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Elevated boron in cod otoliths from the low-salinity Åland Sea: A unique marker for a new population in the Baltic Sea?

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ABSTRACT

Objective: The purpose of this study was to understand the possible provenance of a unique population of Atlantic Cod *Gadus morhua* that is found in the low-salinity Åland Sea region of the northern Baltic Sea. This population consists of large, healthy individuals, in contrast to the Atlantic Cod in the rest of the Baltic Sea.

Methods: We used laser ablation inductively coupled plasma mass spectrometry to measure levels of boron (as B:Ca) in the otoliths of Atlantic Cod in regions throughout the Baltic Sea. We examined both lifetime chronologies and concentrations in the core region that corresponds to birth and early life.

Results: We found that B:Ca concentrations were 31 to 348 times higher in the otoliths of cod that occupy the Åland Sea, including in the core region. These concentrations were much higher than expected given that boron is linearly, positively proportional to salinity, which is higher in the southern Baltic Sea, and other populations displayed very low concentrations by comparison.

Conclusions: Based on the otolith B:Ca as a unique marker, we suggest that the cod that are sampled in the Åland Sea may be a separate population from those that inhabit the rest of the Baltic Sea. This would not prevent it from mixing with other populations but could point to a separate spawning area. The source of the elevated boron is currently unknown, but the widespread occurrence in cod otoliths from the Åland Sea indicates an extensive nonpoint source.

KEYWORDS: Baltic Cod, microchemistry, otolith boron

LAY SUMMARY

In 2021, we found that high levels of boron, an element that is rarely studied in fish otoliths, could distinguish an unusual population of cod that inhabits the low-salinity waters in the part of the northern Baltic Sea that is known as the Åland Sea. Furthermore, the high boron (measured as boron in ratio to calcium) appears to be recent, as Åland Sea otoliths that were collected in 1948 and 2013 contained much lower concentrations of boron, similar to the levels that were found in other sites in the Baltic Sea. The elevated B:Ca in modern Atlantic Cod otoliths from the Åland Sea does not correlate with salinity, in contrast to seawater B:Ca that does so. Although the source of this unique signal is unknown, it serves as a biomarker for a highly unusual population of brackish-tolerant Atlantic Cod.

INTRODUCTION

Atlantic Cod *Gadus morhua*, with their broad geographic distribution, have historically been composed of many populations and subpopulations (Kulatska et al., 2025; Marteinsdóttir & Rose, 2019); despite that, many of the major stocks were dramatically overfished. Often regarded as a semiresident, demersal species, cod populations in fact undertake a variety of migrations and life history patterns as they explore and exploit new habitats. Notably, Atlantic Cod in the eastern portion of their range extend from the Arctic south to the Mediterranean and in salinities ranging from full-strength seawater to oligohaline waters, underscoring the remarkable adaptability of this species.

