



Strontium isotope analysis in prehistoric cod otoliths by laser ablation multi-collector inductively coupled plasma mass spectrometry

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ABSTRACT

Exploitation of aquatic resources, especially fishing, was a fundamental part of human subsistence during the Late Mesolithic Ertebølle culture (5400–4000/3900 cal BC) in Southern Scandinavia. In this pilot study we examine three cod otoliths from two Late Mesolithic locations in eastern Denmark to see whether local environmental conditions are reflected in the strontium ratios of the fish, to source the fish to either the Atlantic or the Baltic Sea and finally, to explore how fishing was conducted in relation to the settlements. We used laser ablation multi-collector inductively coupled plasma mass spectrometry for sequential sampling of the otoliths for strontium isotope analysis. All three otoliths yielded ⁸⁷Sr/⁸⁶Sr values that fall within the range of Baltic Sea water, thus indicating that cod caught by Mesolithic fishers in the Danish straits belonged to the Baltic Sea stock. Our results suggest that cod were not caught in waters immediately adjacent to the archaeological sites but rather came from the Kattegat. We could not detect any substantial change in habitat between juvenile and mature stages of the fish's lives. Our study shows the potential of isotopic analysis to address issues regarding the individual ecological history of fish and human fishing strategies.

1. Introduction

Aquatic resources were a fundamental part of human subsistence for Late Mesolithic Ertebølle peoples of Southern Scandinavia (Fischer et al., 2007). Fishing, especially seems to have played a major role (e.g. Enghoff, 1994), but the precise nature of Ertebølle fishing remains unclear (Pickard and Bonsall, 2004). Determining where and when fish were caught can help to elucidate the nature of the fisheries (both the technology and the participants involved). Recent advances in biomolecular archaeology open new paths to explore the precise nature of prehistoric fishing.

Otoliths are paired calcified (CaCO₃) structures in the ear responsible for hearing and balance in teleost fish (Campana, 1999; Campana and Neilson, 1985) and are well preserved and commonly found in archaeological assemblages with good preservation conditions for skeletal material (Nicholson, 1996). They grow continuously throughout the life of a fish by deposition of metabolically inert incremental layers in which

a variety of trace elements are incorporated (Campana, 1999; Kalish, 1989). Thus, by microchemical analyses on these incremental layers, we can obtain information on the environment to which the fish was exposed in each growth stage (Campana, 1999) and convey a unique source of information on seasonal fishing activities (Hufthammer et al., 2010), historical reconstructions in fish growth patterns (Limburg et al., 2008; Ólafsdóttir et al., 2017), and individual life history (Walther and Limburg, 2012).

Analysis of strontium in fish otoliths has been proved to be a reliable method widely used to study migratory patterns in anadromous and catadromous fish, and describe migrations between habitats with different salinity (Engstedt et al., 2012; Zimmerman, 2005), hypoxia (Limburg et al., 2011, 2015; Limburg and Casini, 2018) and to reconstruct life history and migrations (Daverat et al., 2006; Walther and Limburg, 2012; Secor and Rooker, 2000). This is because the primary source of the Sr, strontium isotopes (⁸⁷Sr/⁸⁶Sr), and the Ca ions in fish otoliths is the ambient water (Bath et al., 2000; Webb et al., 2012; Farrel

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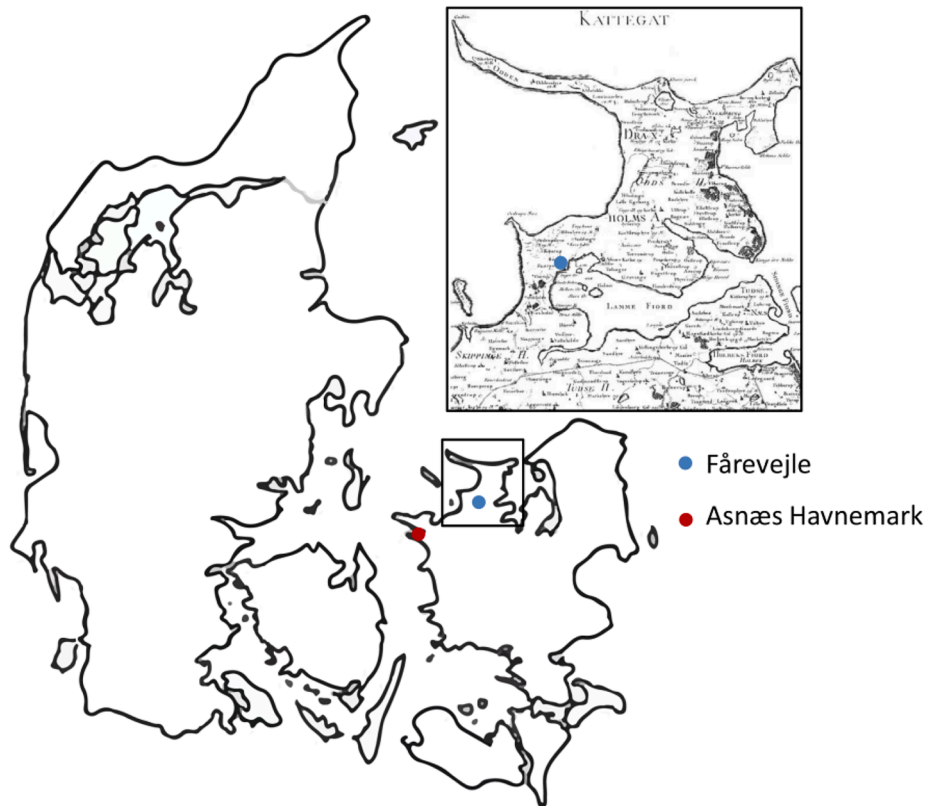


Fig. 1. Map showing the locations of the two sites with an inset detail rendering of the region by Tim Lykkegren, based on a map from 1773 showing the Lammefjord before it was drained. Source: Kongelige Videnskabernes Selskab.

and Campana, 1996), while the contribution of diet is estimated to be much less significant (Engstedt et al., 2012). Additionally, it has been established that the uptake of strontium in otoliths might vary depending on the salinity (Bath et al., 2000; Secor and Rooker, 2000; Diouf et al., 2006; Panfili et al., 2015; Engstedt et al., 2012) and temperature of the water (Limburg et al., 2011; Martin and Wuenschel, 2006).

Strontium concentrations are generally recognized as a proxy for water salinity (Ingram and Sloan, 1992; Andersson et al., 1992; Ning et al., 2017). Because salinity fluctuated in the Baltic Sea through time (Emeis et al., 2003), we expect strontium and carbon isotopes to have fluctuated as well and we assume that salinity fluctuations should be recorded in the otolith growth rings. The strontium isotopic composition of the water becomes higher with lower salinity in the Baltic Sea (Andersson et al., 1992) and therefore we expect to see a similar pattern in the otoliths.

In modern fish populations laser ablation multicollector -inductively coupled plasma-mass spectrometry analysis of strontium has been performed on otoliths to investigate provenance (Outridge et al., 2002; Brennan et al., 2015a; Kerr and Campana, 2014), natal habitats (Brennan et al., 2015b; Rohrla et al., 2014), stock discrimination (Heidemann et al., 2012) and migrations (Walther and Limburg, 2012). To our knowledge the method has not yet been applied to ancient otoliths.

