

# Oxygen Isotope Ratios in Cod Otoliths Used to Reveal Seasonality of Fishing at Late Mesolithic Sites in Denmark

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**ABSTRACT:** Estimation of fish season of capture is fundamental to the study of mobility and resource exploitation patterns of ancient populations that relied heavily on piscine resources. In this study, we examined the contribution of a new isotopic method to further our ability to reconstruct the seasonality of ancient fisheries. Seven cod (*Gadus morhua*) sagittal otoliths were selected as a sample from two Late Mesolithic (Ertebølle) sites in Denmark (Asnæs Havnemark and Fårevejle) to examine cyclical patterns in relative water temperatures estimated by the ratio of oxygen stable isotopes. Our study demonstrated that isotopic analysis of sagittal otoliths has great potential for revealing these patterns and showing when fish were caught. Results indicated that fishing activity occurred during more periods of the year than had been previously estimated from the presence of migratory fishes in the assemblages. In all, our study suggests that fishing played a larger role in the annual subsistence cycle of Ertebølle groups than had been previously acknowledged.

**KEYWORDS:** COD, DENMARK, ERTEBØLLE, FISHING, OTOLITHS, OXYGEN ISOTOPES, SEASONALITY

**RESUMEN:** La estimación de la estación de captura es clave en el estudio de los patrones de movilidad y explotación de recursos de las poblaciones pretéritas que dependían de recursos piscícolas. En este estudio examinamos la aportación de un nuevo método isotópico para incrementar nuestra capacidad de inferencia de la estacionalidad en las antiguas pesquerías. Siete sagitas de bacalao (*Gadus morhua*) fueron seleccionados en dos yacimientos del mesolítico tardío (cultura Ertebølle) en Dinamarca (Asnæs Havnemark y Fårevejle) con el fin de examinar patrones cíclicos de la temperatura del agua estimados a través de la relación de los isótopos estables de oxígeno. Nuestro estudio demuestra que los análisis isotópicos de las sagitas poseen un alto potencial para evidenciar estos patrones y mostrar cuándo fueron capturados los peces. Los resultados indican que la actividad pesquera se produjo durante más periodos del año de los que habían sido previamente postulados a partir de la presencia de peces migradores en las muestras. En conjunto, nuestro estudio apunta a que la pesca desempeñó un papel más importante en el ciclo anual de subsistencia de los grupos Ertebølle de lo que ha sido hasta el momento postulado.

**PALABRAS CLAVE:** BACALAO, DINAMARCA, ERTEBØLLE, PESCA, OTOLITOS, ISÓTOPOS DE OXÍGENO, ESTACIONALIDAD

## INTRODUCTION

The Late Mesolithic Ertebølle period (ca. 5400-4000 B.C.) in Denmark is well-known for its many coastal sites, including *køkkenmøddinger* (kitchen middens), and for a long history of multi-disciplinary archaeological excavations. The importance of marine-focused activities for Ertebølle fisher-hunter-gatherer economies has been noted since the earliest scientific investigations in the 19<sup>th</sup> century started recovering what is now a remarkable archaeological dataset (e.g., Madsen *et al.*, 1900; Andersen, 2008). This includes substantial quantities of shellfish, fish bones, and evidence for fishing technologies and watercraft documented from many sites (Christensen, 1990; Enghoff, 1994; Andersen, 1995; Pedersen, 1995; Ritchie, 2010). Recently, the dietary role of marine resources in the Ertebølle period has been confirmed from isotope analyses of human and dog bones (Tauber, 1981; Richards *et al.*, 2003; Fischer, 2007). Few inland sites with preserved organic remains suitable for examination of subsistence patterns have been excavated, but even here marine resources are sometimes evident (Enghoff, 1998). Despite the impressive record of hundreds of excavated archaeological sites, questions concerning mobility and subsistence strategies during the Ertebølle period remain. Seasonality information is critical for addressing both of these questions. In order to discuss whether Ertebølle groups were relatively more mobile or sedentary, it is essential to determine during which parts of the year sites were occupied. A major impediment to resolving this question stems from the methods used for the reconstruction of seasonality of faunal exploitation. Researchers have reconstructed seasonal rounds from various finds including shellfish growth rings, mammal tooth eruption and wear, epiphyseal fusion, and inferred timing of capture based on when animals were in their prime (e.g., fur-bearing species in the fall and winter) (Rowley-Conwy, 1993; Milner, 2002; Carter, 2009; Enghoff, 2011). Reconstruction of seasonality of fishing has been largely constrained to interpretations based on fish migratory behavior. For example, garfish (*Belone belone*) and mackerel (*Scomber scombrus*) today occur in Danish waters only during the warmer months of the year (Muus & Dahlstrøm, 1964). Assuming that this pattern also existed during the Atlantic period, the presence of these two fishes in Ertebølle assemblages has been used as an indicator of fishing during the late

