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Short communication

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

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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. 5900 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.


## 1. 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 5900 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. 5900 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.,

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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.

## 2. 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-

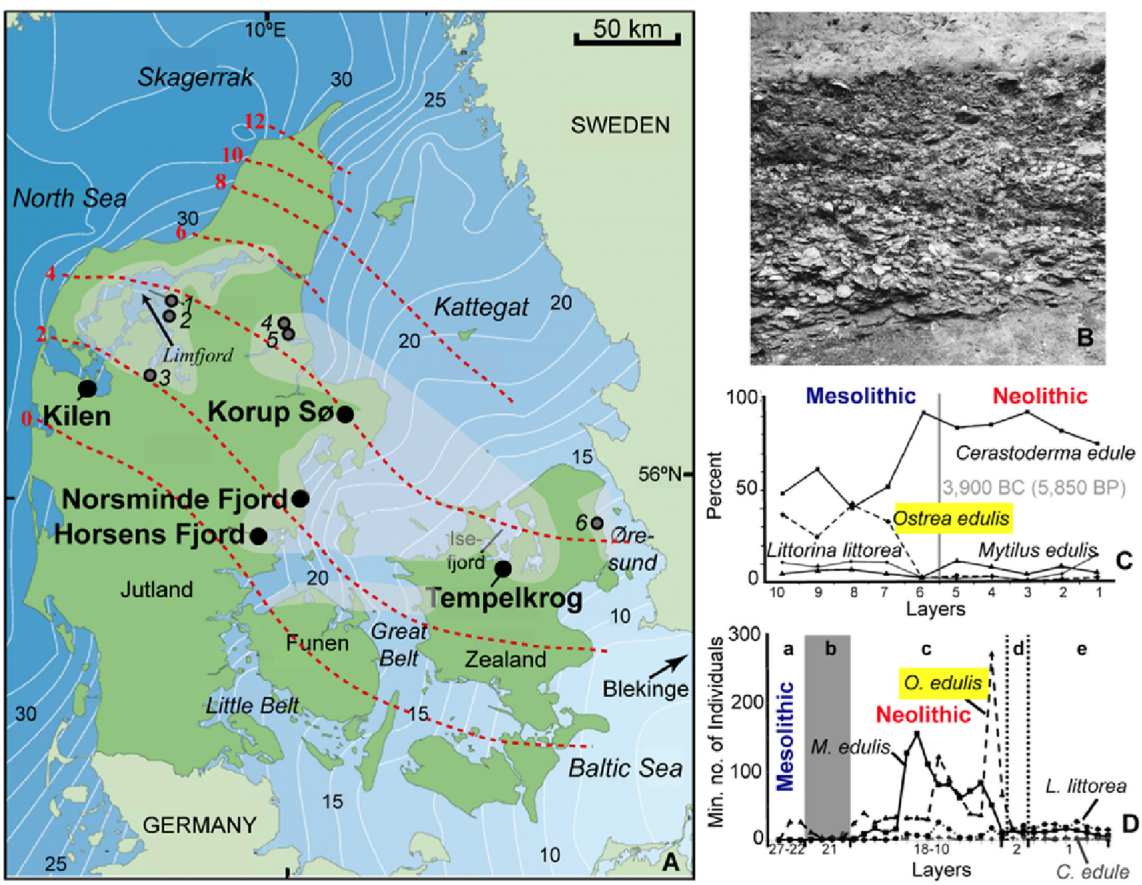


**Fig. 1. Map of Denmark and shell midden data**. A. Location of the five study sites, Kilen, Korup Sø, Norsminde Fjord, Horsens Fjord and Tempelkrog and distribution of late coastal Stone Age shells middens across Denmark (shaded areas). Numbered sites (in italics) 1–5 contain Stone Age shell middens 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. 6200 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. 6800–5500 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. 6500–5200 cal yrs BP/4500–3200 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. 6800 cal yrs BP/4800 B.C.); b. marine sand containing both Mesolithic and Neolithic artefacts; c. Early Neolithic Funnel Beaker Culture shell layers (ca. 5900–5300 cal yrs BP/3950–3350 B.C.); d. compact ash and shell layer and e. brown earth soil with some shell fragments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)