



Life-history characteristics of ide *Leuciscus idus* in the Eastern Baltic Sea

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Abstract Otolith Sr:Ca and Ba:Ca profiles were used in parallel with age data to investigate the life-history characteristics of ide, *Leuciscus idus* (L.) ($n = 111$), in the Väinameri Sea, West Estonia. Sr:Ca profiles were more variable and useful than Ba:Ca profiles. Flexible life-history patterns were observed within and among the three study sites. Most of the individuals (72%) hatched in semi-enclosed bays that are fresh water during spring spawning but are often flooded with brackish water during other seasons. The importance of lotic spawning varied among sites and was the highest (88%) in Matsalu Bay, moderate in Saunja Bay (33%) and lowest (0%) in Käina Bay. Young of the year emigrated from natal sites and entered the sea within the first summer; 95% did so during the first month post-hatch. Juvenile ide undertook non-spawning, freshwater migrations in the following spring; however, the reasons behind this phenomenon remain unknown. As the importance of lotic spawning has significantly decreased and multiple historically important ide spawning rivers lack anadromous runs altogether, it is suggested that actions should be taken to aid the recovery of those imperilled spawning stocks.

KEY WORDS: age, brackish water, cyprinid, Estonia, migration, Sr:Ca and Ba:Ca profiles.

Introduction

The Baltic Sea is one of the largest brackish water bodies in the world. This ecosystem consists of life with marine and freshwater origin and thrives on high productivity of these waters. Unfortunately, this high production comes at a price as most of the regions are affected by eutrophication caused by nutrient pollution from the catchment areas (HELCOM 2010). Eutrophication, together with overfishing and climate change, facilitate alterations in ecosystem function (Möllmann *et al.* 2008; Eriksson *et al.* 2009). For example, the numbers of piscivorous fishes have gone down in many regions (Nilsson *et al.* 2004; Lehtonen *et al.* 2009; Ljunggren *et al.* 2010), whereas the opposite trend is evident for prey species such as roach, *Rutilus rutilus* (L.), silver bream, *Blicca bjoerkna* (L.), gibel carp, *Carassius gibelio* (Bloch), and threespine stickleback, *Gasterosteus aculeatus* L. (Nilsson *et al.* 2004; Vetemaa *et al.* 2005, 2006). This has produced a regime shift in the food chain where top-down control has weakened and bottom-up control prevails (Möllmann *et al.* 2008; Ljunggren *et al.* 2010). Interestingly, the current state does not include the population growth of another

cyprinid, ide *Leuciscus idus* (L.) (Ådjers *et al.* 2006), which are at the historical lows in multiple areas (Vetemaa *et al.* 2006; Eschbaum *et al.* 2014).

Ide is generally considered to be a rheophilic, freshwater species that inhabits large lowland rivers and lakes (Järvalt *et al.* 2003; Winter & Fredrich 2003; Kuliskova *et al.* 2009). However, similar to many other freshwater species inhabiting the brackish Baltic Sea, ide has adapted to life in the sea and to undertake anadromous spawning migrations to fresh waters (Müller & Berg 1982; Järvalt *et al.* 2003). Some populations of such species (e.g. northern pike *Esox lucius* L.) even have totally shifted to spawning in the brackish environment and have lost contact with fresh waters altogether (Engstedt *et al.* 2010). Similarly, some disputable evidence indicates that ide may have reproduced in the brackish coastal waters of Estonia 30–40 years ago (Mikelsaar 1984). General knowledge on the migratory biology of ide is relatively scarce for both freshwater resident (Winter & Fredrich 2003; Kuliskova *et al.* 2009) and anadromous ide (Cala 1975; Eriksson & Müller 1982; Johnson 1982). In the most extensive study on anadromous ide, Cala (1975) studied a population living near the dynamic Øresund Strait and stated that the anadromous runs may

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cover ~50 km in the River Kävlingeån. Potamodromous spawning migrations >100 km are reported from large lowland rivers (Winter & Fredrich 2003; Kuliskova *et al.* 2009). Furthermore, the few sea recaptures of ide that had been tagged in a small river near Umeå (Sweden) were all widely distributed along the coast, meaning that ide may cover long distance in the sea as well (Johnson 1982).