spring or summer (Enghoff, 1994, 2011). The main weakness of this method for determining the seasonality of fishing activity is that both of these species occur in fairly limited numbers in most assemblages. While these species do point to fishing during the summer, it is not clear whether other kinds of species represented among the fish remains were also caught at that time. Since many site assemblages are dominated by fish of the cod family (Gadidae) (Ritchie, 2010; Enghoff, 2011) that, according to historical records, were mainly fished in the cooler months of the year (Drechsel, 1890), their presence raises a question regarding their season of capture. Therefore, analysis of the gadid remains may shed new light on the seasonal rounds and marine exploitation patterns of the Ertebølle period.

### *Otoliths, oxygen isotopes and seasonality*

The value of fish otoliths as paleoenvironmental and seasonal markers has been widely recognized and used in biological and archaeological studies (e.g., Van Neer *et al.*, 2002; Campana, 2005). Enghoff (1994) visually inspected the annual ring growth in gadid (and some pleuronectid) sagittal otoliths to discern seasonal exploitation. Although the patterns observed supported an emphasis on summer fishing, all other seasons of the year were also represented by these analyses (Enghoff, 1994). Recently, the reliability of visual inspection techniques for determining seasonality from otoliths has been questioned (Van Neer *et al.*, 2004). Because of this, a new method of isotopic analysis of samples milled from sagittal otoliths has been developed. The innovative aspect of this method is that it avoids the subjectivity and uncertainty associated with visual inspection methods, because it measures isotopes from multiple samples along a transect of an otolith (e.g., Ivany *et al.*, 2000; Weidman & Millner, 2000; Dufour *et al.*, 2005; Hufthammer *et al.*, 2010). This method will increase our knowledge of fish life histories, especially in determining the season(s) in which fish were caught.

## MATERIALS

This study is based on seven cod (*Gadus morhua*) sagittal otoliths recovered from two sites

in Denmark, Asnæs Havnemark and Fårevejle, both located on the island of Zealand (see Figure 1 and Table 1). Although both sites were repeatedly occupied, all seven of the otoliths used in this project are dated to the Late Mesolithic Ertebølle period based on contextually associated material (see below). The sizes of the fish were reconstructed from a linear regression formula using the length of the otolith to determine the length of the fish (Härkönen, 1986).



FIGURE 1

Map of Denmark with the two archaeological sites used in this study.

#### *The site of Asnæs Havnemark*

The site was identified by an avocational archaeologist who discovered cultural materials eroding out onto the beach. It was excavated during the summer of 2007 under the direction of T. Douglas Price in order to recover samples from the site before it was completely destroyed. Six excavators working for five weeks opened up a series of test pits and dug three trenches. Excavation of the trenches was carried out using shovels and trowels, with the matrix being water-screened in the field through 4 mm mesh-size sieves. Large quantities of flint tools and debitage, Ertebølle and Funnel Beaker (TRB—the first farming culture in Denmark) pottery as well as faunal remains were recovered. Among the faunal remains, fish were especially abundant. Although the squares were excavated according to natural layers, radiocarbon dates indicate that the materials dated to a relatively short (approximately 300 year) time span at the end of the Ertebølle and beginning of the TRB periods (T. Douglas Price, personal communication, March 2008).

