

The shellfish enigma across the Mesolithic-Neolithic transition in southern Scandinavia

Lewis, J.P.^{1*}, Ryves, D.B.¹, Rasmussen, P.^{2,3}, Olsen, J.⁴, Knudsen, K.-L.⁵, Andersen, S.H.⁶, Weckström, K.³, Clarke, A.L.⁷, Andrén, E.⁸ and Juggins, S.⁹

¹Centre for Hydrological and Ecosystem Science, Department of Geography, Loughborough University, Loughborough LE11 3TU, UK.

²Environmental Archaeology and Materials Science, National Museum of Denmark, I.C. Modewegsvej, DK-2800 Kgs. Lyngby, Denmark.

³Department of Glaciology and Climate, Geological Survey of Denmark and Greenland (GEUS), Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

⁴Department of Physics and Astronomy, Aarhus University, Ny Munkegade 120, DK-8000 Aarhus C, Denmark.

⁵Department of Earth Science, Aarhus University, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C, Denmark.

⁶Moesgård Museum, DK-8270 Højbjerg, Denmark.

⁷APEM Aquatic Scientists Ltd, Riverview, A17 Embankment Business Park, Stockport, SK4 3GN, UK

⁸School of Natural Sciences, Technology and Environmental Studies, Södertörn University, SE-141 89 Huddinge, Sweden.

⁹School of Geography, Politics and Sociology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK.

*Corresponding author (J.P.Lewis@lboro.ac.uk)

Abstract

The well-known and widespread replacement of oysters (abundant during the Mesolithic period) by cockles and mussels in many Danish Stone Age shell middens ca. 5,900 cal. yrs BP coincides with the transition to agriculture in southern Scandinavia. This human resource shift is commonly believed to reflect changing resource availability, driven by environmental and/or climatic change at the Mesolithic-Neolithic transition rather than cultural choice. While several hypotheses have been proposed to explain the “Mesolithic-Neolithic oyster decline”, an explanation based on a sudden freshening of the inner Danish waters has received most attention. Here, for the first time, we test and refute this long-standing hypothesis that declining salinity explains the marked reduction in oysters identified within numerous shell middens across coastal Denmark at the Mesolithic-Neolithic transition using quantitative and qualitative salinity inference from several, independent proxies (diatoms, molluscs and foraminifera) from multiple Danish fjord sites. Alternatively, we attribute the oyster decline to other environmental causes (particularly changing sedimentation), ultimately driven by external climatic forcing. Critical application of such high-quality environmental archives can reinvigorate archaeological debates and can aid in understanding and managing environmental change in increasingly impacted coastal regions.

Introduction

A striking but consistent feature of many Danish Stone Age shell middens is a high abundance of the European flat oyster (*Ostrea edulis*), present in Mesolithic (Ertebølle culture) layers, and its widespread replacement about 5,900 cal. yrs BP by species such as the cockle (*Cerastoderma edule*) and the blue mussel (*Mytilus edulis*) in the Early Neolithic layers (Funnel Beaker culture) (Andersen, 2000, 2007; Fischer and Kristiansen, 2002). The

oyster decline is contemporaneous with the introduction of agriculture in southern Scandinavia (ca. 5,900 cal. yrs BP; e.g. Andersen and Rasmussen, 1993) and the concomitant transition from a predominately marine to terrestrial diet for humans (Tauber, 1981; Fischer et al., 2007), and has previously been hypothesised to be a causal factor behind these changes (Rowley-Conwy, 1984; Andersen, 2007). Although the oyster decline has been known for almost 50 years (Andersen, 1976), its cause remains contested. Oysters require higher salinities and temperatures than the species which widely replaced it (mainly cockles and mussels) in the Neolithic layers of many Danish shell middens and subsequently several environmental (as opposed to non-environmental or cultural) hypotheses have been proposed for this transition (Rowley-Conwy, 1984; Bailey and Milner, 2008; Schulting, 2010).

The most commonly cited hypothesis is the declining salinity of inner, accessible coastal waters (Rowley-Conwy, 1984; Andersen, 2007) perhaps associated with lowering of relative sea-level (Christensen, 1995; Berglund et al., 2005) and/or a reduction in tidal amplitude (Nielsen, 1938; Petersen, 1993; Petersen et al., 2005), both ultimately reducing the input of high-salinity water from the North Sea into the inner Danish coastal waters of the Limfjord and Kattegat. *Ostrea edulis* generally requires salinities above 23-25 g L⁻¹ and summer water temperatures above 15°C to spawn successfully (Spärck, 1924; Jensen and Spärck, 1934; Yonge, 1960). In Danish coastal waters today, the European flat oyster is confined to the western part of the Limfjord (which is open to the North Sea in the west) and to the deeper, highly saline and oxic waters of the Kattegat, where the species occurs very sporadically.

Here we use palaeoenvironmental data to test the so-called “salinity hypothesis” mentioned above (hereafter H1). We also use palaeoenvironmental data, regional palaeoclimate data and present-day oyster ecology and habitat information to test two other plausible explanations, namely; (H2) the temperature decline at the end of the Holocene thermal maximum directly affected oyster reproduction and oyster population dynamics and (H3)

increased sedimentation altered the availability of suitable habitats. We also consider two non-environmental, human ecological-cultural hypotheses: firstly, that the substantial rise in population from the start of the Neolithic (Shennan et al., 2013) might lead to over-exploitation of oysters to unsustainable levels and their dramatic decline in the archaeological record (H4); and finally, the cultural rejection of oysters as a food (H5) (paradoxically an opposite driver to H4 but leading to the same observation of an oyster decline in the midden record). We consider these last two briefly in the discussion but focus upon the three main environmental hypotheses for the oyster decline given above (H1-H3), as these can be tested directly using palaeoenvironmental data. Here, we apply state-of-the-art multiproxy palaeoenvironmental techniques to reconstruct key environmental parameters (notably salinity and sedimentation change) from Danish fjord sediments collected either adjacent or in close proximity to Stone Age shell middens (Fig. 1A-D) to test competing environmental hypotheses H1-H3 independently and critically.