The semi-enclosed Baltic Sea (Figure 1) in many ways resembles a vast estuary and is an unusual habitat for Atlantic Cod, given its low salinity compared to that of the open ocean. With a surface area of 349,644 km² (1.7 times the surface area of the Laurentian Great Lakes combined), the Baltic Sea is oligohaline at its northern end (Bothnian Bay, labeled as "31" in Figure 1) and polyhaline as it exits toward the North Sea
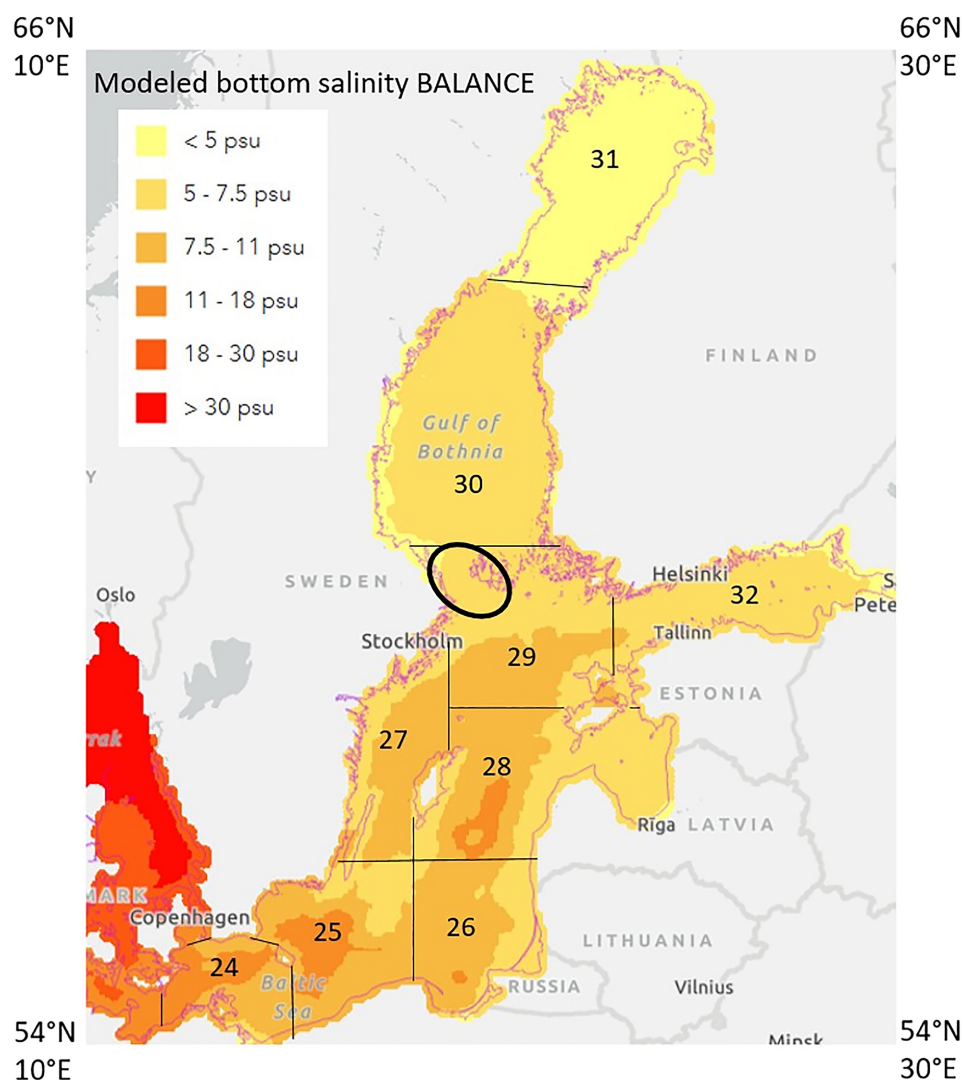
Figure 1. Map of the Baltic Sea showing bottom water salinities. The numbers indicate the subdivisions that are delineated by the International Council for the Exploration of the Sea for sampling. Subdivisions 25–28 and the southern portion of Subdivision 29 comprise the Baltic proper. The Åland Sea is in the northern portion of that subdivision (black ellipse). Salinities were estimated by the Modelled bottom salinity BALANCE, HELCOM Map and Data Service. The Baltic Marine Environment Protection Commission (HELCOM), Helsinki, Finland; https://maps.helcom.fi (accessed December 12, 2024). The metadata are available at https://metadata.helcom.fi/geonetwork/srv/eng/catalog.search#/metadata/fb51cc51-3ec2-40da-9728-714ca66b0e8f.

through a complex of channels, straits, deep zones, and sills and has complex salinity structure at local scales (Kullenberg, 1981). Despite the low salinity, the eastern component of the Baltic Sea Atlantic Cod complex (hereafter, "eastern Baltic cod [EBC]") can be found throughout the Baltic proper. Nissling and Westin (1997) found that EBC could successfully spawn in mesohaline conditions. Spermatozoa were activated at 11–12 psu, and neutral egg buoyancy occurred at 14.5 psu.

The population dynamics of EBC are complex (reviewed in Tomczak et al., 2022), having fluctuated considerably in the 20th century. Favorable conditions in the 1970s and early 1980s, fueled by mild eutrophication, promoted the formation of several strong year-classes. However, continued nutrient loading, climate warming, and overfishing created ecosystemwide tipping points and regime shifts from the 1990s through today (Reusch et al., 2018; Tomczak et al., 2022). Much of the central

Baltic Sea (Baltic proper) has become increasingly hypoxic and anoxic (Hansson & Viktorsson, 2023). Overfishing pressures and hypoxia exposure have led to dramatic reductions in most measures of EBC size at age (Heimbrand et al., 2024; Limburg & Casini, 2018) and condition (Casini et al., 2016; Limburg & Casini, 2019). Fishing largely ceased in 2019, but EBC sizes in the central Baltic Sea continue to shrink. Today, the median size of Atlantic Cod is <30 cm (International Council for the Exploration of the Seas, 2023) and the metrics of condition, hepatosomatic index, and size and age at first reproduction are at all-time lows (Eero et al., 2023).