In addition to the 4 mm mesh-size wet sieving, experience from previous excavations had suggested the need for samples that incorporated a smaller screen size to test the effects of differential recovery. To this end, bulk samples of mainly 2 l were taken from several of the proveniences and washed through nested geologic sieves of 8, 4, 2, and 1 mm sizes. A total of 47,760 specimens were identified from the three trenches at Asnæs Havnemark, representing 17 fish families. In all, 898

Site	Otolith length	Fish length	Seasonality
Asnæs Havnemark	11.5 mm	35 cm	summer
Asnæs Havnemark	14.2 mm	48 cm	winter/spring
Asnæs Havnemark	14.4 mm	49 cm	spring/summer
Asnæs Havnemark	14.4 mm	49 cm	spring?
Fårevejle	16.8 mm	61 cm	?
Fårevejle	17.4 mm	64 cm	winter/spring
Fårevejle	17.8 mm	66 cm	winter/spring?

TABLE 1

List of the seven cod otoliths used in the study, with archaeological provenience, otolith length (mm), estimated fish length (TL) (based on regression formula in Härkönen 1986), and estimated season of capture.

otoliths were recovered and were identified as *G. morhua* (675), *Merlangius merlangus* (46), *Pollachius* sp. (9), *Melanogrammus aeglefinus* (4), and unspecified gadid (164). Four *G. morhua* sagittal otoliths were selected for isotopic seasonality analysis, two from the «culture» layer (estimated fish length of 48 and 49 cm) and two from the «shell» layer (estimated fish length of 35 and 49 cm).

#### *The kitchen midden at Fårevejle*

This site was first excavated by the Second Kitchen Committee in 1896 to 1897 (Madsen *et al.*, 1900). In 2004 and 2005, new investigations were conducted, also directed by T. Douglas Price. The objective was to determine the condition of the midden in light of changes to the water table caused by agricultural activities and to recover information pertaining to the transition from the Ertebølle to the TRB period. In 2004, eight excavators working for six weeks opened up a trench 2 m x 19 m, with additional areas opened by machine to expose stratigraphy and to search for features outside of the shell midden. Deposits in the trench were hand-excavated and water-screened through 4 mm mesh-size sieves to recover artifacts. The midden area in Trench 1 was separated into seven natural layers (and several sub-layers) during excavation based on the color and texture of the matrix; the types and amount of shells in the matrix; the condition of the shell—burnt, crushed, or whole; and the number and size of rocks. Levels 2-4 were mostly Neolithic deposits (based on ceramic typology), whereas level 5 and those levels below dated to the Ertebølle period. Fish remains recovered from 16 m<sup>2</sup> had a total weight of 210 g. One otolith for this project (estimated fish length of 64 cm) was recovered from level 7 (second from the bottom) of this trench.

Work resumed in the summer of 2005, primarily focused on removing a 2 m x 2 m balk that was left in place in the middle of Trench 1 from the first season. An additional 70 g of fish bone material was recovered from Trench 1 (total for both seasons = 280 g). The distribution of fish bones within the midden was not uniform (nor was the thickness of the midden or the individual levels). A second trench (10 m<sup>2</sup>) was opened 8 m away, but few fish remains (ca. 8 g) were recovered in this

area. Two of the otoliths used for this study came from this part of the midden (estimated fish lengths of 61 and 66 cm).

Fish remains recovered from the earlier excavations at Fårevejle included one Anguillidae specimen, 38 Gadidae, and 8 Pleuronectidae (Madsen *et al.*, 1900; Degerbøl, 1945). The recent excavations and analysis resulted in an assemblage of 2,738 identified specimens from 12 different families of fish. These included 38 gadid otoliths: 33 *G. morhua*, 1 *Pollachius* sp., and 4 unspecified gadids. The three largest otoliths of *G. morhua* at the site were selected for isotopic seasonality analysis.

## METHODS

### *Oxygen isotope sampling*

The seven selected otoliths were embedded in Epofix resin, and 500 µm sections were cut using a Buehler low-speed saw with a diamond blade, to make a transverse cut across the otolith core. The sections were polished until the growth increments were visible, which were then photographed using reflected and transmitted light (Figure 2). Lines following the otolith growth increments were traced on the digitized otolith images using ImageJ software (Abramoff *et al.*, 2004). Additional lines were interpolated between these marks, with the aim of defining 10-12 sample areas from the final year of otolith growth. The line coordinates were



FIGURE 2

Thin-section from *Gadus morhua* otolith (64 cm fish from Fårevejle).