Methods and results

Multiproxy palaeoenvironmental analyses (diatoms, molluscs and foraminifera, prepared using standard techniques; see Supplementary Data) were performed on five Holocene sedimentary sequences collected from past (Korup Sø) or present shallow (<6 m) Danish fjord systems from Jutland and Zealand (Fig. 1A and Table 1). Salinity change was quantitatively reconstructed at each site (Fig. 2A; Table 1) using a 210-site coastal pan-Baltic diatom-inferred (DI) salinity inference model. Age-depth models were produced for each site based on multiple ^{14}C datings of terrestrial plant material (Kilen, Tempelkrog, Horsens Fjord, Norsminde Fjord) or shell material (Korup Sø). Full methodological details are provided in Supplementary Data.

The DI-salinity reconstructions infer similar or higher salinity levels than at present over both the late Mesolithic and Early Neolithic period (Fig. 2A), but with no evidence for a salinity decline at the Mesolithic/Neolithic transition (5,900 cal. yrs BP) or even persistently lower

salinity in the Neolithic period. This is corroborated by qualitative mollusc and foraminiferal assemblage data and novel semi-quantitative mollusc-based minimum salinity reconstructions (MI-salinity, Table 1, Fig. 2A; Supplementary Data) available at four of the five sites (not Norsminde Fjord). The Danish molluscan fauna is particularly well studied and this new semi-quantitative approach makes use of long-term observations, distribution and wealth of knowledge of molluscan species-salinity relationships (available in the literature) to produce a semi-quantitative estimate of the lower-range of salinity required to support the fauna found in the fossil dataset.

Statistical analysis of DI and MI-salinity values for each sequence confirms this with only a single case out of 9 comparisons with a significant decrease between the Mesolithic and Neolithic sections, and two cases of salinity increase (1-tailed t-test, $p < 0.05$; Table 1). Moreover, the MI-minimum salinity decline at Korup Sø is gradual rather than dramatic (contrary to H1), likely reflecting local changes to hydrography at this site rather than a regional salinity change as the connection between the site and the sea gradually disappeared due to isostatic uplift, sedimentation and progressive isolation from the Kattegat. The diatom data supports this interpretation, as there is no decrease in DI-salinity at Korup Sø over this period, despite the gradual switch from planktonic to benthic taxa.

Bulk sediment accumulation rates (AR, Fig. 2B) were calculated for each site using the age-depth models. At Horsens Fjord, Norsminde Fjord and Korup Sø, relatively lower sedimentation rates are recorded in older sediments (i.e. before 6,000 cal. yrs BP).

Accumulation rates increase gradually at both Norsminde Fjord and Horsens Fjord from about 6,500 cal. yrs BP, while Korup Sø AR remains low until ca. 5,900 cal. yrs BP, when a three-fold increase occurs. At Tempelkrog, the highest rates occur between ca. 7,000-5,850 cal. yrs BP and decline in the Early Neolithic period. Kilen exhibits a pattern typical of sediment focussing (i.e. movement of sediment from shallower to deeper zones of the fjord), with higher sedimentation rates occurring under deeper water conditions (before ca 7,000 cal. yrs BP), falling as the fjord gets shallower from ca 5,200 cal. yrs BP (Lewis et al., 2013).

Discussion

The high abundance of coastal shell middens dated to the late Stone Age from ca. 7,600 cal. yrs BP (Andersen, 2000, 2007) suggests that environmental conditions were optimal for mollusc growth in general at that time, and for oysters in particular. This includes high salinity ($> 23\text{-}25\text{ g L}^{-1}$), high summer temperatures ($>15^{\circ}\text{C}$) and suitable substrate (Spärck, 1924; Jensen and Spärck, 1934; Yonge, 1960). Our data suggest that suitable salinity conditions extend into the Early Neolithic period (Fig. 2A and Supplementary Data). We observe no evidence of a widespread, sudden decline in salinity at the Mesolithic/Neolithic transition or any period of persistently lower salinity within the Early Neolithic (Fig. 2A), in either the quantitative or qualitative biological data (diatom, foraminiferal and mollusc) presented here.

Other molluscs found in shell middens over the late Stone Age period also argue against any coherent salinity change (Rasmussen, 1958; Nielsen, 2008). Two species of Veneridae (*Ruditapes decussata* and *Politapes aureus*, both previously in the genus *Tapes*), with high salinity requirements and absent in Danish waters today, increase into the Early Neolithic sections of several shell middens (Nielsen, 2008 G. Bailey and N. Milner, unpublished data). *Ostrea edulis* itself exhibits great variability throughout Danish shell middens, with large oysters abundant or dominant in several middens (e.g. Havnø, Visborg and Krabbesholm; Fig. 1A) throughout the Neolithic period, even showing occasional increases in abundances in some cases (e.g. Krabbesholm; Nielsen, 2008). Even within the Norsminde shell midden, where a large oyster decline is evident, oysters (and *Bittium reticulatum*, requiring salinities above 25 g L^{-1}) remain present (and *R. decussatus* increases) in the Neolithic period. Furthermore, *Ostrea edulis* exhibits an almost identical distribution to the corrugated venus (*Venerupis corrugata* previously called *Tapes pallustra*) in the Stone Age in Denmark, which has been attributed to identical substrate affinity, rather than salinity tolerance (Rasmussen,

1958), as these two species have very different salinity tolerance limits, with *V. corrugata* able to live in salinities of $\leq 18 \text{ L}^{-1}$ (Jensen and Spärck, 1934; Rasmussen, 1958).