Archaeological finds, site locations, isotopic dietary studies and other evidence demonstrate the importance of aquatic resources for Late Mesolithic Ertebølle peoples of Southern Scandinavia. While over 50

types of fish have been identified from at least 95 Ertebølle sites, just a handful of them seem to have played a major role in subsistence: gadids (especially cod, *Gadus morhua*), flatfish (e.g., flounder, *Platichthys flesus*), European eel (*Anguilla anguilla*), cyprinids and percids (e.g., perch, *Perca fluviatilis*) (Enghoff, 2011). There are regional differences in which fish were most important, as well as temporal variability, and the impact of taphonomy on the archaeological record cannot be ignored (Enghoff, 2011; Ritchie et al., 2021). A wide variety of fishing equipment including fishhooks, leisters, harpoons, netting technology, fish fences and traps as well as dugout canoes and paddles has been recovered (Andersen, 1995). Fishing during this period has been described as focused on the summer months, but data from otoliths has demonstrated that it occurred in other seasons as well (Enghoff, 1994; Ritchie et al., 2013b). Whether fishing was conducted primarily or exclusively in immediate proximity to sites or also featured expeditions further from shore is also debated (Pickard and Bonsall, 2004). Exploring the underlying environmental conditions for the fisheries is vital, but also complex, given the diversity of site settings as well as changes during the period. Briefly, the Danish waters during this period consist of mostly shallow nearshore areas with somewhat deeper waters farther from shore and a salinity gradient from least saline in the east, closer to the Baltic, becoming saltier to the west as the effects of the North Sea strengthen. Numerous fjords (some extant, others fossil, all different today from what they were during the Late Mesolithic period) were a focus of settlement and some inland waters were also exploited. During the Ertebølle period there were numerous transgressions which had

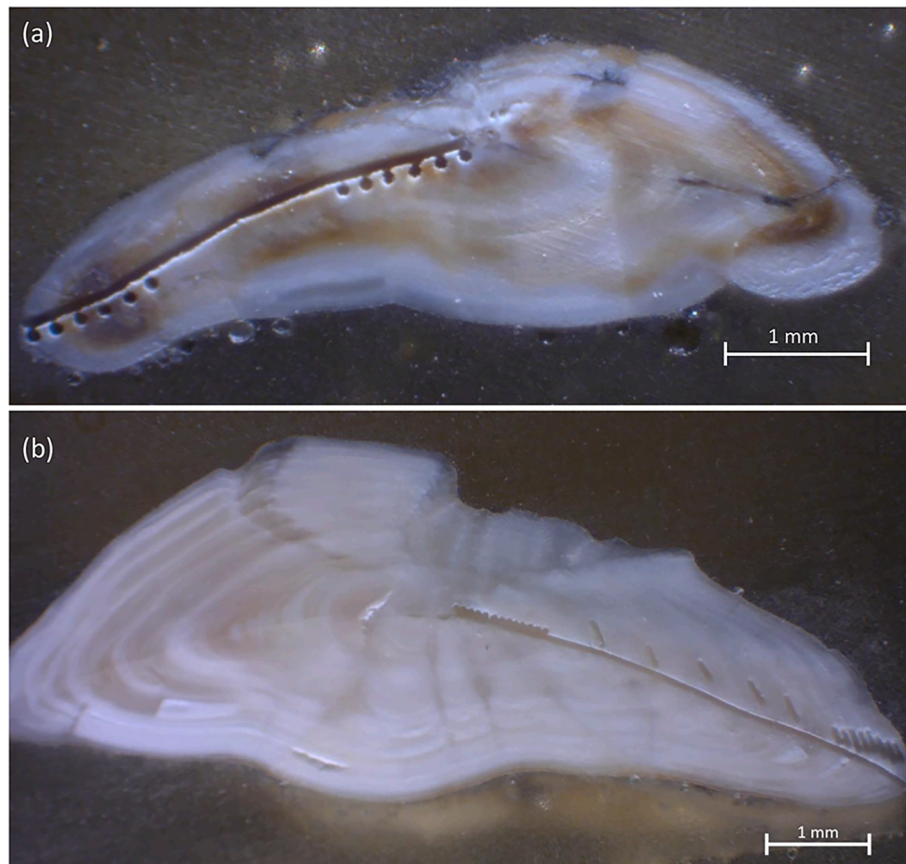


Fig. 2. Fig. 2a) Otolith 3 – Asnæs Havnemærk, b) Otolith 2 - Fårevejle 66 cm. Ablation transect spots and transect line after LA-ICPMS measurements along the growth axis.

significant impacts on the landscape as well as salinity in the adjacent waters (e.g., [Christensen, 1995](#)). Given the major role fishing played in Ertebølle economies, establishing the nature of Ertebølle fisheries can help to understand mobility strategies and other aspects of the lives of these Late Mesolithic people.

In this pilot study we examine three cod otoliths from two Late Mesolithic (Ertebølle, 5400–4000/3900 cal BC) locations in eastern Denmark. Modern algae are sampled for strontium isotopes for comparison, to examine the origin of the fish and to see whether local environmental conditions are reflected in the strontium ratios of the fish. Additionally, we try to source the fish to either the Atlantic or the Baltic Sea. Archaeologically, this information is of interest to address questions of where the Late Mesolithic fishing was conducted in relation to the settlements. Regarding their individual life history, we would like to know if the cod migrate between brackish and marine habitats in the time reflected in the formation of the otoliths and, more specifically, if it is possible to discriminate between spawning location (core of the otolith) and harvest location (edge of the otolith) as has been shown for modern cod based on the strontium concentration ([Heidemann et al., 2012](#)).

2. Material

The otoliths used in this study come from two sites in northwest Zealand, Denmark ([Fig. 1](#)). Asnæs Havnemærk is a coastal settlement not

far from the tip of the Asnæs peninsula, where the waters of Kalundborg Bay meet the Kattegat. Radiocarbon dating shows a period of occupation for the main cultural layer from 4330 to 4040 cal BC ([Price et al., 2018](#)). The faunal remains indicate that fishing was of prime importance, with cod being especially targeted ([Ritchie et al., 2013a](#)). The right sagittal otolith (Otolith 3), from a cod estimated at 49 cm total length based on the length of the otolith ([Härkönen, 1986](#)), was sampled for this project ([Fig. 2a](#)). A previous study of oxygen isotopes on the same otolith from this individual showed a season of catch in early summer ([Ritchie et al., 2013b](#)).

The second site sampled, Fårevejle, is a *køkkenmødding* (shell midden) that at the time of occupation lay on the shore of the now-drained Lammefjord, an arm of the Isefjord ([Fig. 1](#); [Fig. 2b](#)). While the site lay only c. 3 km from the Kattegat in a direct line, sea water would have had to travel a substantial distance to reach all the way back into this part of the fjord system, meaning that freshwater inputs from the surrounding watershed would have been significant in determining the fjord's characteristics, especially in some seasons. The site is a stratified *køkkenmødding* with deposits from both the Late Mesolithic and Early Neolithic, radiocarbon dated to c. 4400–3300 cal BC. The sagittal otoliths sampled for this project come from the Late Mesolithic layers of the midden. One right otolith (Otolith 1), from a cod estimated at 64 cm total length based on otolith length, and one right otolith (Otolith 2), from a cod estimated at 66 cm total length also based on otolith length ([Härkönen, 1986](#)), were sampled.

Table 1

Age estimation of the three sampled cod otoliths with respective matching of LA-ICPMS sampling spots/lines per year of growth.

