

Life history of anadromous burbot (*Lota lota*, Linnaeus) in the brackish Baltic Sea inferred from otolith microchemistry

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Abstract – Strontium to calcium (Sr:Ca) and barium to calcium (Ba:Ca) ratios were quantified in 74 otoliths of brackish water-living burbot *Lota lota*, collected from two regions in the eastern Baltic Sea. Considerable amount of life history plasticity was observed. Ninety-six per cent of analysed burbot were of freshwater origin; only three specimens displayed signs of hatching in low-salinity (1–2) estuarine environment. Most of the juveniles emigrated from freshwater during late winter and spring the next year after birth, while nine individuals did so at the age of 2–3 months. Age and length at maturity (as determined by first freshwater spawning migration) varied from 2–6 years and 189–540 mm, respectively, with most of burbot maturing during the second or third year of life. It is hypothesised that the bulk juvenile downstream migration is triggered by high-flow conditions as evidenced by Ba:Ca peak around the point of freshwater exit. This study provides new information on burbot life history.

Key words: Sr:Ca; Ba:Ca; Estonia; plasticity; Gadiformes

Introduction

The Baltic Sea is one of the most unique water ecosystems in the world. Different organisms of marine and freshwater origin have adapted to its salinity (mostly below 8), prospering together in those nutrient-rich waters. However, as significant saltwater intrusions are rare and future freshwater input is projected to increase, salinities will drop even further (Kjellström & Ruosteenoja 2007; Meier et al. 2012). This will create more favourable conditions to numerous freshwater species inhabiting the coastal sea and make the life for marine species more difficult.

Burbot *Lota lota* (Linnaeus) is a useful indicator species of habitat quality and an important top predator in many coldwater ecosystems (Stapanian et al. 2010). It is the only gadoid species that lives exclusively in freshwaters. However, in some areas, including the Baltic Sea, burbot and many other freshwater species have also adapted a brackish water life phase and are been therefore referred to as anadromous (Müller & Berg 1982) or semianadromous (Koporikov

& Bogdanov 2011) species. Burbot is a second-rate commercial fish, and the official catches are low worldwide (Stapanian et al. 2010). In the Väinameri area (west-Estonian Archipelago Sea), for example, the annual commercial catches average to ca one ton. Like with many other coastal predatory fish species living in the Baltic, for example, pike *Esox lucius* and perch *Perca fluviatilis* (Nilsson et al. 2004; Lehtonen et al. 2009), the numbers of burbot are declining despite low fishing pressure (Stapanian et al. 2010). In Estonia, one of the reasons behind this decline is probably the predation impact from increasing number of cormorants (*Phalacrocorax carbo*) (Eschbaum et al. 2003; Vetemaa et al. 2010). Also, climate change and pollution may be associated with the decline of burbot in some areas (Stapanian et al. 2010).

Due to low commercial interest, little data on different aspects of burbot ecology and management exist, although somewhat more is known about freshwater resident burbot (Paragamian & Bennett 2008; Stapanian et al. 2010). Most of the research carried out on Baltic burbot dates back at least a decade and

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is focused to the Gulf of Bothnia (Hudd & Kjellman 1983, 2002; Pulliainen & Korhonen 1993). One of the aspects that received more attention in the past is burbot migration, although most of the studies are grey literature (Hedin 1983; Hudd & Lehtonen 1987; Müller 1987). However, based on the information obtained from Müller (1982), it is known that runs of anadromous burbot exist even in smallest rivers. According to Lehtonen (1998), two different migratory phenotypes exist along the Baltic coast: (i) individuals that spawn at sea and spend their whole life in the coastal waters and (ii) individuals that spawn in freshwater but otherwise live in the sea. However, the former should be regarded as hypothesis, as no published data on sea-spawning burbot actually exist. All the past burbot migratory studies are based on fish trap data and mark-recapture studies. To our best knowledge, no results on real-time telemetry studies or other methods (e.g., otolith microchemistry) have been published to investigate the movement patterns and spawning biome preference of brackish water-living burbot. Alternative methods should be implemented to obtain a more detailed view on the spatial and temporal movements of burbot and to validate the results obtained by other methods.