We also discount any role played by changing tidal amplitude on salinity (and sedimentation) dynamics within the Danish coastal waters as recent results from tidal modelling suggest that only minor changes have occurred in the tidal amplitude around the North Sea and Baltic coasts over the last 8,000 years (Uehara et al., 2006). Furthermore, we find no evidence amongst any of the biological proxies (in terms of either inferred salinity change or a shift in assemblage composition to more benthic taxa) for a sudden, substantial sea-level change around 6,100 cal. yrs BP as inferred at Blekinge in southern Sweden (Berglund et al., 2005). Rather, our proxy data are more consistent with the muted sea-level fluctuations reconstructed for eastern Denmark at Vedbæk (Christensen, 2001) (Fig. 2A). We therefore reject the salinity hypothesis (H1) as the cause of the oyster decline in the Danish shell middens over the Mesolithic-Neolithic transition.

The other two environmental hypotheses (H2: temperature decline and H3: increased sedimentation) need not in fact be mutually exclusive. Here we argue for a more nuanced, spatially complex alternative that combines these two environmental explanations for the oyster decline. The trends within the shell middens (outlined above) and palaeoenvironmental records presented here (Fig. 2) all exhibit a degree of spatial and temporal variability, but provide evidence for extensive changes in the marine environment at, or near 5,900 cal. yrs BP, at a time when climate was beginning to cool (Snowball et al., 2004; Seppä et al., 2009; Brown et al., 2012) (Fig. 2B). We hypothesise that accessible oyster beds were steadily waning as a resource for hunter-gatherer societies from ca. 6,300 cal. yrs BP, as temperature in particular declined below optimal conditions (H2), but other factors (specifically sedimentation patterns) triggered the sudden oyster decline recorded in shell middens.

Suitable habitat is key to the development of oyster beds. *Ostrea edulis* favours a hard substrate (i.e. coarser silts/sands containing stones and shells) with sparse vegetation cover, and is easily choked by a high flux of fine-grained sediment (Jensen and Spärck, 1934; Yonge, 1960). This contrasts with taxa such as *Cerastoderma edule* and *Mytilus edulis*, which are better suited to living in finer sediments (Jensen and Spärck, 1934). Over the Late Mesolithic/Early Neolithic, sedimentation rates increased (i.e. starting before agriculture developed in coastal catchments) at four of the five sites (though earlier at Tempelkrog, beginning around ~6,900 cal. yrs BP and peaking between ca. 6,400-6,100 cal. yrs BP), increasing the rate of shallowing of these fjords and reducing exchange and sedimentary export (Fig. 2B).

The underlying causes behind increased sedimentation rates in Danish Fjords in the Late Mesolithic/Early Neolithic period need to be investigated further, though it remains likely that these differ between sites for a variety of reasons (as demonstrated by the variable timings in the data presented here; Fig 2B). Individual fjord sedimentation rates are likely to be heavily influenced by topographical features such as fjord area, water depth and water-current systems. After several thousand years of sedimentation since being submerged by the rising sea-levels in the Early Holocene (Petersen, 1981; Christensen, 1995, 2001; Berglund et al., 2005; Bendixen et al., 2015), many of these sites were becoming shallower, and increasingly acting as sediment sinks. Shallowing would also promote macrophyte development, further trapping sediments.

Additionally, changing climate around this time likely also contributed to increased or variable sedimentation rates in these fjord systems. Isotope records from regional lake and peat systems show spatial variability, with some records indicating a more humid Holocene thermal maximum (HTM), followed by drier conditions in the Early Neolithic (e.g. Harrison and Digerfeldt, 1993; De Jong et al., 2006; Olsen et al., 2010), whilst other nearby lakes (e.g. Hammarlund et al., 2003; Seppä et al., 2005) suggest a shift to wetter conditions in southern Scandinavia after ca. 6,100 cal. yrs BP, likely increasing run off and sediment input

from the catchment. Changing hydrological conditions and decreasing temperatures towards the end of the peak period of the HTM (ca. 8,000 BP and 4,000 BP in northern Europe with maximum temperatures between ca. 7,500-6,000 BP; Snowball et al., 2004; Antonsson et al., 2008; Renssen et al., 2012) would have likely altered the local vegetation and subsequently run off rates and fjord-sedimentary inputs. Later (post ca. 5,900 BP), forest clearance might also have been important following the introduction of agriculture into the catchments by a substantially larger population (Shennan et al. 2013), and in some areas forest restructuring following the likely pathogen-related elm (*Ulmus*) decline (Andersen and Rasmussen, 1993; Peglar and Birks, 1993; Rasmussen et al., 2002). Furthermore, beach ridges are believed to have developed at a number of coastal sites around Denmark in the Late Mesolithic/Early Neolithic (including Norsminde Fjord and Bjørnsholm Bay; Andersen, 1989; Andersen and Rasmussen, 1991; Andersen, 1992). As these beach ridges generally form along/near the mouths of fjords and estuaries, they are likely to have reduced the connection of these sites with the open seas and resulted in reduced current flows and lower energy in the system, limiting the sediment removal capacity and encouraging greater deposition within the basin. Under a combination of the above conditions, a positive feedback between increasing sediment accumulation rate and fjord shallowing might develop, eventually leading to the decline or disappearance of once productive, but increasingly stressed and perhaps over-exploited oyster beds from many shallower, accessible coastal areas.

Recently, Shennan et al. (2013) have shown a major increase in human population density around 5,900 BP (following the onset of the Neolithic period) in Denmark. Bailey and Milner (2008) and Nielsen (2008) have both previously suggested that a combination of environmental stress and over-exploitation (hypothesis H5) might be responsible for oyster populations decreasing in size and age in Neolithic layers of the Norsminde Fjord and Krabbesholm shell middens (Fig 1A, D). Measurement of the size and age of molluscs present in shell middens can give an indication of the natural population health and resource

exploitation pressure. In Denmark, these analyses have shown only a gradual decrease in age and size of collected oysters present within the middens over time (and continuing throughout the Neolithic) (Bailey and Milner, 2008; Nielsen, 2008) suggesting slow degradation of natural oyster beds, and perhaps more consistent with changing environmental conditions than over-exploitation. Furthermore, Bailey and Milner (2008) have shown that oyster populations at Norsminde Fjord do not appear to have become particularly stressed (i.e. greater collection of smaller and younger specimens) until later in the Neolithic, and much later than the Mesolithic-Neolithic oyster decline.