imported into the computer-controlled micromill (NewWave Research), which consisted of an adjustable-speed drill and a sample stage that moved in sub-micron step resolution along the X, Y, and Z axes. Discrete samples were milled from the otolith edge and inward, using the edge of the drill bit. Sample depth was set to 150  $\mu\text{m}$ , and sample width varied from 24 to 45  $\mu\text{m}$ , resulting in carbonate samples of approximately 25–45 mg. The milled otolith carbonate was transferred to glass vials and analyzed on a Finnigan MAT 253 mass spectrometer coupled to an automated Kiel device (Kleiven *et al.*, 2008). The data were reported on the VPDB scale calibrated with carbonate standard NBS-19. The long-term analytical precision of the system as defined by the external reproducibility of carbonate standards (>15 mg) over a period ranging from weeks to months, exceeds  $\pm 0.06$  for  $\delta^{18}\text{O}$ , corresponding to less than  $0.5^\circ\text{C}$  when converted to a temperature estimate based on the temperature –  $\delta^{18}\text{O}$  relationship for cod (Høie *et al.*, 2004a; Høie *et al.*, 2004b; Hufthammer *et al.*, 2010).

## RESULTS

### *Oxygen isotope analysis and estimation of season of capture*

Three of the four otoliths analyzed from Asnæs Havnemark displayed clear patterns of cyclical oxygen isotope (temperature) variability that could be confidently used to determine season of catch for the fish while one otolith was difficult to interpret (Figures 3a-d). The 48 cm cod was caught when water temperatures started to warm following their annual low (Figure 3a). This result corresponded to a seasonality indication of late winter or very early spring. One of the 49 cm cod showed a final reading midway between the coolest and warmest parts of the annual cycle (Figure 3b). This indicated that it was caught in late spring or early summer. The cyclic pattern observed in Figure 3c for the smallest cod (35 cm) showed that it was caught when water temperatures were at their highest. This result indicated that the fish was captured during late summer. Because of two samples that were lost during measurement and the absence of a clear annual temperature pattern, interpretation of the results for the second 49 cm fish was difficult (Figure 3d). Although not conclusive, the more positive measurements from the two samples

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closest to the edge of the otolith suggested a season of catch in the spring when water temperatures were just beginning to increase.

Only one of the otoliths from Fårevejle provided unambiguous results, although at least one of the other two otoliths was also useful (Figures 3e-g). The cyclical temperature pattern for the 64 cm fish showed that it was caught when water temperatures had reached their lowest point during the late winter or very early spring (Figure 3e). The samples closest to the edge of the otolith for the 66 cm fish also provided the most accurate readings, suggesting a cool season time of catch (Figure 3f). Still, the lack of a clear cyclical temperature pattern made this interpretation uncertain as it was possible that the samples did not cover a whole year of otolith growth. The last otolith, from the 61 cm fish, also lacked a clear cyclical pattern and, moreover, two samples were missing that were lost during measurements (Figure 3g). Although the sample from the edge of the otolith indicated temperatures just beginning to rise, the ambiguity of the seasonal pattern made it difficult to discern at what time of the year this fish was caught.

## DISCUSSION

The isotope cyclical patterns obtained from the Asnæs Havnemark and Fårevejle otoliths are a valuable contribution to our understanding of seasonality at these two sites. Previous information about the seasonality of fishing activity at Asnæs Havnemark estimated seasonality based primarily on the presence of migratory fishes in the assemblage, mainly garfish (*Belone belone*) and Atlantic mackerel (*Scomber scombrus*) (Ritchie, 2010). Based on these migratory fishes, the Asnæs Havnemark fishery would be characterized as being a summer activity. In light of the rarity of these species at the site, this conclusion is clearly questionable (Table 2). In fact, the combined total of 489 garfish and mackerel specimens in the assemblage obtained with 4 mm mesh-size water-screening represented just over 1% of the fish assemblage. When smaller size mesh sieves were applied, there were no garfish identified, and the mackerel bones (NISP=117) rose to ca. 3.5% of the assemblage (Table 3). Given the dominance of gadids in the assemblage (over 85% when using 4 mm mesh sieving and ca. 68% with a 1 mm mesh

sieve), it is reasonable to question whether the few garfish and mackerel bones accurately character-

ized the seasonality of fishing activity at Asnæs Havnemark.