Otolith	Site	Estimated length (TL)	Sampling spots/lines	Biological age
Otolith 1	Fårevejle	64 cm	1–2	year 1 core
			3–5	year 1
			6	year 2
			7–9	year 3
Otolith 2	Fårevejle	66 cm	10–12	year 4
			1–3	year 1 core
			4–13	year 1
			14–15	year 2
Otolith 3	Asnæs Havneemark	49 cm	16	year 3
			17	year 4
			18	year 5
			19–26	year 6
			1	year 1 core
			2–3	year 1
			4–6	year 2
			7–10	year 3
			11–12	year 4

For reference of the regional water $^{87}\text{Sr}/^{86}\text{Sr}$ values, nine algae samples of the kelp species *Saccharina latissima* were measured by Thermal Ionisation Mass Spectrometry at the Swedish Museum of Natural History. The algae samples were collected from the region of Skagerrak/Kattegat from nine locations along the Swedish west coast from the Norwegian border in the north, down to its distribution range in the south of Sweden (see Fig. A2). The samples were collected in 2018, to study the genetic population structure, connectivity and environmental drivers of local adaptation of this kelp species. Sampling occurred at different depths, 2, 15 and 17 m below sea level.

3. Methods

3.1. Sample preparation

For a previous study, the selected otoliths had been embedded in Epofix resin and sectioned using a Buehler low speed saw with a diamond blade to make a transverse cut across the otolith core. The sections were then polished until the growth increments were visible, sampling

areas were identified and then micromilled to remove material for mass spectrometry to produce data on oxygen isotope ratios (see Ritchie et al., 2013b for a complete description of the methodology of this earlier study). The remaining parts of the otoliths in the epoxy blocks were used for analysis in this project.

3.2. Biological age of cod based on otolith growth rings

In fish, ageing is usually determined by counting pairs of opaque and translucent growth rings in otoliths. A general pattern in otolith growth is the deposition of seasonally alternating opaque and translucent zones, where the translucent layers that are associated with slow growth are formed during the winter and where the opaque layer is associated with fast growth, high food intake and optimum temperature and is deposited during the summer (Campana, 2001). This is the general rule, however, recent studies on modern cod populations have shown that environmental impacts and changes in prey availability and temperature can result in opposite patterns (Fablet et al., 2011) or slightly different patterns with formation of opaque layers during late winter, spring and early summer and deposition of translucent layers in late summer, autumn and beginning of winter (Gjosæter and Danielssen, 2011). Further, spawning during summer might result in an additional zone formation in the summer (Hüsey et al., 2009). In general, somatic growth rates in modern cod is very complex and highly variable as it can be influenced by environmental changes such as temperature increases, hypoxia and decreased salinity (Smoliński et al., 2020; Hüsey et al., 2018) and also correlates with the amount of food consumed (Gjosæter and Danielssen, 2011; Irgens et al., 2020). Faster growth in earlier ages seems to be linked to earlier maturation (Hüsey et al., 2018). Recent studies have shown that elemental analysis on different annuli can be a reliable method of ageing (Heimbrand et al., 2020). However, in this study we consider an opaque-translucent pair to represent one year of growth without determining the season.

By counting the pairs of alternating opaque and translucent zones we can roughly estimate that otolith 1 comes from a fish that was approximately 4–4.5 years old (Table 1). Otolith 2, however, does not show distinct annuli, nevertheless we roughly estimate that the fish was 6–8 years old. Despite that the two fish from Fårevejle have approximately the same size (64 and 66 cm respectively), they seem to have different ages. One explanation could be that the 66 cm fish is female and has spawning annuli. An alternative explanation would be that the 64 cm fish is from the North Sea stock which grow considerably faster than the

Table 2

Sample ID, sampling location and depth of the algae (*Saccharina latissima*) samples. $^{87}\text{Sr}/^{86}\text{Sr}$ results. Normalized to the NBS 987 $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.710248. Aspholmen 1 and 2 are repeats. CIT#39 is “in house” sea water standard. Literature value for world average sea water normalized to NBS987 above gives $^{87}\text{Sr}/^{86}\text{Sr}$ 0.709171 (Mokadem et al., 2015).

Sample	Latitude	Longitude	Depth (m)	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$^{85}\text{Rb}/^{86}\text{Sr}$	C_{Sr} ppm	$^{87}\text{Sr}/^{86}\text{Sr}$ norm. *	Ext. prec. 2 σ
Slevik	59.1758	10.8139	2	7.5	−12.6	0.000001	414	0.709190	0.000013
Ursholmen	58.8345	10.9936	2	5.9	−13.9	0.000001	547	0.709179	0.000013
Hamburgö	58.5412	11.2420	2	5.8	−12.2	0.000012	583	0.709216	0.000013
Tuvesvik	58.2155	11.4114	2	7.3	−14.7	0.000001	590	0.709217	0.000013
Kovikshamn	57.8413	11.6798	2	2.9	−10.9	0.000001	851	0.709541	0.000013
Aspholmen 1	57.6626	11.8365	2	7.5	−15.3	0.000001	722	0.709277	0.000013
Aspholmen 2	57.6626	11.8365	2			0.000001	724	0.709263	0.000013
Sturöd	57.3938	11.909	2	3.8	−16.2	0.000001	759	0.709210	0.000013
Mölle	56.2644	12.4972	15	4.1	−26.5	0.000001	722	0.709211	0.000013
Ven	55.8851	12.6965	17	4.7	−21.1	0.000001	657	0.709207	0.000013
CIT#39 1						0.000001	7.77	0.709181	0.000013
CIT#39 2						0.000001	7.77	0.709170	0.000013