During the past two decades, microchemical analyses of otoliths have become a popular tool in fish ecology studies (Gillanders 2005; Elsdon et al. 2008). In particular, the use of otolith strontium to calcium ratio (Sr:Ca) to infer fish migration patterns between fresh and seawater is probably the most used application (e.g., Zimmerman et al. 2012), although studies on

elemental fingerprinting are also common (e.g., Miller 2007). The premise of using Sr:Ca as a tracker of fish movements is the usually positive relationship between salinity, water Sr:Ca and otolith Sr:Ca (Secor & Rooker 2000; Crook et al. 2006). In some areas, however, Sr:Ca in a low-salinity environment may exceed that of high (Kraus & Secor 2004). Therefore, one should assure that Sr:Ca variation in the study area is as expected. Several studies have also used barium to calcium ratio (Ba:Ca) as a tracker of fish migratory history (Elsdon & Gillanders 2005; Feutry et al. 2012). There should be a negative relationship between salinity and Ba:Ca in the water and otolith (Elsdon & Gillanders 2005), but this depends on estuarine particle dynamics and riverine sediment supply (Coffey et al. 1997).

In this study, we use otolith Sr:Ca and Ba:Ca to investigate different life history traits of brackish water-living burbot. Specifically, we aim to look in to following issues: (i) spawning biome preferences, (ii) age and length at first freshwater emigration and at first freshwater spawning migration and (iii) migration patterns.

Materials and methods

Study sites

Matsalu Bay (MB) together with its estuary system (Fig. 1) is the only real delta estuary in the eastern Baltic Sea. The surface area of the bay is ca 67 km², and it has a relatively long (ca 15 km) salinity gradient increasing steadily from east (0–0.5) to west

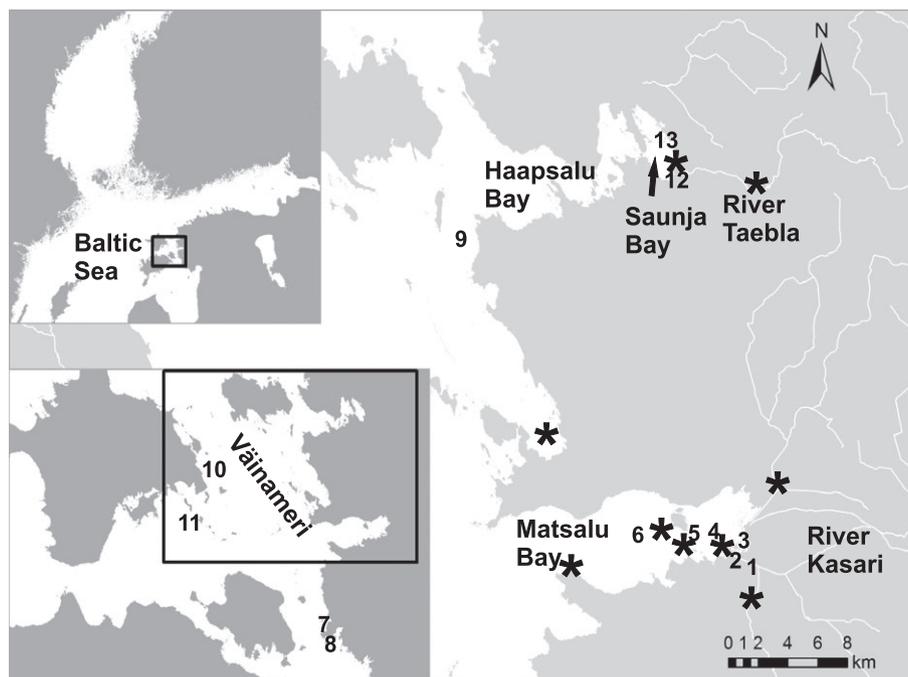


Fig. 1. Location map of the study regions. Collection sites of fish (*) and water samples (1–13) are marked.

(5–6). Occasionally, weak currents from the sea and from the largest river draining into the bay (River Kasari) produce slight deviations to the salinity gradient, but those are temporary (Kumari 1985).