In contrast, in a more northerly, lower salinity, well-oxygenated region of the Baltic Sea known as the Åland Sea there is a remarkably healthy population of EBC (Figure 2; online Supplementary Material Figure S1). This population is characterized by larger sizes, better condition, broader and older age distribution, and a greater growth rate than the EBC

Figure 2. Comparison of eastern Baltic cod (EBC) captured (A) in the Åland Sea versus (B) in the southern Baltic Sea, subdivision 25. The same person (Maddi Garate Olaizola) appears in both photos for scale. We aged the large cod as 13 years old; we did not age the small cod, but it is likely to be around 3 or 4 years old. Photo credits: Y. Heimbrand and O. Löfgren.

in the Baltic proper (Heimbrand et al., 2023). Despite these differences, there are few indications of genetic differentiation (S. Henriksson and C. André, University of Gothenburg, personal communication). Furthermore, whether the Åland Sea population is capable of reproducing in local waters is questioned; there, the salinity ranges from roughly 7 to 7.5 psu, and fertilization experiments that were conducted with individuals of this population found successful hatching at 10–11 psu (A. Nissling, Uppsala University [emeritus] and U. Bergström, Swedish University of Agricultural Sciences, personal communication). However, spawning in proximal waters to the south is a possibility.

In a recent study that focused on multiple stressors to EBC in the Baltic proper, we analyzed the chemistry of cod otoliths and monitored the trace element boron as a possible indicator of incipient ocean acidification in the Baltic (Limburg et al., 2023). Although dissolved boron in water correlates linearly with salinity (Kuliński et al., 2018), we found declining otolith boron (as B:Ca ratios as well as B concentrations) that correlated with concurrent declines in pH and dissolved oxygen and that negatively correlated with salinity and total alkalinity. The declines in B:Ca were found throughout the Baltic proper, even in the more saline portions. We included an out-group of healthy Icelandic cod in that study and concluded that otolith boron in cod correlates with otolith P:Ca, a metric of physiological status in healthy populations, but not in the EBC of that study.

It was therefore a surprise to us when we expanded our survey to include cod from the Åland Sea population from 2021. We found unexpectedly elevated concentrations of boron in otoliths from those individuals. These were 30- to >300-fold higher than in other EBC and 10- to 20-fold higher than in Icelandic cod otoliths. Here we describe our findings and place them into context with the rest of the Baltic cod. We also provide evidence that the elevated boron signal is of recent origin. We suggest that otolith B:Ca serves as a unique biomarker for this present-day population.

METHODS
Study site and sampling

One-hundred-thirty EBC that were collected from five International Council for the Exploration of the Sea (ICES) subdivisions (SD)[1] in the Baltic Sea were included in this study (Table 1). The cod were collected within the environmental monitoring program that is maintained by the Government of Åland, using gill nets in SD 29 (Åland Sea) and the Department of Aquatic Resources, Swedish University of Agricultural Sciences, using gill nets in SD 27, 28, and 29 (Åland Sea) and bottom trawls (Baltic International Trawl Survey SD 24, 25).

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[1]International Council for the Exploration of the Seas Subdivisions are fishery management areas.

Table 1. Locations (International Council for the Exploration of the SEA [ICES] SD = sampling subdivisions in the Baltic Sea), collection years, and number of analyzed cod. The collection years that are marked with an asterisk (*) were used in Limburg et al. (2023).