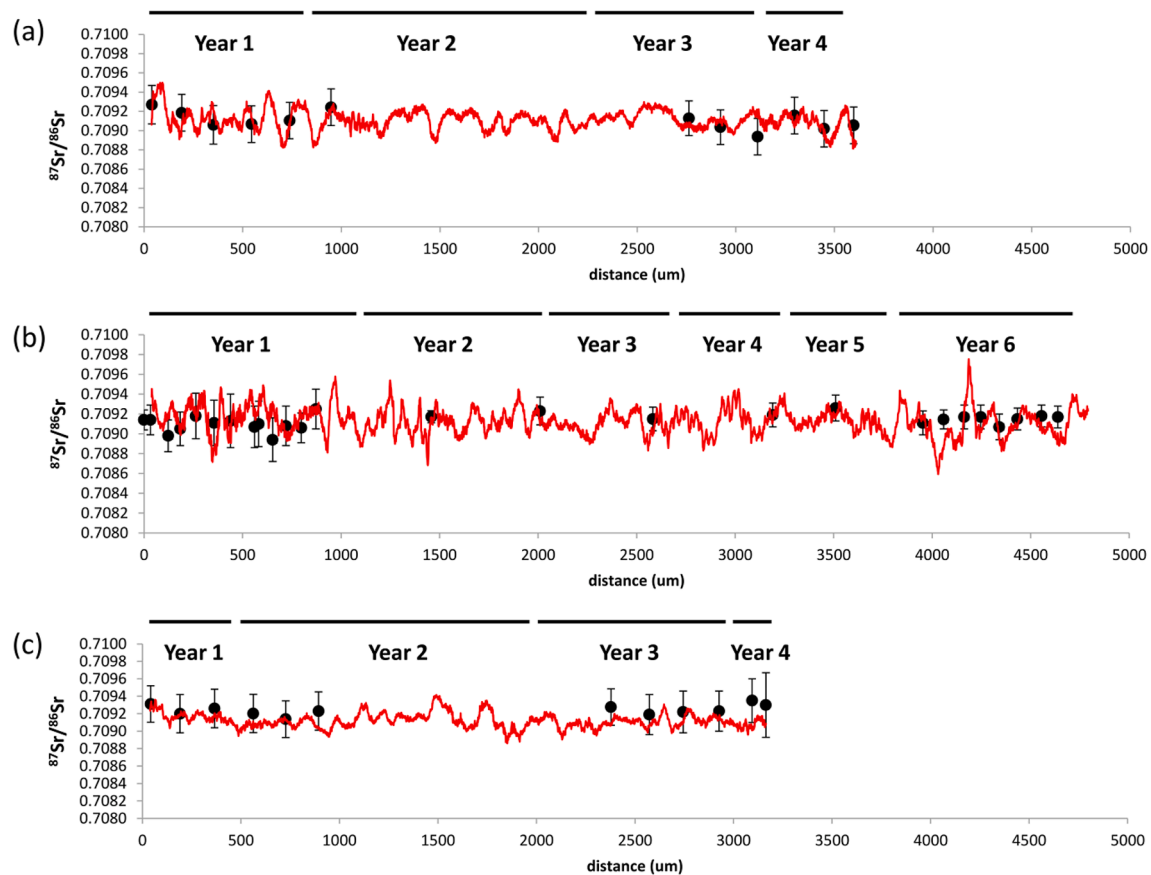


Fig. 3. (a) Otolith 1 Fårvejele; (b) Otolith 2 Fårvejele; (c) Otolith 3 Asnæs Havnemark. Black dots represent the $^{87}\text{Sr}/^{86}\text{Sr}$ values of the transect spots. The red line represents the moving average $^{87}\text{Sr}/^{86}\text{Sr}$ of the transect line sampling (a diagram with the individual measurements is found in Appendix A- Fig. A1). Biological age is indicated above each diagram. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Baltic stock (Daan, 1974; Gjøsæter and Danielssen, 2011, Table VIII; Froese and Pauly, 2020). These issues will be discussed later. Finally, otolith 3 displays a clear deposition of different annuli, indicating that the fish was approximately 3.5 years old.

3.3. Sequential sampling by laser ablation multi-collector inductively coupled plasma mass spectrometry

Strontium isotope ratios were measured on the otoliths at the Vegacenter facility at the Swedish Museum of Natural History (Stockholm, Sweden) using a NWR193 excimer laser ablation system (Electro Scientific Industries, Portland, OR, USA) coupled to a Nu Plasma II multi-collector ICP mass spectrometer (Nu Instruments Ltd, Wrexham, UK). For detailed description of the method and instrument operating conditions see Glykou et al., 2018 (Table S1). The otoliths were mounted in a sample cell and the surface was pre-ablated to remove potential surface contamination. All three otoliths have been sampled by applying two different procedures. A transect line 65 μm width (otolith 2) and 80 μm width (otoliths 1 and 3) was ablated along the growth axis of the otolith from the core to the edge. Parallel and close to the transect line we ablated spots or lines, using a 65 μm (otolith 2) and 80 μm (otoliths 1 and 3) spot or line size. The number of spots/lines varied between the otoliths, 12 spots were ablated on otoliths 1 and 3, and 26 spots/lines on otolith 2. Transect lines were chosen to sample the middle and outer

growth rings of otolith 2 in order to ensure that each sampling line corresponds to the natural growth curve of the ring.

Possible isobaric interferences and isotope fractionation were corrected as outlined in Glykou et al., 2018, Table 2. Two reference materials were measured alongside the samples to verify that all interferences were successfully removed. A primary standard, *Ecnomiosa gerda* that was measured 10 times during the session, was used for normalization to the value determined by Thermal ionization mass spectrometry (TIMS) (0.709168 ± 0.000004 ; Kiel et al., 2014). As a secondary standard a modern oyster shell from Western Australia was measured. The average of 9 measurements during the sampling session yielded 0.70918 ± 0.00013 which agrees well with the accepted value for today's Sr seawater composition (0.709171 ± 0.000004 Mokadem et al., 2015, normalised to a NBS987 value of 0.710248).

3.4. Thermal Ionisation mass spectrometry (TIMS)

The algae samples were analysed on a Thermo Scientific TRITON TIMS using a load of purified sample mixed with tantalum activator on a single rhenium filament. Two hundred 8 sec. integrations were recorded in multi-collector static mode, applying rotating gain compensation. Measured ^{87}Sr intensities were corrected for Rb interference using $^{87}\text{Rb}/^{85}\text{Rb} = 0.38600$ and ratios were reduced using the exponential fractionation law and $^{88}\text{Sr}/^{86}\text{Sr} = 8.375209$. The external precision for

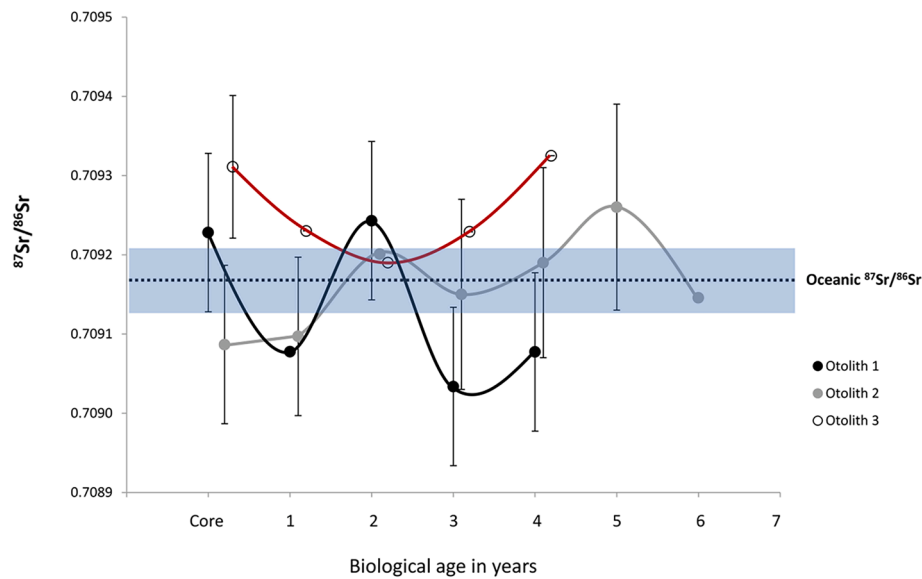


Fig. 4. Summarized $^{87}\text{Sr}/^{86}\text{Sr}$ values of the individual sampling spots after biological age (see Table 1). Error bars present the external precision 2SD (see Table A1). Blue box presents SD of oceanic $^{87}\text{Sr}/^{86}\text{Sr}$ 0.70917 ± 0.00004 (Fig. 5; Mokadem et al., 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$^{87}\text{Sr}/^{86}\text{Sr}$ as judged from running the NBS 987 standard was 18 ppm ($n = 12$). Accuracy correction of the results – normalization to NBS 987 = 0.710248 – was applied, while the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio for the NBS 987 standard during the course of the study was 0.710210 ± 13 ($n = 12$). The dried algae samples were weighed, an ^{84}Sr enriched spike added and then dissolved in 8 M nitric acid and hydrogen peroxide. The solution was dried and re-dissolved in 6 M HCl and purified using Eichrom Sr resin ion exchange (after Delmonte et al., 2008).