Saunja Bay (SB) is the most eastern part of the Haapsalu Bay system (Fig. 1). The former has a surface area of ca 7 km² and the later, ca 50 km². Compared to MB, this system is a rather closed one, where narrow and uplifted straits prevent constant water exchange between the sea and SB. Also, only three small rivers drain into SB, making the whole system not as dynamic as MB. Such conditions create a relatively steep salinity gradient between the saline parts of the Haapsalu Bay system (3–7) and SB (<0.5). During strong westerly winds, however, sea water intrusion to SB may occur.

Fish sampling and processing

A total of 35 burbot were collected from the fyke nets located at the mouth of River Taebila, SB (Fig. 1) at the beginning of the 2011/2012 spawning season (December–January). One burbot was also collected ca 6 km upstream of River Taebila. The fish were killed immediately after capture by severing the central nervous system. Total length (TL, 1 mm) and weight (0.1 g) were recorded, and sex determined by visual examination of the gonad. Sagittal otoliths were extracted, cleaned from adhering tissue and stored dry in microtubes.

For the samples from MB and the draining rivers, otoliths ($N = 38$) from the archives of Estonian Marine Institute (collected in 1978–2005) were used; therefore, no extra sampling was necessary. Unfortunately, no biological data were available for most of the MB burbot. For the estimation of the TL of fish with unknown size, a relationship between known burbot TL and otolith radius (mm) from the transverse section was plotted. The equation used for backcalculation was: $TL = 0.206 \cdot OR - 52.437$, where OR is the otolith radius. The same equation was used for the backcalculation of TL at first seaward and spawning migration. Standard t -test and MW U -test were used to detect any difference between the two study regions.

Otolith preparation and ageing

All the otoliths were embedded into epoxy resin (Epo-fix; Struers A/S, Radovre, Denmark), so that a transverse section could be ground out. To expose the core area, the mount was ground manually with a grinding machine (Metaserv 250; Buehler Ltd., Lake Bluff, IL, USA) from both sides using abrasive papers with grit sizes P400 and P1200. A final polish was carried out with P4000.

Age was determined by counting the translucent zones from unstained and stained (neutral red) otoliths using a stereomicroscope against dark and light background. As burbot is a cold-water species, the first annulus is completed when the second translucent growth zone starts to form. Because burbot is quite stagnant during the summer months (from June to August) and most of the feeding and growth takes place from September to May, the birthday of burbot is set to 15th May (Raitaniemi et al. 2000).

LA-ICPMS and water analysis

The elemental composition of otoliths was quantified with laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) in Oregon State University's WM Keck Collaboratory of Plasma Spectrometry, Corvallis, OR. Before the analysis, all the otoliths were ultrasonically cleaned for 10 min in NANO-Pure[®] water (Barnstead International, Dubuque, IA, USA) and dried in laminar flow hood. 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 for quantifying the concentrations of ⁴³Ca, ⁸⁶Sr and ¹³⁷Ba. The laser was set at 10 Hz with a 40 μm ablation spot size and a scan speed of 10 μm·s⁻¹. Helium was used as a carrier gas. A continuous line scan, which corresponded to the longest radius of a transverse section, was measured from the core area to the edge. Data reduction was achieved by following the methods of Miller (2007). Briefly, counts per second were background subtracted, ratioed to ⁴⁶Ca (used as internal standard) and then standardised to NIST-612 glass standard. For presentation, concentrations were converted to mmol/mol for Sr:Ca and μmol/mol for Ba:Ca. Extreme outliers were removed following the methods of Veinott & Porter (2005). A nine-point running mean followed by a nine-point running median was used to reduce the noise and smooth the data (Sinclair et al. 1998). The precisions (%RSD) of ⁴³Ca, ⁸⁶Sr and ¹³⁷Ba for NIST 612 glass were 13%, 10% and 17%, respectively. Absolute accuracy was estimated from a calcium carbonate standard of known composition developed by US Geological Survey (USGS MACS-2), and the mean values for Sr:Ca and Ba:Ca were 24% and 42% higher than reported.

Water samples were collected from various sites in autumn of 2009 (Table 1), filtered (0.45 μm) and acidified to pH 2 with nitric acid for later analysis. They were analysed using X Series II ICPMS device coupled with CETAC ASX100 autosampler (CETAC Technologies Inc., Omaha, NE, USA). The Sr and Ba quantification in the water was achieved by external calibration using Claritas PPT multi-element

Table 1. Results of the water analyses and approximate salinities in respective locations. Concentrations are expressed as parts per million (ppm). Sampling site numbers correspond to the numbers given in Fig. 1.