If increasing human population (and subsequent over-exploitation) was a primary cause of the oyster decline (H4), then an initial increase in the abundance of oysters present in the shell middens in the Early Neolithic might be expected (i.e. more oysters needed to support a larger population), followed by a rapid shift to smaller, younger specimens as the natural oyster populations became quickly stressed due to over-exploitation. Whilst, human population increase in the Neolithic (Shennan et al., 2013) likely accentuated this gradual pattern of decreasing age and size of oysters evident in Danish shell middens through time (Bailey and Milner, 2008; Nielsen, 2008), the lack of clear evidence for large-scale stress on the shell midden-oyster population at ca. 5,900 BP argues against this as a primary cause of the oyster decline. However, we acknowledge that age-size data of collected molluscs are not available for all shell middens demonstrating an oyster decline, and therefore in some cases earlier, localised population stress due to increasing population and human impact might have occurred. Nonetheless, with the data available we argue that changing environmental conditions (lower temperature and increased sedimentation rates) caused an overall decline in oyster availability, particularly in the near-shore more-accessible oyster beds, meaning that alternative resources were exploited. Furthermore, as the oyster decline is generally synchronous across Denmark, then if localised over-exploitation through population increase was a major driver, then greater variability in the timing of this oyster decline would be expected.

Importantly, whilst the oyster decline was widespread it was not total and oysters remained accessible, and even locally abundant at a few sites, far into the Neolithic period where favourable hydrographic conditions allowed (e.g. at Havnø, Visborg and Krabbesholm, Andersen, 2008; Nielsen, 2008; Figs 1A, C) despite declining temperature. This finally argues against a cultural explanation (or indeed a purely temperature-driven threshold; Fig. 2) for the oyster decline as oysters were clearly not rejected as a dietary component (hypothesis H5). Shellfish were still harvested in many places, despite the occurrence of a cultural shift from a marine to a terrestrially-dominated diet (Tauber, 1981; Fischer et al., 2007). Indeed some oyster-dominated middens re-appeared briefly in Denmark around 4,900-4,400 cal. yrs BP during the Pitted Ware and Single Grave cultural period, although with far fewer shells (Andersen, 2007). However, forest restructuring following the elm decline and early Neolithic forest clearances resulted in sedimentation rates further increasing in many sites across Denmark (at Korup Sø, dramatically so; Fig. 2B), and this marked the end of large-scale oyster harvesting across coastal Denmark.

Conclusions

The oyster decline (evident in many Danish shell middens) is seen as an important marker of a wider human resource shift, attributable to environmental and climate change, without the need to invoke purely cultural hypotheses which may be difficult to test rigorously.

Specifically, we argue that the change is principally the result of accelerated deposition of fine-grained sediments during a period of declining temperatures, rather than reduced salinity. These factors altered conditions within inner coastal waters, fjord systems and local catchments, e.g. increasing sedimentation rates to levels critical for oyster populations to survive.

We have shown here that palaeoenvironmental data can help establish the context for archaeological inquiry, make important contributions to understanding patterns of

archaeological and cultural change, and test competing hypotheses of change. We hope that the unequivocal rejection of the long-standing salinity hypothesis based on qualitative and quantitative salinity inferences and our alternative environmental hypothesis will reinvigorate archaeological debate concerning the introduction of agriculture and human subsistence strategies in southern Scandinavia. Furthermore, understanding the impacts that climate and environmental change has on valuable marine resources is critical for successful and sustainable management of heavily exploited ecosystems such as the Baltic Sea in light of projected changes for this system in future.

Acknowledgements

For data analyses we thank Karin Gutfelt Jensen (diatom analysis at Horsens Fjord), Kaj Strand Petersen (molluscs at all sites), Peter Konradi (foraminifera at Norsminde Fjord), Ole Kisum (foraminifera at Horsens Fjord), Peter Kristensen (foraminifera at Kilen), Beth Stavngaard (sediment physical analyses), Aarhus University ^{14}C dating facilities (for all ^{14}C dates) and Harald Krog (original coring and pollen analyses from Korup Sø). We also thank Bent Odgaard and Ole Bennike for field assistance. This work was carried out under funding from the Carlsberg Foundation (ANS-1283/20 to DBR), the Danish Council for Independent Research-Natural Sciences and Humanities (grants 21-03-0510 and 25-03-0462 to PR), Loughborough University Development Fund (Ph.D. funding for JPL) and the Geological Survey of Denmark and Greenland (for funding of numerous ^{14}C datings). The MOLTEN (European Union grant EVK3-CT-2000-00031) and DEFINE (Nordic Council of Ministers grant 04NUT9) projects and associated project members are also gratefully acknowledged.

References

Andersen, S.H., 1976. Norsminde Fjord undersøgelsen. En arkæologisk undersøgelse af stenalderbebyggelsen i en østjysk fjord i perioden ca. 4500-1500 f.Kr. med særligt henblik

på de kulturelle og erhvervsmæssige forhold. In: Thrane, H. (Ed.), *Bebyggelsesarkæologi*. Skrifter fra Institut for Historie og Samfundsvidenskab no. 17, Odense Universitet, pp. 18-61.

Andersen, S.H., 2000. 'Køkkenmøddinger' (shell middens) in Denmark: a survey. *Proceedings of the Prehistoric Society* 66, 361-384.

Andersen, S.H., 1989. Norsminde. A "Køkkenmødding" with Late Mesolithic and Early Neolithic Occupation. *Journal of Danish Archaeology* 8, 13-40.

Andersen, S.H., 1992. Marin udnyttelse af Limfjorden i stenalderen, Limfjordsprojektet. Rapport nr. 4: Limfjordsfiskeri i fortid og nutid, pp. 65-96.