Ide is classified as least concern in the IUCN Red List (2014), whereas in Estonia, it is classified as data deficient (<http://elurikkus.ut.ee>). In Estonia, catches of freshwater resident and coastal ide peaked in 1920–1930s and 1980s at 54 and 177 t yr⁻¹, respectively (<http://www.agri.ee>). Abundances and catches have constantly decreased since the 1980s in the coastal sea (Vetemaa *et al.* 2006, 2010; Eschbaum *et al.* 2014). However, an increase in juvenile ide has been recorded in some coastal areas in recent years (Eschbaum *et al.* 2014). It is likely that overfishing lead to the collapse of most ide spawning stocks in Estonia (Vetemaa *et al.* 2001). It remains unclear, however, why most of those spawning stocks have not recovered despite a virtual cessation of commercial fishing for ide. Therefore, unfavourable environmental conditions may be inhibiting recovery. For example, Eriksson and Müller (1982) observed large numbers of adult ide migrating up a small Swedish river for spawning, but no descending juveniles were subsequently recorded. Although they caught large numbers of dead or developing eggs and newly emerged larvae, they concluded that reproduction had failed, possibly due to extreme variations in river water pH. They also noted that the individuals in that spawning stock were large (old) and of uniform size. It was also recently demonstrated that some low-density spawning stocks of ide in Estonia are predominantly composed of old individuals (Rohtla *et al.* 2015), and this in turn may hinder successful reproduction in those spawning stocks due to reduced egg quality (Targońska *et al.* 2012). Thus, it is likely that the current state of ide is a result of complex interplay between fishing pressure, environmental factors, species-specific traits and other factors such as interspecies competition and predator–prey relationships. Further studies on migration patterns, natal origins and environmental factors that are needed for successful spawning would help to gain more information for conserving, restoring and managing the anadromous stocks of this large bodied cyprinid.

Otolith microchemistry has recently emerged as a powerful tool for studying fish migration patterns (Secor 2010). Besides recording the age of the fish, otoliths also incorporate and retain different minor and trace elements from the water. These chemical data can be then used to infer migration patterns if elements are incorporated to

the otolith in proportion to the ambient concentrations and differences between study systems exist (Elsdon *et al.* 2008; Walther & Limburg 2012). The strontium-to-calcium ratio (Sr:Ca) is the most frequently used chemical marker because the Sr:Ca ratio in fresh waters is usually several times lower than sea water (Kraus & Secor 2004; Rohtla *et al.* 2014). This allows the movements of diadromous species to be tracked because the ambient Sr:Ca levels are recorded in the otoliths (Shiao *et al.* 2006; Magath *et al.* 2013; Rohtla *et al.* 2014). The barium-to-calcium ratio (Ba:Ca) is often used as an additional marker for interpreting Sr:Ca profiles, but with mixed results (Crook *et al.* 2006; Hamer *et al.* 2006; Rohtla *et al.* 2014; Smith & Kwak 2014). By contrast to Sr:Ca, the Ba:Ca ratio is generally enriched in fresh waters and decreased in sea waters.

In this study, life-history migrations of ide from the Väinameri Sea were reconstructed using otolith Sr:Ca and Ba:Ca profiles. Specifically, the aims were to investigate migrations on a temporal and spatial scale using combined age and chemical data, and assess potential spawning biome preferences, with fresh waters assumed to be the main spawning biome for ide.

Methods

Ide were sampled from three sites in the Väinameri Sea (Fig. 1). Käina Bay (KB) is a semi-enclosed lagoon in which salinity varies from 0 to 4 psu. Water level is regulated by locks situated on the two outlets. KB becomes a freshwater lake during spring snowmelt and is therefore used for spawning by different freshwater species. During summer, water levels may drop to <50 cm, and in winter, the bay often freezes to the bottom. Fish assemblage structure is shaped by predation pressure from common cormorant *Phalacrocorax carbo sinensis* (L.) (Vetemaa *et al.* 2010). Nevertheless, the ide spawning stock in KB is probably the largest and most viable in the entire Väinameri Sea. There are no recent records of ide spawning in nearby rivers, such as occurred historically. Matsalu Bay (MB) is a relatively dynamic system with an east-to-west salinity gradient (0–6 psu) that is 10 km long, and a delta estuary formed by multiple rivers. Ide penetrates these rivers for spawning, but no reproduction in the bay has been recorded. Saunja Bay (SB) is a shallow and semi-enclosed, mostly fresh water, bay with three small inflowing rivers. Winter hypoxia events occur about once every 6 years and may incite major fish kills. According to local fishers, ide spawns in SB only, despite it penetrating the rivers some decades ago. Together with the inflowing rivers, MB and SB act as important spawning and nursery grounds for many freshwater fishes in the Väinameri Sea area.

However, ide stocks are at their historical lows in both bays (Vetemaa *et al.* 2006; Eschbaum *et al.* 2014).

Ide were caught with gillnets (KB and SB) or purchased from local fishers (MB) in 2010–2013 (Fig. 1; Table 1). Immediately after capture, total length (L_T to nearest mm) was measured, sex was determined by dissection, and otoliths (lapillus) were removed from most of the individuals. Some individuals were frozen by the fishers and later thawed for otolith removal. Otoliths were cleaned with tissue paper and stored dry in microtubes. One otolith per fish was embedded into epoxy resin (Epofix; Struers A/S, Radovre, Denmark) so that a frontal section could be ground out from both sides with a grinding machine (Metaserv 250; Buehler Ltd., Lake Bluff, IL, USA) using silicon carbide grinding papers (P400/1200/4000 Buehler, Germany) to expose the core area and growth history. Age was determined by counting the narrow winter growth zones from unstained and stained (neutral red) otoliths using a stereomicroscope against dark and light backgrounds (Rohtla *et al.* 2015).