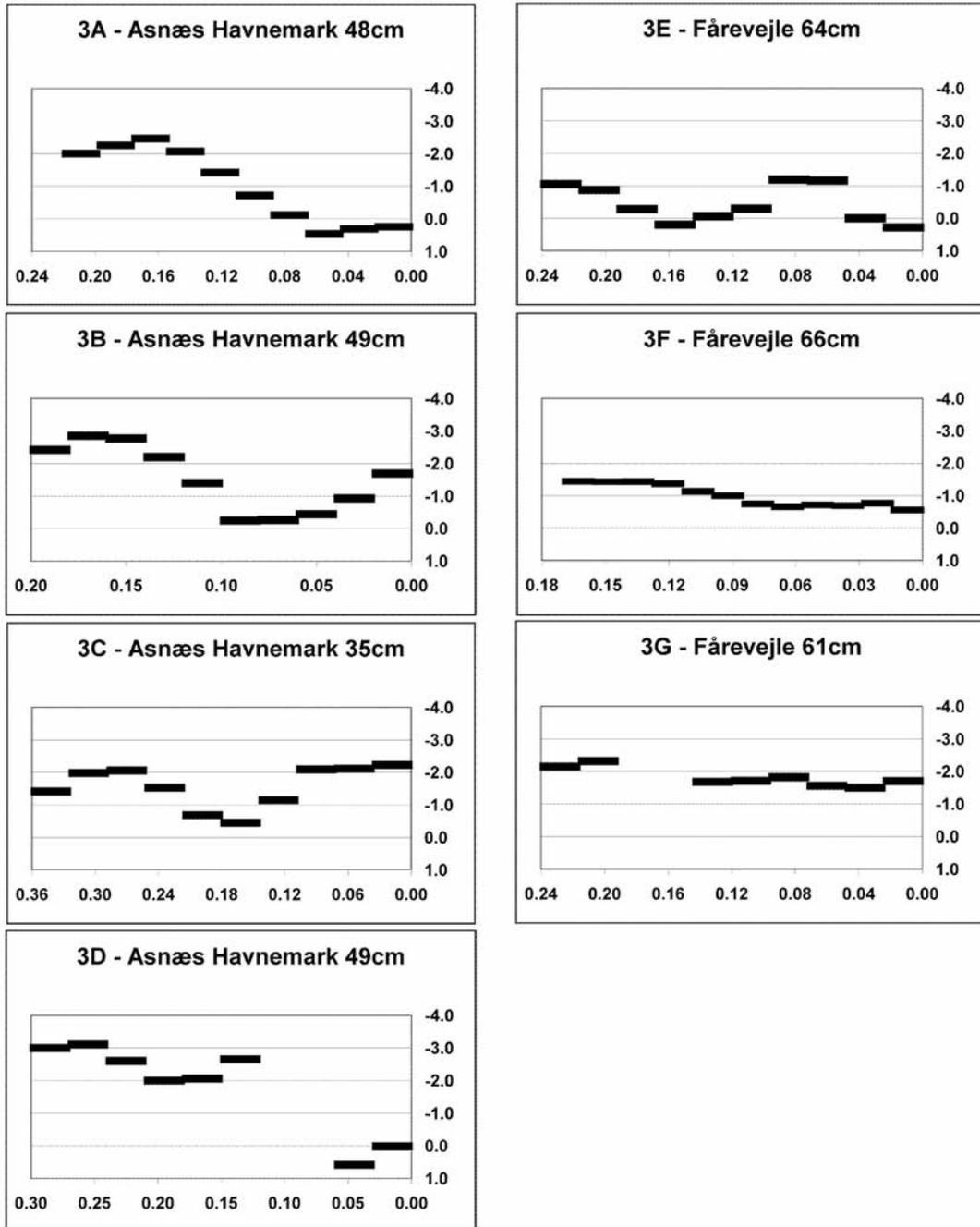


FIGURE 3

Oxygen isotope measurements of the seven cod otoliths used for this study. The x-axis shows the distance from the edge in mm (readings farther to the right are closer to the time of capture). The y-axis shows the  $\delta^{18}\text{O}$  values with the scale reversed so that results higher (more negative) on the axis indicate warmer temperatures.