ICES SD	Collection years	Number of cod
24	2019*	5
25	1976	6
25	2019*	25
25	2020*	7
25	2021*	30
27	2019*	8
28	2020*	6
29	1948	7
29	2013	3
29	2021	33

Otolith chemistry analyses

The otoliths were cleaned, dried, and embedded in EpoFix epoxy. They were subsequently sectioned in the transverse plane with a diamond saw and polished to expose the core. Otolith boron and calcium (monitored on ^{11}B and ^{43}Ca, respectively) concentrations were quantified with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the State University of New York College of Environmental Science and Forestry's Analytical and Technical Services Division. A 193-nm Teledyne CETAC Analyte Excite Excimer Laser Ablation System was coupled to a Thermo iCAP TQ inductively coupled plasma mass spectrometer. Argon is used to create the plasma; helium is used as the carrier gas to increase signal intensity. The laser power was set to 20%, corresponding to 2.03 J/cm^2 fluence, shot at 10 Hz. Transects were made by running the laser with a spot size of 110 µm in diameter at a speed of 7 µm/s; the ablated material was transported with the helium gas into the argon plasma. Background counts of the elements were made by running the setup for 30 s prior to firing the laser.

The daily performance of the system was optimized with a NIST 612 certified glass standard. In each analysis session, we used at least one of three fairly well matrix-matched U.S. Geological Survey reference standards (MAPS-4, MAPS-5, and MACS-3) to calibrate and correct for instrument drift. The standards were ablated twice every 3–5 samples, depending on the otolith size. The limit of detection for ^{11}B was 0.26 mg/kg, and the analyses were above this limit in all otoliths. The otolith material was ablated along a line transect from the otolith core (birth) to the dorsal edge (death) to assess lifelong incorporation of boron (online Supplementary Material Figure S2). In some cases, the transects extended from the ventral side through the dorsal edge to check for symmetry. The results are expressed in ratio to calcium as B:Ca × 10^{-3} (mass basis).

The data were log transformed for a statistical pairwise comparison of group means and used to help visualize differences between the recent Åland otoliths and those from other groups. Entire transects were plotted as a function of distance from the otolith cores. We then extracted the inner core data (0–150 µm) to test for natal differences. Violin-and-box plots visualized the latter. To further explore differences in the core region, we used ANOVA followed by post

Table 2. Means and standard deviations of B:Ca for whole transects and core region representing birth and early larval stage (0–150 µm).

Group	Region	Means × 1,000	Standard deviation
Whole transects			
SD24_2019	SW Baltic	2.11×10^{-4}	9.25×10^{-5}
SD25_1976	S Baltic	1.28×10^{-3}	7.26×10^{-4}
SD25_2019-2021	S Baltic	1.26×10^{-3}	1.49×10^{-3}
SD27_2019	Central Baltic	1.13×10^{-4}	5.70×10^{-5}
SD28_2020	Central Baltic	1.75×10^{-4}	1.04×10^{-4}
SD29_1948	Åland Sea	4.18×10^{-4}	4.14×10^{-4}
SD29_2013	Åland Sea	8.01×10^{-4}	7.51×10^{-4}
SD29_2021	Åland Sea	3.93×10^{-2}	3.71×10^{-2}
Core region (0–150 µ)			
SD24_2019	SW Baltic	3.57×10^{-4}	1.16×10^{-4}
SD25_1976	S Baltic	1.64×10^{-3}	9.16×10^{-4}
SD25_2019-2021	S Baltic	2.02×10^{-3}	1.99×10^{-3}
SD27_2019	Central Baltic	1.44×10^{-4}	5.68×10^{-5}
SD28_2020	Central Baltic	1.68×10^{-4}	7.11×10^{-5}
SD29_1948	Åland Sea	8.08×10^{-4}	4.68×10^{-4}
SD29_2013	Åland Sea	1.07×10^{-3}	9.23×10^{-4}
SD29_2021	Åland Sea	5.23×10^{-2}	4.92×10^{-2}

hoc Tukey's HSD to tests for pairwise differences of otolith ln(B:Ca) among groups. The analyses were performed in R (R Core Team, 2023).

RESULTS

The mean B:Ca ratios of Åland Sea cod in 2021 were 0.0393 × 10^3 and were 31 to 348 times higher than those from the other ICES regions of the Baltic Sea (Tables 2 [see Whole transects] and 3 [see Between-group foldwise differences in lifelong mean B:Ca]). The levels of B:Ca in the Åland Sea otoliths that were collected in 1948 and 2013 averaged 94- and 49-fold lower, respectively, relative to those in the recent otolith collections in 2021 (Tables 2 [see Whole transects] and 3 [see Between-group foldwise differences in lifelong mean B:Ca]). Although the overall levels varied, the recent (2021) B:Ca ratios in Åland Sea cod otoliths were significantly higher than those in all the other areas and periods ($P < 0.05$; Table 2; Figure 3 [ln B:Ca for all groups in the same panel]; Figure S3 [ln B:Ca separated in panels per group]; Figure S4 [raw values of B:Ca separated in panels per group]).