Chemical analyses of otoliths were conducted in the WM Keck Collaboratory of Plasma Spectrometry, Oregon State University, Corvallis, OR. Before the analysis, all the otoliths were ultrasonically cleaned for 15 min in NANOPure[®] water (Barnstead International, Dubuque, IA, USA) and dried in laminar flow hood. The concentrations of ^{43}Ca , ^{86}Sr and ^{137}Ba were quantified with

laser ablation–inductively coupled plasma mass spectrometry (LA-ICPMS). A VG PQ ExCell ICPMS (Thermo Scientific, Waltham, MA, USA) with a New Wave DUV193 excimer laser (New Wave Research, Fremont, CA, USA) was used. The laser was set at 10 Hz with a 40- μm ablation spot size and a scan speed of 5 $\mu\text{m s}^{-1}$. A continuous line scan was traced from the core area to the edge. Helium was used as a carrier gas. A glass reference material (NIST612) was analysed before and after every 6–10 otoliths. Data reduction was achieved by following the methods of Miller (2007) as described in Rohtla *et al.* (2014). A four-point running median was used to reduce the noise and smooth the data.

In the data analysis, the following background information was taken into consideration. Käina Bay Ca, Sr and Ba concentrations in late spring are 36, 0.1 and 0.007 ppm, respectively (M. Rohtla, unpublished data). Relatively low Ca and high Sr concentrations in KB result in a high Sr:Ca_{water} ratio (Table 1). Therefore, it is expected that otolith Sr:Ca natal values will also be significantly higher in KB than in SB and MB. If SB-caught ide are indeed born in the bay, then their otolith Sr:Ca profiles should display lower natal values than KB, but higher values than MB rivers. To test this hypothesis, the mean Sr:Ca values from the natal region (identified as lowest values on the elemental profile)

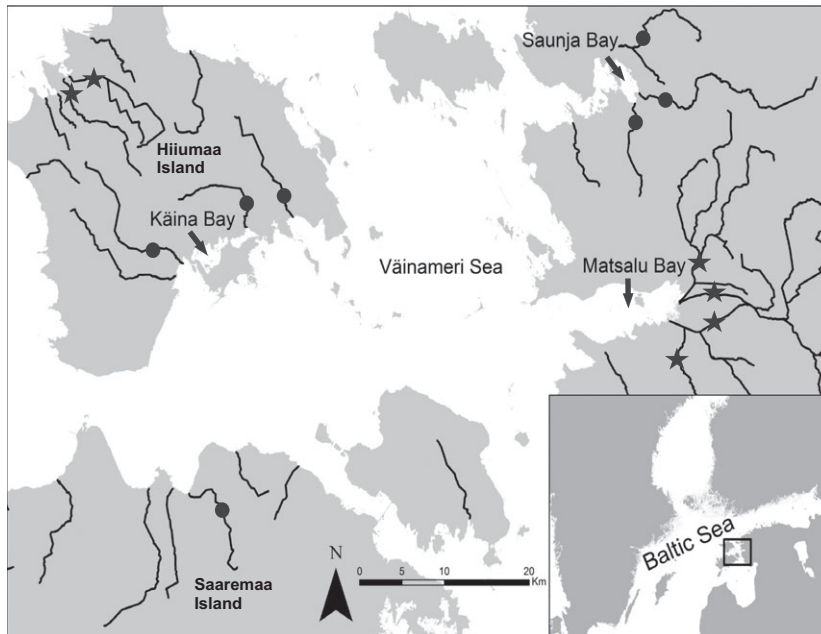


Figure 1. Sampling locations of ide around the Väinameri Sea (marked with arrows). Note that data on known ide spawning rivers are also given. Rivers marked with a star indicate rivers that support more or less significant anadromous runs; those marked with a circle indicate rivers that are historically known as ide spawning rivers, but currently do not support significant anadromous runs. Data are based on information from anglers, unpublished material of Estonian Marine Institute and from Järvekülg (2001).