4. Results

Otolith 1, from an individual 4–5 years old, provided $^{87}\text{Sr}/^{86}\text{Sr}$ values from the spot analysis between ~ 0.7089 and ~ 0.7093 (see Table A1 for the single measurements, SE and uncertainty of measurement). The first two measurements of the innermost part of the core yielded the highest values, ~ 0.7093 and ~ 0.7092 respectively, corresponding to the time of an early larval stage. Three measurements

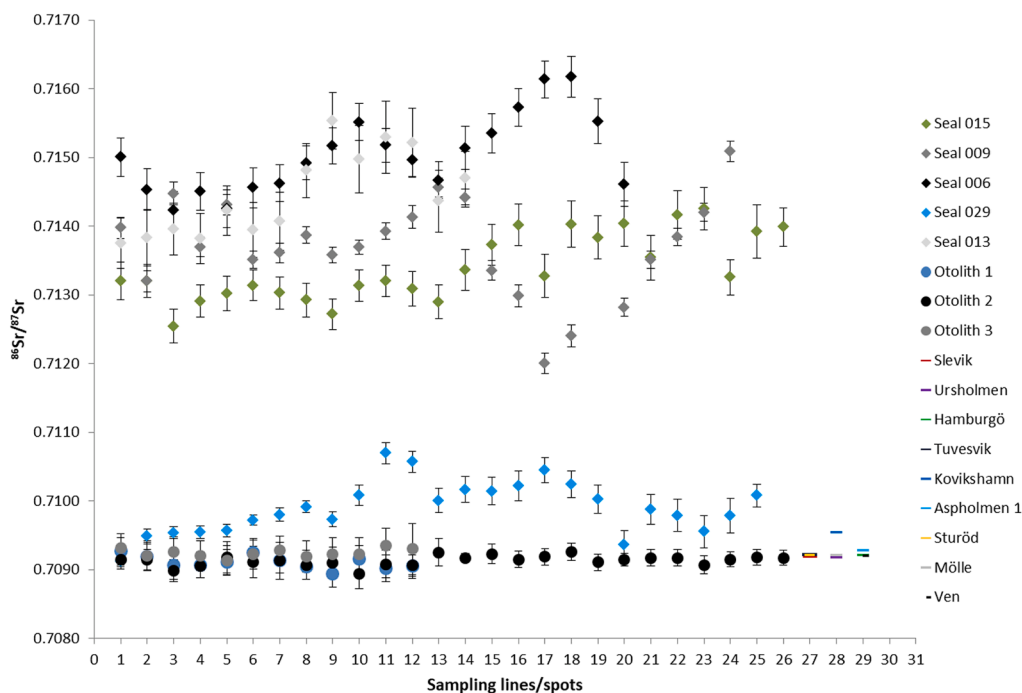


Fig. 5. Seal tooth enamel measurements of $^{87}\text{Sr}/^{86}\text{Sr}$ from the Baltic Sea (Glykou et al., 2018) and measurements of $^{87}\text{Sr}/^{86}\text{Sr}$ from cod otoliths and algae from this study. Error bars present the external precision 2SD - propagated uncertainty calculated by multiplying 2SE of unknowns with 2SD/2SE average of the rodent standard measurements (see Table A1). The x-axis represents the sampling spots from the core to the edge for the otoliths and from the tooth tip to the crown for the seals.

corresponding to the first year of life yielded slightly lower $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of ~ 0.7091 . The sixth measurement, that corresponds to the second year of life, yielded a slight increase of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of ~ 0.7092 . The three measurements (7–9), that correspond to the third year of life, show a continuous decrease from ~ 0.7091 to ~ 0.7089 . Finally, the fourth year of life is represented by three sampling spots yielding $^{87}\text{Sr}/^{86}\text{Sr}$ values from ~ 0.7092 to ~ 0.7091 . The $^{87}\text{Sr}/^{86}\text{Sr}$ values of the transect line and those of the single spot sampling are in good agreement (Fig. 3a). The obtained mean values are not statistically significantly different.

Otolith 2, from an individual approximately 6 years old, provided $^{87}\text{Sr}/^{86}\text{Sr}$ values from the spot analysis between ~ 0.7089 to ~ 0.7093 , thus the range is the same as in otolith 1 (Table A1). However, the formation of different annuli was very diffuse and therefore, roughly six growth rings could be recognized (Fig. 2b). The first three measurements closest to the core, corresponding to the time of an early larval stage, yielded $^{87}\text{Sr}/^{86}\text{Sr}$ values ~ 0.7091 . The same average in $^{87}\text{Sr}/^{86}\text{Sr}$ values was obtained from the first year of life, while the $^{87}\text{Sr}/^{86}\text{Sr}$ values increase during the second year (measurements 14–15), averaging ~ 0.7092 , and then slightly fluctuates during the third and fourth year. The highest $^{87}\text{Sr}/^{86}\text{Sr}$ values, ~ 0.7093 , for this otolith come from the measurement representing the fifth year of life. Finally, the $^{87}\text{Sr}/^{86}\text{Sr}$ values close to the edge of the otolith corresponding to the last year of life are slightly below the oceanic average of ~ 0.7092 . The $^{87}\text{Sr}/^{86}\text{Sr}$ values of the transect line and those of the single spot sampling are in good agreement (Fig. 3b). The obtained mean values are not statistically significantly different.

Otolith 3 from an individual of c. 3.5 years, yielded $^{87}\text{Sr}/^{86}\text{Sr}$ values fluctuating between ~ 0.7091 to ~ 0.7094 (Table A1). The first measurement on the innermost part of the core, corresponding to the time of an early larval stage, yielded the highest value at ~ 0.7093 . The following two measurements within the first year of life yielded a slight decrease reaching $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of ~ 0.7092 . The measurements which correspond to the second year of life yielded fluctuations between ~ 0.7091 and ~ 0.7093 . The two last measurements corresponding to the 4th year of life are slightly increased up to ~ 0.7093 . The $^{87}\text{Sr}/^{86}\text{Sr}$ values of the transect line and those of the single spot sampling are in good agreement (Fig. 3c; Fig. 2a). The obtained mean values are not statistically significantly different.

The algae (*Saccharina latissima*) yielded $^{87}\text{Sr}/^{86}\text{Sr}$ ratios ~ 0.7092 (from 0.70918 to 0.70927) with the exception of the sample from Kovikshamn which yielded 0.70954 and thus substantially deviates from the rest of the samples (Table 2). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between 0.70918 and 0.70927 correspond very well with previous measurements of sea water $^{87}\text{Sr}/^{86}\text{Sr}$ from the same region as reported by Andersson et al. (1992) ~ 0.7092 . The Kovikshamn sample yielded high $^{87}\text{Sr}/^{86}\text{Sr}$ values, most likely reflecting the low salinity water in the sampling area that is affected by the Göta älv River that discharges in the area (Figs. A2, A3). Despite the lower salinity of the surface waters at the region of the two southern sites, the strontium values seem not to be affected by the low salinity. This is most likely due to sampling at lower depths, as the algae are not present at the surface at these locations due to the low salinity. Therefore, the kelp strontium values probably reflect the higher salinity of deeper waters and not surface salinity.

5. Discussion

In the Baltic Sea, strontium ratios vary considerably as a consequence

of large freshwater influxes from rivers which drain basins with sediments of different geological origin (Löfvendahl et al., 1990). While $^{87}\text{Sr}/^{86}\text{Sr}$ increases with lower salinity, it reaches values of > 0.7095 in the Gulf of Bothnia (Andersson et al., 1992; Widerlund and Andersson, 2006, 2011). Close to the large rivers in the north the $^{87}\text{Sr}/^{86}\text{Sr}$ values are even higher than > 0.7095 as a result of riverine influx (Andersson et al., 1992). Most measurements in all three otoliths of our study have $^{87}\text{Sr}/^{86}\text{Sr}$ values that strongly deviate from the average oceanic $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70917 ± 0.000004 (Fig. 4; Mokadem et al., 2015) indicating that all three otoliths belonged to cod from the Baltic Sea stock. Thus, the assumed differences in biological age between the two cod otoliths with comparable size from Fårevæjle are more likely due to different sex of the cod than the cod originating from different stocks, as females grow faster and larger than males (Hüsey, 2011). A recent study on sequential analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ isotopes from teeth from prehistoric grey (*Halichoerus grypus*), ringed (*Pusa hispida*) and harp (*Pagophilus groenlandicus*) seals from the Baltic Sea yielded even higher $^{87}\text{Sr}/^{86}\text{Sr}$ values for the seals than for the cod of this study (Fig. 5). The seals were interpreted as being affected by strontium values commonly found in waters from the Baltic Sea proper and close to riverine discharge areas in southern Sweden and the central Baltic Sea (Glykou et al., 2018). Thus, the distinct strontium isotope ratios between the prehistoric seals and the prehistoric cod from this study most probably reflect distinct geographic distributions in the Baltic Sea and different water sources for strontium, as the cod most probably were hatched close to where they were caught in the Kattegat. Overlaps in some values are not surprising since the $^{87}\text{Sr}/^{86}\text{Sr}$ water values in the Kattegat region are very close to that of the oceanic water due to water exchange with the North Sea and the Atlantic Ocean, as most of the modern algae $^{87}\text{Sr}/^{86}\text{Sr}$ values show (Fig. 5, Fig. A3).