Examining the inner 150 µm of the transects revealed that the cores, which form before hatching (Geffen, 1995), showed that the B:Ca ratios in the Åland Sea cod otoliths were also significantly elevated relative to those in other areas in the Baltic Sea as well as those from earlier years of collection in the same area (Figure 4). Qualitatively, the magnitudes of differences were similar to the overall trends. We note that 150 µm also incorporates a few days' growth, but we did not count the daily increments near the core. Nevertheless, this region represents birth and early larval growth.

We further investigated the pairwise differences of means in the core regions among the surveyed groups (Table 3). For the untransformed B:Ca ratios, only the recent Åland Sea (SD 29) otoliths differed from those of the other groups ($P < 0.05$;

Table 3. Between-group foldwise differences in lifelong mean otolith B:Ca, measured in line transects from the otolith core (birth) to the dorsal edge (death). Core region (0–150 μm). Tukey's HSD was used to indicate the significance of post hoc pairwise comparisons of means (i.e., Tukey–Kramer) test. The tests with $P < 0.05$ are marked in bold. Note that all the samples from subdivision (SD) 29 are from the Åland Sea.

| Group	SD24 (2019)	SD25 (1976)	SD25 (2019–2021)	SD27 (2019)	SD28 (2020)	SD29 (1948)	SD29 (2013)
Between-group foldwise differences in lifelong mean B:Ca							
SD24 (2019)							
SD25 (1976)	6.05						
SD25 (2019-21)	5.96	0.99					
SD27 (2019)	0.54	0.09	0.09				
SD28 (2020)	0.83	0.14	0.14	1.55			
SD29 (1948)	1.98	0.33	0.33	3.70	2.39		
SD29 (2013)	3.80	0.63	0.64	7.09	4.58	1.92	
SD29 (2021)	**186.42**	**30.79**	**31.25**	**347.66**	**224.85**	**94.03**	**49.06**
Between-group differences in mean core ln(B:Ca)							
SD24 (2019)							
SD25 (1976)	**1.33**						
SD25 (2019–21)	**1.14**	−0.18					
SD27 (2019)	−0.94	**−2.27**	**−2.08**				
SD28 (2020)	−0.81	**−2.13**	**−1.95**	0.13			
SD29 (1948)	0.70	−0.62	−0.44	**1.64**	**1.51**		
SD29 (2013)	0.79	−0.54	−0.35	**1.73**	**1.59**	0.08	
SD29 (2021)	**4.43**	**3.11**	**3.29**	**5.37**	**5.24**	**3.73**	**3.65**
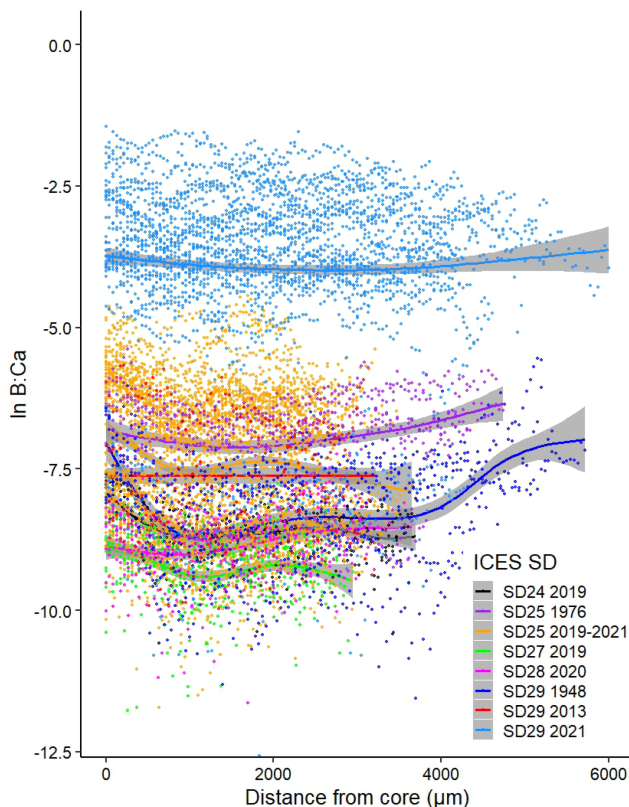
Figure 3. Natural-log-transformed otolith B:Ca measured in line transects from the otolith core (birth) to the dorsal edge (death) of EBC that were caught in International Council for the Exploration of the Sea (ICES) subdivision (SD) 24 ($N = 5$), SD 25 ($N = 62$), SD 27 ($N = 8$), SD 28 ($N = 6$), SD 29 1948 ($N = 7$), SD 29 2013 ($N = 3$), and SD 29 2021 ($N = 33$). Spline smoothing is done for each group.