Family	Vertebra	Other	NISP	% of NISP
Gadidae	32594	5509	38103	85.7%
Anguillidae	3609	340	3949	8.9%
Pleuronectidae	858	40	898	2.0%
Cottidae	497	104	601	1.4%
Scombridae	444	0	444	1.0%
Clupeidae	167	4	158	0.4%
Triglidae	110	26	136	0.3%
Belonidae	41	4	45	0.1%
Squalidae	30	10	40	0.1%
Trachinidae	33	1	34	0.1%
Zoarcidae	18	0	18	0.0%
Salmonidae	13	0	13	0.0%
Cyprinidae	8	0	8	0.0%
Callionymidae	1	0	1	0.0%
<b>Total</b>	<b>38423</b>	<b>6038</b>	<b>44461</b>	

TABLE 2

NISP (number of identified specimens) and relative abundance of the fish assemblage recovered from Asnæs Havneemark using 4 mm mesh sieving.

Family	Vertebrae	Other	NISP	% of NISP
Gadidae	1679	565	2244	68.0%
Anguillidae	543	55	598	18.1%
Scombridae	117	0	117	3.5%
Clupeidae	104	2	106	3.2%
Cottidae	82	14	96	2.9%
Pleuronectidae	54	5	59	1.8%
Gasterosteidae	39	5	44	1.3%
Zoarcidae	12	0	12	0.4%
Trachinidae	9	0	9	0.3%
Triglidae	4	1	5	0.2%
Gobiidae	3	0	3	0.1%
Cyprinidae	2	0	2	0.1%
Salmonidae	1	1	2	0.1%
Syngnathidae	1	0	1	0.0%
Squalidae	1	0	1	0.0%
<b>Total</b>	<b>2651</b>	<b>648</b>	<b>3299</b>	

TABLE 3

NISP and relative abundance of the fish assemblage recovered from Asnæs Havneemark, using effective 1 mm mesh-size sieving.

The cyclical temperature patterns obtained from the otoliths showed that fishing activity was practiced during the summer, as has been previously predicted from the presence of garfish and Atlantic mackerel. Only one of the four otoliths studied, however, was indisputably from the warmest part of the year. The other otoliths examined demonstrated that fishing also occurred during the winter and spring. These results provided, for the first time, clear evidence for fishing activity also during these seasons, site seasonality information that previously was only tentatively indicated by the mammal and bird assemblages (Kurt Gron, personal communication, January 2012).

At Fårevejle, the fish assemblage was also dominated by gadids, while the migratory fish (garfish and Atlantic mackerel) comprised less than 0.7% of the assemblage (Table 4). In contrast to the summer indicators (migratory fishes), the results from one otolith showed a clear late winter or early spring signal, and another otolith was also possibly from this same time of year. These results demonstrated again that fishing activity was not confined to summertime but included late winter/early spring as well. The mammal and bird assemblages from Fårevejle unequivocally showed

site use during the spring and summer, but again only gave tentative indications for use during other seasons (Kurt Gron, personal communication, January 2012). Information from the otolith isotopes was invaluable for demonstrating that the site was in use during the early part of the year as well.

One additional point concerns the  $\delta^{18}\text{O}$  values obtained for the otoliths from the two sites. As observed (Figure 3), there was variability in the average amplitude of  $\delta^{18}\text{O}$ . Whereas the average range of the  $\delta^{18}\text{O}$  values was 2.73 at Asnæs Havneemark, it was only 1.05 at Fårevejle. Even the smallest range at Asnæs Havneemark (1.78 for the 35 cm fish) was greater than the largest range (1.47 for the 64 cm fish) at Fårevejle. A possible explanation for this difference was that, while Asnæs Havneemark was on the coast of the Kattegat, Fårevejle was located on the Lammefjord which may have had slightly brackish waters.

This study confirms previous studies (e.g., Hufthammer *et al.*, 2010), demonstrating the potential of otolith isotopic analysis for providing information about site seasonal activity. Due to the limited number of samples used and the problems encountered with some of the results, archaeologi-

<b>Family</b>	<b>Vertebrae</b>	<b>Other</b>	<b>NISP</b>	<b>% of NISP</b>
Gadidae	1273	307	1580	57.7%
Pleuronectidae	960	83	1043	38.1%
Anguillidae	47	27	74	2.7%
Belonidae	15	2	17	0.6%
Clupeidae	8	0	8	0.3%
Cyprinidae	7	0	7	0.3%
Esocidae	2	1	3	0.1%
Cottidae	2	0	2	0.1%
Scombridae	2	0	2	0.1%
Squalidae	0	1	1	0.0%
Salmonidae	1	0	1	0.0%
<b>Total</b>	<b>2317</b>	<b>421</b>	<b>2738</b>	

TABLE 4

NISP and relative abundance of the fish assemblage recovered from Fårevejle using 4 mm mesh-size sieving.

cal interpretations from this project remain tentative. Furthermore, expanding the technique to include otoliths of other species of fish would be useful to discern if seasonal patterns of exploitation varied according to the exploited species. Clearly, further analyses of fish otoliths in future research studies will increase our understanding of subsistence and mobility during the Ertebølle period.