Cod is a marine species but tolerates brackish water and shows a high degree of adaptability to variable salinity (Kijewska et al., 2016; Tomkiewicz et al., 1998). While the Atlantic cod occupies oceanic water with a salinity of 35 psu, the western Baltic Sea cod lives in waters with a salinity of c. 15 psu (Petereit et al., 2014) and the eastern Baltic Sea cod sub-population occupies the inner/eastern Baltic Sea waters with a salinity down to 5–6 psu (Nissling et al., 1994). However, cod is a species that requires substantially higher salinity for successful reproduction than the average surface salinity of the Baltic Sea water (Westin and Nissling, 1991; Nissling and Westin, 1997). Surface water salinity in the Baltic Sea is low (3–8 psu) but increases with depth, reaching its highest levels below a permanent halocline (10–18 psu) (Nissling and Westin, 1997). Major cod aggregations are observed in an intermediate layer below the halocline and above the oxygen-depleted waters showing that high salinity and oxygen concentration are the main determinants for cod distributions in the Baltic Sea (Tomkiewicz et al., 1998; Voss et al., 2017). Therefore, today only the deeper parts of the southern Baltic are suitable for spawning and cod eggs are found where the salinity is between 17.5 and 21 psu (Petereit et al., 2014; Westernhagen et al., 1988). Main spawning grounds for the western Baltic stock are considered to be the deep, saline waters in the Arkona Basin, the northern Kiel Bight, Great Belt and southern Kattegat (Bleil and Oeberst, 2000; Hüsey, 2011; Petereit et al., 2014) with a spawning season from January to April (Bagge et al., 1994; Muus and Nielsen, 1999). Since the core regions of cod otoliths reflect the hydrographic conditions of their natal origin (Heidemann et al., 2012), the measurements close to the core are expected to represent their spawning/hatching locations. The core regions of the three otoliths yielded slightly different $^{87}\text{Sr}/^{86}\text{Sr}$ values, ~ 0.7091

Otolith 1, ~ 0.7092 Otolith 2 and ~ 0.7093 Otolith 3 (Fig. 4). Strontium can be used as a proxy for salinity and strontium isotope values in the Baltic Sea, as the $^{87}\text{Sr}/^{86}\text{Sr}$ values become depleted with depth as ambient salinity increases, for example reaching $^{87}\text{Sr}/^{86}\text{Sr} \sim 0.7092$ at a depth of > 150 m in the Baltic proper (Andersson et al., 1992). Thus, we would expect cod that spawn at depths with high salinity to carry the strontium isotopic signature of this depth. However, salinity in the Baltic Sea varies not only with depth but also with season depending on complex hydrographic conditions that to a large extent are determined by the seasonal and annual influx of Atlantic water, the distance from the Danish straits, the oxygen rates and seasonal riverine run-off. Besides the seasonal variations of salinity, after spawning in the western Baltic Sea cod eggs and early larvae drift and float northwards in the water column and can reach the Kattegat (Petereit et al., 2014). Such drifts are strongly impacted by seasonal winds and currents that determine their destination (Hüssy, 2011), meaning that strontium measurement in an otolith core could represent a bulk value from the natal area and other water strontium sources during drift. The differences in $^{87}\text{Sr}/^{86}\text{Sr}$ values in the three otoliths most likely reflect exposure to different salinity levels at an early larval stage and thus, are not conclusive of their natal area. We conclude that the fish either originated from different natal areas or, most likely, from the same natal area but from different chronological periods or cohorts with different strontium and/or salinity signatures.

After hatching, cod are advected to the nursery areas that are assumed to be inshore, where the juveniles can feed and grow, protected from predation (Borg et al., 1997; Fahay et al., 1999). The average values of otoliths 1 and 2 during the first year are very similar, slightly below ~ 0.7091 , while the transect lines show a larger variation with values fluctuating between ~ 0.7086 to 0.7095 (Figs. 3, 4) which fit very well to the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope values of Danish surface waters at the region of the Lammefjord that range between 0.7079 and 0.7128 , as part of the strontium derives from pre-Quaternary carbonaceous sediments with low strontium ratios (Frei and Frei, 2011). Thus, these values imply that the cod were foraging in the part of the Lammefjord close to the areas where they were found in the archaeological record.

Interestingly, all three cod otoliths display $^{87}\text{Sr}/^{86}\text{Sr}$ values close to ~ 0.7092 during the second year. Because cod in Danish waters become sexually mature at 2–3 years (Muus and Nielsen, 1999), we interpret this value as the possible spawning time. According to that, spawning could have taken place in the deep waters of the western Baltic Sea, where saline waters that enter the Baltic through the Danish straits have similar values (Andersson et al., 1992). Limburg et al. (2011) found that Sr/Ca ratios in cod otoliths from different time periods from the Neolithic up to modern times increase during the second and third year of life and then decrease again. The authors infer that the increase indicates exposure to colder and saltier water i.e. that cod moves to deeper and saltier water in the Baltic Sea (Limburg et al., 2011, p. E172). This find fits very well to our interpretation, that the $^{87}\text{Sr}/^{86}\text{Sr}$ values close to ~ 0.7092 during the second year reflect the first spawning time which for cod occur in high salinity below the halocline. It is intriguing, however, that this pattern is not repeated in the next years, as we would expect if Mesolithic cod spawned annually like modern cod do. However, assessing biological age by visual inspection of growth rings is problematic and so in the future it would be good to assess strontium and oxygen isotope values together. Concluding, either prehistoric cod had different spawning patterns, or the annual hydrographic conditions in the Baltic Sea varied substantially with different salinity and thus different strontium ratios.

Regarding individual life histories, and specifically the question if cod changed habitat during the course of their lives, none of the three

otoliths yielded any significant differences in the values between the core and edge, indicating that spawning and harvesting areas did not differ substantially in $^{87}\text{Sr}/^{86}\text{Sr}$. Usually, mature cod undertake migrations to deeper and colder waters. If these cod had followed this pattern, we would have expected to see a significant change in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, because strontium is a proxy for salinity and temperature in the Baltic (Limburg et al., 2011). Our results do not confirm a substantial change of habitat between juvenile and mature cod. Similar observations have been previously made for Baltic cod showing that they do not always follow this pattern of changing habitat at maturity, but some individuals can spend later years in lower salinity environments (Limburg et al., 2011). Of course, one can ask if it would be likely to get substantial differences in the $^{87}\text{Sr}/^{86}\text{Sr}$ values for cod as those observed for anadromous species, where freshwater and marine strontium sources can clearly be discriminated in a seasonal pattern (Kennedy et al., 2002). Cod, however, can occupy habitats with no significant differences in salinity throughout the year and may change habitat when it matures. Our results indicate that the three specimens examined in this study did not change habitat over the course of their life, but rather they were moving in waters with similar $^{87}\text{Sr}/^{86}\text{Sr}$ values.