Table 1. For ide *Leuciscus idus* in bays of the Estonian Baltic Sea are given the mean \pm SD, minimum (min) and maximum (max) for total length (L_T) in mm and age in years as well as the female-to-male sex ratio (F:M) and the corresponding water Sr:Ca values (in mmol mol^{-1}) by location of capture. Values for Matsalu and Saunja Bay are calculated from Rohtla *et al.* (2014)

Bay	n	L_T	min–max	F:M	Age	min–max	Sr:Ca _{water}
Käina	59	412 \pm 113	128–521	28:25*	7.3 \pm 4.5	2–24	1.3 _{bay}
Matsalu	25	454 \pm 77	222–568	11:14	10.9 \pm 7.5	3–27	0.4 _{river} 0.6 _{inner inner bay} 2.0 _{outer inner bay} 4.2 _{central bay} 7.5 _{Väinameri Sea}
Saunja	27	522 \pm 69	207–587	10:17	16.2 \pm 8.5	3–29	0.7 _{bay}

*Six individuals were juveniles.

were calculated and compared among sites using ANOVA, followed by a *post-hoc* Tukey's HSD test, given that the assumptions of ANOVA were met. The assumption of no immigration events was made, and therefore, natal values from each site represent a mixture of all possible spawning areas within one site (i.e. both riverine and bay). There may be some temporal variation within natal Sr:Ca values because the sampled specimens vary in age. Finally, to group individual Sr:Ca profiles statistically, the general method of Howland *et al.* (2001) was adopted, but with some modifications, that is the mean, minimum, maximum and range were calculated for each Sr:Ca profile and thereafter a principal component analysis (PCA) was conducted using log-transformed values.

Results

Sr:Ca value of otolith natal region differed significantly among sites (ANOVA, $F_{2,108} = 58.3$; $P < 0.001$) (Fig. 2). As expected, KB ide had significantly higher natal Sr:Ca values than MB and SB ide (Tukey HSD, $P < 0.001$). The latter were statistically indistinguishable (Tukey HSD, $P = 0.17$), although ide from MB generally had lower Sr:Ca natal values than ide from SB. One MB ide had an exceptionally high Sr:Ca natal value (i.e. $3.2 \text{ mmol mol}^{-1}$, Fig. 3d), and this affected the ability to statistically distinguish the two aforementioned sites.

Based on low and stable natal Sr:Ca values of most MB and some SB ide, the river threshold value for ide was determined to be $\leq 0.6 \text{ mmol mol}^{-1}$, which distinguishes the river spawning and bay spawning ecomorphs: 88% ($n = 22$) of individuals from MB, 33% ($n = 9$) of individuals from SB and 0% of individuals from KB were spawned in rivers. The remainder of the fish in each site were spawned in fresh waters with moderate Sr:Ca values (seasonally freshwater bays) or in brackish waters ($n = 80$ in total).

Otolith Sr:Ca profiles revealed that migratory patterns varied among and within sites (Figs 3 and 4). Age and

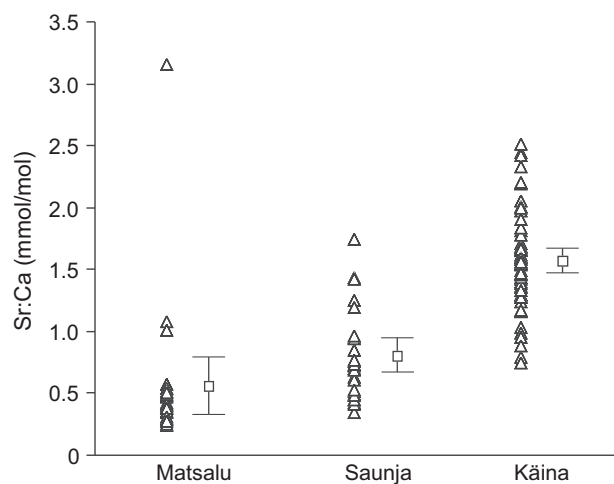


Figure 2. Natal Sr:Ca values from individual ide collected from three sites. Mean \pm 95% CI are also given.

Sr:Ca profile data indicated that young-of-the-year emigration to the sea occurs shortly after hatching, irrespective of location. About 95% of ide emigrate within the first month (Fig. 3b,e,i), but there were few individuals (5%) that stayed in fresh water for a couple of months (Fig. 3a,c). Age and L_T at maturation could not be estimated from the Sr:Ca profiles because of the following: (1) young immature ide seem to undertake spring migrations back to fresh water (Fig. 3f,g,i), and (2) many ide stay on the spawning grounds only for short periods, therefore not allowing Sr:Ca freshwater signal to incorporate fully (Fig. 3b,j,k). Nevertheless, 32% of individuals ($n = 36$) had a Sr:Ca profile where the number of nadirs was equal to the age of fish (Fig. 3e,i,l). These fish were mostly from KB, but several were also from MB. Sr:Ca nadirs were always located on or right before the annulus, indicating that these changes took place in spring. In MB, 40% of ide ($n = 10$) displayed Sr:Ca profiles that consisted of high values during the first part of life (indicating life in the Väinameri Sea) and low values