Andersen, S.H., Rasmussen, K.L., 1991. Bjørnsholm. A stratified Køkkenmødding on the Central Limfjord, North Jutland. *Journal of Danish Archaeology* 10, 59-65.

Andersen, S.H., 2007. Shell middens ("Køkkenmøddinger") in Danish Prehistory as a reflection of the marine environment. In: Milner, N., Craig, O.E., Bailey, G.N. (Eds.), *Shell Middens in Atlantic Europe*. Oxbow Books, Oxford, pp. 31-45.

Andersen, S.H., 2008. A report on recent excavations at the shell middens of Havnø in Denmark. *Mesolithic Miscellany* 19, 2-5.

Andersen, S.T., Rasmussen, K.L., 1993. Radiocarbon wiggle-dating of elm declines in northwest Denmark and their significance. *Vegetation History and Archaeobotany* 2, 125-135.

Antonsson, K., Chen, D., Seppä, H., 2008. Anticyclonic atmospheric circulation as an analogue for the warm and dry mid-Holocene summer climate in central Scandinavia. *Climate of the Past* 4, 215-224.

Bailey, G., Milner, N., 2008. Molluscan archives from European prehistory, In: Antczack, A., Cipriani, R. (Eds.), *Early Human Impacts on Megamolluscs*. BAR International Series, pp. 111-134.

Bendixen, C., Jensen, J.B., Boldreel, L.O., Clausen, O.R., Bennike, O., Seidenkrantz, M.-S., Nyberg, J., Hübscher, C., in press. The Holocene Great Belt connection to the southern Kattegat, Scandinavia: Ancyclus Lake drainage and Early Littorina Sea transgression. *Boreas*. DOI. 10.1111/bor.12154

Berglund, B.E., Sandgren, P., Barnekow, L., Hannon, G., Jiang, H., Skog, G., Yu, S.Y., 2005. Early Holocene history of the Baltic Sea, as reflected in coastal sediments in Blekinge, southeastern Sweden. *Quaternary International* 130, 111-139.

Brown, K.J., Seppä, H., Schoups, G., Fausto, R., Rasmussen, P., Birks, H.J.B., 2012. A spatio-temporal reconstruction of Holocene temperature change in southern Scandinavia. *The Holocene* 22, 165-177.

Christensen, C., 1995. The Littorina transgressions in Denmark. In: Fischer, A. (Ed.), *Man and sea in the Mesolithic. Coastal settlement above and below present sea-level*. Oxbow Books, Oxford, pp. 15-22.

Christensen, C., 2001. Coastal settlement and sea-level change in the Stone Age., In: Jensen, O.L., Sørensen, S.A., Hansen, K.M. (Eds.), *Denmarks Hunting Stone Age – status and perspectives*, Hørsholm Egnsmuseum, pp. 183-193.

Dahl, K., Lundsteen, S., Helmig, S.A., 2003. *Stenrev - havets oaser*. Gads Forlag, Copenhagen.

De Jong, R., Björck, S., Björkman, L., Clemmensen, L.B., 2006. Storminess variation during the last 6500 years as reconstructed from an ombrotrophic peat bog in Halland, southwest Sweden. *Journal of Quaternary Science* 21, 905–919.

Fischer, A., Kristiansen, K., 2002. *The Neolithisation of Denmark. 150 years of debate*. J.R.Collis, Sheffield.

Fischer, A., Olsen, J., Richards, M., Heinemeier, J., Sveinbjörnsdóttir, A.E., Bennike, P., 2007. Coast-inland mobility and diet in the Danish Mesolithic and Neolithic: evidence from stable isotope values of humans and dogs. *Journal of Archaeological Science* 34, 2125-2150.

Hammarlund, D., Björck, S., Buchardt, B., Israelson, C., Thomsen, C.T., 2003. Rapid hydrological changes during the Holocene revealed by stable isotope records of lacustrine carbonates from Lake Igelsjön, southern Sweden. *Quaternary Science Reviews* 22, 353-370.

Harrison, S.P., Digerfeldt, G., 1993. European lakes as palaeohydrological and palaeoclimatic indicators. *Quaternary Science Reviews* 12, 233-248.

Jensen, S., Spärck, R., 1934. Bløddyr II. Saltvandsmuslinger. *Danmarks Fauna* 40, 208.

Lewis, J.P., Ryves, D.B., Rasmussen, P., Knudsen, K.L., Petersen, K.S., Olsen, J., Leng, M.J., Kristensen, P., McGowan, S., Phillipsen, B., 2013. Environmental change in the Limfjord, Denmark (ca 7,500–1500 cal yrs BP): a multiproxy study. *Quaternary Science Reviews* 78, 126-140.

Mertz, E.L., 1924. Late and post-glacial height changes in Denmark (In Danish). *Danish Geological Survey (DGU)* 2. 41, 50.

Nielsen, E.S., 1938. De danske farvandes hydrografi i Litorinatiden. *Dansk Geologisk Forening* 9, 337-350.

Nielsen, N., 2008. Marine Molluscs in Danish Stone Age Middens: A Case Study on Krabbesholm II. In: Antczak, A., Cipriani, R. (Eds.), *Early Human Impact on Megamolluscs*. BAR International Series. Hadrian Books Ltd, Banbury, Oxford, UK, pp. 157-167.

Olsen, J., Noe-Nygaard, N., Wolfe, B.B., 2010. Mid- to late-Holocene climate variability and anthropogenic impacts: multi-proxy evidence from Lake Bliden, Denmark. *Journal of Paleolimnology* 43, 323-343.

Peglar, S.M., Birks, H.J.B., 1993. The mid-Holocene *Ulmus* fall at Diss Mere, South-East England - disease and human impact? *Vegetation History and Archaeobotany* 2, 61-68.

Petersen, K.S., 1993. Environmental changes recorded in the Holocene molluscan faunas from Djursland, Denmark. *Scripta Geologica Special Issue* 2, 359-369.

Petersen, K.-S., 1981. The Holocene marine transgression and its molluscan fauna in the Skagerrak-Limfjord region, Denmark. *Special Publications International Association of Sedimentologists* 5, 497-503.