Site	Number	Salinity	Sr	Ba	Ca	Sr:Ca ($\times 10^{-3}$)	Ba:Ca ($\times 10^{-3}$)
Matsalu Bay							
Kasari River (main channel)	1	<0.5	0.045	0.028	45	1	0.6
Kasari River (side channel)	2–3	<0.5	0.046–0.059	0.027	78–82	0.6–0.7	0.3
Inner bay	4	1	0.088	0.026	63	1.4	0.4
Borderline of inner and central bay	5	2	0.314	0.033	72	4.4	0.5
Central bay	6	3	0.812	0.032	89	9.1	0.4
Väinameri	7–11	5–6	1.223–1.504	0.022–0.03	75–111	12.0–17.5	0.2–0.4
Haapsalu Bay							
Saunja Bay	12–13	<0.5	0.101–0.108	0.013–0.018	65–72	1.4–1.6	0.2

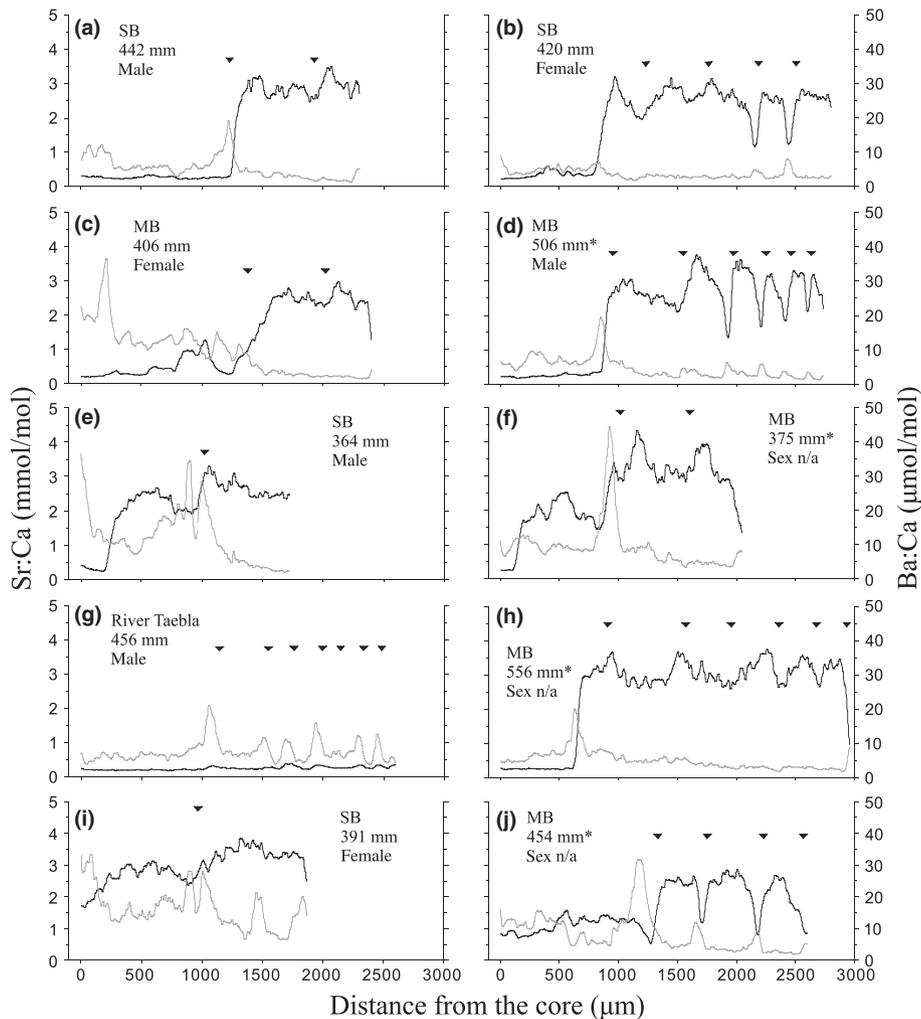


Fig. 2. Examples of Sr:Ca (black line) and Ba:Ca (grey line) profiles of sampled burbot: (a–d) typical chemical profiles of burbot; (e–f) early migrants; (g) freshwater resident burbot, note the annual Ba:Ca peaks and also the reduced growth rate compared to anadromous individuals; (h) burbot with delayed maturity; and (i–j) brackish water-born individuals. SB, Saunja Bay; MB, Matsalu Bay. Arrowheads indicate the annulus. An asterisk (*) denotes individuals with backcalculated total length.