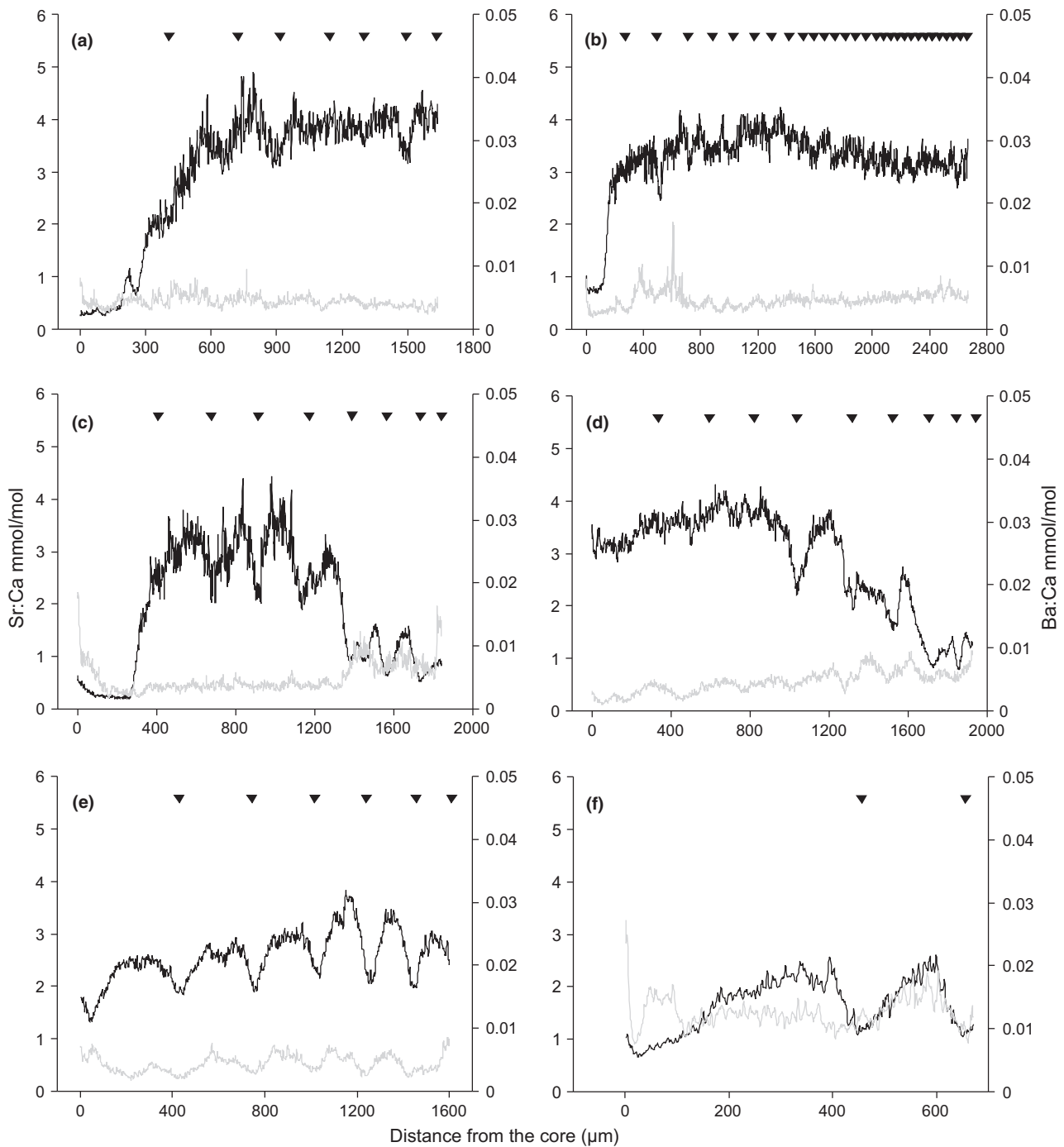


Figure 3. Representative otolith Sr:Ca (—) and Ba:Ca (—) profiles quantified in ide collected from three sites around Väinameri Sea, Baltic Sea: (a) Saunja Bay, 480 mm L_T , male with a riverine Sr:Ca natal value; (b) Saunja Bay, 547 mm L_T , female with a bay Sr:Ca natal value; (c) Matsalu Bay, 462 mm L_T , female with a riverine Sr:Ca natal value; (d) Matsalu Bay, 498 mm L_T , female with an exceptionally high Sr:Ca natal value; (e) Käina Bay, 433 mm L_T , female with Sr:Ca nadirs equalling the age and coinciding Ba:Ca profile; and (f) Käina Bay, 151 mm L_T , juvenile making non-spawning migrations to the bay. (g) Saunja Bay, 207 mm L_T , female (juvenile) making non-spawning migrations to the bay that are not visible in the Sr:Ca profile. Note that the scale for Ba:Ca is different from the rest; (h) Saunja Bay, 522 mm L_T , male with Sr:Ca nadirs nearly equalling the age; (i) Matsalu Bay, 537 mm L_T , male with Sr:Ca nadirs nearly equalling the age; (j) Matsalu Bay, 518 mm L_T , male that initially lived in higher salinities, but switched to lower salinities later in life; (k) Käina Bay, 475 mm, male with minimal Sr:Ca nadirs; and (l) Käina Bay, 484 mm L_T , male with Sr:Ca nadirs equalling the age and no variation in Ba:Ca. Note that scale values on x-axis vary with otolith (fish) size. Triangles denote the annuli.