Petersen, K.S., Rasmussen, K.L., Rasmussen, P., von Platen-Hallermund, F., 2005. Main environmental changes since the Weichselian glaciation in the Danish waters between the North Sea and the Baltic Sea as reflected in the molluscan fauna. *Quaternary International* 133, 33-46.

Rasmussen, E., 1958. Past and Present Distribution of *Tapes (Venerupis) pullastra* (Montagu) in Danish Waters. *Oikos* 9, 77-93.

Rasmussen, P., Christensen, K., Møller, J.D., 2002. Elmesyge i geologisk perspektiv. *Naturens Verden* 1, 36-40.

Rasmussen, P., Petersen, K.S., Ryves, D.B., 2007. Environmental change in Danish marine waters during the Roman Warm Period inferred from mollusc data. *Geological Survey of Denmark and Greenland Bulletin* 13, 21-24.

Renssen, H., Seppä, H., Crosta, X., Goosse, H., Roche, D.M., 2012. Global characterization of the Holocene Thermal Maximum. *Quaternary Science Reviews* 48, 7-19.

- Rowley-Conwy, P., 1984. The Laziness of the Short-Distance Hunter: The Origins of Agriculture in Western Denmark. *Journal of Anthropological Archaeology* 3, 300-324.
- Schulting, R., 2010. Holocene environmental change and the Mesolithic-Neolithic transition in north-west Europe: revisiting two models. *Environmental Archaeology* 15, 160-172.
- Seppä, H., Hammarlund, D., Antonsson, K., 2005. Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. *Climate Dynamics* 25, 285-297.
- Seppä, H., Bjune, A.E., Telford, R.J., Birks, H.J.B., Veski, S., 2009. Last nine-thousand years of temperature variability in Northern Europe. *Climate of the Past* 5, 523–535.
- Shennan, S., Downey, S.S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., Manning, K., Thomas, M.G., 2013. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nature Communications* 4:2486.
- Snowball, I., Korhola, A., Briffa, K.R., Koç, N., 2004. Holocene climate dynamics in Fennoscandia and the North Atlantic. In: Batterbee, R.W., Gasse, F., Stickely, C.E. (Eds.), *Past climate variability through Europe and Africa*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 364-397.
- Spärck, R., 1924. *Undersøgelser over Østersens (Ostrea edulis) Biologi i Limfjorden, særlig med Henblik paa Temperaturens Indflydelse paa Kønsskiftet*. Centraltrykkeriet, København.
- Tauber, H., 1981. ^{13}C evidence for dietary habits of prehistoric man in Denmark. *Nature* 292, 332-333.
- Uehara, K., Scourse, J.D., Horsburgh, K.J., Lambeck, K., Purcell, A.P., 2006. Tidal evolution of the northwest European shelf seas from the Last Glacial Maximum to the present. *Journal of Geophysical Research-Oceans* 111, C09025.
- Yonge, C.M., 1960. *Oysters*. Collins, London.

Table and Figure captions

Table 1. Proxy summary. Summary of biological proxies analysed over the study period from the five Danish coastal sites (ca. 7,400-5,000 BP), with an assessment of salinity change over the Mesolithic-Neolithic transition (Meso-Neo salinity change). See Supplementary Data for stratigraphic profiles of proxies. Salinity change is inferred using qualitative (diatoms, foraminifera, molluscs), semi-quantitative (mollusc-inferred (MI) minimum salinity inference) and quantitative approaches (diatom-inferred salinity), and is qualified by proxy preservation, and temporal resolution. Molluscs at Norsminde Fjord are too scarce to permit a reliable salinity inference. Individual stratigraphic plots for proxies are shown in Supplementary Data. * = Temporal resolution of MI-min salinity inferences based on amalgamated 10 cm slices. One-tailed t-tests on Mesolithic and Neolithic data series were applied after testing for unequal variances; n.s. = not significant ($p > 0.05$); values in *italics* indicate a positive salinity difference between Neolithic and Mesolithic sections (i.e. higher salinity in Neolithic sections).

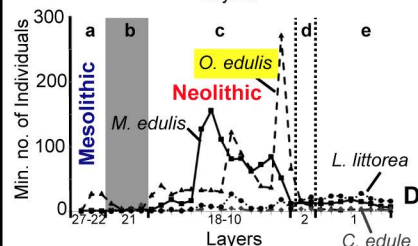
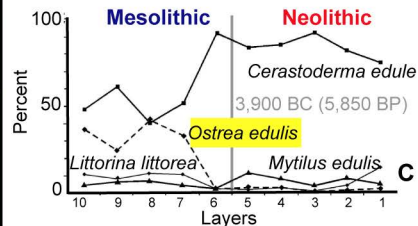
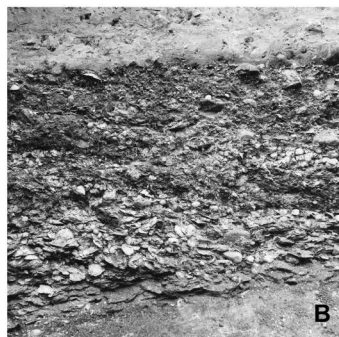
Fig. 1. Map of Denmark and shell midden data. A. Location of the five study sites, Kilen, Korup Sø, Norsminde Fjord, Horsens Fjord and Tempelkrog and distribution of late coastal Stone Age shells middens across Denmark (shaded areas). Numbered sites (in italics) 1-5 contain Stone Age shell middens with abundant oysters: 1. Bjørnsholm Bay 2. Ertebølle, 3. Krabbesholm, 4. Visborg, 5. Havnø. Site 6 (Vedbæk) shows the location from which the Danish sea-level curve displayed in Fig. 2A originates. Isolines show the modern surface salinity (in g L^{-1} ; black numbers along isolines) gradient in the Kattegat and adjacent coastal waters. Isobases for the highest level of the *Littorina* Sea (ca. 6,200 yrs BP) above present sea-level in Denmark are shown by dotted (red) lines; in metres (red numbers) after Mertz (1924) and Christensen (2001). Map modified from Dahl et al. (2003) and Rasmussen et al. (2007). B. Photo of a section through the late Stone Age (ca. 6,800-5,500 cal. yrs BP) Norsminde Fjord shell midden (courtesy of S.H. Andersen). C. Percentage abundance of key molluscs present in stratigraphic layers of the Late Stone Age Norsminde Fjord shell midden