Surprisingly, the two otoliths from the site Fårevejle, that at the time of occupation was situated on the shore of the now-drained Lammefjord (Fig. 1), did not yield average $^{87}\text{Sr}/^{86}\text{Sr}$ values that would correspond to the less saline water of this region during the last year of life. Otolith 1 yielded $^{87}\text{Sr}/^{86}\text{Sr}$ values between ~ 0.7092 to ~ 0.7091 and otolith 2 yielded values slightly below the oceanic average of ~ 0.7092 from the last year of life that are close to the oceanic average and the water values of Kattegat-Skagerrak (Fig. 4; see also map in Glykou et al., 2018). This implies that the fish might not have been caught in close proximity to the site (in brackish fjord waters) but further north, in open water. This is in contrast to otolith 3 from Asnæs Havneemark, that belonged to a fish that spent time closer to the shore areas as it yielded $^{87}\text{Sr}/^{86}\text{Sr}$ values slightly above 0.7093 from the last year of life and so it fits to the $^{87}\text{Sr}/^{86}\text{Sr}$ water values of the Danish straits (Frei and Frei, 2011). This could indicate that we are dealing with at least two distinct fishing strategies between the inhabitants of the two sites.

6. Conclusions

This pilot study shows that cod caught by Mesolithic fishers in the Danish straits belonged to the Baltic Sea. At least in the case of Fårevejle, located on the Lammefjord, our results suggest that cod were not caught in waters immediately adjacent to the site but rather came from the Kattegat. Our results do not indicate any substantial change in habitat between juvenile and mature stages of the fish lives, but this needs to be verified through sampling more otoliths. Further analysis is needed to be done by correlating strontium isotope ratios with Sr/Ca ratios because Sr/Ca ratios vary as a function both of salinity and temperature (Limburg et al., 2011) as well as with oxygen isotopes.

CRediT authorship contribution statement

Aikaterini Glykou: Conceptualization, Validation, Formal analysis, Investigation, Writing - original draft, Funding acquisition. **Kenneth Ritchie:** Conceptualization, Resources, Writing - review & editing. **Matthew S. Hargrave:** Resources, Writing - review & editing. **Wouter Visch:** Resources, Writing - review & editing. **Kerstin Lidén:** Conceptualization, Supervision, Writing - review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Figures

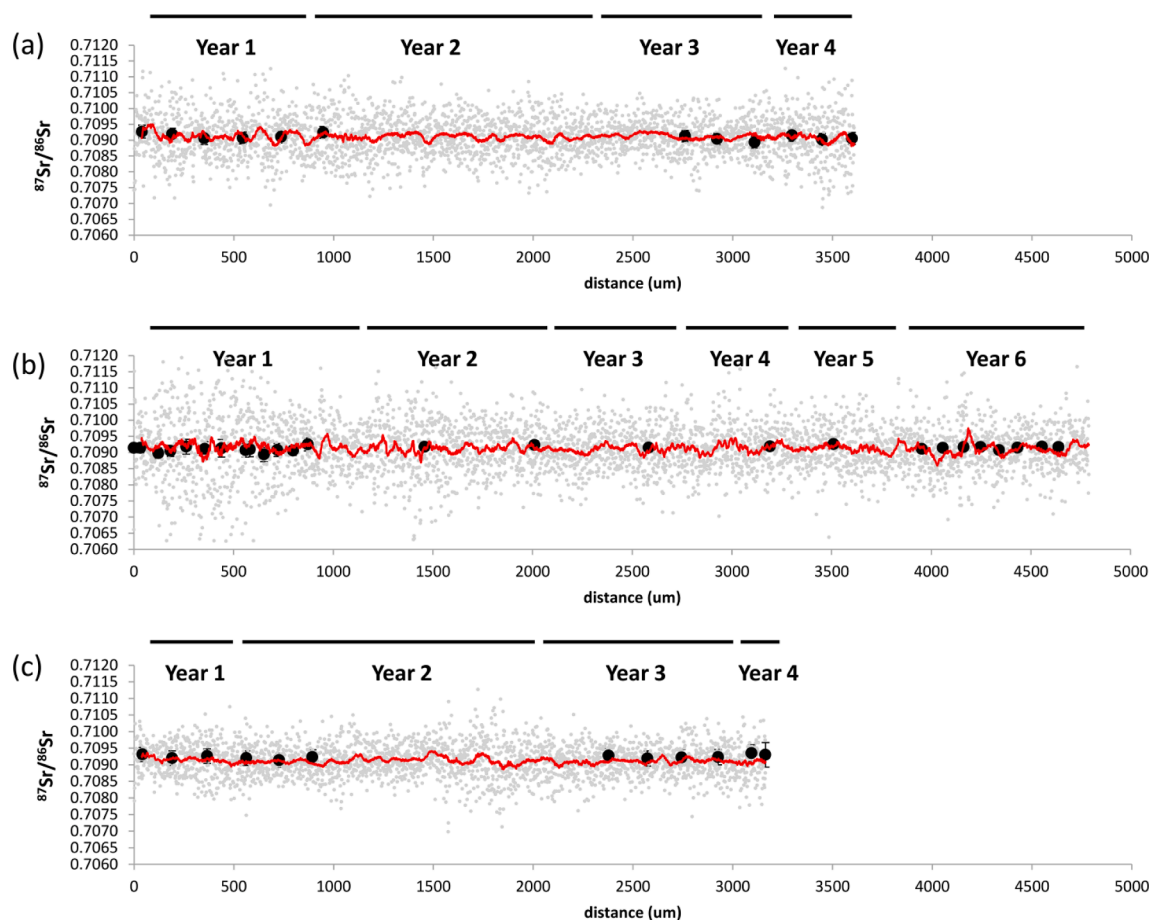


Fig. A1. (a) Otolith 1 Fårevejle; (b) Otolith 2 Fårevejle; (c) Otolith 3 Asnæs Havnemark. Black dots represent the $^{87}\text{Sr}/^{86}\text{Sr}$ values of the transect spots. The red line represents the moving average $^{87}\text{Sr}/^{86}\text{Sr}$ of the transect line sampling. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