standards CLMS-1 and CLMS-2 (SPEX CertiPrep Inc, Metuchen, NJ, USA). Quality control was carried out with National Institute of Standards and Technology water standard 1643e. Analytical accuracy and precision for Ca, Sr and Ba were within 5% and 2%, respectively.

Results

Strontium concentrations and Sr:Ca in the water increased with salinity, but no obvious relationship between salinity and Ba and Ba:Ca was detected (Table 1). The low and stable Sr:Ca values of

Table 2. Total length and age of burbot collected from Saunja and Matsalu Bay (including the river samples), and the results of backcalculations expressed as mean ± SD and range.

	TL (mm)	Age (years)	TL at first freshwater exit (mm)	Age at first freshwater exit (years)	TL at maturity (mm)	Age at maturity (years)
Saunja Bay	407 ± 57	2.5 ± 1.2	156 ± 48	0.7 ± 0.2	385 ± 50	2.1 ± 0.5
	301–532	1.7–7.7	50–231	0.1–1.0	282–493	1.7–2.7
	<i>N</i> = 36	<i>N</i> = 36	<i>N</i> = 34	<i>N</i> = 34	<i>N</i> = 35	<i>N</i> = 35
Matsalu Bay	384 ± 104	3.3 ± 1.5	134 ± 46	0.8 ± 0.3	323 ± 87	2.4 ± 1.0
	76–556	0.3–7	50–199	0.1–1.2	189–540	1.4–5.7
	<i>N</i> = 38	<i>N</i> = 38	<i>N</i> = 33	<i>N</i> = 33	<i>N</i> = 26	<i>N</i> = 26

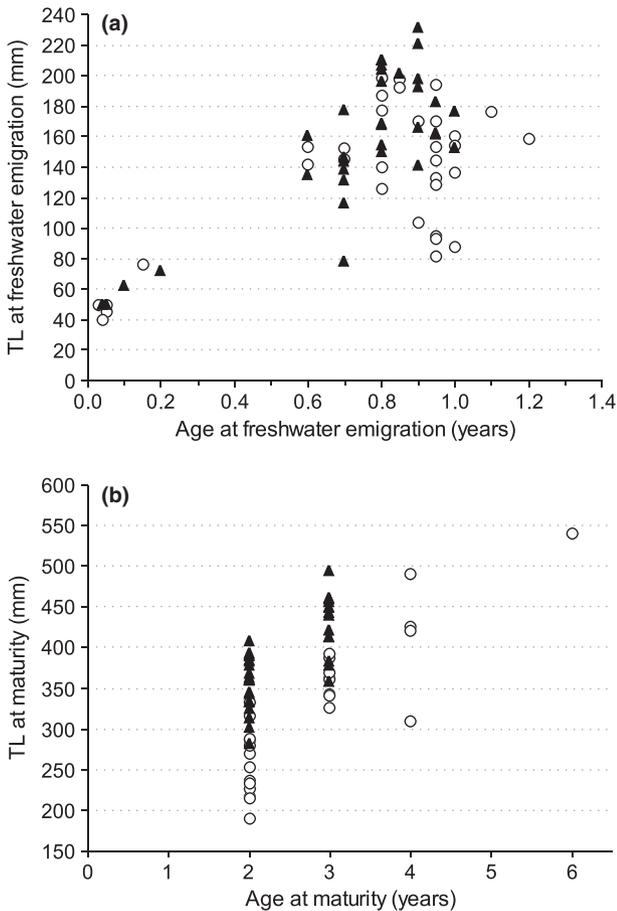


Fig. 3. Backcalculated metrics of Matsalu Bay (circles) and Saunja Bay (triangles) burbot: (a) age and total length at freshwater emigration and (b) age (in full years) and total length at maturity.

freshwater resident burbot (*N* = 5) were used to determine the freshwater threshold of 0.5×10^{-3} (calculated as mean + 1 SD). This is the same threshold that was also determined for MB pike (Rohtla et al. 2012).