between ca. 6,500-5,200 cal. yrs BP/4,500-3,200 B.C. (from Bailey and Milner, 2008). D. Minimum numbers of individuals (MNI) of key molluscs present in stratigraphic layers of the Late Stone Age Krabbesholm shell midden (from Nielsen, 2008). Numbered sections: a. Mesolithic-Ertebølle oyster-dominated layer (ca. 6,800 cal. yrs BP/4800 B.C.); b. marine sand containing both Mesolithic and Neolithic artefacts; c. Early Neolithic Funnel Beaker Culture shell layers (ca. 5,900-5,300 cal. yrs BP/3,950-3,350 B.C.); d. compact ash and shell layer and e. brown earth soil with some shell fragments.

Fig 2. Coastal proxy data. A. Palaeosalinity inferred from diatoms (labelled DI; or blue line) and molluscs (labelled MI; or brown line) for each site over the study period, along with regional sea-level curves from Vedbæk, East Zealand, Denmark (Christensen, 2001), and Blekinge, south east Sweden (Berglund et al., 2005). Dotted reference line refers to the average DI-salinity at each site over for the Ertebølle period (ca. 5,900-7,400 cal. yrs BP). Black arrows indicate modern surface salinity (MSS) at the study sites. The modern surface salinity for Tempelkrog is based on the average for the wider Isefjord (Fig. 1). Kilen is now a semi-isolated brackish lake (since AD 1856) and therefore the MSS is taken from the adjacent Struer Bay (See SF1, Supp. data). Korup Sø has no MSS as it is no longer a fjord system. **B.** Sediment accumulation rates at the five study sites (7,400-5,000 cal. yrs BP) based upon the independent ¹⁴C age-depth models and pollen-inferred composite air temperature for Denmark (Brown et al., 2012). Abbreviations of archaeological divisions (after Fischer and Kristiansen, 2002): EN = Early Neolithic (ca.5,900-5,300 cal. yrs BP), MNA = Middle Neolithic A (ca.5,300-4,800 cal. yrs BP).

Site	Proxy	No. of samples	Resolution range (~years)	Avg. resolution (~years)	Meso-Neo salinity change	t-test p-value
Kilen	Diatoms (and DI-salinity)	47	5-160	50	None	n.s.
	Molluscs	296	5-20	10	None	
	MI-min salinity inferences*	88	20-60	25	Increase	$p < 0.05$
	Foraminifera	21	60-250	120	None	
Korup Sø	Diatoms (and DI-salinity)	30	5-340	80	None	n.s.
	Molluscs	27	30-400	90	Gradual decrease	
	MI-min salinity inferences	27	30-400	90	Gradual decrease	$p < 0.001$
Norsminde Fjord	Diatoms (and DI-salinity)	37	10-230	60	None	n.s.
	Molluscs	22	50-200	90	(Poor preservation)	
	Foraminifera	28	10-240	90	None (poor preservation)	
Horsens Fjord	Diatoms (and DI-salinity)	32	60-90	80	Gradual increase	$p < 0.01$
	Molluscs	116	10-50	20	None	
	MI-min salinity inferences*	19	105-155	126	None	n.s.
	Foraminifera	31	10-90	70	None	
Tempelkrog	Diatoms (and DI-salinity)	10	110-620	250	None (low resolution)	n.s.
	Molluscs	181	10-20	15	None	
	MI-min salinity inferences*	36	45-100	66	None	n.s.