## CONCLUSIONS

Stable oxygen isotope analysis of samples milled from otoliths is an innovative method for determining fish season of catch at archaeological sites. The seven cod otoliths sampled from two coastal Late Mesolithic Ertebølle sites in Denmark demonstrated their potential for identifying the seasonality of cod (*G. morhua*) exploitation. At the site of Asnæs Havneemark, where the fish assemblage was heavily dominated by gadids, fishing was shown to have occurred from late winter until late summer. Results at Fårevejle were less definitive but did demonstrate that fishing was conducted during the period of the year when water temperatures were at their lowest. These results showed that fishing activity during the Ertebølle period was practiced not only during summer, as was previously reconstructed from migratory species, but also in late winter/early spring.

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## REFERENCES

- ABRAMOFF, M.D.; MAGELHAES, P.J. & SUNANDA, J.R. 2004: Image Processing with ImageJ. *Biophotonics International* 11: 36-42.
- Archaeofauna 22 (2013): 95-104
- ANDERSEN, S.H. 1995: Coastal adaptation and marine exploitation in Late Mesolithic Denmark – with special emphasis on the Limfjord region. In: Fischer, A. (ed.): *Man and the Sea in the Mesolithic*: 41-66. Oxbow Books, Oxford.
- ANDERSEN, S.H. 2008: Shell Middens («Køkkenmøddinger»): The Danish Evidence. In: Antczak, A. & Cipriani, R. (eds.): *Early Human Impacts on Megamolluscs*: 135-156. B.A.R. (International Series) 1865. Oxford.
- CAMPANA, S.E. 2005: Otolith science entering the 21<sup>st</sup> century. *Marine and Freshwater Research* 56: 485-495.
- CARTER, R. 2009: One pig does not a winter make. New Seasonal evidence at the Early Mesolithic sites of Holmegaard and Mullerup and the Late Mesolithic site of Ertebølle in Denmark. In: McCartan, S.; Schulting, R.; Warren, G. & Woodman, P. (eds.): *Mesolithic Horizons*: 115-121. Oxbow Books, Oxford.
- CHRISTENSEN, C. 1990: Stone Age dug-out boats in Denmark: Occurrence, age, form and reconstruction. In: Robinson, D. (ed.): *Experimentation and Reconstruction in Environmental Archaeology*: 119-142. Oxbow Books, Oxford.
- DEGERBØL, M.A. 1945: *Subfossile Fisk fra Kvartærtiden i Danmark*. Videnskabelig Meddelelser Bind 106. Copenhagen.
- DRECHSEL, C.F. 1890: *Oversigt over vore Saltvandsfiskerier*. Danskfiskerimuseum, Grenaa.
- DUFOUR, E.; PATTERSON, W.P.; HØØK, T.O. & RUTHERFORD, E.S. 2005: Early life history of Lake Michigan alewives (*Alosa pseudoharengus*) inferred from intra-otolith stable isotope ratios. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2362-2370.
- ENGHOFF, I.B. 1994: Fishing in Denmark during the Ertebølle Period. *International Journal of Osteoarchaeology* 4: 65-96.
- ENGHOFF, I.B. 1998: Freshwater fishing at Ringkloster, with a supplement of sea fishes. *Journal of Danish Archaeology* 12: 99-106.
- ENGHOFF, I.B. 2011: *Regionality and biotype exploitation in Danish Ertebølle and adjoining periods*. Scientia Danica Series B. Copenhagen.
- FISCHER, A. 2007: Coastal fishing in Stone Age Denmark – evidence from below and above the present sea level and from human bones. In: Milner, N.; Craig, O. & Bailey, G. (eds.): *Shell Middens of Atlantic Europe*: 54-69. Oxbow Books, Oxford.
- HUFTHAMMER, A.K.; HØIE, H.; FOLKVORD, A.; GEFFEN, A.; ANDERSSON, C. & NINNEMANN, U.S. 2010: Seasonality of human site occupation based on stable oxygen isotope ratios of cod otoliths. *Journal of Archaeological Science* 37: 78-83.