Diverse array of life history profiles was observed (Fig. 2). General movement patterns were readily interpreted using Sr:Ca data alone; however, Ba:Ca data provided additional information. Vast majority (96%) of analysed burbot were of freshwater origin; only one specimen from SB and two specimens from

MB hatched in brackish water (Fig. 2i,j). Most of burbot descended to the sea during late winter and spring the following year after birth (Table 2; Fig. 3a). However, from both locations, a total of nine individuals showed precocious migration patterns (i.e., descending during first summer) (Fig. 2e,f). There were no significant differences between SB and MB in TL and age at freshwater emigration when precocious migrants were included (*t*-test; *P* = 0.06 and 0.6, respectively), but significant differences were found when precocious migrants were excluded from the analysis (*t*-test; *P* = 0.02 in both cases) with burbot from SB descending at younger age and larger size.

Most of sampled burbot matured during second or third year of life. Age and length at maturity (determined as first freshwater migration) varied more in MB sample (Table 2, Fig. 3b). Total length at first reproduction was significantly greater in SB burbot than in MB burbot (*t*-test; *P* < 0.001), but no significant age differences were detected (MW *U*-test; *P* = 0.2). Ten MB individuals displayed signs of delayed maturation (Fig. 2h) with five of them not yet matured despite being in suitable reproductive age (3–4 years) and length (388–497). No rest years between consecutive spawning seasons were detected (Fig. 2b,d).

Ba:Ca profiles displayed inconsistent patterns, being helpful in some individuals but not necessarily in others (Fig. 2). Many individuals possessed a Ba:Ca peak at the point of freshwater exit (Fig 2a,d). Ba:Ca peaks were annual in freshwater residents (Fig. 2g).

Discussion

Considerations about Sr:Ca data

Ninety-six per cent of burbot analysed in this study were of freshwater origin. This contrasts to earlier beliefs that a significant part of Baltic Sea burbot population can complete their lifecycle solely in the sea (Lehtonen 1998). It is worth noting, though, that Lehtonen's (1998) statement on lifetime sea residency is based on two earlier studies (Hudd & Lehtonen 1987; Müller 1987) that do not even mention the

possibility of burbot spawning in brackish water. Therefore, based on our data, we argue that the sea-residency hypothesis is invalid, at least on a Baltic scale. Only a small fraction of burbot population seems to hatch in low-salinity (1–2) estuarine environment and even they return to freshwater for spawning (Fig. 2i,j). It is possible that these fish were also spawned to freshwater, but they were drifted to brackish water very soon after hatching (or even during embryonic development). Pelagic yolk-sac larvae of burbot have been observed in lotic environments (Dillen et al. 2008).

Most of analysed burbot descended to the sea during late winter and spring the following year after birth (Table 2, Fig. 3a). However, nine individuals showed precocious migration patterns (i.e., descending during first summer). The factors behind this early emigration are unclear, but it could be that these fish were simply forced to descend due to nonoptimal conditions (e.g., lowering water levels). From a trap-net data collected in River Ängerån (Sweden), it is known that the bulk juvenile downstream migration occurs from August to January (Eriksson & Müller 1982); however, no sampling was conducted from February to May. This contrasts to the results presented in our study, as both earlier and especially later migrants dominated. One of the main reasons behind this discrepancy could be the difference in river discharges, which are several times smaller in River Ängerån than in River Kasari and Taebila. This could potentially influence the timing of downstream migration in River Ängerån, especially in winter, when water levels are in the lows.

Juvenile burbot from SB emigrated from freshwaters at younger age and at larger size than the juveniles from MB. This fast growth rate of SB burbot is also evidenced by low age and large size at first reproduction. One possible explanation to the extremely high growth rates in SB may be simultaneous fluctuations in both burbot and potential prey species population densities, which in combination have been shown to increase mean length-at-age (Kjellman & Hudd 1996). Unfortunately, no such data are available for the present study. Lastly, it has to be stressed that most of the MB burbot were collected more than 20–30 years ago, and therefore, the growth conditions and population dynamics may have been different at that time.