Table 3 [Between-group foldwise differences in lifelong mean B:Ca]). More significant differences were apparent in the log-transformed data (Table 3 [Between-group differences in mean core ln(B:Ca)]). Those other differences notwithstanding, the recent Åland Sea (SD 29) group stands out on its own (Figure 4).

DISCUSSION

We found much higher levels of B:Ca in nearly all the transects of EBC that were captured in the Åland Sea in 2021. Three otoliths exhibited levels that were comparable to those in the samples that were collected in the Baltic proper (B:Ca $\approx 0.0005–0.0015 \times 10^{-3}$), but most were orders of magnitude higher (Figure 3; Figures S3 and S4), particularly in the core region (Figure 4; Figure S2). An early collection of cod from SD 25 in 1976 shows otolith B:Ca that is comparable to that in samples that were collected during 2019–2021 in the same area. Interestingly, the otoliths of seven cod that were collected in SD 29 in 1948 and another three that were collected in 2013 were lower in B:Ca, within the range of cod that were collected in SD 25. This suggests that the elevated boron source to the otoliths is a recent phenomenon.

The anomalously elevated levels of boron in recently caught Åland Sea cod are puzzling, as this region is low in salinity (at 100–300 m depth, mean salinity for the period 2000–2024 = 7.14 psu ± 0.38 [mean ± SD], range 6.37–8.75 psu; data retrieved from Baltic Nest; Wulff et al., 2013; Figure S1). In general, Baltic Sea boron concentrations are tightly, positively correlated with salinity, as elsewhere (Kuliński et al., 2018). Limburg et al. (2023) found that cod otolith B:Ca in the Baltic proper (central and southern parts) has declined since the late 1990s, but even the high levels before the 2000s rarely exceeded B:Ca ratios of 0.01×10^{-3}.
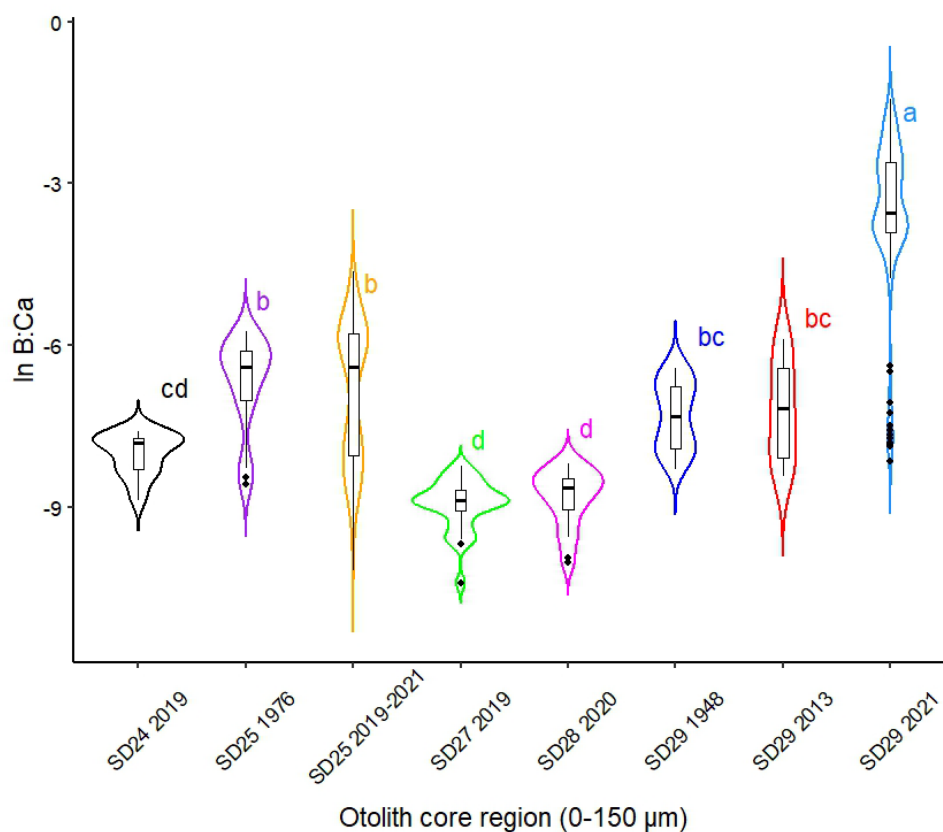
Figure 4. Violin-and-box plots with black dots corresponding to outliers of ln(B:Ca) in the otolith core region (0–150 μm) for different International Council for the Exploration of the Sea subdivisions (SD) in the Baltic Sea: SD 29_2021 is the Åland Sea for 2021. The letters indicate groups that were identified by Tukey HSD tests. The recent data for the Åland Sea differ from those for the other groups, including the older Åland Sea observations from 1948 and 2013.