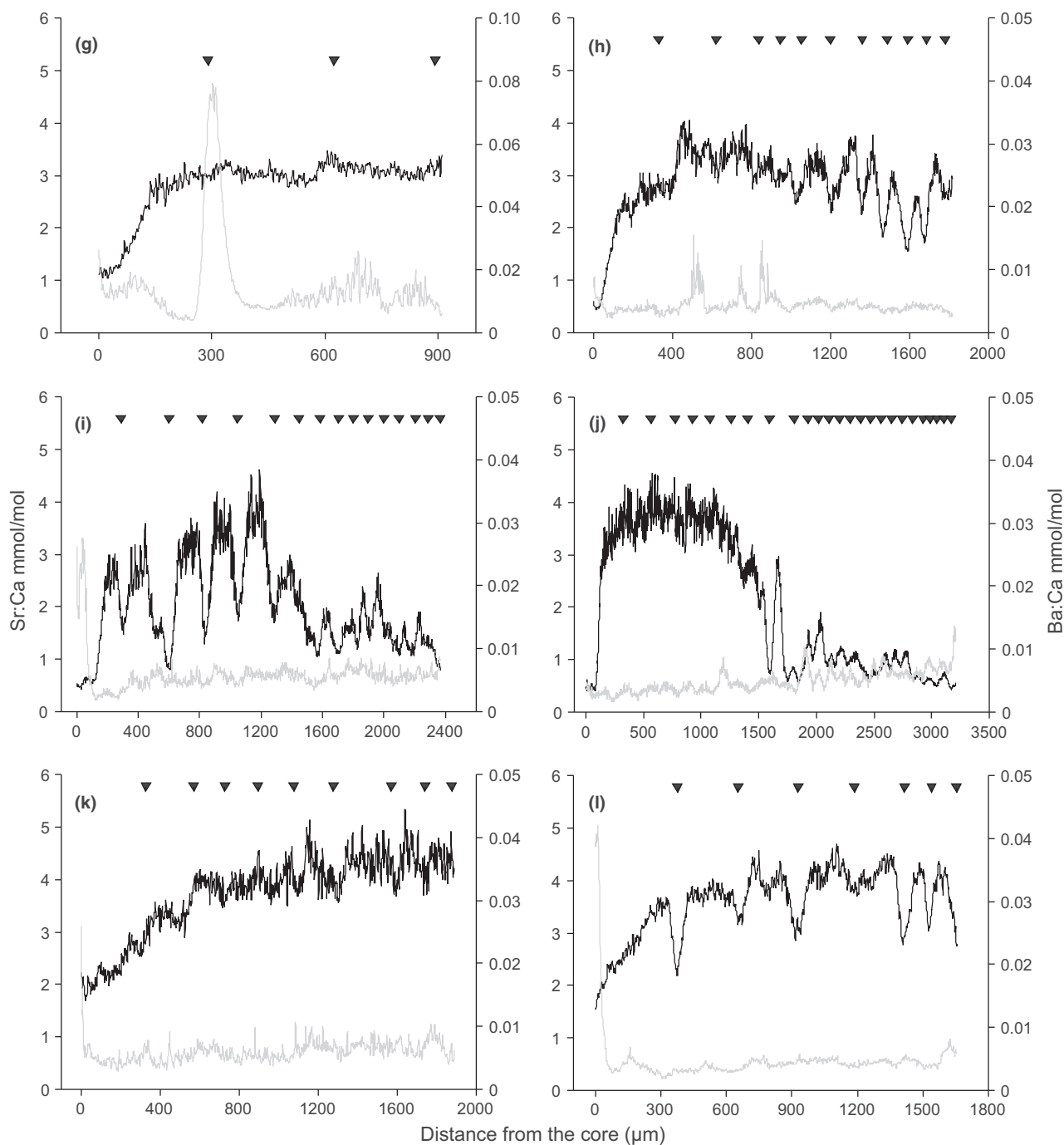


Figure 3. continued.

during the latter part of life (indicating life in inner bay) (Fig. 3d,j). Similarly, some KB ide had lower Sr:Ca absolute values than others (Fig. 3e,f), possibly indicating life in a region with lower salinities. Otolith Ba:Ca profiles were also obtained, but these were inconsistent. For example, some individuals displayed Ba:Ca oscillations that coincided with Sr:Ca oscillations in the otolith

(Fig. 3c,e,j), whereas most did not (Fig. 3h,i,l). Therefore, Ba:Ca data were excluded from further analysis and interpretation.

Principal component analysis on different Sr:Ca profile parameters revealed relatively distinct groups, although there was considerable overlap (Fig. 4), with PC1 and PC2 accounting for 95% of the variation.