Table 1

Figure 1

A. Salinity and sea-level

B. Sediments and temperature

DI = Diatom-inferred salinity
 MI = Mollusc-inferred minimum salinity

Diatom- and mollusc-inferred salinity

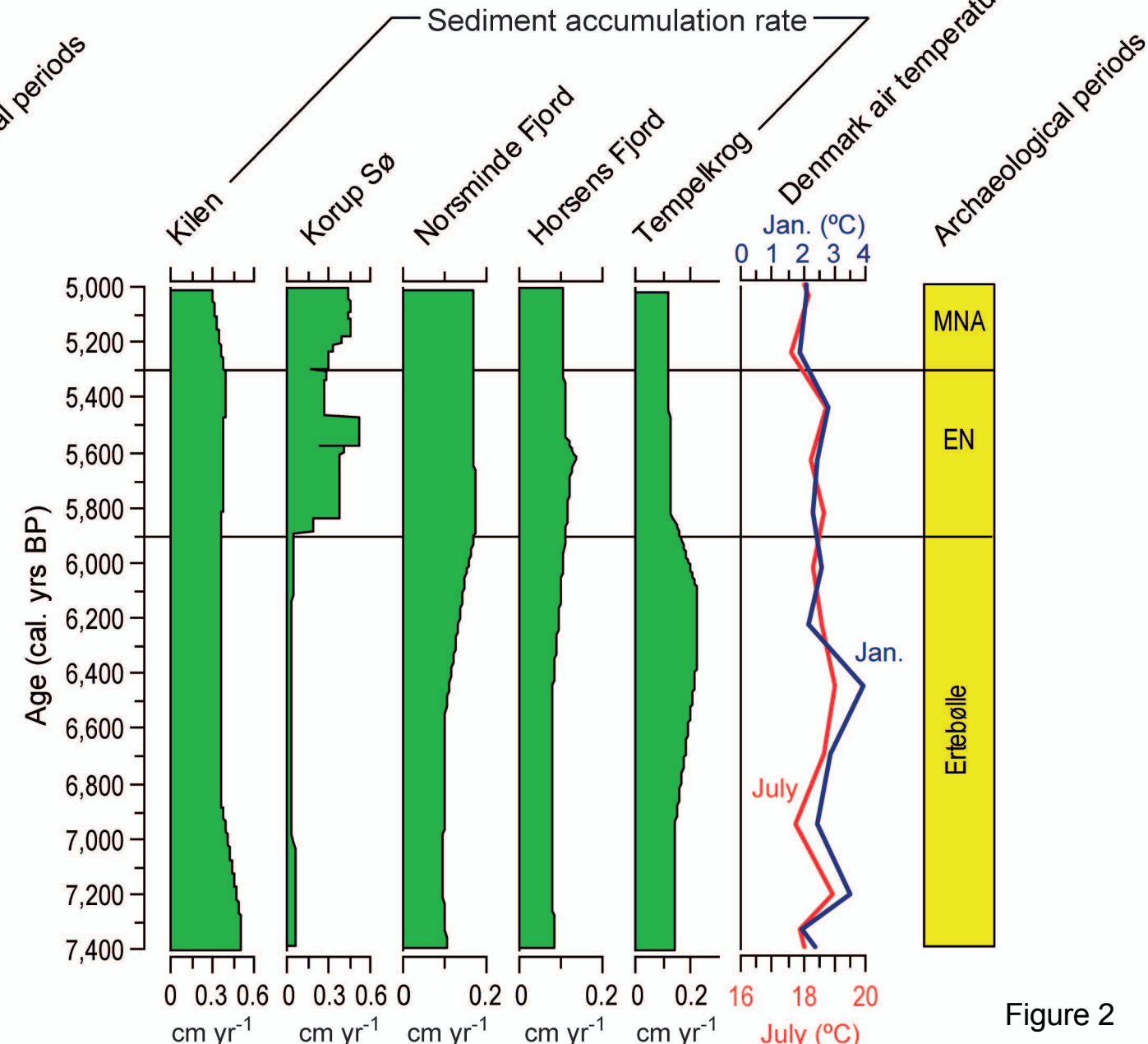
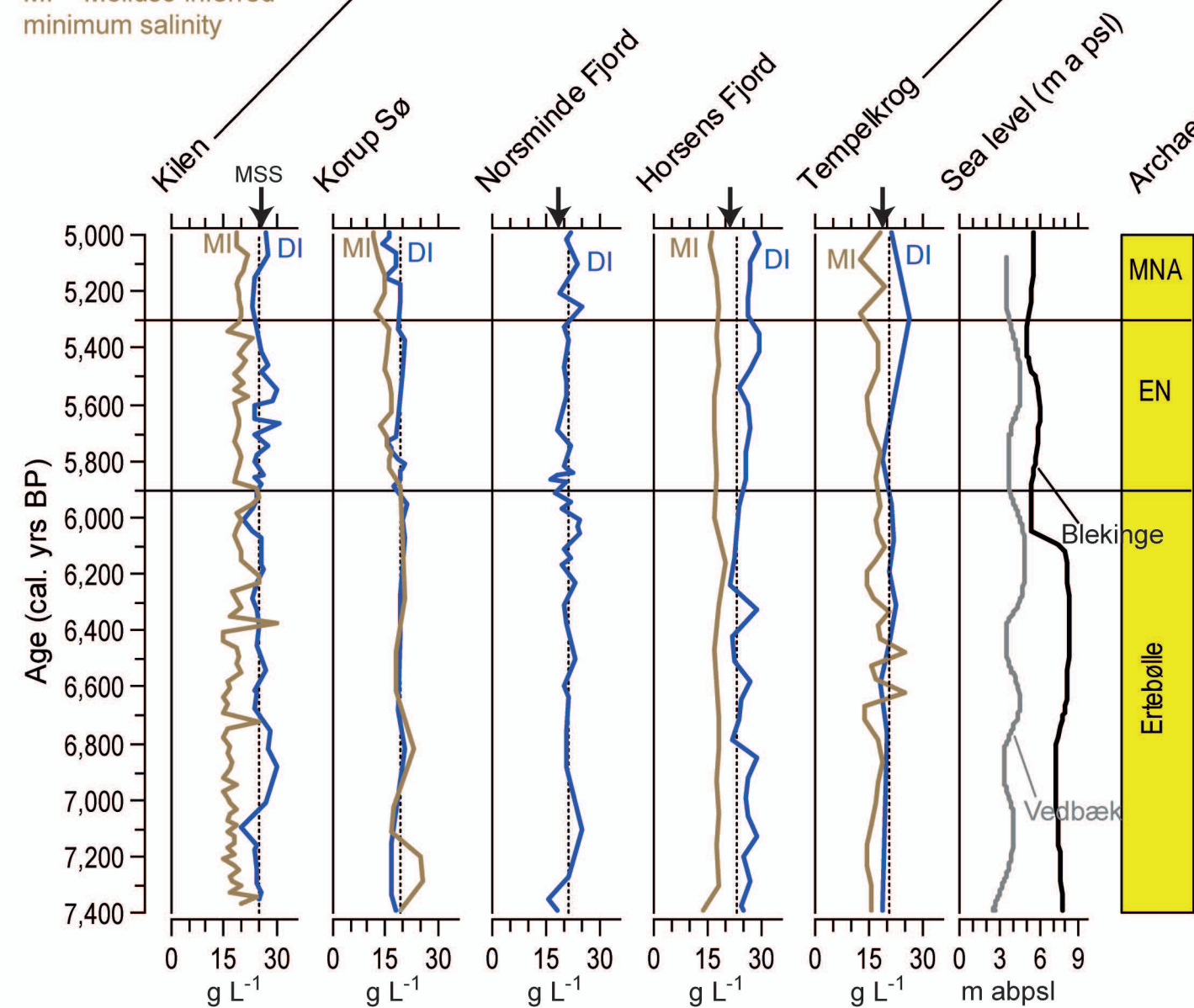


Figure 2