- HØIE, H.; DAHL, C.A.; FOLKVORD, A. & KARLSEN, Ø. 2004a: Precision and accuracy of stable isotope signals in otoliths of pen reared cod (*Gadus morhua* L.) when sampled with high resolution micromill. *Marine Biology* 144: 1039-1049.
- HØIE, H.; OTTERLEI, E. & FOLKVORD, A. 2004b: Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). *ICES Journal of Marine Science* 61: 243-251.
- HARRKØNEN, T. 1986: *Guide to the Otoliths of the bony fishes of the Northeast Atlantic*. Danbiu Aps, Hellerup.
- IVANY, L.; PATTERSON, W. & LOHMANN, K. 2000: Cooler winters as a possible cause of mass extinctions at the Eocene/Oligocene boundary. *Nature* 407: 887-890.
- KLEIVEN, H.F.; KISSEL, C.; NINNEMANN, U.S.; RICHTER, T.O. & CORTIJO, E. 2008: Reduced North Atlantic deep water coeval with the glacial lake Agassiz freshwater outburst. *Science* 319: 60-64.
- MADSEN, A.P.; MØLLER, S.; NEERGAARD, C.; PETERSEN, C.G.J.; ROSTRUP, E.; STEENSTRUP, K.J.V. & WINGE, H. 1900: *Affaldsdynger fra Stenalderen i Danmark Undersøgte for Nationalmuseet*. C.A. Reitzel, Copenhagen.
- MILNER, N. 2002: *Incremental Growth of the European Oyster *Ostrea edulis**. B.A.R. (International Series) 1057. Oxford.
- MUUS, B.J. & DAHLSTRØM, P. 1964: *Havfisk og Fiskeri*. G.E.C. Gads Forlag, Copenhagen.
- PEDERSEN, L. 1995: 7000 years of fishing: stationary fishing structures in the Mesolithic and afterwards. In: Fischer, A. (ed.): *Man and the Sea in the Mesolithic*: 75-86. Oxbow Books, Oxford.
- RICHARDS, M.P.; PRICE, T.D. & KOCH, E. 2003: Mesolithic and Neolithic Subsistence in Denmark: New Stable Isotope Data. *Current Anthropology* 44(2): 288-295.
- RITCHIE, K.C. 2010: The Ertebølle Fisheries of Denmark, 5400-4000 B.C. Unpublished PhD dissertation, University of Wisconsin-Madison.
- ROWLEY-CONWY, P. 1983: Sedentary hunters; the Ertebølle example. In: Bailey, G. (ed.): *Hunter-Gatherer Economy in Prehistory*: 111-126. Cambridge University Press, Cambridge.
- ROWLEY-CONWY, P. 1993: Season and Reason: The Case for a Regional Interpretation of Mesolithic Settlement Patterns. In: Peterkin, G.L.; Bricker, H.M. & Mellars, P. (eds.): *Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia*: 179-188. Archaeological Papers of the American Anthropological Association Number 4. Washington, D.C.
- TAUBER, H. 1981: 13C evidence for dietary habits of prehistoric man in Denmark. *Nature* 292: 332-333.
- VAN NEER, W.; ERVYNCK, A.; BOLLE, L.; MILLNER, R. & RIJNSDORP, A. 2002: Fish Otoliths and their Relevance to Archaeology: An Analysis of Medieval, Post-Medieval and Recent Material of Plaice, Cod and Haddock from the North Sea. *Environmental Archaeology* 7: 61-76.
- VAN NEER, W.; ERVYNCK, A.; BOLLE, L. & MILNER, R. 2004: Seasonality Only Works in Certain Parts of the Year: the Reconstruction of Fishing Seasons through Otolith Analysis. *International Journal of Osteoarchaeology* 14: 457-474.
- WEIDMAN, C.R. & MILLNER, R. 2000: High-resolution stable isotope records from North Atlantic cod. *Fisheries Research* 46: 327-342.