability (Westin, 2003; Sjöberg *et al.*, 2009, 2017; Marohn *et al.*, 2013; present study). Furthermore, evidence from studies with the American eel (*Anguilla rostrata*) suggests that eels restocked to freshwater may have significantly lower potential for successful spawning migration if translocated from distant donor areas (Stacey *et al.*, 2015). And when the eels do escape the freshwater gauntlet, new hazards await in the sea where lost energy and high *A. crassus* infection rates (Kangur *et al.*, 2010; Marohn *et al.*, 2013) may impair the ability to perform vertical migrations necessary for avoiding predators and coastal fishing (Westerberg *et al.*, 2007; Sjöberg *et al.*, 2009).

Some countries have already modified their restocking programmes so that a significant share of eels is also restocked directly to the sea (e.g. Denmark, Germany, Finland, Sweden) or eels are restocked only to freshwater systems without migration obstacles (Latvia). Therefore, it is important for eel conservation that other countries will follow this practice and modify their EMPs. If restocking as measure is used at all, then restocking to the brackish coastal ecosystems or to free-flowing rivers disemboguing directly to the sea should be prioritized. For Estonia this means that besides coastal waters eels should also be restocked to West-Estonian River Basin District where no migration obstacles are present (e.g. River Pärnu and River Kasari basins).

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Wider implications

The results of this study add to the growing body of evidence suggesting that restocking eels to freshwaters may be futile as a conservation measure in some situations. Furthermore, for the first time, we have demonstrated that the targets set within an active EMP may not actually be met, although indirect estimates of escapement suggest the otherwise. This of course has implications for the Estonian EMP specifically and calls for further studies, but it also demonstrates the ambiguity and uncertainty involved at the root level of these calculations if adequate quality control and restocking efficiency estimation measurements are not taken. At the entire eel continental range level, out of 86 EMUs that reported all silver eel biomass parameters in 2017, 20% reached or exceeded the target level of 40% of escapement (ICES, 2018). The 40% target level should perhaps be most rigorously monitored in EMUs which restock eels that have been translocated away from their natural migration destination. For example, 15 countries restocked glass eels in 2017 (ICES, 2019). However, whatever the main restocking aim is, yellow eel based model calculations on the theoretical biomass of escaping silver eels should be validated by direct or indirect estimation about the actual silver eel biomass that reaches the sea.

To better our understanding on how different restocking practices contribute to the escaping silver eel biomass future work should concentrate on estimating actual escapement at vital geographical locations on eel migratory route. In the context of individual EMUs these locations should be river estuaries/mouths. In the context of the Baltic and Mediterranean Sea, these locations should be Danish Straits and Strait of Gibraltar, respectively. Only when this, somewhat easier task, is completed and yielded positive results, we can move on to the harder task and study if and to what extent restocked eels actually contribute to spawning.

Data availability statement

Data available on request.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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