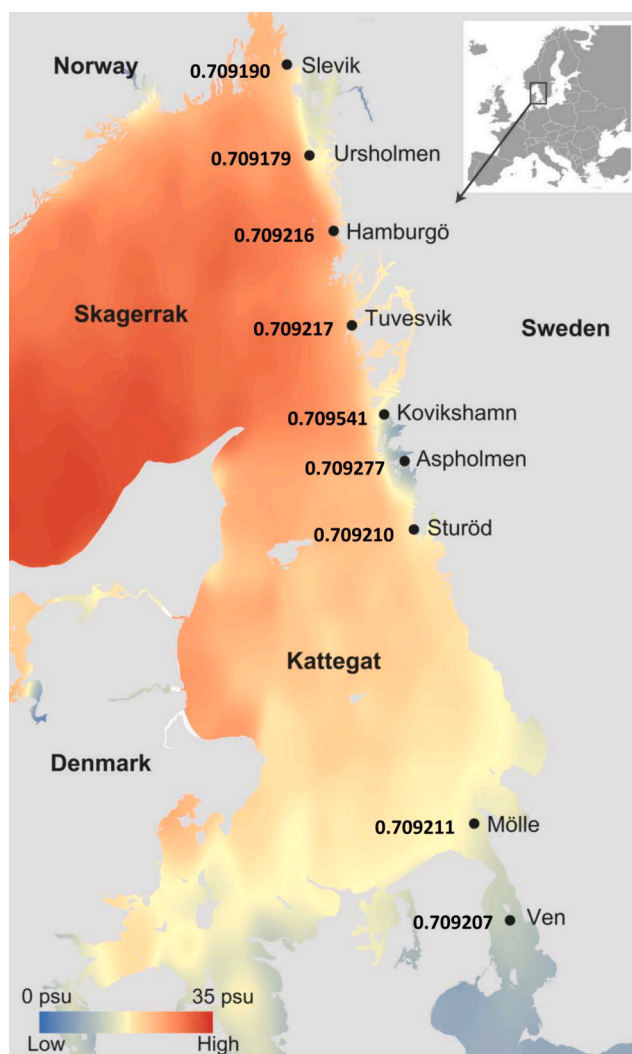


Fig. A2. Map of sampling sites for *Saccharina latissima* in the Skagerrak-Kattegat region of the North Sea. The background heat map shows diffusion interpolation of minimum salinity values from the ICES data-base (1980–2018). The background heat map colour is surface water and therefore not representative for the two southern sites that were sampled at lower depths, as kelp is not present at the surface on these locations due to the low salinity. The numbers represent the $^{87}\text{Sr}/^{86}\text{Sr}$ results of the algae of each site (more information in Table 2). Map: Per Bergström, University of Gothenburg.

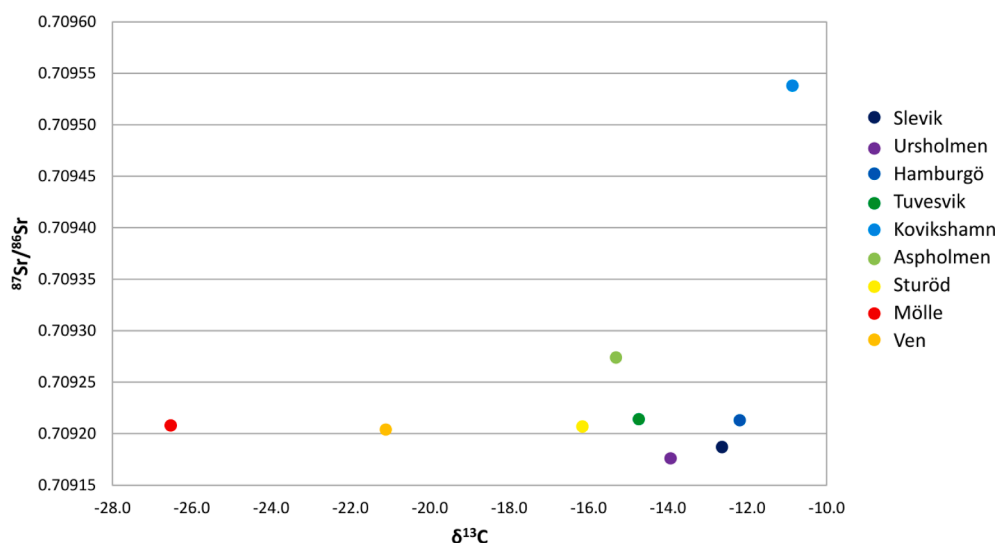


Fig. A3. Graph representing the $^{87}\text{Sr}/^{86}\text{Sr}$ vs. $\delta^{13}\text{C}$ values for each site the *Saccharina latissima* was sampled in the Skagerrak-Kattegat region of the North Sea.

Table

Table A1

All $^{87}\text{Sr}/^{86}\text{Sr}$ measurements for each sample. *propagated uncertainty calculated by multiplying 2SE of unknowns with $2\text{SD}/2\text{SE}_{\text{average}}$ of the rodent standard measurements.

Sample	Biological age	line number	$^{87}\text{Sr}/^{86}\text{Sr}$	2SE	Prop.2SE	total Sr (V)	$^{84}\text{Sr}/^{86}\text{Sr}$
Otolith 1	year 1 core	1	0.70927	0.00011	0.0000070	10.96	
	year 1 core	2	0.70919	0.00009	0.0000053	11.51	
	year 1	3	0.70906	0.00010	0.0000044	12.55	
	year 1	4	0.70907	0.00010	0.0000044	12.95	
	year 1	5	0.70911	0.00009	0.0000041	13.93	
	year 2	6	0.70924	0.00010	0.0000046	11.76	
	year 3	7	0.70913	0.00008	0.0000047	10.47	
	year 3	8	0.70904	0.00007	0.0000051	12.01	
	year 3	9	0.70894	0.00009	0.0000048	13.66	
	year 4	10	0.70916	0.00010	0.0000044	10.11	
	year 4	11	0.70902	0.00010	0.0000055	9.19	
	year 4	12	0.70906	0.00010	0.0000046	10.72	
mean							0.05646
Otolith 2	year 1 core	1	0.70914	0.00010	0.000012	4.47	
	year 1 core	2	0.70914	0.00015	0.000012	4.49	
	year 1 core	3	0.70898	0.00016	0.000015	3.97	
	year 1	4	0.70905	0.00017	0.000017	4.02	
	year 1	5	0.70918	0.00023	0.000015	3.68	
	year 1	6	0.70911	0.00023	0.000016	3.83	
	year 1	7	0.70913	0.00027	0.000017	4.05	
	year 1	8	0.70907	0.00021	0.000017	4.58	
	year 1	9	0.70910	0.00023	0.000013	4.81	
	year 1	10	0.70894	0.00022	0.000017	4.39	
	year 1	11	0.70908	0.00020	0.000010	5.90	
	year 1	12	0.70906	0.00015	0.000011	6.62	
	year 1	13	0.70925	0.00020	0.000011	6.28	
	year 2	14	0.70917	0.00006	0.000004	9.09	
	year 2	15	0.70923	0.00014	0.000008	5.25	
	year 3	16	0.70915	0.00012	0.000005	8.75	
	year 4	17	0.70919	0.00012	0.000007	6.35	
	year 5	18	0.70926	0.00013	0.000007	6.53	
	year 6	19	0.70911	0.00012	0.000008	6.80	
	year 6	20	0.70915	0.00010	0.000005	11.40	
	year 6	21	0.70917	0.00012	0.000005	8.91	
	year 6	22	0.70917	0.00012	0.000006	8.31	
	year 6	23	0.70907	0.00013	0.000005	9.98	
	year 6	24	0.70915	0.00011	0.000004	10.82	
	year 6	25	0.70918	0.00011	0.000005	10.38	
	year 6	26	0.70917	0.00011	0.000005	10.27	
mean							0.05643
Otolith 3	year 1 core	1	0.70931	0.00009	0.0000079	9.75	
	year 1	2	0.70920	0.00011	0.0000061	10.13	
	year 1	3	0.70926	0.00011	0.0000050	12.32	
	year 2	4	0.70920	0.00010	0.0000044	14.45	
	year 2	5	0.70914	0.00008	0.0000040	16.05	
	year 2	6	0.70923	0.00011	0.0000042	15.04	
	year 3	7	0.70928	0.00009	0.0000113	7.30	
	year 3	8	0.70919	0.00013	0.0000103	7.55	
	year 3	9	0.70922	0.00015	0.0000101	9.74	
	year 3	10	0.70923	0.00013	0.0000073	11.41	
	year 4	11	0.70935	0.00016	0.0000155	13.70	
	year 4	12	0.70930	0.00032	0.00017	14.85	
mean							0.05648

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