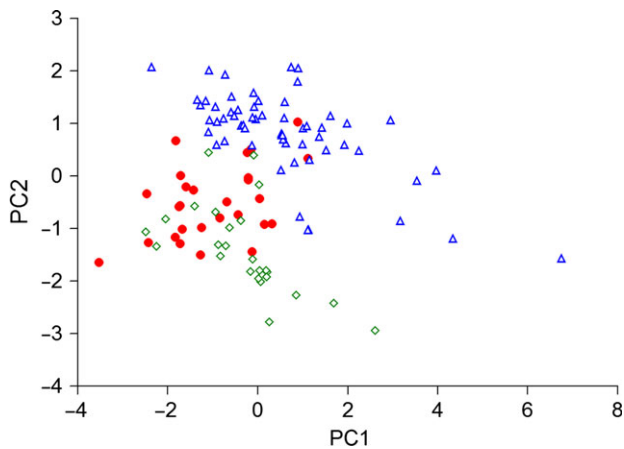


Figure 4. Principal component analysis on individual Sr:Ca profile mean, minimum, maximum and range values for ide collected from Käina Bay (triangles), Saunja Bay (squares) and Matsalu Bay (diamonds).

Several ide specimens from MB and SB were grouped among or in close proximity to the KB's multivariate space. This could mean that these ide originated from KB. The seven KB individuals grouped outside the main KB cluster were juveniles that had experienced lower Sr:Ca values (e.g. Fig. 3f).

Discussion

The Sr:Ca freshwater threshold determined for riverine ide is similar to the value reported for northern pike and burbot, *Lota lota* L., from the same systems (Rohtla *et al.* 2012, 2014; M. Rohtla, unpublished data). In the context of the present study, it is important to use the term 'river' and not 'freshwater' for thresholds because ide reproduction in Estonia also takes place in bays that in spring contain fresh waters with moderate Sr:Ca values (Table 1; see also Järvalt *et al.* 2003) – salinity measurements in KB and SB have confirmed this (R. Svirgsden, unpublished data). Also, although the natal Sr:Ca values were mostly higher than the riverine threshold (except in MB), the great majority of the sampled ide were hatched in fresh waters. The ide is not an obligatorily rheophilic species in terms of spawning, and because KB and SB are also more or less frequently flooded by sea water during other seasons, it results in ambient Sr:Ca values that are permanently higher than riverine values, most likely due to sediment deposition of marine elements. This is also reflected in the water samples and otoliths as demonstrated in the present study. Note, however, that there is some disputable evidence that ide can spawn in the brackish waters of the Baltic Sea with no direct freshwater input (Mikelsaar 1984).

In the present study, there were few individuals per site with high Sr:Ca natal values (most notably Fig. 3d), which could mean that some of them were spawned in brackish water. However, it has been demonstrated that the eggs and newly hatched larvae of river spawning ide can be flushed to the sea immediately after spawning (Eriksson & Müller 1982). If those early life stages can survive such habitat transition and some Estonian rivers disembogue directly to salinities 4–7, then it is possible that at least one specimen from MB (Fig. 3d) is a drifter. In that case, this specimen would also be an immigrant, because no river in MB drains directly to high salinities. The matter of immigration was also addressed in the Sr:Ca profiles (Fig. 4), and this also indicated that some of MB and SB ide may originate from KB. Immigration events are highly likely as ide is capable of long migrations (Winter & Fredrich 2003; Kuliskova *et al.* 2009) and MB and SB are ideal targets for strays due to low abundances of ide in those sites. Further study on these issues is needed.

The importance of lotic spawning varied between sites. None of the ide sampled from KB had Sr:Ca natal values indicative of river values. This result is strengthened by information from anglers, who report that no ide has been caught from nearby rivers for ~10 years. By contrast, 33% ($n = 9$) and 88% ($n = 22$) of the sampled ide from SB and MB, respectively, originated from rivers. This result was to be expected in MB (i.e. active spawning rivers), but somewhat surprising in SB. Anglers have not reported catching any ide in the rivers of SB for ~15 years. Of the nine SB fish with riverine natal values, six were <15 years old (min–max = 6–11). Therefore, it is likely that some river spawning does exist, perhaps in the rivers that are not exploited by anglers. Also, the possibility that these six individuals are immigrants, for example from MB, cannot be ruled out. The factors responsible for substantially decreased importance of riverine spawning are unknown. However, unsuitable environmental conditions and natural blockage of river mouths (due to ground uplift and dense vegetation) are the most plausible explanations.