Most of the analysed burbot matured during the second or third year of life. This is the same result as reported for burbot caught from the coast of southern Finland (Lehtonen 1998). However, ten individuals from MB displayed signs of delayed maturity. One could argue that those fish simply spawned in brackish water during the first years and suddenly ‘decided’ to spawn in freshwater. Although the possibility of a significant part of burbot population

spawning in brackish water during first reproductive years cannot be totally ruled out, it is unlikely as nearly all the sampled burbot were born in (and thus spawned to) freshwater. Furthermore, there is evidence for late maturity amongst burbot from Lake Peipsi (Estonia), where individuals may mature as large and as old as 60 cm and 7 years, respectively (Ojaveer et al. 2003). Laboratory experiments are needed to quantify the hatching success and survival of larvae at different salinities.

Considerations about Ba:Ca data

The use of Ba:Ca as a proxy for salinity resulted in controversial, but also interesting results. We found no variation in ambient Ba:Ca (Table 1), but this is probably because Ba is removed from the system as the summer commences (Stecher & Kogut 1999). Also, otolith Ba:Ca data were not that consistent and variable as expected, but still provided complementary information (Fig. 2). Most interestingly, we recorded distinct Ba:Ca peaks at freshwater emigration in many individuals and noticed that these peaks were always laid down during late winter or spring. As this is the period when most of burbot descend (based on Sr:Ca profiles), it could mean that coinciding Ba:Ca peaks reflect high temporal or spatial environmental availability of Ba. It is known that Ba concentrations in running waters exhibit seasonal variation under various discharge rates (Colbert & McManus 2005; Wang et al. 2009), and fish otoliths can record those peaks (Hamer et al. 2006; Tabouret et al. 2011). As the snowmelt period and the resulting high riverine runoff occurs in late winter and spring, it can be hypothesised that freshwater emigration is actually triggered by high-flow conditions. Variations in river discharge have been shown to influence the migration of adult burbot (Slavík & Bartoš 2002; Paragamian et al. 2005). Alternatively, Ba:Ca peaks at freshwater emigration could depict prolonged residence in the river-mouth area, where elevated concentrations may occur (Coffey et al. 1997; Wang et al. 2009). Additional water sampling in winter and spring is required to properly address these hypotheses.

Burbot life history

Burbot life history traits (e.g., age and length at freshwater emigration and at first reproduction) displayed considerable plasticity. This result is principally verified by Paragamian & Wakkinen (2008) who reported multiple burbot movement patterns in a river–lake system of North America, using telemetry and limited sample size. Although widespread in salmonids (e.g., Thorpe 1994), it is only recently when such examples amongst nonsalmonid fish have

emerged (Daverat et al. 2006, 2012; Feutry et al. 2012). For example, Daverat et al. (2012) have shown that European flounder *Platichthys flesus* may spawn in coastal, brackish or freshwater environments, and multiple habitat use patterns exist. Similar results are also reported for pike from the Baltic Sea (Engstedt et al. 2010; Rohdla et al. 2012). As organisms with complex life histories are most affected by climate change (e.g., salmonids, Crozier et al. 2008), burbot faces similar problems in the future. For example, discharge levels of Baltic rivers are projected to increase, especially in winter (Kjellström & Ruosteenoja 2007). This could alter the spawning migrations and also the timing of freshwater emigration, therefore potentially decreasing recruitment.

Conclusion

The findings of this study provide new information on burbot ecology and draw attention to flexible life history strategies. Large majority of burbot still require freshwater for spawning in the brackish Väinameri system. Most of juveniles emigrate from freshwater during late winter and spring at the age of 8–11 months, while precocious migrants are also present. Emigration was often accompanied by Ba:Ca peak, and it is therefore hypothesised that high-flow conditions may trigger freshwater emigration. Maturity is achieved during second or third year of life, but some individuals delay it for couple of years. As burbot is an important top predator in aquatic ecosystems, these results provide a basis for fisheries managers and conservationists dealing with this anadromous winter spawning species.

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