As the locations wherein elevated B:Ca is found extend across the Åland Sea, an area of greater than 5,000 km², we hypothesize that there are one or more non-point sources of boron loading to this region and that these sources are recent. Furthermore, the low B:Ca ratios in Åland Sea cod that were collected in 1948 and in 2013 add further evidence of the recency (i.e., 2019 and onward) of elevated boron. The elevated boron's source is presently unknown, although riverine fluxes have increased globally due to anthropogenic activities (Park & Schlesinger, 2002). It is used in the paper industry as a whitener and as a fertilizer in some forests, including conifer forests in Scandinavia (Bhatt, 2021).

Another unknown is the route by which boron is taken up by cod and incorporated into the otolith. Whereas many elements are absorbed directly from the water via passage across the gills (Campana, 1999), trophic pathways are also possible, with absorption of elements from the gut (Hüssy et al., 2021). We note that *Saduria entomon*, a large, benthic isopod that is a favorite prey of Baltic cod, is present in the well-oxygenated Åland Sea and is often found in the stomachs of cod that are caught there. In contrast, *Saduria* is currently absent from large parts of the Baltic proper because of the hypoxia and anoxia that spreads across the seafloor (Lindmark et al., 2023). In fact, *Saduria* can be considered an indicator species for good oxygen status (Rousi et al., 2019). That significantly elevated B:Ca ratios occur in the Åland cod otolith cores suggests a spawning

population that is separate from the more southerly Baltic cod population. This presents another unknown, as fertilization experiments to date have not been successful at 7–8 psu, the salinity of the Åland Sea (Nissling and Bergström, personal communication). There is speculation that water of sufficient salinity (9–10 psu) may occasionally reach areas just south of the Åland Sea. Nevertheless, cod have been observed in the spawning stage in the Åland Sea as recently as June 2024 (Y.H., personal observation), and further investigation is desirable.

Future refinements in genetic markers may eventually show whether the Åland Sea cod represent a separate population. Regardless, the elevated otolith boron identifies a special group of cod that thrive in this low-salinity region, an example of the remarkable plasticity of this cosmopolitan species of the North Atlantic. Furthermore, we suggest that this group warrants a precautionary management approach to avoid the risk of losing it and its unique characteristics.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

DATA AVAILABILITY

Data are available upon request.

ETHICS STATEMENT

Ethical guidelines and legal requirements were followed, as we used no live fish in this specific study. The samples (otoliths) came from biological archives and were originally collected by other research projects from the 1940s to the 2020s during scientific research expeditions for fisheries management purposes. Since 2003, the number of fishes that were caught during fish surveys have been reported to the Swedish Board of Agriculture, but before that they were not regarded as experimental animals. Since 2012, the Swedish marine fish surveys have had permissions from regional ethical boards (permit numbers 255-2012, 126-2015, 5.8.18-06684/2020, 2021/92). Permit numbers from the Government of Åland were ÅLR 2021/1966, 5a § LL (2019:71) and LL (2015:49).

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CONFLICTS OF INTEREST

We have no conflict of interest to declare.

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