All the sampled ide emigrated from natal areas and entered the sea during the first few months of life. Most of them did so within the first month. According to Cala (1975), juvenile ide in the River Kävlingeån spend the first year of its life in the river and then descend to the southern part of Øresund Strait – an area where salinity varies from 10 to 20 psu. Therefore, it is likely that in such areas, ide stay in fresh waters for a year to attain greater size before coping with high salinities in the sea. Larger individuals are generally more capable of adapting to the increased osmoregulatory demands (Beckman *et al.* 2003; Mojazi *et al.* 2009). However, the results of

the present study, and to lesser extent the results of Eriksson and Müller (1982), point towards a different life-history strategy in the Väinameri and Bothnian seas. The seawater salinity in both of these study systems is <6 psu, and it seems that such salinities are tolerable to early life stages of ide. Although Eriksson and Müller (1982) did not document any juvenile downstream migration *per se* (as for roach, which descended from August to December), they did observe large numbers of drifting ide eggs and newly hatched larvae near the river mouth. Early life stages of river spawning whitefish, *Coregonus lavaretus* (L.), and smelt, *Osmerus eperlanus* (L.), can also drift or emigrate to the sea soon after hatching (Sörmus & Turovski 2003; Quigley *et al.* 2004). The adaptive value of such early migrations is unknown, but this strategy could allow ide to take full advantage of productive sea habitats (McDowall 2007). Alternatively, as ide share their spawning grounds with other, more abundant cyprinids, it may be that competition forces this strategy on ide. For example, roach juveniles occupy their natal areas over summer and start their seaward migration 2–7 months post-hatch (Eriksson & Müller 1982). Emigration at small size definitely has its downsides (e.g. increased predation risk, stress), and this in turn may hinder the population recovery in systems where spawning stocks are small or declining (e.g. in MB and SB).

A diverse array of life-history patterns was observed as described by otolith Sr:Ca profiles. In addition to some variation in age (and therefore length) at natal area emigration, several other variable traits were observed. Ide usually mature at 6–7 years of age in Estonian coastal waters (Järvalt *et al.* 2003). Spawning migrations to fresh waters can be recorded with Sr:Ca profiles if the fish stay in the spawning areas for an extended period (Rohtla *et al.* 2014). It seems that these requirements are not fully met in ide because not all the individuals possessed clear Sr:Ca nadirs. Also, these nadirs were already observed on or at the end of the first annulus (i.e. age-1 fish in the spring). This means that juvenile ide migrate to fresh waters for purposes other than spawning. This result is supported by information from anglers, who report catching juvenile ide in rivers during annual spring spawning migration of adult roach and ide. However, the adaptive value of this phenomenon remains unknown. The most likely explanation is that freshwater migration by juveniles is the result of schooling, whereby juveniles move to the spawning grounds with the adults (i.e. a type of collective navigation; see Berdahl *et al.* in press). Fishers have reported large mixed shoals of juvenile and adult ide in the coastal waters of Estonia. Alternatively, it can be hypothesised that ide juveniles undertake spring

migrations to fresh waters for feeding at optimal (warmer) thermal conditions, such as found in freshwater wetlands, rivers and bays in spring. Finally, it must be also noted that the number and extent of Sr:Ca nadirs varied individually among and within sites (Fig. 3). This means that individual ide differ in terms of how long they stay in fresh waters (probably from a few days to a couple of weeks). Indeed, fishers of the River Nasva separate anadromous ide into four groups based on their size and the date they enter the river (Mikelsaar 1984).

Multiple individuals from MB had high Sr:Ca (sea water) values when they were young, but switched to waters of significantly lower Sr:Ca when they were older. This phenomenon most likely reflects changes in salinity and therefore the occupied region in the sea. As MB is a relatively long estuary with an east-to-west salinity gradient, it can be suggested that these fish switched to a life in the inner reaches of the bay rather than moving to the outer bay and Väinameri Sea. The reasons behind this are unknown, but it is likely that when certain body size is attained, predation pressure from piscivorous fishes, birds and mammals decreases and fish can use the shallower inner parts of the bay. Food competition should also be smaller in the inner part of MB as the numbers of potential competitors are low (Vetemaa *et al.* 2006).

To conclude, ide is a species capable of using variety of habitats of variable salinity and the potential for long migrations. The present study adds to the multiple otolith microchemistry studies that have shown that the migratory life history of fishes can be far more diverse than previously believed (e.g. Limburg *et al.* 2001; Daverat *et al.* 2006; Mai *et al.* 2014; Rohtla *et al.* 2014). Although ide can arguably also reproduce in brackish waters, the results of present study point towards freshwater reproduction only. However, multiple historically important spawning rivers are currently not used by ide, which at two of the study sites have mostly shifted to spawning in seasonally freshwater bays. This draws attention to the problems associated with rivers used for spawning fish stocks (e.g. unsuitable environmental conditions, inaccessibility of rivers) and calls for the resolution of these issues. As ide seems to be very flexible in terms of spawning migration strategy and habitat choice in the sea, it is reasonable to anticipate that ide spawning stocks will recover and be more viable if riverine spawning grounds are restored. Future studies should try to address the issues concerning the extent of sea migrations and natal homing. Salinity experiments will be required to determine the fate of the (potentially) sea-spawned or drifted eggs and larvae in different salinities.

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